

Research Article

Functionally novel invasive predator eradicates herbivores of a littoral community

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Abstract

In the Archipelago Sea as in most other parts of the Baltic Sea, the bladder wrack (*Fucus vesiculosus*) is a foundation species of the littoral communities of the rocky shores. It sustains a community of epiphytic algae, herbivorous crustaceans and molluscs and various fish. Recently we have noticed a steep decline in the occurrence of the herbivorous crustaceans and molluscs in many sites in the Archipelago Sea. We hypothesise that a key factor contributing to this decline is the recent introduction of the Harris mud crab (*Rhithropanopeus harrisi*), which was first sighted in 2009 in this region. Importantly, because there are no native crabs in the northern parts of the Baltic Sea, the mud crab is a completely novel kind of predator in the ecosystem and the herbivorous crustaceans and molluscs may be particularly susceptible to it. Here, we document a dramatic decline of the typical herbivores occurring on the bladder wrack, possibly indicating an ongoing regime shift, by comparing our recent samples from across the Archipelago Sea with data collected a decade before the sighting of the mud crab. Moreover, we demonstrate a spatio-temporal association between the decline, particularly of the key herbivore species, the isopod *Idotea balthica*, and the establishment of the mud crab. We also present experimental evidence for a strong predator-prey link between the mud crab and the isopod *I. balthica*. Finally, we discuss the possible consequences of the community change and scrutinise alternative explanations for our observations.

Key words: Mud crab, Baltic Sea, herbivory, *Idotea balthica*, ecosystem function

Introduction

Marine species introductions have become more and more frequent with a forecasted multi-fold global increase in invasion risk with the growing maritime shipping (Pysek et al. 2020; Sardain et al. 2019). A vast majority of introduced species become widely established and have ecological impacts (Garcia-Berthou et al. 2005). These include changes in biotic interactions, such as higher mortality of native species by invasive consumers (Paolucci et al. 2013; Salo et al. 2007) with subsequent effects on abundance and ecosystem function. Ecosystem functioning may be altered by changes in primary production, trophic transfer of matter and energy, habitat structure, and disturbance regimes (Pysek et al. 2020).

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Similar to other European Seas, the Baltic Sea has received introduced species with an accelerating rate (Galil et al. 2014) and by now 191 species have been introduced according to the AquaNIS database (AquaNIS 2015). In most cases, the introductions and subsequent establishment and spread of invasive species have been documented and they have been suggested to have potentially deleterious ecological effects on the native community (reviewed by Olenin et al. 2017). However, little is known about their actual impact on ecosystems (Ojaveer et al. 2021). Thus, there is an urgent need to assess the ecological consequences and risks of invasive species. One of the current invasives widening its range is the Harris mud crab (*Rhithropanopeus harrisi*). It was first observed in the Baltic Sea in Germany, Denmark, Poland and Kaliningrad in 1950s (AquaNIS 2015), but in the Archipelago Sea as recently as in 2009. After its first appearance in the Archipelago Sea in the coastal southwestern Finland it has quickly increased in abundance in its newly established sites and is quickly widening its distribution range (Forsström et al. 2018; Fowler et al. 2013).

In the Baltic Sea, the mud crab inhabits a variety of benthic habitats but shows a preference for macrophytes such as macroalgal stands dominated by *Fucus vesiculosus* (Gagnon and Boström 2016; Kotta et al. 2018; Nurkse et al. 2018; Riipinen et al. 2017). It interacts with the native benthic community, preying on mussels, snails and crustaceans (Forsström et al. 2015; Hegele-Drywa and Normant 2009; Jormalainen et al. 2016). Importantly, in the northern Baltic Sea, the mud crab represents a completely novel kind of predator as there are no native brachyuran crabs. Therefore, the native prey lacks common evolutionary history with the predator in the Baltic Sea and may lack effective anti-predation adaptations, which may lead to a considerably high predation mortality (Sih et al. 2010). Intense predation on herbivores may also affect primary producers through trophic cascades (Gallardo et al. 2016; Walsh et al. 2016). Because Baltic Sea biotic communities are species poor, they may be particularly sensitive to such influences.

Herbivory is a very important regulating factor of producer abundance and community composition in marine littoral environments (Hillebrand et al. 2007; Poore et al. 2012; Shurin et al. 2006). Together with distinct trophic levels, linear food chains, and strong predator-prey interaction it can create conditions where cascading trophic effects are likely to arise. Bladder wrack (*F. vesiculosus*) is a foundation species and an important producer species of the benthic food web in rocky littoral habitats of the Archipelago Sea. It is inhabited by several gastropod, amphipod and isopod herbivores that feed on bladder wrack, filamentous algae and on periphyton thereby transferring the primary production in the food web. The mud crab is a novel predator in this community, and observation of a single, newly invaded site suggested a collapse in the abundance of gastropod and crustacean herbivores (Jormalainen et al. 2016). However, we lack a spatially comprehensive assessment on the effects of mud crab invasion of native herbivores in this community.

Members of our group have been involved in research on littoral communities and species in the Archipelago Sea over the past three decades (e.g. Jormalainen and Tuomi 1989; Jormalainen et al. 1995; Merilaita and Jormalainen 2000; Merilaita 2001; Korpinen et al. 2008; Haavisto and Jormalainen 2014). Therefore, we possess considerable insight about the occurrence and abundance of the littoral species in this area. In autumn 2020 when collecting the isopod *Idotea balthica* from bladder wrack stands for another study, we noticed that they were much harder to obtain in adequate numbers at several sites. Here, the overall abundance of herbivorous crustaceans and molluscs were substantively much lower than we would have expected based on sampling conducted in previous decades. As a first attempt to establish this change, its extent in the community, and its possible connection to the mud crab, we estimated the abundance of *I. balthica*, the key

herbivore in the rocky littoral bladder wrack stands, both within and outside the current distribution range of the recently introduced mud crab *R. harrisi* in the Archipelago Sea. For comparison, we also present data on abundance of invertebrates, including *I. balthica*, on bladder wrack within the same area before the introduction of the mud crab. To provide evidence for the causal link between the spread of the introduced mud crab and the decline of the isopod *I. balthica*, we conducted an experiment to quantify the mortality of the isopod caused by the crab. We document a dramatic change in the occurrence and abundance of the key littoral herbivore *I. balthica* within the invasion range of the mud crab, which likely concerns the entire herbivore community in bladder wrack communities. We discuss its reasons and potentially harmful consequences for ecosystem function.

Methods

From the 7th of September to the 1st of December 2020, we sampled bladder wrack (*F. vesiculosus*) across the Archipelago Sea from 21 rocky littoral sites with a dense bladder wrack stand (Table 1). Our sampling area included the current core distribution range of *R. harrisi* in coastal Finland and extended outside of the range towards the south, south-west and north. Of all the sampling sites 17 were located within the current core distribution area of *R. harrisi* and four were located

Table 1. Sampling sites and dates of bladder wrack in 2020, with sample total volumes (Vol., in liters) and no. of replicate containers (Cont.), site location with respect to *R. harrisi* core distribution range, occurrence of *R. harrisi* in the sample, density of *I. balthica* and a qualitative description of *T. fluviatilis* abundance in the sample. “-” marks cases when the occurrence information was not recorded. Sites are sorted by increasing distance from the site of first observation of the *R. harrisi*, Naantali, in the coastal Finland.

Site	Coordinates	Date	Vol./ Cont	Location relative to <i>R. harrisi</i> core range	<i>R. harrisi</i> in the sample	<i>I. balthica</i> density #/100 l	<i>T. fluviatilis</i> in the sample
Anttiskauri	60°23'07.9"N, 22°03'02.4"E	8.9.	44/1	within	present	0	-
Hanka	60°17'01.1"N, 21°57'31.1"E	8.9.	44/1	within	present	0	-
Orhisaari	60°16'27.0"N, 21°59'29.1"E	8.9., 23.9.	160/3	within	present	0	-
Reksaari	60°23'33.9"N, 21°39'53.4"E	11.9.	58/1	within	missing	0	-
Vähä-Kuusinen	60°17'45.5"N, 21°50'04.4"E	11.9.	44	within	present	0	-
Korpinkarit	60°16'48.6"N, 21°50'26.2"E	11.9.	44/1	within	present	0	-
Kuhala	60°23'31.7"N, 21°38'02.1"E	11.9.	58/1	within	present	0	-
Pähkinäinen	60°19'44.4"N, 21°42'32.5"E	11.9.	58/1	within	present	0	-
Vuori-Sakoluoto	60°23'47.4"N, 21°38'20.7"E	11.9.	58	within	present	0	-
Högholm	60°14'39.1"N, 21°59'11.1"E	8.9.	44/1	within	present	0	-
Katava	60°14'02.2"N, 21°57'16.9"E	1.12.	58/1	within	missing	0	missing
Ekholm	60°12'57.3"N, 21°59'58.6"E	1.12.	58/1	within	missing	0	missing
Björkholm	60°12'45.4"N, 21°55'45.6"E	1.12.	58/1	within	present	0	missing
Björkholma	60°11'04.0"N, 22°15'20.7"E	1.12.	58/1	within	missing	0	missing
Bergholm	60°08'36.6"N, 22°02'28.8"E	16.10.	116/2	within	present	2 ± 2	-
Gulskär	60°07'16.6"N, 22°07'00.2"E	16.10.	349/6	within	present	13 ± 12	few
Bergö	60°06'53.4"N, 21°47'16.0"E	21.9.	58/1	within	present	0	missing
Boskär	60°01'57.6"N, 21°46'31.9"E	21.9.	349/6	outside	present	86	abundant
Färö	59°54'44.4"N, 21°46'55.2"E	21.9., 30.9.	349/6	outside	missing	86 ± 51	abundant
Jurmo	59°49'33.5"N, 21°35'04.3"E	25.9., 30.9.	378/6.5	outside	missing	95 ± 77	abundant
Rihtniemi, Rauma	61°04'05.1"N, 21°18'17.1"E	22.9.	153/3	outside	missing	130	few

outside (Fig. 1). The Archipelago Sea is non-tidal, and we collected bladder wrack from dense stands at shallow depths of 0.5–1.5 meters, filling containers with a known volume (44 or 58 l; Table 1). The known volume allowed us to estimate the density of the counted animals and to compare sites sampled with variable effort. We then extracted all non-sessile macroinvertebrates from the algae by shaking the thalli in the containers, recorded the number of *I. balthica* and *R. harrisii* and made a qualitative note (“missing”, “few” referring to up to dozens or “abundant” referring up to hundreds of individuals) regarding the occurrence of *Theodoxus fluviatilis* that is a common snail herbivore feeding mainly on periphyton but also on *Fucus* zygotes and germlings (Malm et al. 1999).

For comparing the occurrence of macroinvertebrates on bladder wrack stands prior to the introduction of the Harris mud crab in the Archipelago Sea, we use data collected for another study (Korpinen et al. 2010) in August–September 1998 (eleven years before the first observation of the mud crab). These data were collected from six sites (60°14'18.5"N, 22°03'13.6"E; 60°15'55.1"N, 22°04'27.4"E; 60°08'25.2"N, 22°02'29.3"E; 60°08'15.8"N, 22°05'25.0"E; 60°08'00.9"N, 22°05'32.0"E; 60°07'16.8"N, 22°07'11.2"E; map of the sites in Korpinen et al. 2010) located within the area covered by our 2020 sampling, within the current core range of *R. harrisii* (i.e., where the density of observations is above the average in Fig. 1a). Both samplings took place after the summertime reproductive period, mainly in September, when the abundances of macroinvertebrates on bladder wrack typically peak (Haavisto and Jormalainen 2014; Korpinen et al. 2010). While the sampling in 1998 was conducted truly quantitatively by enclosing individual bladder wrack algae in mesh-net bags underwater, and counting and identifying all invertebrates from the wet-weighed algae, the 2020 sampling was semi-quantitative and based on pooled volume of large quantity of bladder wrack sampled from the surface. However, the sampling method used in 2020 is an effective collection method of *I. balthica* used widely in numerous studies (see Discussion), capable of capturing individuals even during times of their lowest abundances. The sampling in 2020 included a multi-fold amount of bladder wrack thalli ($n = \text{hundreds}$) compared to sampling in 1998 ($n = 39$). Thus, although the abundances are not given in entirely comparable units, we are confident that the 2020 sampling method, due to its efficiency and intensity, revealed the true occurrence of *I. balthica*. Hence, we have no reason to suspect that it would have underestimated the abundance when compared with the sampling in 1998.

We used the contingency table G-test to test the inter-dependency between the occurrences of *I. balthica* and the mud crab. For that, we cross-tabulated the numbers of sites where *I. balthica* either occurred or was missing within and outside of the mud crab core distribution range. Using the sites where *I. balthica* was found, we compared its density inside and outside of the mud crab core distribution range using one-way ANOVA.

To demonstrate the predator-prey interaction between mud crab and *I. balthica* and to quantify its intensity, we conducted a predation experiment. We collected naïve *I. balthica* from two populations, Rihtniemi and Jurmo (Table 1), outside the current mud crab distribution range. Mud crabs we collected from the vicinity of the Archipelago Research institute on Seili Island (60°14'21.9"N, 21°58'01.3"E) where we conducted the experiment. We set up a total of eight 24 liter aquaria, four for the isopods originating from Rihtniemi and four for the isopods from Jurmo. The aquaria had a seminatural habitat of three bladder wrack thalli, three fist-sized stones and four pieces of plastic tubes placed on the bottom of the aquaria to provide additional shelter for the crabs. Water temperature was 18 °C, salinity 5.8–6‰, with continuous water circulation and a 13:11 h day:night light-rhythm. In each aquarium, we put 25

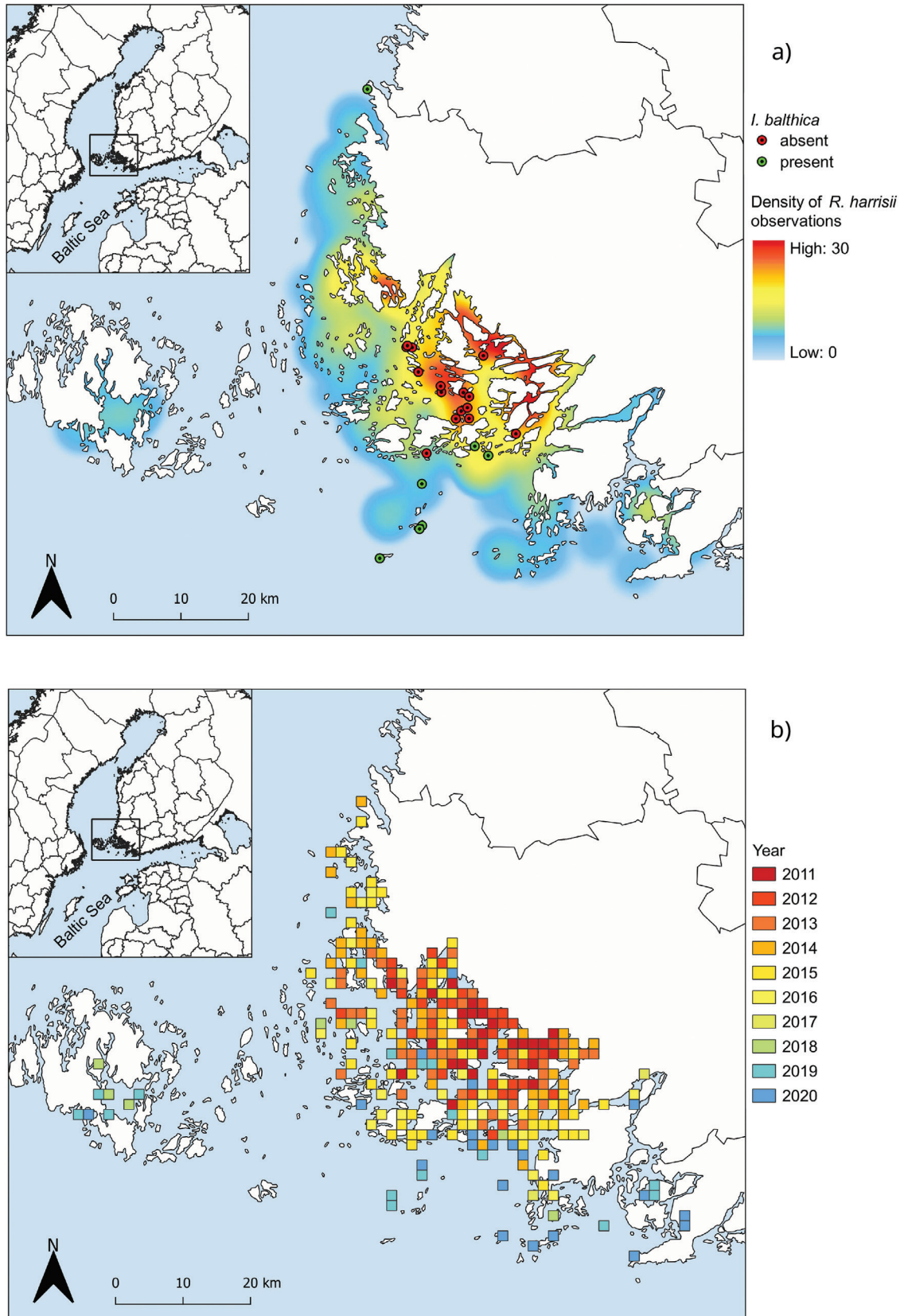


Figure 1. The progress of invasion of the mud crab *Rhithropanopeus harrisi* in coastal Finland from the first observation in Naantali harbor in 2009 to the situation in 2020, as reflected by the citizen science Finnish invasive alien species observation database, the portal maintained by the Natural Resource Institute Finland (<https://vieraslajit.fi/>). In (a), the numbers of reported observations (total no. of observations 566) of mud crabs show as a heat map. Overlaid are the sampling points of *Idotea balthica* with the occurrence of the species in the fall 2020. In (b), spreading of the distribution range in terms of the year of the first observation are shown on the map with a 3 × 3 km grid.

I. balthica individuals representing the natural body-size distribution (body length, mean \pm SD in mm, n; Jurmo: 13.6 ± 2.43 , 200; Rihtniemi: 15.6 ± 2.53 , 191). Four of the aquaria served as a control, and in the other four we added four mud crabs in each after the isopods had settled on the algae. Before the start of the experiment, the mud crabs had starved for 24 h. Mud crabs were chosen so that they represented four different size classes (carapax width, mean \pm SD in mm, (1): 11.8 ± 1.4 , n = 11; (2): 14.6 ± 1.6 , n = 11; (3) 15.6 ± 1.1 , n = 10; (4): 18.1 ± 1.1 , n = 11). One crab of each size-class was put in every aquarium. We followed the survival by counting all isopods every second day over a period of 18 days. In few cases where a crab died during the experiment, we replaced it immediately with a similar-sized individual.

We analysed the survival data using Cox proportional hazard model, implemented by SAS 9.4 Prg-procedure (Allison 2010). Mud crab predation and population were used as fixed effects and aquarium as a random factor.

Results

In 1998, before the introduction of the Harris mud crab, the early fall bladder wrack community in the Archipelago Sea harboured abundant herbivorous invertebrates (Fig. 2). The herbivorous crustaceans, *I. balthica* and gammarids were abundant, averaging 50 and 74 individuals with a maximum of 209 and 464 individuals, respectively, per an average-sized bladder wrack alga (Fig. 2). The occurrence of *I. balthica* in the bladder wrack stands was ubiquitous: it was found in all the stands,

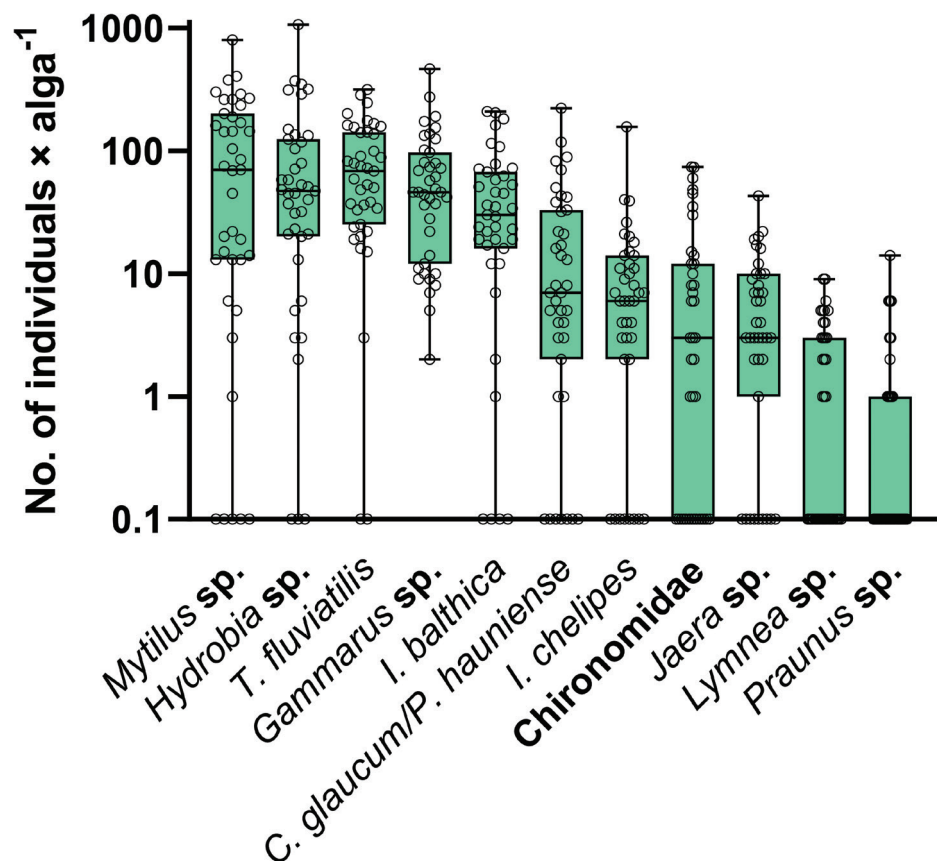


Figure 2. The invertebrate community found on *F. vesiculosus* in August–September 1998. The data from six sites within the Archipelago Sea is combined. Box-plots show 25% and 75% percentiles, median and minimum and maximum values as well as actual data points; points along the horizontal axis are zero values. Each point shows the number of individuals found in one alga; the average size (fresh-weight, mean \pm SD) of sampled algae was 167 ± 93 g, n = 39. Data are redrawn from Korpinen et al. (2010).

and of the 39 bladder wrack thalli collected, only four individual algae lacked *I. balthica* completely. Thus, *I. balthica* were found in 90% of the thalli, and typically in dozens and often over a hundred individuals per an individual alga. The bivalve *Mytilus trossulus* and the snails *Hydrobia* sp. and *T. fluviatilis* were even more numerous with average abundances of 126, 110 and 88, respectively.

Establishment of the mud crab has had a negative effect on the abundance and occurrence of *I. balthica*. When relating the location of the sampling sites of 2020 to the current core distribution range of the mud crab (i.e., where its density is above the average in Fig. 1a), *I. balthica* was found at all four sites located outside of the core distribution range, but only at two out of the 17 sites inside of it (Table 1). Thus, the occurrence of *I. balthica* was significantly dependent on the distribution of the mud crab ($G^2 = 12.8$, $df = 1$, $P = 0.0003$). At the two sites located close to the current southern margin of the core distribution range and where *I. balthica* co-occurred with the mud crab, the density of *I. balthica* was substantially lower (7.5 ± 2.17 individuals/100 l, $n = 2$) than at the sites outside (99.2 ± 10.4 ind./100 l, $n = 4$) the mud crab core distribution range ($F_{1,4} = 70.3$, $P = 0.001$). In this comparison, one site (Boskär) was considered belonging to the outside of the core distribution range, although we found one mud crab there in our relatively high sampling volume (Table 1). This is because we consider that the mud crab has entered that site very recently: our observation was the first one from the site and the only other observations of the crab from that area, within 13 km radius of our sampling site, were from the previous year (Fig. 1b).

Although we did not record quantitatively the abundance of *T. fluviatilis* in our samples, and cannot therefore test the spatial differences statistically, there appears to be a pattern: At all sites outside the core distribution range of the mud crab, we found *T. fluviatilis* and it was typically abundant (Table 1), whereas inside the core range it was typically absent.

The experiment revealed that mortality of *I. balthica* due to predation by the mud crab was high, as their survival decreased quickly in the aquaria with mud crabs compared to the control aquaria (Fig. 3; predation: Wald $\chi^2 = 61.9$, $P < 0.0001$, $df = 1$). Overall survival differed between the two populations (Fig. 3; population: Wald $\chi^2 = 4.62$, $P < 0.05$, $df = 1$). However, predation decreased survival similarly in both isopod populations (Fig. 3; predation-by-population -interaction: Wald $\chi^2 = 1.67$, $P = 0.20$, $df = 1$). Notice that survival dropped to 50% already two days after the start of the experiment in the crab predation aquaria. During the 18 days of the experiment, the mud crabs ate in total about 82 isopods, averaging over five isopods per an individual crab, i.e. one isopod every third or fourth day. We also frequently observed the crabs catching, handling and consuming isopods.

Discussion

We found a dramatic difference between the invertebrate samples collected before and after the introduction of mud crab *R. harrisi* in the Archipelago Sea. We further showed experimentally the existence of a strong predator-prey link between *R. harrisi* and the key herbivore *I. balthica*: predation rate was one prey individual per a crab every third day, high enough to kill all *I. balthica* from an average-sized bladder wrack within a few months. Although effect-sizes observed in experiments cannot be generalized in the nature as such, this provides evidence both for the potential of the mud crab to regulate its prey species and for causality between the dynamics of the mud crab and the isopods. *Idotea balthica*, that used to be highly abundant in bladder wrack stands, had either become locally extinct or occurred in very low abundance in the region overlapping with the current range of established distribution of the in-

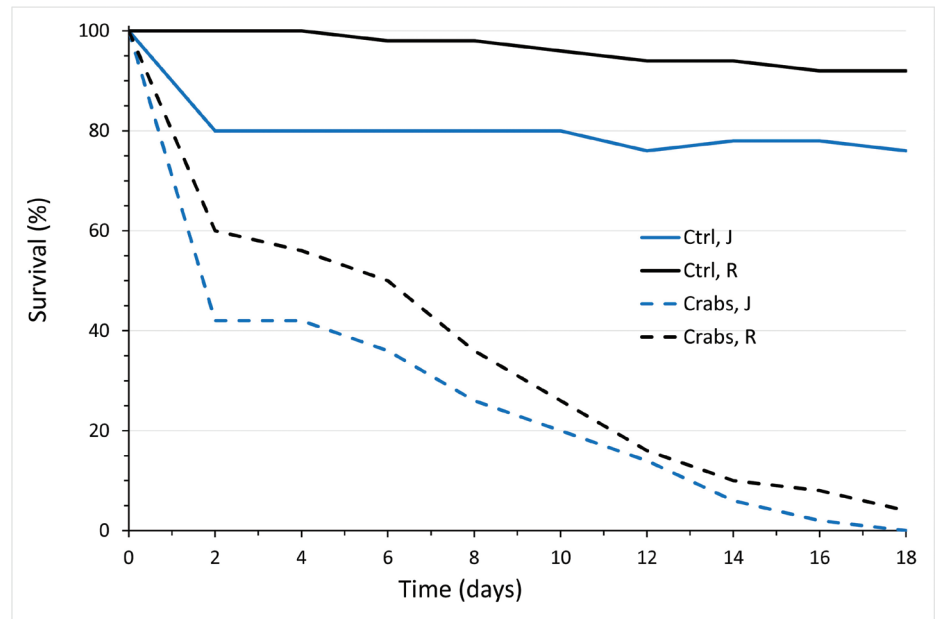


Figure 3. Survival of *I. balthica* during 18 days from the start of the experiment in control aquaria (Ctrl) and in aquaria with mud crabs (Crabs). In both control and predation treatment level, at the start there was 50 *I. balthica* individuals from both the two populations, both outside the mud crab distribution range (Jurmo (J) and Rihniemi (R)). These were divided into eight aquaria of 25 individuals each. In addition, in each predation aquaria there were four mud crabs.

vasive mud crab. We conducted the 2020 sampling in the fall, after the reproductive season of *I. balthica* during summer, at the time of its peak abundance (Korpinen et al. 2010). The nearly complete absence of the species and particularly the generation born during the summer in most of the sampling sites, indicates the extent of the collapse. In the samples collected in 1998, eleven years before the introduction of the mud crab, *I. balthica* was found in every sampled bladder wrack stand, and typically in a very high abundance. *Idotea balthica* has been a very common and abundant herbivore in seaweed as well as seagrass habitats throughout the coastal Baltic Sea (De Wit et al. 2020; Kotta et al. 2019; Leidenberger et al. 2012; Vesakoski et al. 2008), and its past commonness in the Archipelago Sea is well documented both here and in numerous other studies that have sampled hundreds (e.g. Jormalainen et al. 2001; Jormalainen and Tuomi 1989; Merilaita 2001; Merilaita and Jormalainen 2000; Tuomi and Jormalainen 1988; Vesakoski et al. 2008; Vesakoski et al. 2009) to thousands (Jormalainen et al. 1995) of *I. balthica* for laboratory experiments or estimated their abundance in the field (Gagnon et al. 2016; Haavisto and Jormalainen 2014; Korpinen et al. 2008; Korpinen et al. 2010). In the 2020 sampling, the six sites (out of 21) where we found *I. balthica*, their abundances varied from 2 to 130 individuals/100 l of bladder wrack. In the 1998 sampling, we found an average 50 individuals per one average sized bladder wrack (196 g wet weight), equalling about 25 000 individuals/100 l of bladder wrack. This suggests that also the abundances, when the species was present, were orders of magnitude smaller in 2020 than in 1998.

The decline of *I. balthica*, the key herbivore in the community, and herbivores in general as hinted here and by an earlier study (Jormalainen et al. 2016) is of great concern from a conservation point of view and raises ecological and evolutionary concerns. Isopods together with amphipods and gastropods have an important role as grazers in the Baltic Sea macrophyte communities. *Idotea balthica* is the only abundant grazer able to feed on the fully developed parts of the thallus of the bladder wrack. Grazing by *I. balthica* can have both negative and positive effects on bladder wrack: Grazing

can be substantial as over 60% of the biomass can be grazed at the time of the peak abundance of the isopod in the fall (Haavisto and Jormalainen 2014; Jormalainen and Ramsay 2009). Increased density of *I. balthica* has formerly been suggested to be one of the factors contributing to previous declines in bladder wrack abundance (Engkvist et al. 2004; Kangas et al. 1982; Nilsson et al. 2004; Salemaa 1987). However, direct grazing of the thallus (Haavisto et al. 2017) and even waterborne cues of grazing (Haavisto and Jormalainen 2019) can induce resistance against grazing in bladder wrack, providing population persistence especially when faced with seasonally high grazing pressure. Thus, although grazing may remove a substantial amount of bladder wrack biomass, the alga has evolved ways to deal with the high grazing pressure.

Another ecologically important function of the grazers is that they generate indirect benefits to large perennial macrophytes, such as the bladder wrack, by grazing on periphytic and filamentous macroalgae and microalgae that compete with macrophytes for light, nutrients and substrates. Small juvenile *I. balthica* feed solely on filamentous and periphytic algae (Salemaa 1986) while in their later life-stages they feed on a number of filamentous algae in addition to bladder wrack (Boström and Mattila 2005; Jormalainen et al. 2001; Kotta et al. 2000). Grazing of epiphytes by *I. balthica* is beneficial for eelgrass (Jaschinski and Sommer 2008) and grazers in general have positive effects on eelgrass (Hughes et al. 2004) and on bladder wrack (Korpinen et al. 2007) through removal of competitors. For example, grazing of periphytic microalgae by the snail *T. fluviatilis* from the bladder wrack thallus doubled the growth rate of bladder wrack (Honkanen and Jormalainen 2005). Thus, a drop in herbivore abundance will affect the top-down regulation of producer community by changing competitive interactions among algae.

Our observation on the collapse of the populations of the most important herbivore species and a possible collapse of one of the most abundant herbivorous gastropods, *T. fluviatilis*, suggests a major change in littoral ecosystem function caused by the predation effect of the invasive mud crab. This means the deterioration of trophic transfer of matter and energy from producers to herbivores, i.e. loss of producer-herbivore -link. Consequently, there will be less benthic-pelagic coupling through invertebrate herbivore - fish predator -interaction and an increased flux of producer biomass directly to decomposers. This is likely to increase the biomass of benthic drifting algal mats (Vahteri et al. 2000), benthic oxygen demand and CO₂ production, and exacerbate benthic hypoxia and acidification in coastal ecosystem (Melzner et al. 2013). Already as it is, coastal episodic hypoxia has increased for the last 50 years in the Baltic Sea, including the Archipelago Sea, due to anthropogenic eutrophication (Conley et al. 2011).

In addition to local extinction, also a steep decline in abundance can endanger local populations as it depletes genetic variation and thus reduces the potential of evolutionary adaptation of local populations to changing conditions. Local differences both in its colour morph frequencies (Merilaita 2001) and in the ability to utilize host species as food (Vesakoski et al. 2009) suggest that *I. balthica* is imposed to locally varying selection. Moreover, fast global change in the Baltic Sea, including eutrophication, acidification, change in temperature and salinity, introduction of the mud crab, the round goby and other invasive species (Reusch et al. 2018) are and will be changing the conditions and selection imposed on the littoral herbivores. This underlines the importance of maintaining adequate genetic variation and potential for evolutionary adaptation in persistence of species under environmental change (Chevin et al. 2010). If the native prey are capable of evolutionary responses to decrease predation mortality imposed by the invasive predator, the invasive species may decline after its initial rise to high densities, the native populations may persist and increase in abundance and the invasion may proceed

to a more persistent, less harmful stage ('boom-bust' -dynamics of invasion, Strayer et al. 2017). However, the ability for evolutionary responses may be compromised if the genetic variation is depleted by the magnitude of the initial collapse.

Our data strongly suggest a correlation between the establishment of the invasive mud crab and the decrease and local extinctions of *I. balthica* and possibly snails. However, our data do not enable the demonstration of causality, and therefore we also need to consider other possible explanations, that are related to climate change, changes in faunal community composition and biotic interactions. Sea surface temperatures have increased in Baltic Sea at a very fast rate of up to 0.6 °C per decade since 1980 (Reusch et al. 2018). While the increase in average temperature may lead to gradual changes in littoral faunal communities with time, the occasional extreme temperatures can cause rapid changes. Marine heatwaves, during which the water temperature exceeds the 90th percentile of the local 30-year temperature distribution for several days, have increased with the climate change (Frolicher et al. 2018). The most severe heatwave in the Baltic Sea was recorded in the Gulf of Finland in the summer 2018 (Humborg et al. 2019). There is still little knowledge on the effects of heatwaves on marine organisms in general (Frolicher and Laufkötter 2018), but increased mortality seems to be largely limited to sedentary benthic species (Garrahou et al. 2009; Pansch et al. 2018) that cannot move quickly enough to cooler, deeper water. Pansch et al. (2018) simulated southern Baltic Sea marine heatwaves in a mesocosm experiment and tested their effect on littoral macrofauna. They found that several sessile species were negatively affected, but neither one nor three heatwaves that lasted for up to four days and reached 25.2 °C affected the survival of *I. balthica*. In the year of the highest recorded heatwave in 2018, the surface water temperature in the inner Archipelago Sea monitoring point located in the middle of the current mud crab core distribution range exceeded 23 °C twice, with the maxima of 24.2 and 23.8 °C (Seili Environmental monitoring programme, Odas profiling buoy datasets. 2018. Turku University/ Turku University of Applied sciences, Turku. https://saaristomeri.utu.fi/odas_en/). Therefore, it seems unlikely that heatwaves could explain the decrease of *I. balthica* observed here.

There have been other recent changes in the littoral biota that may have affected the composition of invertebrate communities through predator-prey interactions: First, another introduced species, the round goby (*Neogobius melanostomus*) has expanded its distribution range in coastal Finland. It was found for the first time in Finnish coastal waters in the Archipelago Sea and Gulf of Finland in 2005, and in 2014 its distribution ranged from the Sea of Bothnia to the eastern Gulf of Finland (HELCOM fact sheet: Puntila et al. 2018). The round goby occurs in the littoral environment and its juveniles prefer shallow macrophyte habitats (Henseler et al. 2020). Medium-sized (5–10 cm) round gobies feed on benthic crustaceans and gastropods, whereas larger individuals feed more on polychaetes, bivalves, fish and spawn (Hempel et al. 2019; Henseler et al. 2020). Its habitat use together with the wide diet implies that the round goby may potentially affect abundance of littoral herbivores and their community composition. Corresponding effects of round goby have been found in stream and lake ecosystems (Barrett et al. 2017; Kipp et al. 2012; Kipp and Ricciardi 2012; Lederer et al. 2006; Lederer et al. 2008; Pennuto et al. 2018) as well as suggested in the Gulf of Riga in the Baltic Sea (Nurkse et al. 2016; Nurkse et al. 2018). However, if predation by round goby alone were behind the decrease of *I. balthica*, we would expect it to have happened throughout our study area due to its earlier introduction and rapid spread and establishment in the area. In particular, round goby was found around our northernmost sampling point close to the city of Rauma already in 2013, but despite that the site had the highest *I. balthica* abundance. Furthermore, spreading and increase of the round goby cannot explain decreasing abundance on *T. fluviatilis* as it preys hardly at all on it (Nurkse et al. 2016).

Another fish, the three-spined stickleback (*Gasterosteus aculeatus*) has increased rapidly in abundance in the northern Baltic Sea. In 2011, its density in the pelagic regions surrounding the Archipelago Sea was 4- to 45-fold compared to 1990 (Bergström et al. 2015; Olsson et al. 2019). The pelagic population of the stickleback are composed of pre-spawning juveniles, which migrate to littoral environment to feed and reproduce typically at the age of two years. They feed on herbivorous crustaceans and may generate cascading effects on autotrophs (Eriksson et al. 2011; Sieben et al. 2011). Coastal abundance of stickleback has increased in the Gulf of Finland (Candolin and Voigt 2020) and in the Archipelago Sea (Gagnon et al. 2017), and, in the latter, increase in abundance was most pronounced in the outer Archipelago, a pattern parallel to that in the coastal Sweden (Eklöf et al. 2020). Interestingly, in Gagnon et al. (2016), the study area “the outer archipelago” matches our study area outside the core distribution range of the mud crab while the “inner archipelago” is inside the core of mud crab distribution range. However, the abundance of the stickleback was 10- to 100-fold in the outer compared to the inner archipelago. If the increased stickleback predation were to explain the decrease of *I. balthica* we would expect a different spatial pattern of change from what we observed, namely decrease of *I. balthica* in the outer instead of the inner archipelago.

Consequently, we find an increase in fish predation by the round goby invasion or increased abundance of the three-spined stickleback as unlikely explanations for the collapse of *I. balthica*. The herbivorous crustaceans and molluscs of the Archipelago Sea have coexisted with predatory fish for a long period and have likely evolved anti-predatory adaptations against them. Hence, it seems more likely that a completely novel kind of predator, the mud crab, and the lack of recent shared coevolutionary history with it may predispose these herbivores to an unusually high predation mortality and local extinctions.

To conclude, although we cannot completely reject alternative single causes, or, combinations of multiple heatwaves, history of eutrophication and the changing ecological settings with multiple new predators working together, we consider the recent introduction and spread of the mud crab in the Archipelago Sea as the most straightforward and likely cause for a collapse of the key herbivore population and possibly to that of other herbivore species. The collapse comes with several ecological and evolutionary consequences. It may expose the native herbivore species to local extinctions and deplete genetic variation, decreasing the potential for adaptation to changing conditions. Deterioration of the herbivore function leads to trophic transfer of matter and energy shifting to decomposition instead of consumers, with likely impairment of littoral benthic-pelagic coupling and increase in benthic hypoxia. These are the consequences at the relatively early stage of invasion when the mud crab abundance has quickly increased, but it is hard to predict the long-term development. In the region, the mud crab is a novel predator and also a novel prey for native predators. Behavioural and evolutionary responses of the native species, if they are to occur, may alter the progression of the invasion from the early harmful stage to a less harmful one. There are no reasonable means to manage the mud crab invasion in the already invaded regions, but we may learn a lot by closely following the consequences of the progressing invasion.

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Authors' contributions

VJ, SM, VH and EK collected the data, VJ analyzed the data and produced the first manuscript version, SM, VH and EK contributed to the manuscript and all authors agreed the submission.

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