



Analysis of potential distribution and impacts for two species of alien crabs in Northern Europe

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Received: 4 December 2018 / Accepted: 7 June 2019 / Published online: 28 June 2019
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Abstract The Asian shore crab (*Hemigrapsus sanguineus*) and the brush-clawed shore crab (*H. takanoi*) both originate from east Asia but have in recent years established viable populations throughout coastal European waters. The two species are highly competitive and can occur in very high densities. Both species have been linked to the decrease of otherwise abundant native species such as the European shore crab (*Carcinus maenas*) and the common periwinkle (*Littorina littorea*). As both crabs are relatively new in European coastal waters, little is known about the full distribution range that may be achieved by these crabs and the ecological impact that may follow with an invasion of coastal habitats. In this study we investigated the potential distribution of *Hemigrapsus* in coastal waters of Northern Europe and the potential impact on the native competitor *C. maenas*. To this end we collected crabs on the Swedish west coast and on Helgoland and used these for behavioural experiments. We also collected new observation records of both species in Sweden and used these occurrences for building ecological niche models. We report that the

potential distribution range of both *H. sanguineus* and *H. takanoi* extends from western Sweden to eastern Ireland (east–west) and southern Norway to western France (north–south). We also found evidence that *H. takanoi* can establish viable populations in nutrient-rich inshore areas of the western and southern Baltic Sea and that competition by *H. sanguineus* is likely to affect abundances of *C. maenas* in the areas where these species co-occur.

Keywords *Hemigrapsus sanguineus* · *Hemigrapsus takanoi* · Invasive species · Ecological niche modelling · Competition · *Carcinus maenas*

Introduction

Non-indigenous species (NIS) are a global issue and the number of NIS has increased during the last decades (Cohen and Carlton 1998; European Environment Agency 2015; Zenetos et al. 2012). European waters are especially susceptible for invasive species from Asia and North America and the main invasion vectors are ballast water and transportation across the Suez Canal (Gollasch and Nehring 2006).

The Asian shore crab (*Hemigrapsus sanguineus*) was first discovered in Europe in 1999, found in Le Havre, France. The individuals found were already mature and breeding, thus it is believed that they

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10530-019-02044-3>) contains supplementary material, which is available to authorized users.

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arrived in Le Havre in 1998 at the latest (Breton et al. 2002). Since then, *H. sanguineus* has spread along the continental coast of North western Europe, from Northern France to the German North Sea coast and has recently been found in England, Wales and Scotland (Marine Biological Association 2017; Berggren and Karlsson 2017; Dauvin 2009a; Seeley et al. 2015). The species have also been found in the Black Sea by the coast of Romania and in the Mediterranean Sea off the coasts of Croatia and Tunisia (Amor et al. 2017; Micu et al. 2010; Schubart 2003), these were however only a few or a single individual.

The brush-clawed shore crab (*Hemigrapsus takanoi*) was first found in La Rochelle, France, in 1994. This species was then known as *Hemigrapsus penicillatus* since *H. takanoi* was first described as a species in 2005 by Asakura and Watanabe (2005). *H. penicillatus* is currently not present in Europe. The current distribution of *H. takanoi* in Europe reaches from north-eastern Spain to the Swedish west coast as well as south-eastern England, and western and eastern Scotland. In addition, there is one observation from the German coast facing the Baltic Sea (Marine Biological Association 2017; Berggren and Karlsson 2017; Geburzi et al. 2015; Noël et al. 1997; Wood et al. 2015).

Both crabs originate from east Asia and are considered invasive alien species (IAS) as they are highly competitive in many of the locations where they have become established. Outside of Long Island, USA, the presence of *H. sanguineus* has reduced the number of the common periwinkle (*Littorina littorea*) by 80% and the native flatback mud crab (*Eurypanopeus depressus*) by 95% (Kraemer et al. 2007). At this location, *H. sanguineus* was observed in an average abundance of 120 crabs/m², and at one instance more than 300 crabs/m². Additionally, during both spring and fall of 2016, mean densities above 300 crabs/m² were recorded in Rhode Island, USA, (O'Connor 2018), further indicating the potential density of the species.

As both crabs are relatively new in European coastal waters, little is known about the full distribution range that may be achieved by these crabs and the ecological impact that may follow with an invasion of coastal habitats. The goal of this study was to investigate aspects of potential distribution and impact for both invasive *Hemigrapsus* species in Northern

Europe. To this end we designed competition experiments with a dominant native competitor, the European green crab *Carcinus maenas*, identified important environmental factors that influence the distributions of *H. sanguineus* and *H. takanoi*, and modelled potential distribution areas of both crabs in Northern Europe.

Materials and methods

Field sampling

Hemigrapsus sanguineus were collected by hand and with traps on the island of Helgoland, Germany, between the 2nd and 4th of August 2017. Crabs were collected during the day at low and incoming tide. The traps were placed in the subtidal zone at approx. 0.3–0.5 m depth for 1 h, meanwhile crabs were collected by turning rocks in the intertidal zone. The traps were constructed out of PVC pipe (approx. 500 mm long and 100 mm Ø) with a funnel (25 mm Ø opening) in one end and a 1 mm steel mesh in the other end. In the middle of the PVC pipe a drill out cylindrical tube was fitted, containing a crushed *Mytilus edulis*. The traps were weighted down by two heavy chains, attached to each side of the trap (total weight of approx. 5 kg).

The crabs were then brought to the Sven Lovén Centre for Marine Infrastructure—Kristineberg, Sweden by transport in an electrical cooling bag, set to 10 °C to minimize activity and potential cannibalism, filled up with *Fucus* spp. The transportation took approx. 48 h, no crabs died during transit.

Individuals of *C. maenas* were collected by hand and with the use of traps, in Smalsund, outside of Kristineberg on the 9th of August 2017. The traps were of the same design as those used in Helgoland. Traps were deployed in the subtidal zone at a depth of 0.2–0.5 m and left them for approx. 1 h, during which crabs were collected by turning rocks in the intertidal.

The crabs were kept in separate holding tanks before and during the experiments. The water in the tanks was filtrated sea water with a salinity of 25 ± 1 PSU and a temperature of 19 ± 1 °C. At the time of collection, the waters in Helgoland had a salinity of 33 PSU and a temperature of 19 °C.

Competition experiments with *Carcinus maenas*

Experiments started on the 15th of August, 11 days after the last sampling day for *H. sanguineus* and 6 days after the sampling of *C. maenas*. The experiments comprised three stages (early invasion, mid invasion, late invasion) always containing 10 crabs per aquaria but with different proportions of species and sex depending on the stage (Table 1). These stages are to reflect on the different species ratios during a potential invasion: invader species in minority, in equal number to the native, and eventually in majority. The sex ratio for both is based on the sex ratio of *C. maenas* found in the field along the Swedish west coast (Jungblut and Karlsson unpubl. data).

Crabs used in the experiments had both chelae intact and at least 2 legs on each side of the body, no newly moulded crabs were used. The carapace width (CW) of crabs used in the experiments had the same dimensions in both species: 20–35 mm CW for males, and 15–25 mm CW for females. To distinguish males and females apart during the experiment, red nail-polish was applied to the carapace of the females. Crabs were randomly collected from the holding tanks. Due to limited number of *H. sanguineus*, crabs were returned to the holding tank after the experiment. Hence these crabs may have been used multiple times. However, after each round of experiments, all crabs were feed *M. edulis* and then rested for at least 48 h until the next experiment started.

Three experimental aquaria were recorded simultaneously using a Logitech C920 webcam and the recording software OBS 20.0.1. The aquaria used had a surface area of 0.1 m² (210 × 475 mm), resulting in a density of ~ 100 crabs/m², a density common in the field. In each aquarium a thin layer of filtered shell-sand (1–5 mm grain size) without organic matter was used as a substrate.

The first experiment assessed if *H. sanguineus* can actively dislodge *C. maenas* and/or restrain its food sources at any of the three invasive stages. To this end,

all crabs were kept without food in holding tanks with filtered seawater for 48 h. Thereafter, the animals were transferred to the experimental aquaria and a *M. edulis* (length 80 ± 10 mm with one side crushed) was placed in each aquarium. The aquaria were then recorded for 30 min. At 1, 5, 10, 15, 20, 25 and 30 min into the recording, presence or absence of feeding on the mussel was noted for each crab species and each of its sexes.

The mussels were then removed, and a man-made shelter was placed in each aquarium. The shelter was constructed by a PVC pipe (150 mm in length and 67 mm in diameter) which was attached to a plastic slab (200 × 125 mm) to keep the pipe in place. The shelter was then covered in a layer of sand and the crabs were then left for 30 min to settle down after being disturbed and then recorded for 30 min. At 1, 5, 10, 15, 20, 25 and 30 min into the recording presence or absence of crabs in the shelter was noted for each species and each sex. A minimum of half of the crab needed to be covered by the shelter to be considered “sheltered”. After the end of the experiment, the crabs were relocated to their holding tanks.

For each group (e.g. *C. maenas* males), a mean feeding ratio/hiding ratio was calculated based on the presence (1) or absence (0) at the food location/inside the man-made shelter at each time point (1, 5, 10 min etc.). This was done separately for each of the 6 replicates (aquaria). These 6 replicates were used to calculate the 95% confidence interval as well as a pairwise *t* test assuming unequal variance (Table S1).

Ecological modelling

Species and environmental data

The selected geographical area for this study include the coastal waters of Europe from the French west coast in the south to the Faroe Islands in the north, and also the Baltic Sea. Occurrence records (presence only) were obtained by sampling the Swedish West

Table 1 Number of crabs from each group present in each invasion stage

Species	Number of individuals per invasion stage (% IAS)		
	Early (30%)	Mid (50%)	Late (70%)
<i>Hemigrapsus sanguineus</i> (male + female)	2 + 1	4 + 1	5 + 2
<i>Carcinus maenas</i> (male + female)	5 + 2	4 + 1	2 + 1
Sum	10	10	10

coast, through the literature (Dauvin et al. 2009; Dauvin 2009b; Van den Brink et al. 2012) as well as from the Global Biodiversity Information Facility (GBIF 2017a, b). Records obtained by the authors and collaborators were submitted to GBIF through the Swedish Species Gateway (<http://www.Artportalen.se>). All occurrence records were carefully revised and verified before being used in the models, while unverified records were discarded.

We used gridded environmental data available as global marine layers through Bio-Oracle (<http://www.bio-oracle.ugent.be/>) with a resolution of 5 arc-min (Tyberghein et al. 2012). These data layers are generated from monthly satellite data (Aqua-MODIS and SeaWiFS; <https://oceancolor.gsfc.nasa.gov/>) as well as in situ measured oceanographic data from the World Ocean Database 2009 (Boyer et al. 2009). We also used marine layers from AquaMaps (<http://www.aquamaps.org/download/main.php>) with a resolution of 30 arc-min (Kaschner et al. 2008). These layers were built from long-term averages of temporally varying environmental variables (Ready et al. 2010).

Environmental data was obtained using version 2 of the BioClim workflow (<http://purl.ox.ac.uk/workflow/myexp-3725.2>) available at the BioVeL portal (Hardisty et al. 2016). The workflow was used to retrieve environmentally unique points (Nix 1986; Vestbo et al. 2018) from the species occurrence files for a set of 14 environmental data sets (abbreviations used throughout the article are given in parentheses), including the following. Bio-Oracle (5 arc-min): Mean dissolved oxygen in ml/l (Oxy), Mean nitrate [NO₃] [NO₃ + NO₂] in µmol/l (NO₃), Mean phosphate in µmol/l (PO₄), Maximum sea surface temperature in °C (Max SST), Minimum sea surface temperature in °C (Min SST), Sea surface temperature range in °C (Range SST), Mean calcite concentration in mol/m³ (CaCO₃), Maximum chlorophyll A concentration in mg/m³ (Max ChlA), Minimum chlorophyll A concentration in mg/m³ (Min ChlA), Range of chlorophyll A concentration in mg/m³ (Range ChlA). AquaMaps (30 arc-min): Mean ice concentration in % (Ice), Mean sea surface salinity in PSU (SSS), Mean sea surface temperature °C (SST), Mean chlorophyll A concentration in mg/m³ (Mean ChlA). Chlorophyll A data sets were included as chlorophyll acts as a proxy for phytoplankton, and thus reflects the amount of nutrition in the water.

Statistical analysis

Initially, we conducted a correlation analysis (data not shown) as well as a principal component analysis (PCA) on log-transformed data using the R statistical environment 3.0.2 (R Core Team 2013). Both analyses were performed to identify the variables explaining the variation in the data set, and which can be used as predictor variables in the modelling. The PCA was also used to compare the environmental space occupied by the two species and estimated as a 9 and 10-dimensional hypervolume (Fig. S1). We used all non-correlated variables that were represented (with > 5%) in the first two components of the PCA to build the niche models.

Ecological niche modelling

We used version 20 of the ecological niche modelling (ENM) workflow (<http://purl.ox.ac.uk/workflow/myexp-3355.20>) to describe and compare the geographical and environmental space occupied by the two species and to estimate the potential distribution maps (PD) with favourable biotic and environmental conditions in the study region. We did not consider demographic, dispersal, or substrate properties that may also be used in species distribution modelling (Peterson et al. 2011; Reiss et al. 2014). For more information on the ENM workflows see De Giovanni et al. (2015), Holl et al. (2013), Leidenberger et al. (2015) and Vestbo et al. (2018). We executed parallel analyses with two ENM algorithms, Maximum Entropy v. 1.0 (Phillips et al. 2006; Phillips and Dudík 2008), and Support vector machine v. 0.5 (Schölkopf et al. 2001).

Models were created using each species' maximum distribution range within the study region and the set of predictor variables identified in the PCA. Maxent models were set to run with 10,000 background points (including input points) drawn from the mask. Feature selection was automated, allowing the algorithm to combine feature types when fitting a model, and perform 500 iterations. Tolerance for detecting model convergence was set to 0.00001, while sample threshold was set to 80 (product), 10 (quadratic), and 15 (hinge). SVM models were set to execute the C-SVC algorithm with radial basis kernels, gamma values 1/k (where k is the number of layers), and a cost

value of 1. All models were set to produce a probabilistic, instead of binary output.

For each species, we ran both algorithms across the above-specified environmental layers. Models were tested using fivefold cross-validation based on the area under the curve (AUC) value and omission error rate (false negative rate, OE), and subsequently projected using the same layers (native projections). The results of the ENMs were visualized as potential distribution maps (PD) maps, showing the suitable environment of a species in the region of interest. Overall, we executed 4 niche models (2 algorithms, 2 species).

Raster maps created by the niche modelling algorithms were processed using the qGIS software package v. 2.6 Brighton (Quantum GIS Development Team 2014). We produce PD maps as consensus from the raster values of both algorithms, where red indicates agreement between both algorithms according to lowest presence threshold in each cell (Pearson et al. 2007).

Results

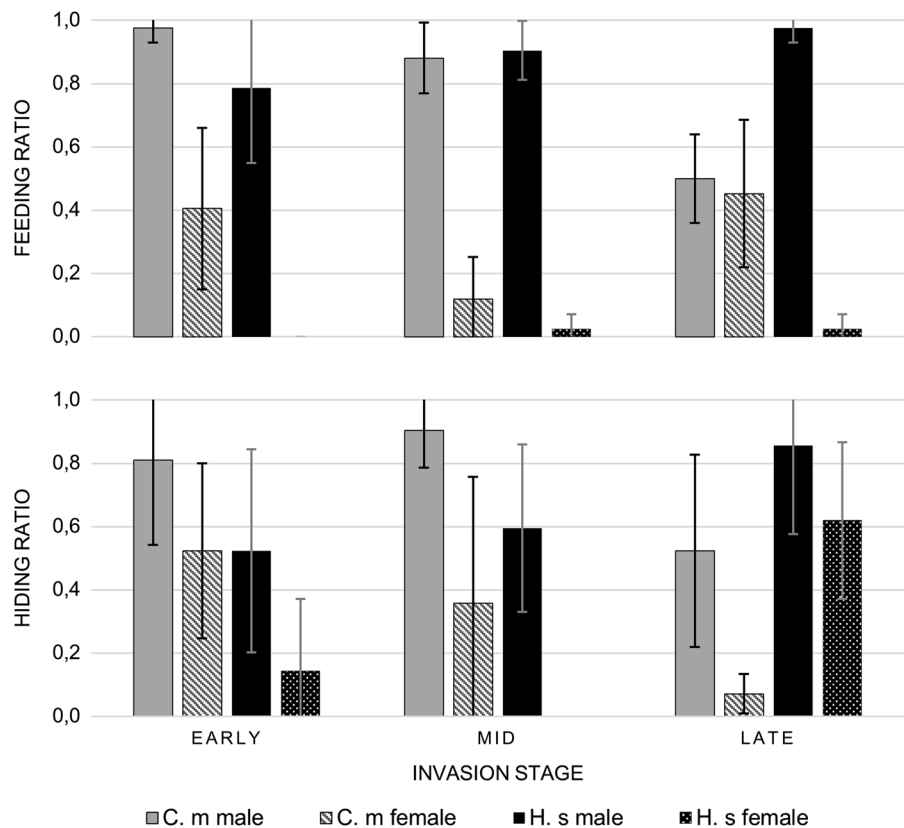
Behavioural experiments

Food competition

Male *C. maenas* showed a significant decrease in feeding ratio between the mid- and late invasion stage. The late invasion stage feeding ratio was also significantly different to the early invasion stage's feeding ratio (Fig. 1). Likewise, female *C. maenas* had a significant increase in feeding ratio between the mid- and late invasion stage (Fig. 1), while no significant changes in feeding ratio were observed with either *H. sanguineus* groups (Fig. 1).

Male *H. sanguineus* had a significantly higher feeding ratio compared to male *C. maenas* at the late invasion stage (Fig. 1). Female *H. sanguineus* had significantly lower feeding ratio compared to female *C. maenas* at the early- and late invasion stage (Fig. 1). All crabs survived the experiments.

Fig. 1 Feeding ratio and hiding ratio as means for each group of crabs for each invasion stage. Error bars show 95% confidence interval



Shelter competition

Female *H. sanguineus* had a significant increase in hiding ratio between the mid- and late invasion stage. The late invasion stage hiding ratio was also significantly different to the early invasion stage's hiding ratio (Fig. 1). Female *C. maenas* had a significant decrease in hiding ratio when comparing early- and late invasion stage. No significant changes in hiding ratio were observed with either male group (Fig. 1).

Female *H. sanguineus* had a significantly higher hiding ratio compared to female *C. maenas* at the late invasion stage (Fig. 1). No significant differences in hiding ratio were observed between the male groups (Fig. 1). All crabs survived the experiments.

Ecological niche models

The predictor variables selected by the PCA were the same for both species: mean nitrate concentration (NO₃), minimum SST (Min SST), mean calcite concentration (CaCO₃) and minimum chlorophyll A concentration (Min ChlA). We also added mean surface salinity (SSS) to both models to increase the accuracy of the predictions in the Baltic Sea, which has a strong salinity gradient. The ENM models performed well in the cross-validation returning high AUC values and low omission errors (Table 2). The resulting PD maps were very similar for the two species with suitable environment throughout the Northern European continental coast between Northern France and eastern Denmark, as well as along the south coast of Norway and west coast of Sweden (Fig. 2). In the south, the potential distribution extends to the Atlantic coastline of France. In the British Isles, large areas of suitable environment are found in much of eastern and western England, Wales, southern Scotland and eastern Ireland. In the Baltic Sea, no suitable environment was found for *H. sanguineus*.

Fig. 2 Potential distribution (PD) maps showing species occurrence and suitable environment for **a** *Hemigrapsus sanguineus* and **b** *Hemigrapsus takanoi*. Areas with suitable environment as calculated by the consensus from two models (Maxent and SVM) are marked red

However, for *H. takanoi*, suitable environment was found in the large estuaries of the Southern Baltic Sea, e.g. in the Szczecin Lagoon, the Vistula Lagoon, and the Curonian lagoon.

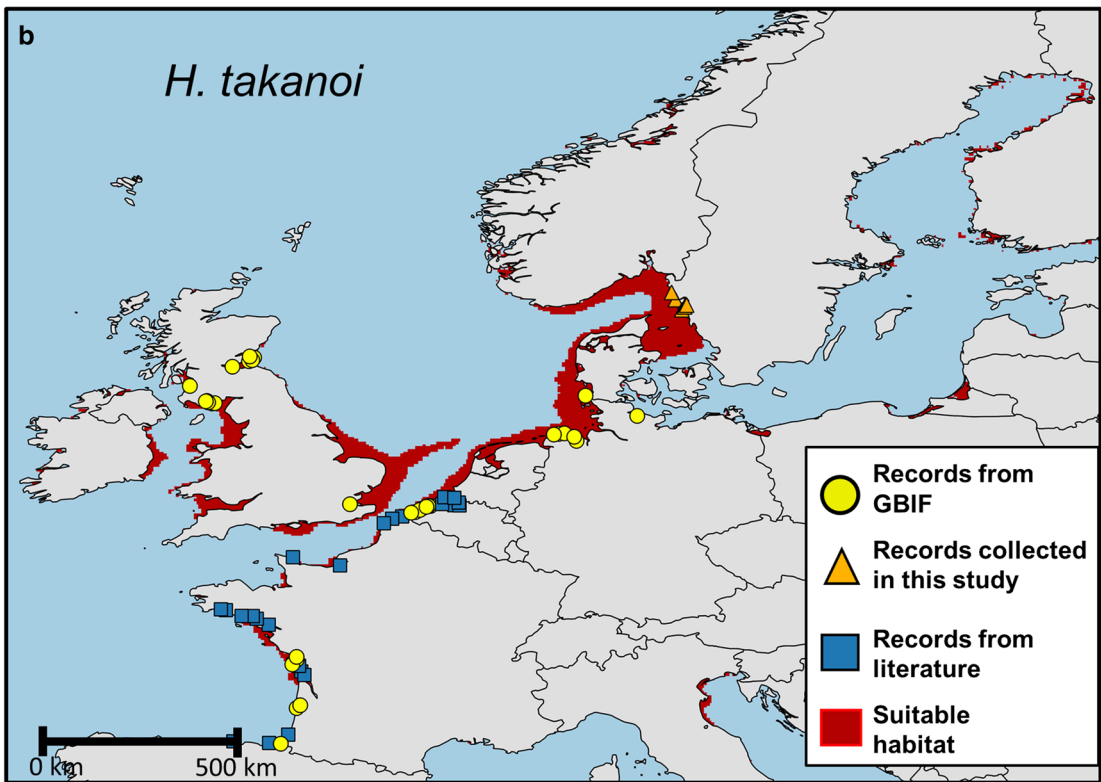
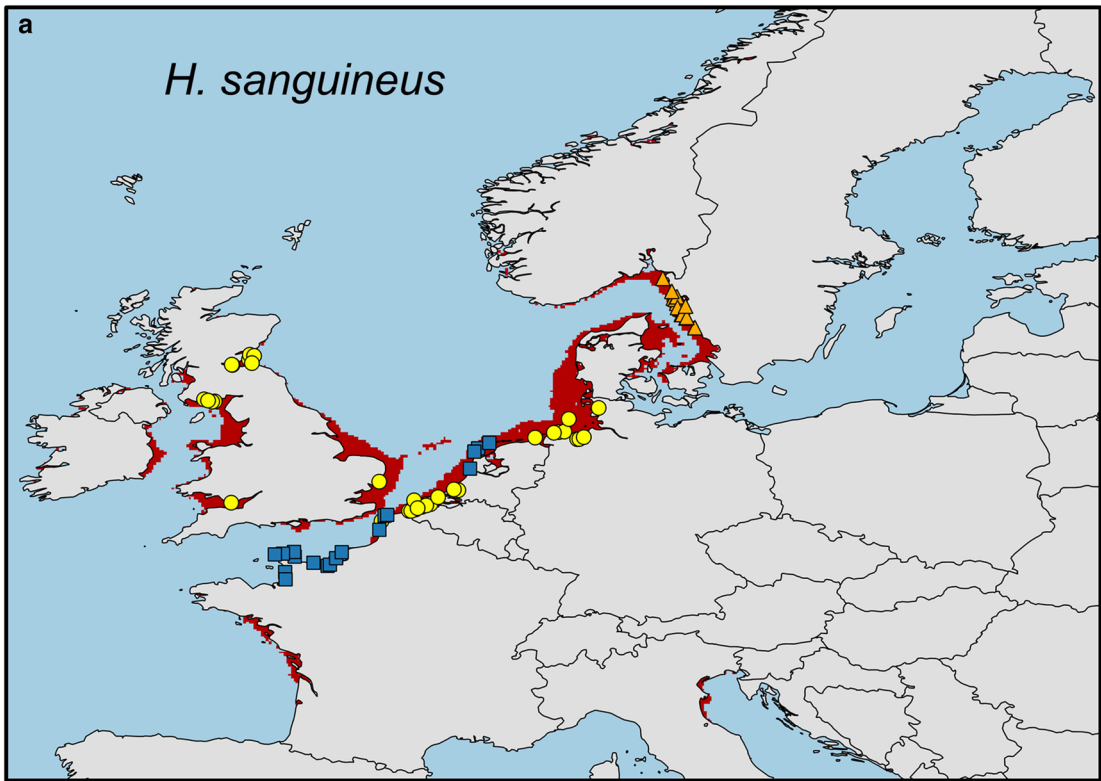
Discussion

Behaviour and potential ecological impact of *Hemigrapsus*

The behavioural experiments show that male *H. sanguineus* competes well with male *C. maenas*, even when outnumbered 2 to 5 (Fig. 1). This will benefit the species's establishment, as then even few individuals may be able to compete for food in areas with large abundances of *C. maenas*. In areas along the American east coast, where *H. sanguineus* occurs together with the likewise invasive green crab (*C. maenas*) it has been observed that *H. sanguineus* outcompetes juvenile *C. maenas* in the competition for shelter. When *H. sanguineus* was not present, 97% of all *C. maenas* were found under rocks and when *H. sanguineus* was present, 22% of *C. maenas* were found under rocks (Jensen et al. 2002). Furthermore, *H. sanguineus* has been found to prey on juvenile *C. maenas* (Lohrer and Whitlatch 2002a). In Europe, in the Dutch delta, *H. takanoi* occurs in high numbers and is believed to contribute to the decrease of *C. maenas* in the area (Van den Brink et al. 2012). Previous experimental studies have also shown that the presence of *H. sanguineus* alters the food preference of *C. maenas*,

Table 2 Results of model tests for all four models of current distribution as indicated by area under the curve (AUC), omission error rate (OE) and number of occurrence records (n)

	<i>Hemigrapsus sanguineus</i> (n = 53)		<i>Hemigrapsus takanoi</i> (n = 43)	
	AUC	OE	AUC	OE
MaxEnt	0.9940	1.818	0.9713	2.222
SVM	0.9903	3.636	0.9865	2.222



changing it from mainly mussels to red algae. This could have a negative impact on *C. maenas*, as a reduction in mussel consumption can result in lower growth rates (Ponati and Adelung 1980).

Female *H. sanguineus* had a low feeding ratio throughout all invasion stages, and if they do not feed, the females cannot produce offspring to sustain the population. It could be that females have a different food preference compared to the males and do not prey on bivalves. Previous studies have suggested that *H. sanguineus* mainly is herbivorous (Griffen 2011; Griffen et al. 2012; Tyrrell and Harris 2000), which could explain the low feeding ratio in this study.

If *H. sanguineus* establish itself along in the eastern extensions of the North Sea (Skagerrak and Kattegat), it may reduce the numbers of *Littorina* snails in some areas, as it has done in areas of the US (Kraemer et al. 2007), as well as *M. edulis* (Lohrer and Whitlatch 2002b). When comparing a single crab, previous studies have been inconclusive about whether *H. sanguineus* has an equal or higher feeding rate on *M. edulis* compared to *C. maenas*, supported by DeGraaf and Tyrrell (2004) but opposed by MacDonald et al. (2007) as well as Lohrer and Whitlatch (2002b). However, as *H. sanguineus* can occur in higher abundances compared to *C. maenas*, the impact on prey species such as *M. edulis* can potentially become higher. For native species feeding on algae (e.g. *Littorina* spp.), *H. sanguineus* might become, not only a predator but a competitor as it also feeds on algae, especially during its juvenile stage (Griffen 2011; Griffen et al. 2012; Tyrrell and Harris 2000). Further, *H. sanguineus* over all seem to feed more on animal tissue in laboratory experiment than in field experiments (Griffen 2011).

During the food competition experiment, differences in behaviour could be observed between the male *C. maenas* and *H. sanguineus*. *C. maenas* showed a more aggressive behaviour, not only towards *H. sanguineus* but also intraspecific aggression, and often used its chelae to pinch any crab which came close. However, *H. sanguineus* did not display that type of aggressive behaviour. *H. sanguineus* instead shoved other crabs out of its way and wedged itself in between the other crabs and the food. Once it started feeding, it used its big chelae to push away other crabs. This behaviour was however rarely seen towards its own species. Similar behaviour has been documented by Jensen et al. (2002), who wrote that *H. sanguineus*

dislodged *C. maenas* from the food and then used its legs to fend off the competitor. Previous studies have also shown that *H. sanguineus* exhibits a higher conspecific tolerance than *C. maenas* (Hobbs et al. 2017), which is highly beneficial for *H. sanguineus* as it facilitates the species to exist in higher densities compared to *C. maenas*.

The effectiveness of male *H. sanguineus* can be seen when comparing the early and late food experiment (Table S1), where male *C. maenas* had a higher feeding ratio (not significantly) despite being 5 to 2. When male *C. maenas* were in minority (despite feeding at 1 min in all replicates), male *H. sanguineus* had a significantly higher feeding ratio ($P = 0.0007$).

There was a distinct difference in behaviour between the sexes of *H. sanguineus*, where males were active and competed well, while females were passive and competed poorly (Fig. 1). This is something which, to our knowledge, has not been reported in the literature before. It suggests that a species' behaviour may vary strongly between the sexes, and future studies may further investigate the behavioural differences between males and females to improve our knowledge of *H. sanguineus*' foraging behaviour.

The potential stress on the collected *H. sanguineus* due to a change in salinity, cannot be completely disregarded and could have affected the results of the experiments. However, this is not deemed probable as the crabs had 9 days to acclimatize to the new salinity (25 ± 1 PSU). Additionally, *H. sanguineus* is found in waters of similar salinity and have shown to tolerate lower salinities in experiments (Gerard et al. 1999; Jungblut et al. 2015; Ledesma and O'Connor 2001; McDermott 1999).

Potential distribution range of *Hemigrapsus*

Both *Hemigrapsus* species prefer areas with high productivity and with high levels of nitrate as indicated by the selected predictor variables. The areas are often found in near coast environments like estuaries, archipelagos, and lagoons (Fig. 2). The presence of large cities and ports in these areas as well as the traffic between them will likely facilitate further spreading of both species and may allow these crabs to establish new populations in areas that could not be reached by natural dispersal. Besides high productivity and nitrate, both species prefer areas with high amounts of calcite. This may be a factor limiting the

distribution in the north, along the south-western coast of Norway, as calcite levels are low in these areas (source, Bio-Oracle).

Our ENMs suggest that both species will be able to expand their distribution ranges northwards to the southern coast of Norway, as well as southward into the Öresund and Belt regions between Denmark and Sweden (Fig. 2). Noticeably, *H. takanoi* finds suitable environment even in semi-enclosed lagoons along the southern coast of the Baltic Sea. Here, the alien crab could have a greater chance of establishment and impact due to the low species diversity of the area (Paavola et al. 2005). *H. takanoi* has already been found in the Baltic Sea, in Kiel (Geburzi et al. 2015), and it is likely that the species has arrived there via the Kiel Canal, which connects the Wadden Sea with the Baltic Sea. If this is the case, the species could rapidly increase in numbers in the bay of Kiel. In order to establish populations further east, e.g. in the Szczecin Lagoon, the Vistula Lagoon, or the Curonian lagoon, larvae or juveniles will need to travel with vessels, as the predominant surface current flows from east to west. However, many ferry lines commute between these hotspots, e.g. between Kiel and Kleipeda and may support further spread if ballast water is not treated.

In the British Isles, both species have been recorded in southern England and southern Scotland (Marine Biological Association 2017; Seeley et al. 2015). Most of the coast of England and the complete coastline of the Irish Sea were deemed suitable according to the models and the many ports in the area could facilitate dispersion, which could lead to a rapid colonization of the region. Along the French west coast both species find suitable environment according to our models, but only *H. takanoi* have so far been recorded in the region (Dauvin et al. 2009; Noël et al. 1997). It is possible that the Brittany peninsula acts as a barrier, restricting natural southward dispersal of *H. sanguineus* from the English Channel (Fig. 2). If so, there is a risk that also in this region maritime traffic may facilitate the transfer of larva to the Atlantic coast.

Future studies

Future studies should investigate the invasion process more in-depth, incl. ecological relations to other species than *C. maenas*. Doi et al. (2009) reported that *H. takanoi* could crush larger mussels

(*Xenostrobus securis*) than that of similar sized *Carcinus aestuarii*. If both *Hemigrapsus* species have a wider range in sizes of *M. edulis* and *Littorina* spp. on which they can prey compared to *C. maenas* (> 35 mm in carapace width) then they could increase the predation pressure on molluscs in the intertidal and upper subtidal zones. Experiments examining size preference of these prey species are therefore needed. In addition, evolutionary studies may help to understand the potential of the species to fully adapt to Baltic conditions. Investigating *H. sanguineus*' and *H. takanoi*'s abilities to adapt to new environments, similar to the studies done on *C. maenas* by Best et al. (2017) and Tepolt and Somero (2014). Finally, population genetic studies similar to that of Reusch et al. (2010) may prove helpful to better understand the invasive pathways of *Hemigrapsus*, which is likely to be caused by a combination of regional currents and ship traffic.

Acknowledgements We would like to acknowledge and thank Simon Jungblut for making it possible for the first author to visit Helgoland and collect *H. sanguineus* as well as for the help when collecting the crabs. This study is supported by the EU's Seventh Framework Program Project BioVeL (www.biovel.eu, Grant No. 283359), the Swedish LifeWatch program funded by the Swedish Research Council (Grant No. 829-2009-6278).

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