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Abstract Native fauna in species poor communities, such as those of the Baltic Sea, may be particularly vulnerable to the effects of species invasions. However, the interspecific interactions that result in the negative impacts on native species tend to be poorly understood. One contributing factor to this knowledge gap may be that the vulnerability of native species can vary between different life-history stages. For example, the parental care phase is often risky both for the developing offspring and care-giving parents. Accordingly, we investigated the interactions between invasive mud crabs, *Rhithropanopeus harrissii*, and native nest-building littoral fish, with a special focus on the sand goby, *Pomatoschistus minutus*. Firstly, our field survey demonstrated that while the recently established mud crab and native nest-building fish have different habitat and depth optima, their distributions also have a considerable overlap, with a high potential for interactions between them. Secondly, our laboratory experiments indicate that the crabs are

likely to impact the fish negatively, especially by taking over occupied nests, as well as pre-occupying nesting resources that are of very limited supply in the studied population. We did not find evidence for successful predation on eggs guarded by male sand gobies naive to the mud crabs. Collectively, the results suggest that the invasive crabs have high potential to negatively impact native fish. Furthermore, the results support the scenario that the parental phase can be a particularly vulnerable life-history stage in face of novel selection pressures, such as species invasions.

Keywords (separated by '-') Baltic Sea - Benthic fish - Competition - Mud crab - Nest - Reproductive behaviour

Footnote Information

2 **The impact of an invasive mud crab on brood success**
3 **of nest-building fish in the Northern Baltic Sea**

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Abstract Native fauna in species poor communities, such as those of the Baltic Sea, may be particularly vulnerable to the effects of species invasions. However, the interspecific interactions that result in the negative impacts on native species tend to be poorly understood. One contributing factor to this knowledge gap may be that the vulnerability of native species can vary between different life-history stages. For example, the parental care phase is often risky both for the developing offspring and care-giving parents. Accordingly, we investigated the interactions between invasive mud crabs, *Rhithropanopeus harrissii*, and native nest-building littoral fish, with a special focus on the sand goby, *Pomatoschistus minutus*. Firstly, our field survey demonstrated that while the recently established mud crab and native nest-building fish have

different habitat and depth optima, their distributions also have a considerable overlap, with a high potential for interactions between them. Secondly, our laboratory experiments indicate that the crabs are likely to impact the fish negatively, especially by taking over occupied nests, as well as pre-occupying nesting resources that are of very limited supply in the studied population. We did not find evidence for successful predation on eggs guarded by male sand gobies naive to the mud crabs. Collectively, the results suggest that the invasive crabs have high potential to negatively impact native fish. Furthermore, the results support the scenario that the parental phase can be a particularly vulnerable life-history stage in face of novel selection pressures, such as species invasions.

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Introduction

Invasive species are one of the leading global threats to biodiversity (Sakai et al. 2001; Clavero and García-Berthou 2005). For instance, invasive predators have been found to have a greater negative impact on prey populations than similar native predators (Salo et al. 2007). However, the vulnerability of native species is likely to vary depending on their life-history stage (Ficetola et al. 2011, 2012; Siesa et al. 2014),

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50 contributing to the difficulty of predicting the impacts
51 of interactions between invaders and natives. The
52 phase of parental care (when present) may be a
53 particularly susceptible life-history stage, in terms of
54 affecting the fitness of two generations. For example,
55 parents of native species may react incompetently
56 towards novel predators of offspring due to a lack of
57 joint evolutionary history with them (Cox and Lima
58 2006; Freeman and Byers 2006; Sih et al. 2010; Wong
59 and Candolin 2015). Such suboptimal responses are
60 seen in a biparental Neotropical cichlid fish, *Amphilo-*
61 *phus zalius*, when the parents are facing an intro-
62 duced, potential predator of their offspring (Lehtonen
63 et al. 2012). Similarly to predators, novel competitors
64 could conceivably decrease the fitness of the parents,
65 e.g. by interfering with their reproductive behaviours.

66 Native fauna in communities with low species
67 diversity are thought to be particularly vulnerable to
68 the effects of species invasions (Stachowicz et al.
69 1999; Leppäkoski and Olenin 2000; Strauss 2014).
70 Such communities can also provide excellent oppor-
71 tunities to assess novel species interactions and, in the
72 longer term, evolutionary change in traits such as anti-
73 predator behaviours. One of the most recent invaders
74 in the species poor community of the Northern Baltic
75 Sea (as described by Paavola et al. 2005) is the mud
76 crab *Rhithropanopeus harrissii* (Fowler et al. 2013),
77 also known as the 'white-fingered mud crab', 'the
78 estuarine mud crab', 'Harris mud crab', and 'dwarf
79 mud crab'. From hereon, we refer to the species simply
80 as 'mud crab'. This mud crab species is native to the
81 Atlantic coast of North America (Williams 1984),
82 from where it has recently proliferated around the
83 globe, mostly via the ballast waters of ships (Roche
84 and Torchin 2007).

85 The mud crab was first found on the coast of
86 Finland, in the Northern Baltic Sea, in 2009, and has
87 since been expanding its local range, and as a result,
88 now occupies multiple habitats (Fowler et al. 2013).
89 Regarding their preferred habitat, mud crabs have
90 previously been found to select vegetated boundary
91 areas over more bare substratum, cover provided by
92 the bladder wrack, *Fucus vesiculosus*, over cover by
93 other local algae (Aarnio et al. 2015; Nurkse et al.
94 2015), and cavities provided by stones over shelter
95 provided by vegetation (Riipinen et al. 2017). The
96 mud crab also has a high potential for impacting native
97 species within the invaded habitats, as it has been
98 found to predate on native immobile and mobile fauna

(Forsström et al. 2015; Lokko et al. 2016), and isotope
analyses suggest that the diet of larger mud crabs
(> 12 mm) corresponds to a relatively high position
(that of a secondary consumer) in the food web (Aarnio
et al. 2015). Recently, mud crabs were also found to
have a drastic effect in the community associated with
the habitat forming brown alga bladder wrack, with a
decrease in local species diversity, as well as decline in
the growth of the bladder wrack, during a 3-year rapid
increase of mud crab numbers (Jormalainen et al.
2016). Given the mud crab's preference for crevices
amongst rocks as shelters (Riipinen et al. 2017;
personal observations), the species also has a high
potential to interact with native species that may have a
period of stationary egg defence in a nest or crevice
along the seafloor. Not only might this omnivorous crab
species predate on fish eggs, but it may also interfere
with parental care strategies (e.g. egg fanning), in
addition to competing for suitable cavities and other
potential nesting resources with species such as gobies
(e.g. the common goby, *Pomatoschistus microps*),
sticklebacks (e.g. the three-spined stickleback, *Gas-*
terosteus aculeatus) and sculpins (e.g. the European
bullhead, *Cottus gobio*). In this regard, we expect that in
cases when suitable hiding cavities are in short supply,
as is the case on most sandy substrate bottoms in the
Northern Baltic Sea (Forsgren et al. 1996; Lehtonen and
Lindström 2004), mud crabs should have the potential
to have negative impacts on such fish species by
expelling the egg-guarding male from the nesting
cavity it is occupying.

One particularly well-studied nest-building fish,
with a wide distribution range along the European
coasts (Miller 1986), is the sand goby, *Pomatoschistus*
minutus. It is the most common species of littoral fish
in many parts of the Baltic Sea (Jansson et al. 1985;
Zander 1990; Sundell 1994; Parmanne and Lindström
2003) and an important node in the food web of the
littoral zone (Fonds 1973), as demonstrated by the
wide array of parasites that have adapted to exploit it
as an intermediate host (Zander et al. 1993). In many
areas, sand gobies compete intensively for suit-
able nesting resources, such as mussel shells, which
are small and sparsely distributed in the Northern
Baltic Sea (Forsgren et al. 1996; Singer et al. 2006;
Wong et al. 2008), or flat stones lying on fine sand
(Lehtonen and Lindström 2004). Similarly to e.g.
common gobies, the male sand goby first prepares a
nest by displacing sand from under a nesting resource

(typically $< 100 \text{ cm}^2$ in surface area). It attracts females to lay eggs in a mono-layer onto the roof of the nesting chamber, and then guards the nest and cares for the eggs until they hatch. Nesting behaviours of gobies (e.g. black gobies, *Gobius niger*) in areas of rocky, hard substrate are similar, except that the male needs to use existing crevices as there is no fine sand to displace (Lehtonen and Lindström 2004; Järvi-Laturi et al. 2008). In the case of the sand goby, the use of the rocky substratum type appears to be a unique, local adaptation to a low abundance of nest predators (Lehtonen and Lindström 2004; Järvi-Laturi et al. 2008). In particular, sand gobies seem to be using such cavities under and amidst stones for breeding only in the Northern Baltic Sea (Zander 1990; Lehtonen and Lindström 2004), where formidable predators of goby eggs, marine crabs and dogwhelks, *Nucella lapillus*, have thus far been absent, not withstanding the rare occurrence of non-breeding individuals of the Chinese mitten crab, *Eriocheir sinensis* (see Bonsdorff 2006). Given the above, we expected that the invasive mud crab may impact the breeding of nest-building and cavity-breeding fish, if the fish and crabs co-occur within the same areas and habitats.

The aim of the current study was to use the recent invader, the mud crab *R. harrissii*, as a model to investigate the influence of newly established crabs on local nest-building fish. In this context, ‘nest-building fish’ are broadly defined as any fish species that uses a crevice or other nesting resource on the seafloor during parental care of eggs or juveniles. We first surveyed multiple habitat types and water depths in the field to identify the species of fish that co-occur with the mud crab, particularly focusing on the overlap between mud crabs and nest-building fish. We also conducted two laboratory experiments to investigate (i) whether mud crabs compete with sand gobies for the type of structures that sand gobies use for nesting, (ii) whether the presence of mud crabs influences nest-building of sand gobies naive to crabs, and (iii) whether the presence of mud crabs affects survival of sand goby eggs.

189 Methods

190 Field study

191 The field study was carried out in June–August in
192 2012, in the surroundings of the Archipelago Research

Institute of the University of Turku, on the Finnish coast of the Baltic Sea (lat. $60^{\circ}14.2'N$; long. $21^{\circ}57.5'E$; Fig. 1). Here, the aim was to investigate the extent to which the invasive mud crab co-occurs with native nest-building fish. For this purpose, we used data from a field study by the Finnish Environment Institute’s Marine Research Centre, with other aspects of that study, i.e. assessment of methods for monitoring marine invasive species, being presented elsewhere (Forsström et al., unpublished data).

The approach in the field study was to catch small, seafloor-oriented species, such as benthic fish and invasive mud crabs, using traps (see below for trap details). The traps were placed in three different habitats, each represented by three distinct ‘locations’ (Fig. 1), with three different depth categories sampled at each location. Hence, in total we had $3 \times 3 \times 3 = 27$ sampling sites. Each sampling site, in turn, had either two slightly different traps ($n = 22$ sampling sites, see below for information about the two trap types) or only one trap ($n = 5$ sampling sites with an ‘American trap’, see below). Hence, $n = 49$ traps were included in the study. The distance between the nearest traps was always $\geq 3 \text{ m}$, whereas the distances between the nine locations (three per habitat type) are shown in Fig. 1.

The three habitat types sampled for the survey—soft substrate, sandy substrate and *Fucus* habitat—represent typical benthic environments in the area, with different animal and macrophyte communities inhabiting each of them. Previous findings suggest that both mud crabs and breeding individuals of nest-building fish can be found in most, if not all, of these habitats (Lehtonen and Lindström 2004; Fowler et al. 2013; Gagnon and Boström 2016; Riipinen et al. 2017). *Soft substrate habitat* had a layer of organic material and silt on the bottom, typically combined with low water clarity and the common reed, *Phragmites australis*, as the dominant macrophyte. *Sandy substrate habitat* was characterised by relatively fine-grained sand with patches of vascular plants, such as the eelgrass, *Zostera marina*, and low densities of stones and rocks. Finally, *hard substrate habitat*, from hereon *Fucus habitat*, was covered with coarser gravel or rock substrate and had a moderate to high density of the bladder wrack, *F. vesiculosus*, growing on the seafloor, forming an important perennial environment for benthic fauna. While no detailed underwater maps of the region are available, underwater habitats are

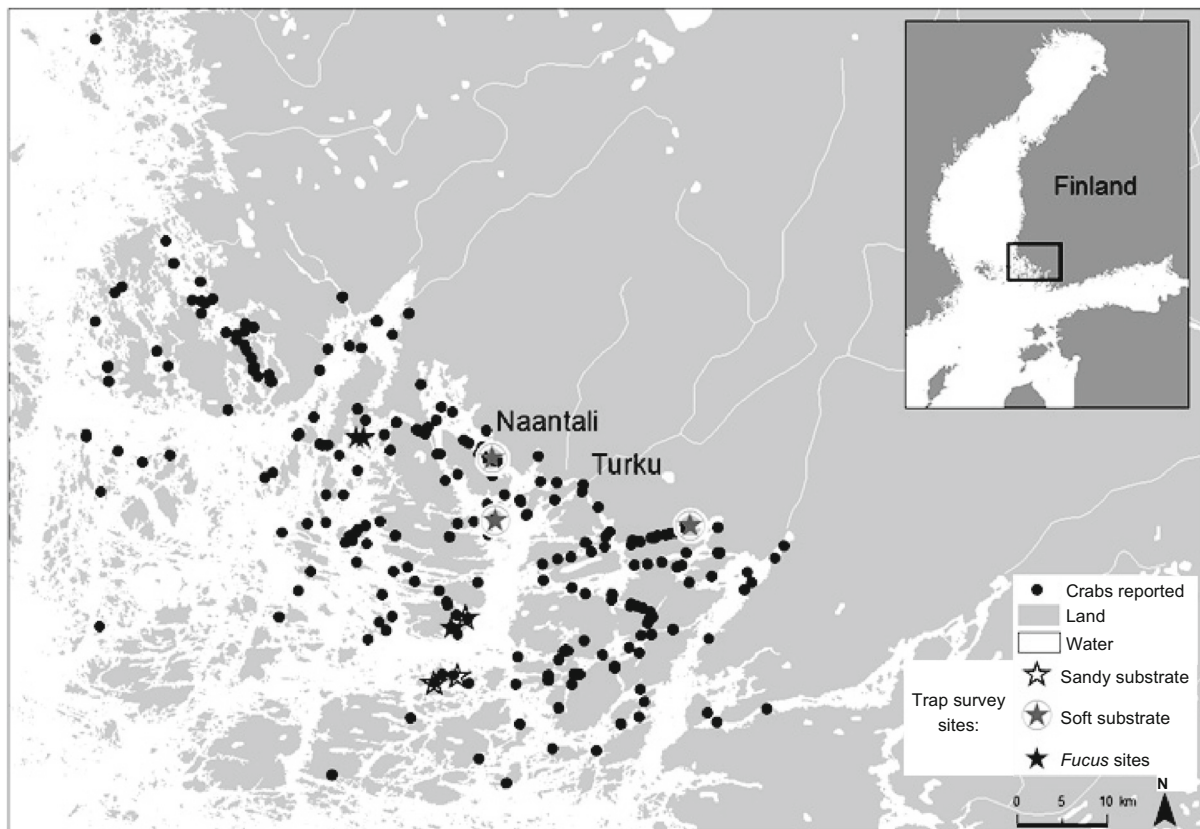


Fig. 1 The 9 locations of the field survey cover 3 types of habitats, as indicated by the star symbols. In addition, black dots show observations of mud crabs on the Finnish coast between

2011 and 2014, as reported by the general public (data collected and provided by the Finnish Environment Institute)

242 likely to be highly affected by the fragmented island
243 mosaic of the archipelago (Fig. 1), with soft substrate
244 areas being more common than the other two habitat
245 types within the area covered by the survey (personal
246 observations).

247 The three sampling depth categories, 1, 1.5–2 and
248 3–4 m, covered the typical depth range in which all
249 three habitat types can be found, and in which many
250 littoral fish have been found to occur during the
251 reproductive season (Lappalainen and Urho 2006).

252 The traps, placed on the seafloor, were filled with
253 pieces of clay flowerpots and lava rocks to provide a
254 network of cavities, with animals being able to move
255 in (and out of) the traps through holes in the walls and
256 ceiling. The dimensions of the traps were
257 30 cm × 30 cm × 30 cm. They had either both the
258 ceiling and walls made of 1 cm × 1 cm plastic mesh
259 with 2–3 larger holes of approximately 2 cm × 2 cm
260 in each wall ('mesh trap'), or the 1 cm × 1 cm mesh

ceiling was combined with plastic walls with
261 2 cm × 2 cm holes (9 holes per wall; 'American
262 trap'). Crabs of various sizes, including those having
263 carapace width of > 2 cm, commonly enter such
264 traps, because their movement is limited by the
265 narrowest dimension of their carapace (rather than
266 its width), while the distance between the opposite
267 corners of a 1 cm × 1 cm grid is $\sqrt{2}$ cm. The bottom
268 of all traps was covered with plastic sheets. Because
269 such traps capture aquatic fauna by providing attrac-
270 tive places of shelter, they are also sometimes called
271 'habitat traps' (sensu Fowler et al. 2013).
272

273 Each trap was checked approximately once a week
274 (in total 2–7 times, except for 1 trap that got lost after
275 the first check). When we checked traps, they were
276 lifted quickly to a boat and their contents were emptied
277 into a bucket with seawater. Because the traps were
278 filled up with pieces of clay pots, and had their bottom
279 parts covered with plastic sheets, the traps caught a
279

280 wide range of aquatic animals, including mud crabs
281 and fish, even without wrapping at the time they were
282 lifted out of the water. After carefully removing the
283 trap filling materials from the bucket, the catch was
284 immediately filtered through a 1 mm sieve. All
285 animals discovered with this method were then moved
286 to labelled sample containers and identified later.

287 Experiment 1: nest building behaviour

288 The laboratory experiments were conducted at the
289 Tvärminne Zoological Station of the University of
290 Helsinki (lat. 59°50.7'N; long. 23°15.0'E), in June
291 2012, during the breeding season of the local sand
292 goby population. Sand gobies were chosen as the
293 model system because the species readily exhibits the
294 full range of breeding behaviours within a short
295 timeframe in aquarium conditions (see e.g. Lehtonen
296 2012), and occurs in high numbers across multiple
297 habitats, making it readily available for experimental
298 set-ups. The aim of experiment 1 was to investigate
299 whether the presence of the invasive mud crab affects
300 the motivation of fish naive to its presence, in terms of
301 investment in nest building or adjustment of nest
302 characteristics. For this purpose, we used male sand
303 gobies from the proximity of the Tvärminne field
304 station, where mud crabs do not yet occur (as of 2016).
305 The fish were exposed to the following three treatment
306 levels: presence of a mud crab, presence of a brown
307 shrimp, *Crangon crangon* (also known as the 'sand
308 shrimp', 'common shrimp' and 'bay shrimp'), which
309 is a native shrimp that is known to predate at least on
310 unguarded goby eggs (Chin-Baarstad et al. 2009), and
311 a control treatment in which intruders were absent.

312 Sand gobies, as well as brown shrimp used in this
313 study, were collected in shallow sand bottom areas
314 using a hand-trawl (see Lehtonen and Kvarnemo
315 2015) and dip nets. At the station, both gobies and
316 shrimp were housed in several aquaria (50–100 l),
317 with the gobies being separated by sex. All aquaria
318 were kept under natural light conditions and were
319 supplied with continuous flow-through of seawater.
320 Before the commencement of the experiment, sand
321 gobies were fed twice a day with live mysid shrimp,
322 whereas brown shrimp were fed with frozen chirono-
323 mid larvae. Mud crabs used in our laboratory exper-
324 iments were caught ~ 100 km northwest on the
325 Finnish coast (lat. 60°24.5'N; long. 22°26.4'E) using
326 traps similar to those of the field study, and then

transported to the field station. The mud crabs were
housed in separate sex stock tanks similar to those
used for housing gobies and brown shrimp, and were
fed with frozen chironomid larvae.

Immediately prior to the onset of the experiment,
gobies, mud crabs and shrimp were weighed using an
electronic balance. The carapace width of mud crabs
was also measured using a calliper. At the onset of each
trial, one sand goby male was placed into an experi-
mental arena measuring 18 cm × 25 cm × 20 cm
(length × width × water depth), with a 4 cm layer of
fine sand as the substratum. In each arena, a ceramic tile
(measuring 10 cm × 10 cm) was placed on top of the
substratum in the middle of the tank as a nesting
resource. Such tiles are similar in size to flat stones that
sand gobies often use for nest construction in the wild
(Lindström 1992; Lehtonen and Lindström 2004; Wong
et al. 2008), and have previously been used successfully
as sand goby nesting resources both in the wild and
laboratory (Wong et al. 2008; Lehtonen et al.
2013, 2015). Each male sand goby was haphazardly
assigned to one of the three treatments. In the mud crab
treatment, one crab ($n = 38$ replicates; mean carapace
width ± SD: 17.6 ± 3.5 mm; weight ± SD: 2.66 ±
1.07 g) was released in the arena at the same time with
the male goby ($n = 38$; weight: 0.97 ± 0.21 g, corre-
sponding to ~ 5 cm of total length). Crabs of that size
are not large enough to predate on adult gobies (Lissåker
and Kvarnemo 2006). In the brown shrimp treatment,
one brown shrimp ($n = 38$; weight: 1.32 ± 0.32 g,
corresponding to ~ 5 cm body length) was released
into the arena at the same time with the male goby
($n = 38$; weight: 1.06 ± 0.34 g). In the control treat-
ment, only the male goby was introduced ($n = 36$;
weight: 1.11 ± 0.29 g). One individual of a species in
each tank corresponds to natural densities of these
animals in the wild. In particular, it is uncommon that a
comparable area of seafloor area is occupied by more
than one nesting sand goby male (e.g. Lehtonen and
Lindström 2004). One brown shrimp within a compa-
rable area of seafloor is also very typical on sandy
substrata (personal observations). Densities of the
invasive mud crabs, in turn, are highly site dependent
(Fowler et al. 2013; Gagnon and Boström 2016).

We checked all tanks every 3–4 h between 09:00
and 21:00 for signs of nest building. Nests were not
checked between 21:00 and 9:00. A male was deemed
to have initiated nest building when it started to pile
sand on top of, and excavate under, the tile (Wong

376 et al. 2008; Japoshvili et al. 2012; Lehtonen et al.
 377 2013). If a male did not start to build a nest within
 378 48 h, the replicate was terminated. Nest characteristics
 379 were assessed for replicates in which the male did start
 380 to build a nest within 48 h. After the first signs of nest
 381 building, the male was left in the tank for another 24 h
 382 to complete his nest (nest building typically takes from
 383 one to a few hours). We then measured the following
 384 two ecologically relevant and commonly used mea-
 385 sures of nest construction in gobies (see Japoshvili
 386 et al. 2012): (1) the amount of sand the male piled on
 387 top of the tile, and (2) the width of the nest entrance
 388 (also called ‘nest-opening’ sensu Svensson and
 389 Kvarnemo 2003). To measure the amount of sand
 390 piled on top of the tile, we carefully collected the sand
 391 by lifting the tile into a tray. The sand was later dried
 392 for 36 h at 60 °C, after which its dry weight was
 393 measured using an electronic balance (Lehtonen and
 394 Wong 2009; Lehtonen et al. 2015). The width of the
 395 nest entrance was measured using a ruler.

396 Experiment 2: egg survival

397 The aim of this experiment was to quantify the
 398 survival of sand goby eggs when the eggs were tended
 399 by a male (1) in the presence of a mud crab, (2) in the
 400 presence of a brown shrimp or (3) in the absence of
 401 any intruders. In all treatments, one male sand goby
 402 was placed into a tank, which measured 18 cm ×
 403 25 cm × 20 cm (length × width × water depth) and
 404 had a 4 cm layer of fine sand on the bottom. The male
 405 was provided with two identical nesting resources of
 406 halved clay flowerpots (diameter: 6.5 cm), lined with
 407 a piece of transparent acetate onto which eggs are
 408 attached during spawning. Such artificial nesting
 409 resources are readily accepted by sand gobies in both
 410 laboratory conditions and the field (Forsgren et al.
 411 1996; Lehtonen and Lindström 2007; Japoshvili et al.
 412 2012). The purpose of the second clay pot was to
 413 function as a potential shelter for the intruder (mud
 414 crab or shrimp). Egg survival was assessed by
 415 photographing the acetate film as soon as eggs were
 416 laid on it and then again after 7 days, which is close to
 417 a typical hatching time (Fonds and Van Buurt 1974;
 418 Lehtonen and Lindström 2007). The numbers of eggs
 419 were later counted from the two photographs. The
 420 most important sources of egg losses were likely to be
 421 filial cannibalism by the focal goby male and egg
 422 predation by the intruder (Lissåker and Kvarnemo

2006; Lehtonen and Lindström 2007; Chin-Baarstad
 et al. 2009).

All focal males were given at maximum 48 h to
 initiate nest building. If the goby did not initiate nest
 building within 48 h, the replicate was restarted with
 another individual. When a male had finished building
 the nest, a female goby that had her belly distended
 with eggs ($n = 53$; weight: 1.03 ± 0.30 g) was added
 into the tank. As soon as the fish had spawned, the
 female was removed and the transparent film with the
 eggs was photographed (Olympus XZ-1 digital cam-
 era), and the eggs were then carefully placed back into
 the nest (Lehtonen and Lindström 2007). At this point,
 an intruder was introduced: a mud crab ($n = 19$, cara-
 pace width: 17.3 ± 2.0 mm, weight: 2.27 ± 0.77 g;
 sand goby weight: 0.94 ± 0.30 g) in the crab treat-
 ment, a brown shrimp ($n = 17$, weight: $1.58 \pm$
 0.50 g; sand goby weight: 1.02 ± 0.28 g) in the
 shrimp treatment. To control for the potential distur-
 bance of introducing the intruder, the same amount of
 water but without an intruder was poured into control
 treatment replicates ($n = 17$; sand goby weight:
 1.03 ± 0.32 g). After 48 h, the tanks were again
 disturbed with a hand net and the intruders in the crab
 and shrimp treatments were removed. This was done
 to replicate invader densities in which they are not
 constantly present throughout the brood cycle of the
 fish, and also to allow the focal male goby to be fed
 without an intruder, as described below.

During the nest building phase, the males in all
 treatments were fed 4 frozen chironomid larvae daily.
 Feeding was suspended when the female was added in
 the tank and then resumed after the intruder presence
 period had ended (the same schedule was followed in
 the control replicates). The trials were completed after
 7 days of egg care and gobies and brown shrimp were
 then released back to the sea, whereas the invasive
 mud crabs were euthanized.

Statistical analyses

When analysing the field survey data, we considered
 whether or not a trap, when checked, had caught any
 individuals of the species of interest, i.e. we consid-
 ered binomial absent/present data. The occurrence of
 mud crabs and nesting fish at the different depths and
 habitats was analysed using a generalized mixed
 model with a binomial distribution and the species
 type (mud crab/nesting fish), depth category (1 m/

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470 1.5–2 m/3–4 m) and habitat (soft/sand/*Fucus*) as fixed
 471 effects, and trap type ('American trap'/ mesh trap') as
 472 a covariate. The covariate was added to account for 5
 473 of the 27 sampling sites (location × depth combina-
 474 tions) having only one of the two trap types. Similarly,
 475 to account for the procedure of counting both mud
 476 crabs and fish captured by the same 1–2 traps at each
 477 sampling site, 'sampling site ID' was added as a
 478 random effect. We then proceeded with stepwise refits
 479 of the model, each time excluding the least significant,
 480 highest order interaction term, using χ^2 -tests with
 481 $p = 0.05$ as the cut-off point (Crawley 2007). We used
 482 R 3.2.2 software (R Development Core Team) for the
 483 field survey analysis.

484 The effect of the intruders on the time until the start
 485 of nest building in experiment 1 was analysed using a
 486 Cox proportional hazards model, 'right censoring'
 487 (Lagakos 1979) the 60 replicates in which a nest was
 488 not built within 48 h. Treatment and male weight were
 489 used as explanatory factors. To investigate nest
 490 characteristics, we ran a linear model for the amount
 491 of sand on nest (i.e. nest elaboration) and nest entrance
 492 width separately. In both cases, we had the treatment
 493 and male weight as fixed effects. Sand weight was log-
 494 transformed for improved normality. We then
 495 assessed whether the models could be refitted without
 496 the treatment × weight interaction by using a χ^2 -test
 497 (with $p = 0.05$ as the cut-off point).

498 For experiment 2, egg survival was assessed by
 499 using both the number of eggs present at the end of the
 500 experiment and the number of 'failures', i.e. the
 501 difference between initial and final number of eggs in
 502 the nest. As the data did not meet assumptions of a
 503 binomial distribution due to over-dispersion, we
 504 applied a generalized model with quasi-binomial
 505 distribution. Treatment and male weight were used
 506 as explanatory variables and model simplification was
 507 conducted as above. Experiments 1 and 2 were
 508 analysed using R 3.0.2 software (R Development
 509 Core Team).

510 **Results**

511 **Field study**

512 Our traps caught in total of 561 mud crabs and the
 513 following nest-building fish: 98 individuals of black
 514 gobies, 3 sand gobies, 1 common goby, 1 three-spined

stickleback, and 1 ninespine stickleback, *Pungitius* 515
pungitius. The traps also caught 6 individuals of other 516
 littoral fish species that do not build nests. 517

518 The generalized mixed model indicated that nest- 518
 building fish and mud crabs significantly differed in 519
 their habitat and depth preferences, with both species 520
 category × habitat ($\chi^2 = 36.1$, $df = 2$, $p < 0.001$) 521
 and species category × depth ($\chi^2 = 9.14$, $df = 2$, 522
 $p = 0.010$) interactions being significant. In particu- 523
 lar, nesting fish were the most common in shallow 524
 water and sandy habitats, whereas mud crab catches 525
 were higher in the other two habitat types (Fig. 2) and 526
 deeper water (Fig. 3). Nevertheless, there was con- 527
 siderable overlap between the distribution of mud 528
 crabs and nesting fish across the different depths and 529
 habitats, with 96% (25 out of 26) of the traps that had 530
 nesting fish also having mud crabs, either at the same 531
 time or another time those traps were checked (Figs. 2, 532
 3). 533

Experiment 1: nest building behaviour 534

535 Neither intruder treatment (Cox proportional hazards 535
 model, treatment effect, $\chi^2 = 3.11$, $df = 2$, $p = 0.21$; 536
 Fig. 4), male weight ($\chi^2 = 1.40$, $df = 1$, $p = 0.24$), 537
 nor their interaction ($\chi^2 = 1.36$, $df = 2$, $p = 0.51$) 538
 had a significant effect on time until the gobies started 539
 nest building (Likelihood ratio test on the full 540

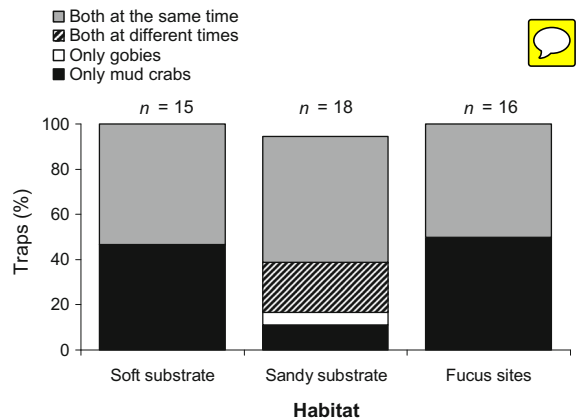


Fig. 2 The proportion of traps in the three habitat types with only mud crabs (black area), mud crabs and nest-building fish at the same time at least in one trap check (grey area), mud crabs and nest-building fish in the same trap but never at the same time (striped area), and only nest-building fish (white area). A column height less than 100% indicates the proportion of traps that caught neither mud crabs nor fish. The total number of traps is shown above each bar

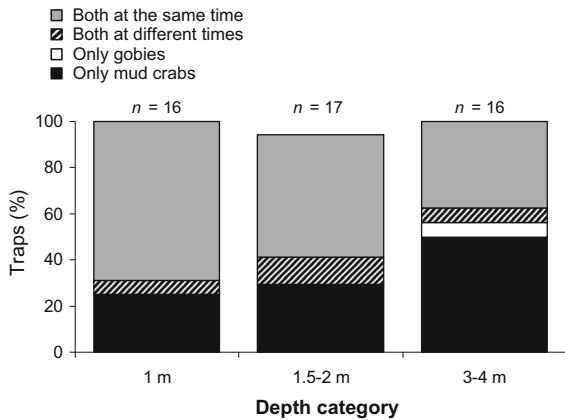


Fig. 3 The proportion of traps in the 3 depth categories with only mud crabs (black area), mud crabs and nest-building fish at the same time at least in one trap check (grey area), mud crabs and nest-building fish in the same trap but never at the same time (striped area), and only nest-nest-building fish (white area)

model = 5.87, $df = 5$, $p = 0.32$). The results were the same for a model fitted without the interaction term. The number of males that built a nest within 48 h was 22 out of 36, 15 out of 38, and 17 out of 38 in the control, brown shrimp, and mud crab treatments, respectively (G test of independence with Williams' correction, $G^2 = 3.70$, $df = 2$, $p = 0.16$). The mud crab took over the nest and completely destroyed the nest entrance in 5 out of the 17 crab treatment replicates in which the male had built (or started to build) a nest. This implies that the 95% confidence interval for the probability of a nest take-over in the

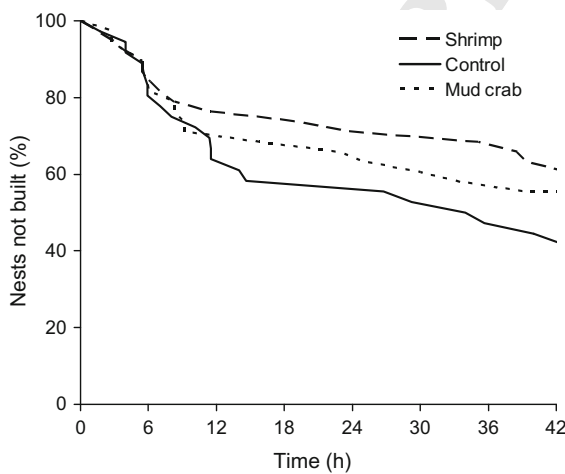


Fig. 4 Nest building over time in experiment 1. The solid, dotted and dashed lines indicate the control, mud crab, and brown shrimp treatments, respectively

presence of a mud crab was 0.103–0.560 (assessed by a binomial test). The probability for a nest take-over in the control treatment (without an intruder) was 0, and we are also not aware of the brown shrimp taking over sand goby nests. The 5 take-overs with a mud crab present resulted in the treatments to differ in the rate of nest destructions (G test of independence with Williams' correction, $G^2 = 11.17$, $df = 2$, $p = 0.004$). In two additional mud crab replicates, in which the male was not recorded to have built a nest, the mud crab was using the nesting resource (i.e. tile) as a hiding place at the end of the trial. We do not know whether the mud crab occupied the tile before any nest-building attempts by the goby male or whether the crab took over the tile during initial stages of a nesting attempt.

The amount of sand on those nests that were not taken over during the first 24 h after the onset of nest building was independent of the treatment (after exclusion of a non-significant treatment \times male weight interaction, linear model, $F_{2,46} = 0.003$, $p = 1.0$). The males piled 38 ± 38 g ($n = 22$), 32 ± 25 g ($n = 14$) and 45 ± 36 g ($n = 12$) of sand on the nest ridge in the control, brown shrimp and crab treatments, respectively. There was a non-significant tendency for heavier males to pile more sand on the nest ($F_{2,46} = 3.893$, $p = 0.055$). In the model with a non-significant interaction removed, nest entrance width did not significantly differ among the treatments (linear model, $F_{2,42} = 0.165$, $p = 0.85$), with the entrance widths of 23 ± 10 mm ($n = 22$), 23 ± 8 mm ($n = 14$) and 21 ± 5 mm ($n = 10$), in the control, shrimp and crab treatments, respectively. There was a non-significant tendency for larger males to have wider nest entrances ($F_{1,42} = 2.891$, $p = 0.096$). In two crab and one shrimp replicate, the goby had completely closed the nest entrance, resulting in nest entrance measures to be missing in these replicates.

Experiment 2: egg survival

In the model without the non-significant interaction, neither intruder treatment (generalized linear model, $F_{1,49} = 0.663$, $p = 0.52$) nor male size ($F_{1,49} = 0.723$, $p = 0.40$) had an effect on the proportion of eggs surviving over the 7 day period (Fig. 5). The mud crab took over the goby nest with eggs in one replicate, indicating that the 95% confidence interval for the probability of a nest take-over in the presence of a mud

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600 crab was 0.001–0.260 (binomial test). This means that
 601 the rate of nest takeovers did not significantly differ
 602 between experiments 1 and 2 (Fisher's exact,
 603 $p = 0.081$). As above, no signs of nest take-overs
 604 were expected, or recorded, in the two other
 605 treatments.

606 Discussion

607 Our results show that the invasive mud crab co-occurs
 608 with several species of littoral fish, especially gobies,
 609 along the coastal areas that it has invaded. In the
 610 laboratory, mud crabs took over and destroyed
 611 between 5% (1 out of 19 in experiment 2) and 29%
 612 (5 out of 17 in experiment 1) of the nests built by male
 613 sand gobies. Despite this threat to the nests, motivation
 614 of the goby to build a nest did not seem to be affected
 615 by the presence of a mud crab, as there was no
 616 significant difference between the proportion of males
 617 that built a nest (and hence initiated a breeding
 618 attempt) in the three treatments.

619 For assessing the potential ecological impact of
 620 invasive species to natives, it is important to know
 621 how likely the two are to encounter each other. In this
 622 respect, the field survey indicated a considerable
 623 overlap in the distribution of nest-building fish and
 624 mud crabs, as demonstrated by 52% of the traps
 625 capturing both nesting fish and mud crabs at the same
 626 time at least once (Figs. 2, 3). However, the peaks of
 627 fish and mud crab distributions differed. It is possible
 628 that the presence of mud crabs in a trap (or sampling
 629 site) affected the likelihood of nesting fish to seek

shelter in the same trap. This, in turn, could have
 inflated the differences in the distributions of mud
 crabs and fish. More generally, the presence of
 individuals of other species in the traps may have
 affected subsequent accumulation of individuals of
 other species. Our statistical analyses, however, were
 not designed to detect the presence (or absence) of
 such patterns. It is also important to note that the traps
 were optimised to catch a wide array of benthic
 invasive animals, and their efficiency in catching fish
 was likely to be species specific. For example, our fish
 catch was heavily dominated by black gobies,
 although at least a subset of the sampled sandy
 substrate and *Fucus* (i.e. rocky substrate with bladder
 wrack) areas were inhabited by dense populations of
 sand gobies and three-spined sticklebacks, respec-
 tively (personal observations). In this respect, black
 gobies may have been particularly prone to being
 caught by the traps we used, or their presence may
 have negatively affected the occurrence of other
 nesting fish in the same traps. Even if this was the
 case, our results show considerable overlaps in the
 small scale distributions of invasive mud crabs and
 native nest-building fish. In particular, the results
 indicate that at each of the assessed habitat type and
 depth, there is a high potential for encounters between
 mud crabs and nest-building fish, despite the differ-
 ences in their peak distributions.

Nest-building behaviour (see below for details) was
 not affected by the presence of a mud crab or brown
 shrimp, and although the proportion of surviving eggs
 was the lowest in the crab treatment, the difference
 between treatments in hatching success was not
 significant. Hence, our results suggest that, unlike
 crabs of similar size that are native on the Swedish
 west coast (Lissåker and Kvarnemo 2006), mud crabs
 do not seem to be effective predators on sand goby
 eggs while the eggs are guarded by the male.
 Similarly, the lack of treatment difference probably
 indicates that the presence of a mud crab did not
 significantly compromise the efficiency of male
 parental behaviours, such as egg fanning (see Lissåker
 and Kvarnemo 2006; Järvi-Laturi et al. 2008). Mud
 crabs may nevertheless have important cumulative
 effects on nesting fish. To demonstrate this, we may
 consider the results of the crab treatments over the two
 lab experiments: in these, 15 of the 38 gobies
 successfully started nesting, on average 17.3% of
 nests were destroyed over the two experiments, and

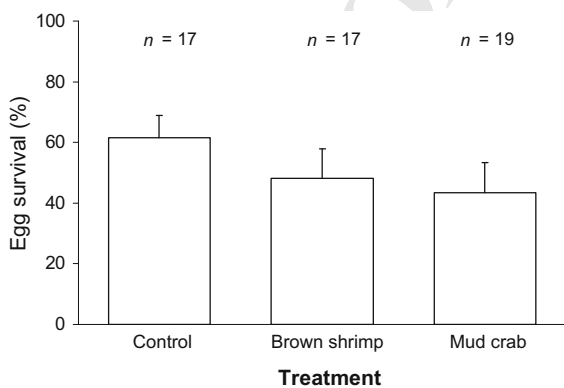


Fig. 5 Egg survival in the three treatments in experiment 2. Means of proportional survival with standard errors and sample sizes are shown

679 egg survival in Experiment 2 (for nests that were not
680 destroyed) was 48.3%, giving a cumulative success of
681 $0.395 \times 0.827 \times 0.483 = 0.158$ (15.8%) of the full
682 potential. The same figure for the control treatment
683 was 22/36 building activity, no nests destroyed and
684 61.1% egg survival, resulting in an overall success of
685 $0.611 \times 1 \times 0.611 = 0.373$ (37.3%) of the theoreti-
686 cal full potential. Hence, the cumulative comparison
687 suggests that the reproductive success of sand gobies
688 may be more than twice as high in the absence of mud
689 crabs than in their presence. In this respect, the most
690 important single effect of mud crabs seems to be that
691 they are capable of, and willing to, take over sand goby
692 nests, presumably to use them as a shelter. As
693 suitable nesting structures are a common limiting
694 resource for reproduction in sand gobies, and poten-
695 tially other nesting fish, in the Northern Baltic Sea
696 (Forsgren et al. 1996; Lehtonen and Lindström 2004),
697 an abundant mud crab population could be expected to
698 negatively affect breeding attempts of such fish.

699 Previous studies suggest that at least some nesting
700 species have the capacity to adapt the design of their
701 nests according to the local environmental conditions.
702 For example, three-spined sticklebacks built smaller
703 and more streamlined nests in flowing than still water
704 (Rushbrook and Barber 2008). In the context of egg
705 predation, sand gobies on the western coast of Sweden
706 reduced the size of their nest entrances in the presence
707 of shore crabs, *Carcinus maenas* (Lissåker and
708 Kvarnemo 2006). In the current study, male sand
709 gobies did not adjust the size of nest entrance (or the
710 amount of sand on top of the nest) in the presence of
711 mud crabs. This difference between the populations in
712 the response to (relatively similar) crabs might imply
713 that because sand gobies in the Northern Baltic
714 (including the study population) are naive to the
715 presence of crabs, and they do not adequately adjust
716 their behaviour in crabs' presence (see Cox and Lima
717 2006; Freeman and Byers 2006; Sih et al. 2010; Wong
718 and Candolin 2015). Besides such naivety of local
719 sand gobies, other factors may have also contributed to
720 the lack of observed adjustments of nesting behaviours
721 in the presence of mud crabs. For example, beha-
722 vioural adjustments might have been too minute to be
723 detected by our sample sizes, sand goby males in the
724 Northern Baltic Sea may show an overall low level of
725 responsiveness to potential egg predators, and the
726 adjustments of nest building in experiment 1 could
727 also have been larger if there had been eggs present in

the nest. In this respect, an interesting scope for future
studies is to assess whether prolonged presence of mud
crabs in the community will select for changes in
nesting (behaviour) of sand gobies and other nesting
fish.

Successful nest take-overs by mud crabs, and the
potential cumulative effects of their presence, imply
that the species might have a negative effect on an
array of native species of nest-building fish. Due to the
significance of these small fish in food webs (Fonds
1973; Zander et al. 1993), even a mere decline in their
abundance could induce unpredictable changes in the
functions of local communities (see also Forsström
et al. 2015; Jormalainen et al. 2016). Furthermore, the
highly unusual, novel pattern of habitat use by sand
gobies in the Northern Baltic Sea—reproduction using
crevices amidst stones on rocky bottom habitats—may
be attributed to the absence of marine egg predators
such as crabs and dogwhelks in this low salinity
environment (see Lehtonen and Lindström 2004;
Järvi-Laturi et al. 2008, 2011). Therefore, it is possible
that the arrival of mud crabs will impact individuals
displaying this unique behaviour particularly strongly.
However, there are also more nesting opportunities for
gobies in the rocky habitat (Lehtonen and Lindström
2004), potentially diluting the effects of crevice
competition with mud crabs. In this respect, the
conditions in our experiment 1 (nest take-over rate
29%) may have corresponded to a high crab density, as
the mud crab was present at the onset of nest building
and there was no extra shelters in the tank. In contrast,
during experiment 2 (5% take-overs), the interactions
with the intruder took place only after egg-laying in a
tank with an additional shelter structure. Hence, the
conditions in the latter experiment could be reminis-
cent of lower crab densities, or higher nesting structure
availability. Our setup was not designed to detect
differences in the rate of destroyed nesting efforts
between the experiments and, indeed, no such differ-
ence was found. Therefore, more investigations are
needed to assess potential density-dependent impacts
of mud crabs.

Many crab species are considered to be habitat
engineers in the sense that they alter the availability of
resources for other species (Jones et al. 1994). For
example, their burrows can change the structure of the
sediment or substrate, in other words, cause 'biotur-
bation' (Wallentinus and Nyberg 2007; Smith and
Green 2015). Such habitat alterations can negatively

777 impact other species that use cavities on seafloor for
 778 nesting and/or shelter. In this respect, our results
 779 indicate that crabs may affect benthic fish either by
 780 occupying suitable nesting and shelter cavities, by
 781 taking over nest cavities already occupied by fish, or
 782 by disturbing individuals that are in the parental phase.
 783 Hence, the interaction between nesting fish and mud
 784 crabs (in relation to shelter use) can be considered
 785 amensalistic: mud crabs can affect fish negatively
 786 when seeking cavities and especially by destroying
 787 nests, while not directly benefitting from the destruc-
 788 tion of the nests. In the Baltic Sea, the most
 789 notable fish species that may be affected in such a
 790 way are gobies (such as the common goby, the black
 791 goby and the two-spotted goby, *Gobiusculus flaves-*
 792 *cens*) and sticklebacks (such as three-spined stickle-
 793 back and ninespine stickleback). It is worth noting that
 794 black gobies, which were most commonly caught with
 795 mud crabs, are typically larger than sand gobies and
 796 are therefore potentially highly capable of defending
 797 their shelters and nesting crevices against mud crabs.
 798 More generally, our results support the idea that one
 799 reason contributing to the vulnerability of species poor
 800 communities to the effects of species invasions
 801 (Stachowicz et al. 1999) could be the lower ability
 802 of species in such communities to cope with invaders
 803 claiming key resources (here: shelters and nesting
 804 cavities).

805 To conclude, our study demonstrates that there is a
 806 potential for interactions between the invasive mud
 807 crab and nest-building fish, as mud crabs and fish
 808 overlap extensively in their habitat use. The mud crabs
 809 may impact these littoral fish by accumulation of
 810 multiple negative effects over the reproductive cycle
 811 of the latter, and especially by taking over nests and
 812 occupying crevices that fish would otherwise use for
 813 nesting. However, we did not find significant predation
 814 by mud crabs on guarded sand goby eggs. Despite the
 815 lack of demonstrated direct predation, the results
 816 support the hypothesis that the parental phase can be a
 817 particularly vulnerable life-history stage in face of
 818 novel selection pressures, such as those caused by the
 819 invasive mud crab. We suggest that future research
 820 should assess whether mud crabs have additional
 821 impacts on littoral fish (whether or not these build
 822 nests), such as competition for the same food resources
 823 or indirect cascade effects by reduction of the
 824 abundance of herbivores.

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