



Prey preferences, consumption rates and predation effects of Asian shore crabs (*Hemigrapsus takanoi*) in comparison to native shore crabs (*Carcinus maenas*) in northwestern Europe

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Abstract

The Asian brush-clawed shore crab *Hemigrapsus takanoi* was introduced to the northern Wadden Sea (southeastern North Sea) in 2009 and now represents one of the most abundant brachyuran crab species. Abundance studies revealed an increase of mean crab densities on mixed reefs of native blue mussels (*Mytilus edulis*) and Pacific oysters (*Magallana gigas*) from 18 individuals m⁻² in 2011 to 216 individuals m⁻² in 2020. Despite its current high densities only little is known about the feeding habits of *H. takanoi*, its effects on prey populations and on the associated community in the newly invaded habitat. We summarize results of individual field and laboratory experiments that were conducted to assess feeding habits and consumption effects caused by Asian brush-clawed shore crabs and, additionally, compare the feeding ecology of *H. takanoi* with the one of the native shore crab *Carcinus maenas*. Field experiments manipulating crab densities revealed that both crab species affected the recruitment success of blue mussels, Pacific oysters and Australian barnacles (*Austrominius modestus*) with highest number of recruits at crab exclusion. However, endobenthic polychaetes within the reefs were differently affected. Only the native *C. maenas* caused a significant reduction in polychaete densities, whereas the introduced *H. takanoi* had no effect. Additional comparative laboratory studies revealed that single *C. maenas* consume more juvenile blue mussels than Asian brush-clawed shore crabs of the same size class. When offering amphipods as a mobile prey species, we found the same pattern with higher consumption rates by *C. maenas* than by *H. takanoi*. For Asian but not for native shore crabs, we detected a sex-dependent feeding behavior with male *H. takanoi* preferring blue mussels, while females consumed more amphipods. Considering mean crab densities and feeding behavior, our results suggest that despite lower consumption rates of single crabs, Asian brush-clawed shore crabs can cause stronger impacts on prey organisms than the native *C. maenas*, because *H. takanoi* exceeds their densities manifold. A strong impact of the invader on prey populations is supported by low amphipod occurrence at sites where *H. takanoi* density is high in the study area. Thus, the introduced Asian brush-clawed shore crab is an additional consumer with significant effects on the associated community of mixed reefs of mussels and oysters in the Wadden Sea.

Keywords Invasion ecology · *Magallana gigas* · *Mytilus edulis* · Oyster reefs · Predator–prey interactions

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Introduction

Worldwide, the introduction and spread of non-native species cause changes in diversity and species interactions in recipient ecosystems (Pyšek and Richardson 2010; Lowry et al. 2013), and this is also well known for coastal habitats (Ruiz et al. 1997; Cohen and Carlton 1998; Gollasch 2006; Williams and Grosholz 2008). Effects on native coastal communities can be caused by direct and indirect

interactions between introduced and native species (Lohrer and Whitlatch 2002; Buschbaum et al. 2016; Reise et al. 2017a). For example, introduced predators directly prey on indigenous species or may compete with native predators for limited food sources (Ruiz et al. 1999; Grosholz 2002; Gregory and Quijón 2011; David et al. 2017; Howard et al. 2017). Introduced predators can also cause facilitative effects on native species by preying on snails and, therefore, indirectly reducing grazing pressure on native macroalgae (Trussell et al. 2002; Griffen and Byers 2009).

Predatory brachyuran crab species represent one of the most common taxonomic group of introduced species in coastal ecosystems (Galil 2009; Karatayev et al. 2009; Brockerhoff and McLay 2011; Hänfling et al. 2011; Rato et al. 2021). A prominent example is the European shore crab *Carcinus maenas* (L.), which is a globally successful invader of coastal ecosystems and can cause ecological but also economic effects in the recipient ecosystems (Grosholz and Ruiz 1995; Grosholz et al. 2000; Carlton and Cohen 2003; Klassen and Locke 2007; Lovell et al. 2007; Kimbro et al. 2009). Further examples are the Asian brush-clawed shore crab *Hemigrapsus takanoi* Asakura & Watanabe, 2005 and the Asian shore crab *Hemigrapsus sanguineus* (de Haan, 1835), which have been introduced to coastal areas of northern Europe in the 1990s, presumably by shipping (Gollasch 1999; Obert et al. 2007; Landschoff et al. 2013; Geburzi et al. 2018). Both species originate from the northwestern Pacific Ocean, and in the southeastern North Sea, crabs have first been detected in 2004 in the southern and in 2009 in the northern part (Gollasch 1999; Gittenberger et al. 2010; Obert et al. 2007; Landschoff et al. 2013). Investigations on the spatial occurrence of both crab species in the intertidal zone of the Wadden Sea revealed that *H. sanguineus* is most abundant in artificial habitats such as coastal protection structures (Landschoff et al. 2013; Jungblut et al. 2017; Geburzi et al. 2018). By contrast, *H. takanoi* achieves highest abundances in natural epibenthic mixed reefs of native blue mussel (*Mytilus edulis* Linnaeus, 1758) and introduced Pacific oysters (*Magallana gigas* Thunberg, 1793), which is also a preferred habitat for native shore crabs *C. maenas* (Kochmann et al. 2008; Van den Brink et al. 2012; Markert et al. 2014).

Due to the co-occurrence of both species in mixed reefs of mussels and oysters, the focus of this study is on the feeding ecology of *H. takanoi* and the comparison with that of *C. maenas*. This allows the identification of potential overlap in food preferences of both crab species with resulting cumulative effects on prey populations. Existing comparative investigations on the feeding ecology of Asian brushed-shore crabs in the Wadden Sea mainly deal with prey selection of differently sized native blue mussels (Bouwmeester et al. 2020) and reveal an increase in prey size in relation to carapace width for both the non-native *H. takanoi* and for *C. maenas*. Additionally, it was shown that crabs of both species within one size class prefer the same sized mussels. Consumption rate experiments with *H. takanoi* in the Baltic Sea report a higher feeding rate of males

on blue mussels compared to females (Nour et al. 2020) indicating that food preferences of males and females can be different. Such sex-dependent consumption behavior is also known for *C. maenas* and other decapod crabs (Ropes 1968; Elner 1980; Eggleston 1990). However, further detailed information on feeding ecology and prey preferences of the introduced Asian brushed-shore crab as well as consequences on native coastal communities in northwestern Europe are limited.

Therefore, the aim of this study was to investigate prey preferences of female and male Asian brush-clawed shore crabs *H. takanoi* in comparison to the European shore crab *C. maenas* in the European Wadden Sea (coastal area of the southeastern North Sea). In laboratory experiments, we offered selected key species associated with mixed reefs of mussels and oysters and quantified the consumption rates of both crab species. Additionally, we conducted crab density manipulating experiments in the field to study predation effects of *H. takanoi* on the associated community of oyster reefs under natural conditions. Finally, to gain insights into the population development of *H. takanoi* in comparison to the native *C. maenas*, we compared the density trajectories of both species on a mixed reef of mussels and oysters from 2011, i.e., shortly after the successful establishment of *H. takanoi* in the survey area, to 2020.

Material and methods

Study area

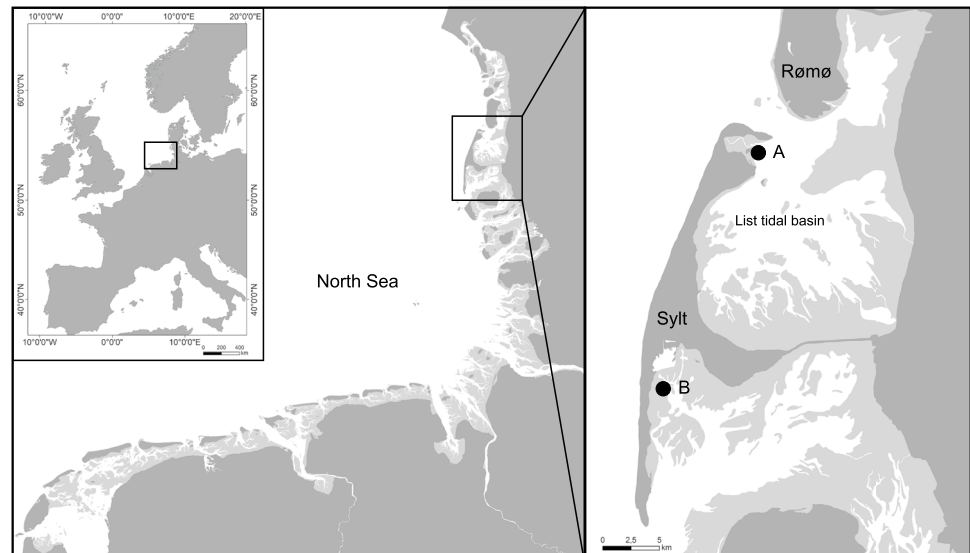
All surveys and experiments were conducted in intertidal mixed reefs of native mussels *M. edulis* and introduced Pacific oysters *M. gigas* near the northern part of the island of Sylt in the northern Wadden Sea (German Bight, southeastern North Sea, Fig. 1). The area is located in the cold temperate region with a mean annual water temperature of about 9 °C, a summer average of 15 °C, and a winter average of 4 °C. The tides are semidiurnal and average tidal range is about 1.8 m. Salinity ranges between 31 psu in summer and 28 psu in winter. Further information about hydrography, geology, sediments, and biota of the study site is given in Gätje and Reise (1998). In the Wadden Sea, the biogenic epibenthic reef structures are the preferred natural habitat of the native European shore crab *C. maenas* and the introduced Asian brush-clawed shore crab, *H. takanoi*, which is an established member of this community since 2009 (Landschoff et al. 2013).

Survey

Population development of *Carcinus maenas* and *Hemigrapsus takanoi* at site A

Densities of both crab species were annually surveyed at site A (Oddewatt, Fig. 1) in early summer (May–June) from 2017 to 2020. We randomly placed a frame (25 cm × 25 cm)

Fig. 1 The island of Sylt in the southeastern North Sea. The two sampling sites (A Oddewatt, B Puan Klent) are located at the eastern site of the island. Light grey areas represent the intertidal zone



on the bottom, and all substrate and organisms within the frame (including the upper approximately 5 cm of sediment) were transported to the laboratory, where the samples ($n=6$) were sieved (mesh size 0.5 mm). The remaining crabs in the sieve were identified to species level. Afterwards, crabs of both species were counted and carapace width was measured to the nearest 0.1 mm with digital calipers. Additionally, we used density data of both species provided by Landschoff et al. (2013), which have been gained with the same method and at the same site in 2011.

Field survey on relationship between *Hemigrapsus takanoi* and mobile prey density at site A and B

To study potential effects of *H. takanoi* on mobile prey species in mixed oyster reefs, we simultaneously quantified the density of *H. takanoi* and amphipods *Gammarus* spp. at study sites A (Oddewatt) and B (Puan Klent) at low tide conditions in June 2018 (Fig. 1). Amphipods represent abundant and mobile organisms within epibenthic structures in the Wadden Sea and are a potential prey of *Hemigrapsus* spp. (Blasi and O'Connor 2016).

Crabs and amphipods were collected from parts of the mixed oyster reefs, which were overgrown by the bladder wrack *Fucus vesiculosus* forma *mytili* (Nienburg) because amphipods show a preference for algal covered bivalve beds (Albrecht and Reise 1994). Six random samples were taken from each oyster reef by using a 25 × 25 cm steel frame (625 cm²). All organism within the frame and the top 5 cm of sediment were transported to the laboratory and each sample was sieved (mesh size 1.0 mm). The algae *F. vesiculosus* forma *mytili* within each sample was washed over the sieve with fresh water to remove all attached amphipods. All remaining *H. takanoi* and amphipods in the sieve were

counted. Algal biomass was weighted after removing amphipods and crabs.

Field predation experiments at site A

To study predation effects of native *C. maenas* and introduced *H. takanoi* on the associated species community of mixed oyster reefs, three field caging experiments were conducted between 2017 and 2019 at mixed mussel and oyster reefs at site A (Oddewatt, Fig. 1). An overview on the field experiments with detailed information on the specific approaches and methods is given in Table 1.

Predation experiment on blue mussel recruits

The effects of both crab species on blue mussel recruitment (settlement and early post-settlement survival) were investigated with a cage enclosure experiment in the field. We used cylindrical cages (15 cm in diameter, 15 cm high) with walls and roofs made of plastic mesh with 3-mm mesh size. On 28 May 2019, the cages were carefully fixed to the mixed reefs of mussel and oysters using three iron rods per cage (50 cm in length, 6 mm in diameter).

The experiment included five treatments with six replicates each: (1) no crabs in the cages, (2) cages with two male *C. maenas* with a carapace width of 10–50 mm, and (3) cages with two female and four male *H. takanoi* with a carapace width of 10–40 mm. The crab densities in the cages correspond to the natural ratio of *C. maenas* and *H. takanoi* in the surrounding oyster reef quantified in spring 2019. However, used densities in the experiment were about twofold higher than natural densities in order to determine a measurable effect. Additionally, we adapted the size range of both crab species in the cages to the natural size distribution

Table 1 Detailed overview on the three field cage experiments conducted on oyster reefs at site A. Information on predator species, number of replicates per treatment (Ht = *Hemigrapsus takanoi*, Cm = *Carcinus maenas*), date and duration of the experiment, and the corresponding figure in the text are given

No	Field experiments	Crab species	Sex	Carapace width (mm)	Crabs cage-1	Reef composition within the cages	Treatment	No of replicates per treatment	Duration and start of experiment	Fig
1	Predation experiment on blue mussel recruits	<i>H. takanoi</i> <i>C. maenas</i>	f/m m	10.0–40.0 10.0–50.0	2/4 2	4 <i>M. edulis</i> 2 <i>M. gigas</i>	Inclusion Ht Inclusion Cm Exclusion Open cage Untreated area	6	14 weeks 05/2019	4
2	Predation experiment on barnacles and juvenile oysters	<i>H. takanoi</i> <i>C. maenas</i>	m m	15.0–20.0 15.0–20.0	1 1	1 <i>M. gigas</i>	Inclusion Ht Inclusion Cm Exclusion	6	5 days 09/2018	5
3	Predation experiment on endobenthic polychaetes	<i>H. takanoi</i> <i>C. maenas</i>	f/m f/m	11.0–20.0 25.0–50.0	3/3 2/1	3 <i>M. edulis</i> 3 <i>M. gigas</i>	Inclusion Ht Inclusion Cm Exclusion Open cage Untreated area	6	8.5 weeks 03/2017	6

at the time of the experiment and also considered the comparatively high numbers of female *H. takanoi* in our experimental set up to simulate the natural conditions as well as possible. Two treatments served as a control of possible cage artefacts: (4) open cages with holes of 10 × 10 cm in the walls so that crabs could freely pass into and out of the treated area and (5) untreated areas of the same size as cages.

To provide natural reef conditions and a suitable settlement substrate for *M. edulis*, each cage contained four living *M. edulis* and two *M. gigas*. All bivalves were cleaned from any epigrowth before the beginning of the experiment. The experimental set up was randomly organized, and a distance of 2 m was kept between the cages to enable independency of the experimental units. After an experimental period of 14 weeks on 4 September 2019, all remaining crabs and blue mussel recruits in the cages were counted. The mean survival rates of *H. takanoi* (44 ± 4%) and *C. maenas* (44 ± 16%) in the cages were largely the same.

Predation experiment on barnacles and juvenile oysters

To investigate predation effects of *C. maenas* and *H. takanoi* on the non-native Australian barnacle *Austrominius modestus* (Darwin) and juvenile Pacific oysters *M. gigas*, we conducted an enclosure field experiment in September 2018 by using the same oyster reefs and cages as in the predation experiment on blue mussel recruitment (see the “[Predation experiment on blue mussel recruits](#)” section). The Australian barnacle was the most abundant barnacle species in the study area at the time of investigation. We used six different treatments with six replicates each: (1) cages with a single male *H. takanoi* and a defined number of barnacles, (2) cages with a single male *C. maenas* and a defined number of barnacles, (3) cages with single male *H. takanoi* and a defined number of juvenile oysters, and (4) cages with a single male *C. maenas* and a defined number of juvenile oysters. For this experiment with one crab per cage, only male individuals of both crab species with intact claws were used, because of the morphological differences between male and female crabs, which may result in different feeding behavior (Klassen 2012; Bouwmeester et al. 2020). Two treatments checked for natural mortality of barnacles and oysters: (5) cages with barnacles but without crabs and (6) cages with juvenile oysters but without crabs. All crabs of both species in the cages had a carapace width of 15–20 mm. To offer a defined number of barnacles and juvenile oysters in the cages, we collected oysters with a maximal shell length of 12–15 cm, which were overgrown with recently settled *A. modestus* (size 1–3 mm in diameter) and juvenile *M. gigas* (shell length 2–5 mm). From these oysters, we removed any epigrowth except either for juvenile barnacles or oysters. All remaining barnacles or oysters were counted. At the beginning of the experiment on 6 September 2018, each

cage contained a single oyster with either 40–80 attached *A. modestus* or 50–75 attached juvenile *M. gigas*. After an experimental time period of 5 days on 11 September 2018, we quantified survival in the cages by counting all remaining living barnacles and juvenile *M. gigas*. The survival rate of *H. takanoi* and *C. maenas* in the cages was 100% in this experiment.

Predation experiment on endobenthic polychaetes

To examine consumption effects of *C. maenas* and *H. takanoi* on endobenthic polychaetes in a mixed reef of mussels and oysters, we conducted an enclosure field experiment by using the same mixed oyster reefs and cages as in the predation experiments on blue mussel recruits, barnacles, and oysters (see the “[Predation experiment on blue mussel recruits](#)” and “[Predation experiment on barnacles and juvenile oysters](#)” sections). With this experiment, we aimed to imitate natural population structures (density and sex ratio) of both crab species in the cages at the time of the experiment in spring 2017. Therefore, we used both female and male individuals and adapted the number of crabs in the cages, sex, and size structure to the natural conditions at the study site. We used five treatments with six replicates each: (1) no crabs in the cages, (2) cages with three female and three male *H. takanoi*, and (3) cages with two female and one male *C. maenas*. Two treatments served as a control of possible cage artefacts: (4) open cages with holes of 10×10 cm in the walls so that crabs could freely pass into and out of the treated area and (5) untreated areas of the same size as cages. All *H. takanoi* had a carapace width of 11–20 mm and *C. maenas* of 25–50 mm. To keep the conditions as similar as possible in the treatments, each cage contained three blue mussels with a shell length of 3–4 cm and three oysters with a shell length of 8–10 cm, which were cleaned from any epigrowth at the beginning of the experiment on 23 March 2017. After 8.5 weeks on 21 May 2017, the remaining crabs in the cages were counted. The survival rate in the cages was $89 \pm 5\%$ for *H. takanoi* and $72 \pm 14\%$ for *C. maenas*, respectively. Afterwards, sediment samples were taken with a tube cover (8 cm in diameter) to a depth of 10 cm at the center of each experimental plot. The samples were sieved (mesh size 0.5 mm), and all remaining polychaetes in the sieve were counted.

Laboratory predation experiments

To focus on specific aspects of the feeding ecology of *H. takanoi* in comparison to the native *C. maenas* and to investigate differences in prey choice of female and male crabs of both species, we conducted three laboratory experiments. Before starting the experiments, all organisms were collected in the field and kept in aquaria with seawater in climate

chambers. All experiments were conducted using a natural light dark cycle and constant temperature conditions (15°C). Organisms (crabs, blue mussels, and amphipods) were acclimated to experimental conditions for at least 3 days and were fed daily. Mussels were fed with algae suspension (Instant Algae Iso 1800TM, Shellfish Diet 1800 TM), crabs were fed with mussel, and oyster flesh and amphipods were fed with fucoid macroalgae.

All crabs were starved for 24 h prior to the experiment to standardize hunger levels. Only intact and not freshly moulted crabs were used. All feeding trials lasted for 24 h. The respective crabs and prey items were added to aquaria (11 cm length, 11 cm width, 18 cm height), and after 24 h, the remaining prey organisms were counted. In pilot studies, the maximum feeding rate of both crab species was determined for blue mussels and amphipods to avoid food limitation in the course of the experiments. For all experiments, we used a control treatment, i.e., aquaria with prey organisms but without crabs. Survival rate of prey organisms was 100% in all controls of all laboratory experimental approaches. An overview on the three laboratory experiments with detailed information on the specific approaches and methods is given in Table 2.

Consumption of *Mytilus edulis* and the amphipod *Gammarus locusta* by *Hemigrapsus takanoi*

To compare consumption rates of introduced *H. takanoi* on amphipods (*Gammarus locusta* Linnaeus, 1758) and juvenile blue mussels (*M. edulis*), we conducted a no-choice experiment. Single *H. takanoi* individuals were separately offered 30 blue mussels (shell length 8–11 mm) and 10 *G. locusta* (body length 5–14 mm) within one aquarium, respectively. To explore potential gender differences in consumption, we offered both prey items to female and male *H. takanoi*.

The experiment with blue mussels as prey was 30 times replicated for both sexes. The experiment with amphipods as prey was 13 times replicated for female crabs and 15 times replicated for male *H. takanoi*. Crab carapace width of both sexes was 15–20 mm. Six control treatments were performed without any crab to control the natural mortality of both prey species.

Prey preference of *Hemigrapsus takanoi* between *Mytilus edulis* and *Gammarus locusta*

To investigate whether *H. takanoi* prefers juvenile blue mussels or amphipods (*G. locusta*) as prey, we conducted a choice experiment. Within one aquarium, we simultaneously offered a single crab 30 juvenile mussels (shell length 8–11 mm) and 10 amphipods (body length 5–14 mm). Again, we tested for gender differences in *H. takanoi* and performed this experiment with female and male crabs

Table 2 Detailed overview on the three laboratory consumption experiments. Information on predator species, prey organisms in the aquaria, number of replicates per treatment, date and duration of the experiment, and the corresponding figure in the text are given

No	Laboratory experiments	Crab species	Sex	Carapace width (mm)	Prey item	Prey size (mm)	Prey number aquarium-1	No of replicates per treatment	Duration and start of experiment	Figure
1	Consumption rate of <i>M. edulis</i> and <i>G. locusta</i> by <i>H. takanoi</i>	<i>H. takanoi</i>	f	15.0–20.0	<i>M. edulis</i>	8.0–11.0	30	30	24 h	7
			m	15.0–20.0			30	30	09/2018	
2	Prey preference of <i>H. takanoi</i> between <i>M. edulis</i> and <i>G. locusta</i>	<i>H. takanoi</i>	f	15.0–20.0	<i>G. locusta</i>	5–14	10	13		8
			m	15.0–20.0			10	15	24 h	
3	Comparison of consumption rates of <i>M. edulis</i> and <i>G. locusta</i> by <i>H. takanoi</i> and <i>C. maenas</i>	<i>H. takanoi</i>	f/m	15.0–22.0	<i>G. locusta</i>	5–14	10	15	24 h	10
		<i>C. maenas</i>	f/m	17.0–22.0	<i>M. edulis</i>	8–11	30	9	09/2018	
		<i>H. takanoi</i>	f/m	13.0–21.0	<i>M. edulis</i>	8–11	30	30	24 h	10
		<i>C. maenas</i>	f/m	21.5–38.0	<i>G. locusta</i>	5–14	60	8	08/2019	
	f/m	15.3–18.3			10	6 (C. m m, n=5)	24 h	05/2020		
		f/m	16.2–18.2							

(carapace width 15–22 mm for both sexes), with 15 replicates each. Six control treatments were performed without any crab to control the natural mortality of both prey species.

Comparison of consumption rates of *Hemigrapsus takanoi* and *Carcinus maenas* on *Mytilus edulis* and *Gammarus locusta*

To compare consumption rates of *H. takanoi* and *C. maenas* on blue mussels and amphipods under the same experimental conditions, we conducted an additional no-choice experiment. Single crab individuals were separately offered 30 blue mussels (*H. takanoi*) or 60 blue mussels (*C. maenas*) (shell length 8–11 mm) and 10 amphipods (body length 5–14 mm) within one aquarium, respectively. To explore potential gender differences in consumption, we offered both prey items to female and male *H. takanoi* as well as to female and male *C. maenas*. Crab carapace width of both species and sexes was 13–38 mm. Replicates for the respective treatments varied from five to nine (Table 2). Six control treatments per prey species were performed without any crab to control the natural mortality of *M. edulis* and *G. locusta*.

Statistical analysis

All statistical analyses were conducted in the statistical software R (version 3.6.3, R Development Core Team 2017), and the predefined functions from the “stats” (R Core Team 2013); “ppcor” (Kim 2015); “MASS” (Venables and Ripley 2002); “ggplot2” (Wickham 2009); “car”; and “carData” (Fox and Weisberg 2019) packages were used to perform the analyses. The data are given as arithmetic means with standard error (SE). Effects were considered to be statistically significant if p value was < 0.05.

To test, whether there is a relationship between the densities of *H. takanoi* and amphipods *Gammarus* spp. in our field density survey, we pooled all our samples from both study sites (A Oddewatt, B Puan Klent) and correlated mean crab density per m² to amphipod densities with a Spearman correlation test.

All field experiments were analyzed by using a one-way analysis of variance ANOVA, and the Levene test was used to test for homoscedasticity of variances. Data of all experiments were heterogeneous in variances and, therefore, log transformed to achieve homoscedasticity of variances. In one case (predation experiment on barnacles), variances remained heterogeneous despite transformation. Therefore, we used the non-parametric Kruskal–Wallis test and analyzed different survival rate of barnacles between the experimental treatments by using a Wilcoxon signed rank test. Data of all other experiments were homogenous in variances after transformation, and we used the Turkey’s Honest

Significant Difference (HSD) multiple comparison test for pairwise comparisons between the treatments.

All laboratory experiments were analyzed by using non-parametric Mann–Whitney U-tests for all pairwise comparisons.

Results

Field density surveys

Density development of *Carcinus maenas* and *Hemigrapsus takanoi* at site A

The survey data revealed different density patterns for the native *C. maenas* and the non-native *H. takanoi* on an intertidal mussel reef in the northern Wadden Sea in the time period from 2011 to 2020 (Fig. 2). The two species showed contrasting developments: The maximum density of *C. maenas* was 38 ± 7 individuals m^{-2} in 2011 and decreased to 5 ± 3 individuals m^{-2} in 2020. The density of *H. takanoi*, by contrast, increased from a mean density of 18 ± 5 individuals m^{-2} in 2011 to a maximum of 248 ± 49 individuals m^{-2} in 2018 and remained at about 200 individuals m^{-2} until 2020.

Density of *Gammarus* spp. and *Hemigrapsus takanoi* at sites A and B

In June 2018, six samples on mixed oyster reefs were taken at two different sites to quantify amphipod and *H. takanoi* densities. At site A (Oddewatt), the mean density of

Gammarus spp. was 45 ± 25 individuals m^{-2} , while at site B (Puan Klent), amphipod densities were higher with 261 ± 38 individuals m^{-2} (Fig. 3). The densities of *H. takanoi* showed an opposite pattern with a mean density of 248 ± 49 individuals m^{-2} at site A and 53 ± 7 individuals m^{-2} at site B. We found a negative correlation between densities of *H. takanoi* and *Gammarus* spp. in the pooled samples of both study sites ($n = 12$, Spearman's rank correlation: $r = -0.828$, $p < 0.001$). The mean algal biomass within the samples did not significantly differ between the two study sites (Mann–Whitney U-test: $p = 0.262$) and was 310 ± 37 g m^{-2} at site A and 408 ± 25 g m^{-2} at site B, respectively.

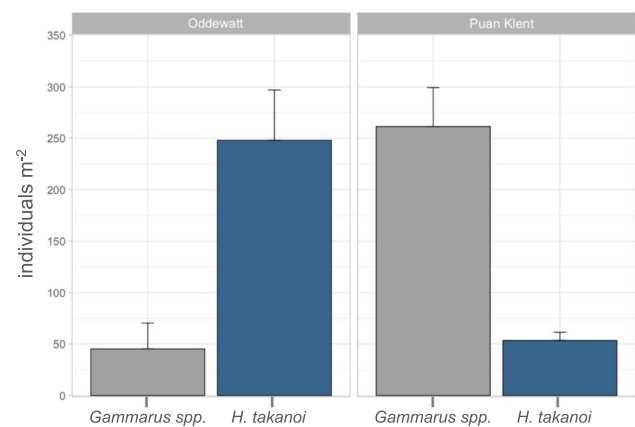
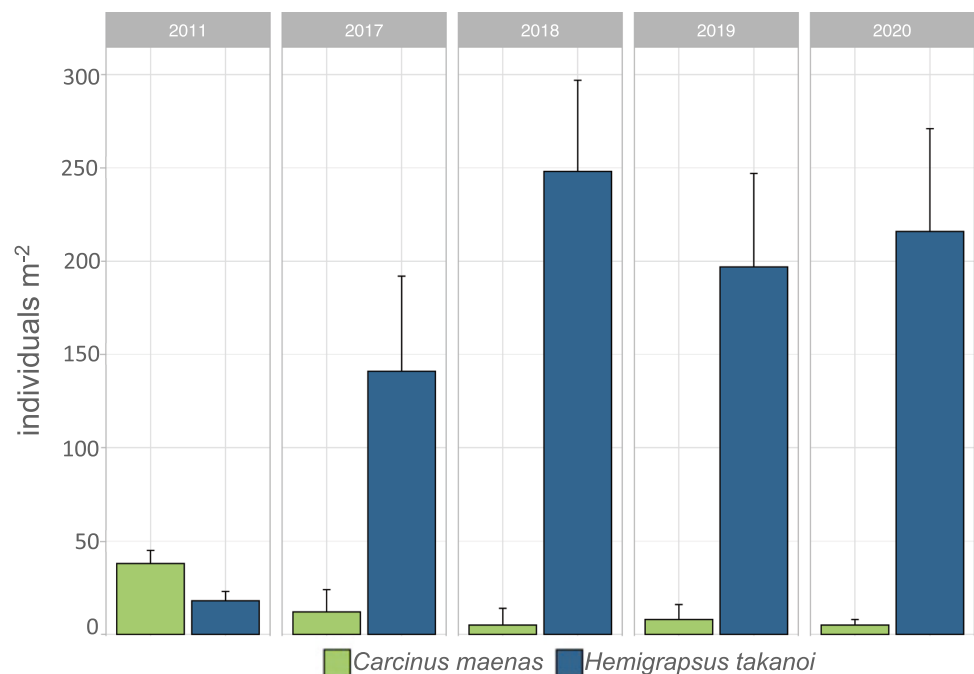


Fig. 3 Mean densities m^{-2} (\pm SE) of *Hemigrapsus takanoi* and the amphipod *Gammarus* spp. at sites A and B in June 2018

Fig. 2 Mean densities m^{-2} (\pm SE) of *Carcinus maenas* and *Hemigrapsus takanoi* on an intertidal mixed reef of mussel and oysters (site A) in May to June from 2011 to 2020



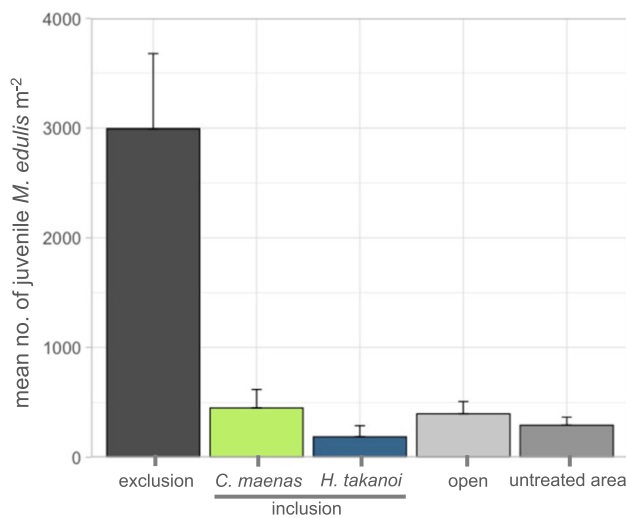


Fig. 4 Mean densities m^{-2} (\pm SE) of juvenile blue mussels *Mytilus edulis* in a field cage experiment at an intertidal mixed oyster reef after an experimental period of 14 weeks in spring/summer 2019. Five treatments were used: one predator exclusion treatment; two inclusion treatments with *Carcinus maenas* and *Hemigrapsus takanoi* in the cages, respectively; two control treatments with open cages and untreated areas

Field experiments

Predation experiment on blue mussel recruits

The number of mussel recruits significantly differed between the treatments (one-way ANOVA: $F = 9.489$, $df = 4$, $p < 0.001$, Fig. 4). Most blue mussels recruited in the absence of crabs (exclusion treatment) with a mean density of 2994 ± 684 individuals m^{-2} , which was significantly higher than recruitment of *M. edulis* in all other treatments (Tukey's test: $p < 0.001$, for all comparisons). The number of juvenile mussels in the treatment with enclosed native *C. maenas* (450 ± 168 individuals m^{-2}) was higher than in the treatment with enclosed non-native *H. takanoi* (185 ± 102 individuals m^{-2}), but differences were not significantly different. We also found no significant differences between crab inclusion treatments, open cages (397 ± 112 individuals m^{-2}), and untreated areas (291 ± 76 individuals m^{-2}) (Tukey's test: $p > 0.3$ for all comparisons).

Predation experiment on barnacles and juvenile oysters

The survival rate of barnacles *A. modestus* differed between the three experimental treatments (Kruskal–Wallis test: $p < 0.001$, Fig. 5). Highest barnacle survival rate was detected in the absence of crabs with a mean survival of $99.38\% \pm 0.62\%$ $cage^{-1}$, and survival rate was significantly lower in the treatments with enclosed native *C. maenas* ($77.40\% \pm 3.89\%$ $cage^{-1}$, Wilcoxon signed rank test: $p = 0.004$) and non-native *H. takanoi*

($83.14\% \pm 3.13\%$ $cage^{-1}$, Wilcoxon signed rank test: $p = 0.004$) in the cages, respectively.

Survival rate of juvenile Pacific oysters *M. gigas* was also significantly different between cages with native *C. maenas* ($70.95\% \pm 4.60\%$ $cage^{-1}$), cages with non-native *H. takanoi* ($67.45 \pm 2.47\%$ $cage^{-1}$), and cages without crabs ($96.74 \pm 1.46\%$ $cage^{-1}$; one-way ANOVA: $F = 54.28$, $df = 2$, $p < 0.001$, Fig. 5). We found significantly lower survival rates of juvenile oysters in cages with native *C. maenas* and non-native *H. takanoi* (Turkey's test $p < 0.001$, respectively) in comparison to cages without crabs.

The survival rate of *A. modestus* and *M. gigas* in cages with native *C. maenas* was not significantly different from the survival rate in cages with non-native *H. takanoi* (*A. modestus* Turkey's test, $p = 0.273$; *C. gigas*, Turkey's test, $p = 0.515$).

Predation experiment on endobenthic polychaetes

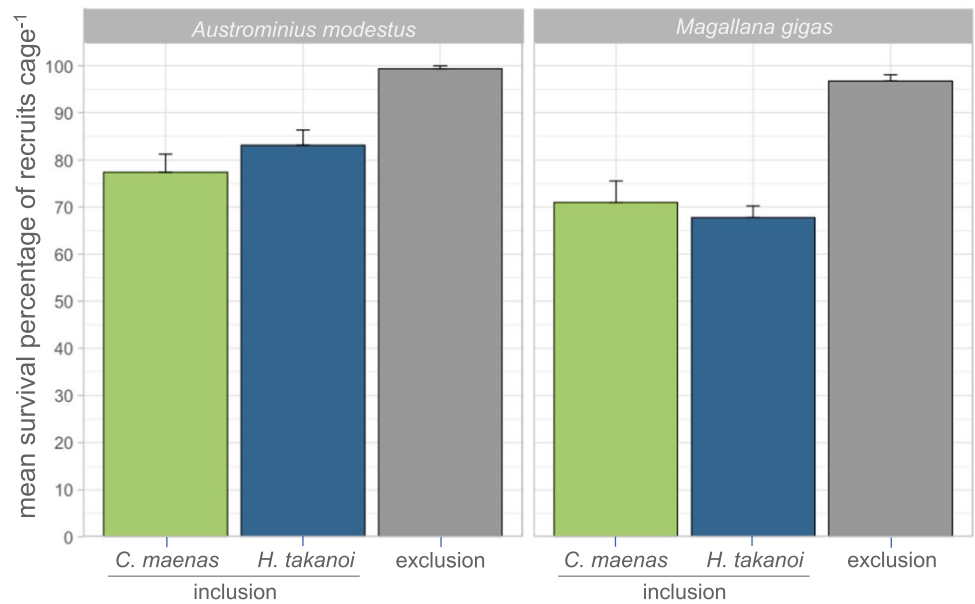
The mean number of polychaetes in the sediment samples significantly differed between the treatments (one-way ANOVA: $df = 4$, $F = 2.877$, $p = 0.043$, Fig. 6) and was lowest in cages with native *C. maenas* (2817 ± 1237 individuals m^{-2}). The number of polychaetes in cages with non-native *H. takanoi* (6266 ± 15 individuals m^{-2}) was not significantly different from cages without crabs (6863 ± 1884 individuals m^{-2} ; Tukey's test: $p = 0.986$). Interestingly, polychaete densities were 2.8-fold higher in open cages (8122 ± 2359 individuals m^{-2}) and 3.5-fold higher in untreated areas ($10,112 \pm 1810$ individuals m^{-2}) than in cages with the native *C. maenas*, although this species also had access to both control treatments. Maybe, our used density of *C. maenas* in the cages was higher than the natural density in the surrounding environment, although this has been adjusted before the experiment. In our analysis, we did not differentiate between different polychaete species but most abundant were *Tharyx killariensis* (Southern, 1914), *Capitella capitata* (Fabricius, 1780), and *Scoloplos armiger* (Müller, 1776).

Laboratory experiments

Consumption rate of *Mytilus edulis* and *Gammarus locusta* by *Hemigrapsus takanoi*

In a no-choice experiment, female *H. takanoi* consumed significantly more amphipods *G. locusta* than *M. edulis* (Mann–Whitney U-test: $p < 0.001$), while male *H. takanoi* consumed more blue mussels than amphipods (Mann–Whitney U-test: $p < 0.001$, Fig. 7). Comparing the sexes, the consumption of amphipods *G. locusta* by female and male *H. takanoi* was significantly different (Mann–Whitney U-test: $p < 0.001$). Female crabs consumed about twice as many

Fig. 5 Mean survival percentage cage⁻¹ (\pm SE) of juvenile *Austrominius modestus* and juvenile *Magallana gigas* in a field caging experiment with three different treatments: two inclusion treatments (*Carcinus maenas*, *Hemigrapsus takanoi*) and one control (without predators) at the end of 5 days exposure in September 2018



amphipods (8.00 ± 0.37 amphipods crab⁻¹ d⁻¹) than male individuals (4.06 ± 0.47 amphipods crab⁻¹ d⁻¹). The consumption of blue mussels by female and male crabs was also significantly different (Mann–Whitney U-test: $p < 0.001$). Male crabs consumed about 10 times more blue mussels (14.83 ± 0.96 blue mussels crab⁻¹ d⁻¹) than female conspecifics (1.43 ± 0.22 blue mussels crab⁻¹ d⁻¹).

Prey preference of *Hemigrapsus takanoi* between *Mytilus edulis* and *Gammarus locusta*

In this choice experiment, female *H. takanoi* consumed significantly more amphipods *G. locusta* (7.13 ± 0.42

amphipods crab⁻¹ d⁻¹) than blue mussels *M. edulis* (1.40 ± 0.37 blue mussels crab⁻¹ d⁻¹, Mann–Whitney U-test: $p < 0.001$, Fig. 8). Male *H. takanoi* showed an opposite pattern with lower consumption of *G. locusta* (3.53 ± 0.72 amphipods crab⁻¹ d⁻¹) in comparison to *M. edulis* (23.2 ± 2.43 blue mussels crab⁻¹ d⁻¹, Mann–Whitney U-test: $p < 0.001$, Fig. 8). Thus, the choice experiment confirmed the pattern from the no-choice experiment (see the “Consumption rate of *M. edulis* and *G. locusta* by *H. takanoi*” section).

Personal observations during the course of the experiment revealed that female and male *H. takanoi* use different techniques to open blue mussels. Male Asian brush-clawed shore crabs crushed the mussels into many small pieces by using their powerful claws (Fig. 9a,c). Female conspecifics opened the shells at the posterior end and removed the mussel flesh from the opening, leaving the mussel shell largely intact (Fig. 9b,d).

Comparison of consumption rates of *Mytilus edulis* and *Gammarus locusta* by *Hemigrapsus takanoi* and *Carcinus maenas*

In an additional no choice experiment, native *C. maenas* consumed significantly more *M. edulis* than non-native *H. takanoi* (analyzed over both sexes: Mann–Whitney U-test: $p < 0.012$, Fig. 10a). While female (28.0 ± 7.85 blue mussels crab⁻¹ d⁻¹) and male (26.62 ± 7.97 blue mussels crab⁻¹ d⁻¹) *C. maenas* did not consume different numbers of *M. edulis*, female *H. takanoi* (3.88 ± 1.88 blue mussels crab⁻¹ d⁻¹) consumed fewer blue mussels than male Asian brush-clawed shore crabs (9.0 ± 2.88 blue mussels crab⁻¹ d⁻¹), although in this experiment, the difference was not

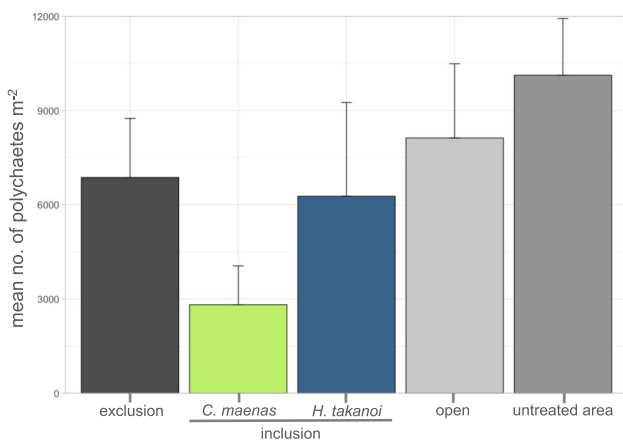
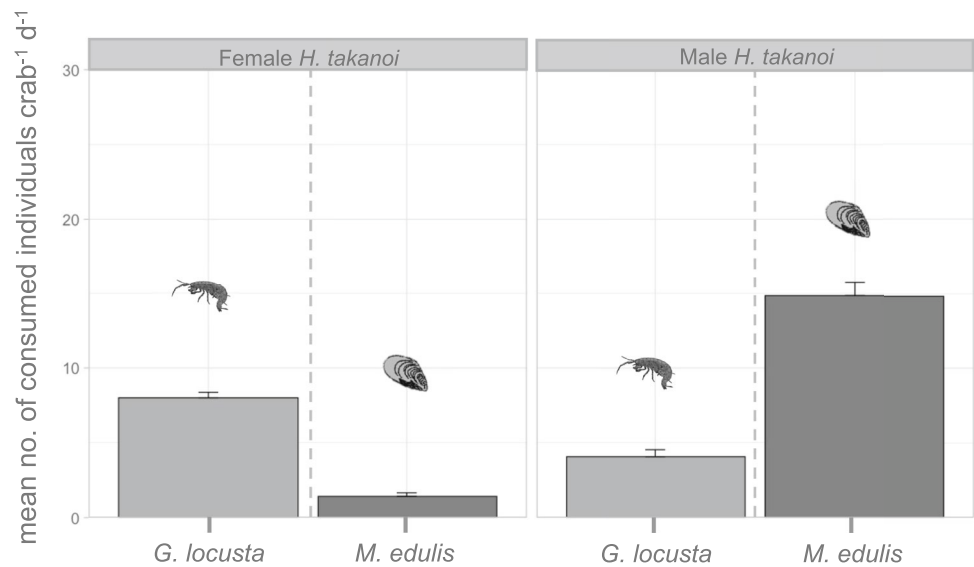


Fig. 6 Mean densities (\pm SE) of polychaetes m⁻² in a field cage experiment at an intertidal mixed oyster reef after an experimental period of 8.5 weeks in spring 2017. Five treatments were used: two inclusion treatments (*Carcinus maenas*, *Hemigrapsus takanoi*), one exclusion treatment (without predators), and two control treatments (open cages and untreated areas)

Fig. 7 Consumption (mean number \pm SE) of *Gammarus locusta* and *Mytilus edulis* by female and male *Hemigrapsus takanoi* in a laboratory no-choice experiment

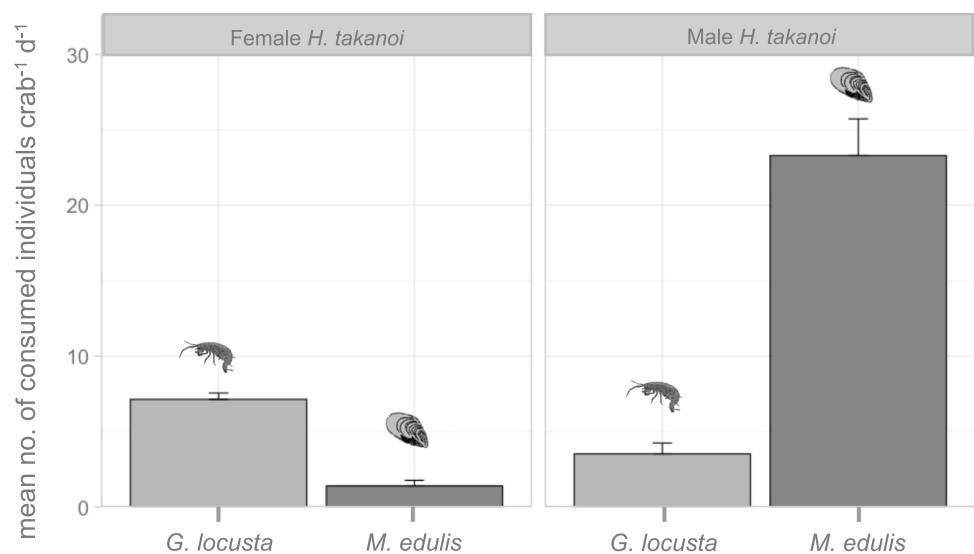


significantly different (Mann–Whitney U-test: $p = 0.182$; compare the “Consumption rate of *M. edulis* and *G. locusta* by *H. takanoi*” section).

The consumed number of amphipods was also significantly different between native *C. maenas* and introduced *H. takanoi* with higher consumption rates in *C. maenas* than in *H. takanoi* (analyzed over both sexes: Mann–Whitney U-test: $p = 0.006$, Fig. 10b). Female and male *C. maenas* consumed no significant different numbers of amphipods. Female *H. takanoi* (6.00 ± 0.57 amphipods crab⁻¹ d⁻¹) consumed similar numbers of amphipods than female (6.67 ± 0.92 amphipods crab⁻¹ d⁻¹) and male *C. maenas* (6.80 ± 0.73 amphipods crab⁻¹ d⁻¹), but consumption was significantly higher than of male *H. takanoi* (1.83 ± 0.40 amphipods per crab d⁻¹, Mann–Whitney U-test:

$p < 0.003$). In this case, the low consumption rate of amphipods by male *H. takanoi* mainly caused the significant difference between both crab species. Comparison of consumption rate of mussels and amphipods by female *C. maenas* as well as male *C. maenas* revealed no significant difference between the sexes (Mann–Whitney U-test: $p > 0.136$, for both comparisons). Female Asian brush-clawed shore crabs consumed more amphipods than blue mussels although the difference was not significantly different (Mann–Whitney U-test: $p < 0.085$). Male *H. takanoi* showed a contrasting pattern with higher consumption of *M. edulis* than *G. locusta*, but this difference was also not significantly different (Mann–Whitney U-test: $p < 0.064$). However, the pattern of prey preferences for female and male *H. takanoi* was the same as in the previous experiments.

Fig. 8 Consumption (mean number \pm SE) of *Gammarus locusta* and *Mytilus edulis* by female and male *Hemigrapsus takanoi* in a laboratory choice experiment



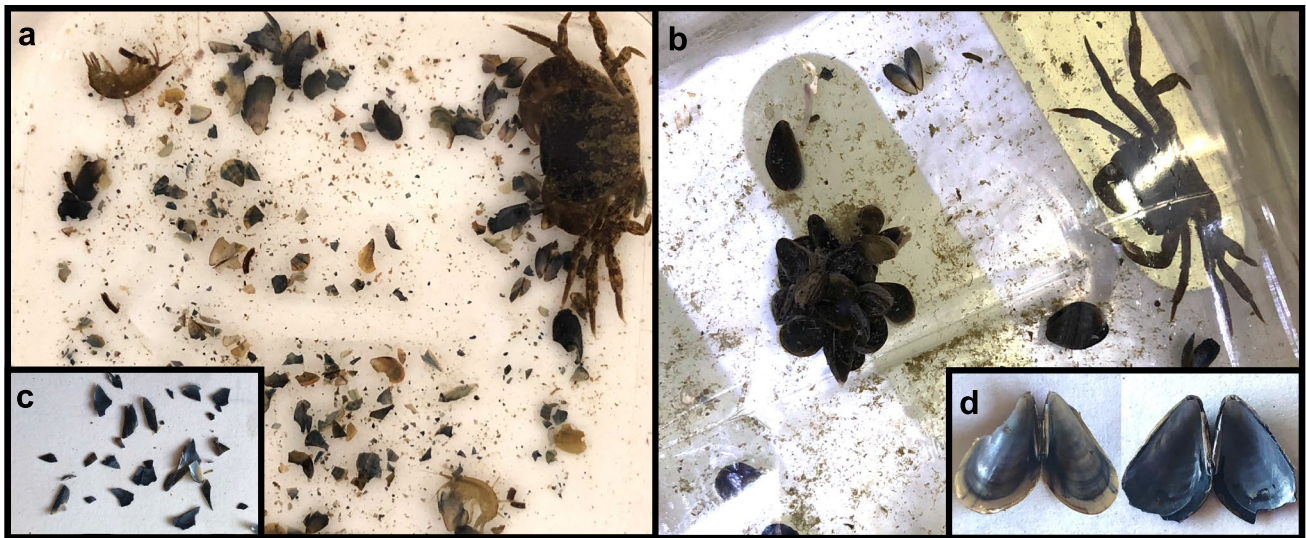


Fig. 9 The strategy of *Hemigrapsus takanoi* for preying on mussels is different in male (a) and female (b) Asian brush-clawed shore crabs. Male crabs crack the whole shell, resulting in many shell fragments

(c). Female crabs open *Mytilus edulis* shells at the posterior end of the mussels, leaving the shells largely intact (d)

Discussion

The results of this study reveal a strong density increase of introduced Asian brush-clawed crabs in the northern Wadden Sea during the last decade, whereas densities of

native *C. maenas* have decreased. Both crab species show an overlapping food spectrum of epibenthic prey organisms with higher consumption rates per crab for *C. maenas*. The occurrence of endobenthic polychaeta worms, by contrast, was only affected by native shore crabs.

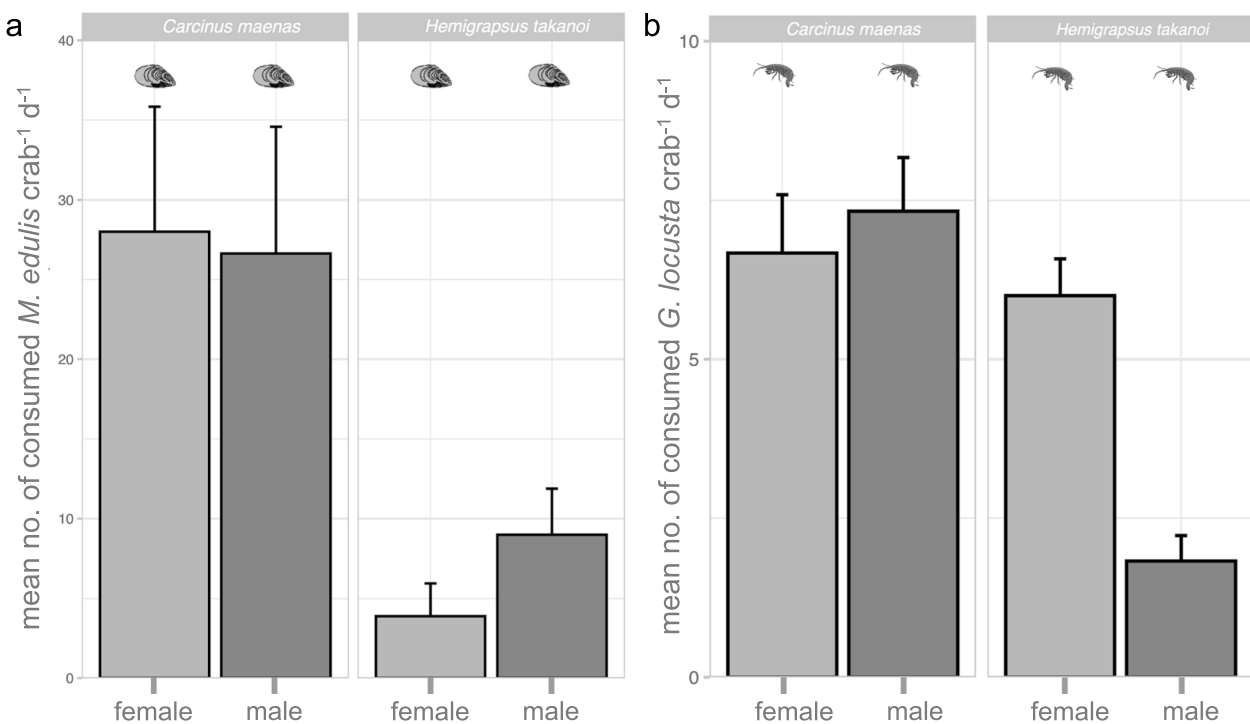


Fig. 10 Consumption (mean number ± SE) of *Mytilus edulis* (a) and *Gammarus locusta* (b) by *Carcinus maenas* and *Hemigrapsus takanoi* in a laboratory no-choice experiment (note the different y-axis scaling of (a) and (b))

Population development of Asian and native shore crabs

Since its first detection in 1993, the Asian brush-clawed shore crab *H. takanoi* now occurs at many coastal habitats in western Europe (Gollasch 1999) and strongly increased in abundance of more than 100 individuals m^{-2} at different sites in the Wadden Sea (Schückel et al. 2013; Geburzi et al. 2018; Bleile 2019). Shortly after the introduction into a new environment, invasion trajectories of non-native species regularly show a lag phase with low abundances, followed by an exponential density increase (Mack et al. 2000; Blackburn et al. 2011; Reise et al. 2017b). A subsequent adjustment phase is triggered by behavioral and evolutionary adaptations and often results in population dynamics with fluctuating density levels (Reise et al. 2017a). Such a pattern was also shown by *H. takanoi* in our study area at site A with still low abundances of about 20 individuals m^{-2} in 2011 and a subsequent strong density increase until 2018. Since then, densities remain relatively stable with values of about 225 individuals m^{-2} . Our study focused on one site, but since 2011, a strong density increase of *H. takanoi* has also been observed at many further oyster reefs in the northern Wadden Sea (Möller 2017), suggesting that the investigated oyster reef and found invasion trajectory of *H. takanoi* are representative for the study area.

Asian brush-clawed shore crabs need epibenthic structures, and mixed reefs of *M. edulis* and *M. gigas* offer such a habitat with ideal growth and living conditions for the newcomer (Landschoff et al. 2013). Furthermore, low intraspecific competition and reduced predation pressure by native shore crabs facilitated the high recruitment success and the comparatively high survival probability of juvenile *H. takanoi* on the reefs (Geburzi et al. 2018). Since the introduction of *H. takanoi*, the native *C. maenas* has to share one of its preferred habitats with the invader. In 2011, densities of *C. maenas* in mixed reefs were still higher than of the non-native *H. takanoi*, but decreased in the following years, while densities of *H. takanoi* strongly increased. At site A in 2020, densities of *H. takanoi* were finally many times higher than of *C. maenas*. This development may be caused by high predation pressure of adult Asian brush-clawed shore crabs on native *C. maenas* recruits (Lohrer and Whitlatch 2002; van den Brink and Hutting 2017; Geburzi et al. 2018) and competition for food sources. However, also other factors or multiple as well as combined effects may have been responsible, because a decline in *C. maenas* was already observed in the southern Wadden Sea before the introduction of *H. takanoi* (Van den Brink et al. 2012). Reasons for the previous decrease of *C. maenas* are still unknown, but it also may have made the enormous increase in Asian brush-clawed shore crabs possible in the first place (Van den Brink et al. 2012). The current pattern with a dominance of *H.*

takanoi in mixed reefs will presumably persist because the presence of Asian brush-clawed shore crabs enhances the recruitment of juvenile conspecifics (Geburzi et al. 2018).

However, despite decreasing densities in oyster reefs, it seems not likely that the occurrence of native shore crabs is endangered by the spread of *H. takanoi* on a Wadden-Sea wide scale. In contrast to Asian brush-clawed shore crabs, *C. maenas* also achieves high densities in other habitats than mixed reefs of mussels and oysters such as bare sedimentary tidal flats and seagrass beds that also serve as nursery grounds for native shore crabs (Polte et al. 2005; van den Brink and Hutting 2017). Additionally, a large part of the adult *C. maenas* population lives in the subtidal zone and provides a high number of planktonic larvae, which settle in the above-mentioned habitats.

Prey preferences of introduced and native crabs

Beside direct predation effects between introduced *H. takanoi* and native *C. maenas*, also competition for food may affect the occurrence of both species in mixed reefs of mussels and oysters (van den Brink and Hutting 2017). Both species show an overlapping food spectrum but with partly different prey preferences. While the native *C. maenas* feeds on both epibenthic and endobenthic prey items such as polychaetes, the introduced *H. takanoi* mainly consumes epibenthic organisms. The broader food spectrum of *C. maenas* may offer a competitive advantage over *H. takanoi*. Despite the competitive advantage, however, densities of *C. maenas* have decreased on the oyster reef at site A in the last 10 years, suggesting that competition for food with *H. takanoi* has presumably not caused the density development of *C. maenas*. This assumption is supported by the fact that both crab species can also use other food sources such as algae and carrion (Knudsen 1964; Moore and Howarth 1996). Indeed, we regularly observed Asian brush-clawed shore crabs and native shore crabs feeding on just died mussels and oysters being common on the reefs.

The introduction of *H. takanoi* and its preferred consumption of epibenthic organisms cause an increased predation pressure on sessile and mobile organisms above the sediment surface within an oyster reef. Therefore, associated species such as sessile barnacles attached to the bivalve shells and motile amphipods may suffer from high Asian brush-clawed shore crab densities and may show lower densities in comparison to the situation before the establishment of *H. takanoi*. The increased consumption of epibenthic organisms could also explain the negative correlation between the densities of *H. takanoi* and amphipods. Although this pattern was also observed at other sites in the northern Wadden Sea (K. Reise, personal communication), this result has to be considered with caution. We have only investigated a limited number of oyster reefs, and we have no additional

information on other predators and the sex ratio of *H. takanoi* at these sites, which also may affect amphipod densities. Generally, associated species of epibenthic structures in the Wadden Sea often reveal high interannual variations (Buschbaum 2000), and whether densities of barnacles, amphipods, and further species will decrease in the long run cannot be yet answered by our investigations but should be subject in forthcoming more long-lasting studies.

The increased predation pressure may not only affect oyster reef associated organisms but also the habitat-forming species itself. In our field experiments, *H. takanoi* and *C. maenas* revealed a significant reduction of native *M. edulis* and non-native *M. gigas* with lower densities of both bivalve species at crab presence in the cages. This treatment also excluded further potential consumers of juvenile blue mussels such as starfish. However, potential other predators than crabs did not additionally reduce the number of mussel recruits in untreated areas and open cages. This result indicates that crab predation was the main factor, which affected blue mussel recruitment success. However, not only the cumulative impact of *H. takanoi* and *C. maenas* is important but also the temporal occurrence and recruitment of both crab species in oyster reefs. The native *C. maenas* occurs from late spring to autumn on intertidal oyster reefs, but spends the winter months in the sublittoral zone and shows a temporal restricted recruitment phase in July and August. By contrast, the introduced *H. takanoi* inhabits intertidal oyster reefs all year round with continuous recruitment that peaks in September (Geburzi et al. 2018). Thus, predation effects by Asian brush-clawed shore crabs on mussels and oysters are not limited in time and may also reduce the number of bivalves during the winter months. Additionally, temporal mismatch between bivalve recruits and predatory juvenile *C. maenas* may cause high recruitment success in *M. edulis* (Strasser and Günther 2001). With the permanent presence of juvenile and adult *H. takanoi* on oyster reefs, this temporal refuge for bivalve recruits seems to have ceased. The resulting higher predation pressure must be compensated by mussel and oyster recruitment. Otherwise, the structure and spatial extent of oyster reefs will be affected in the long term, but this can only be determined by ongoing studies.

Differences between sexes

In our laboratory experiments, both crab species consumed amphipods and blue mussels. While the sex of *C. maenas* did not significantly influence the consumption rate, the food preference of *H. takanoi* was different between female and male individuals. Male Asian brush-clawed shore crabs consumed fewer amphipods than female crabs of the same size class, but consumption of blue mussels was higher in male compared to female *H. takanoi*.

The different consumption patterns of female and male *H. takanoi* can be explained by sexual dimorphism in the shape of the chelae (Mingkid et al. 2006; Markert et al. 2016). Male *H. takanoi* have larger and stronger claws than similar-sized females (Nour et al. 2020). The filigree and tweezer-like claw shape of female crabs likely facilitate the catching of small mobile prey items, while the big claw of males is less suited for catching amphipods but advantageous for cracking mussels. The different food preferences of female and male *H. takanoi* show that not only the total density of a predator species but also the sex ratio is important when considering the effects on specific prey species. For example, in our laboratory experiments, the consumption of blue mussels by female *H. takanoi* was quite low, and, therefore, mainly male Asian brush-clawed shore crabs should be considered to exert the predation pressure on *M. edulis* (see Fig. 7). In the northern Wadden Sea, densities of male *H. takanoi* were not significantly higher than of female conspecifics, although slight differences in the sex ratio may occur (Schückel et al. 2013; Goedknecht et al. 2017) that we considered in our field experiments by adjusting the number of females and males in the cages to field densities at the respective times of the experiments. Interestingly, Nour et al. (2020) investigated the sex ratio of *H. takanoi* in the Western Baltic Sea and revealed that females were dominant over males (mean sex ratio of 1.4:1), but this ratio also shows strong seasonal changes with resulting predatory effects on population dynamics of blue mussels *M. edulis*. Therefore, sex specific investigations of introduced predatory species are essential to assess their effects on native prey organisms in invaded habitats.

Consumption rates and synthesis

Our results show that *H. takanoi* is nowadays a well-established and permanent non-native predator on oyster reefs in the Wadden Sea and will presumably have a persistent impact on the associated community of mixed reefs of mussels and oysters but also on the habitat structuring bivalves itself.

In our field experiments, we aimed to adapt the densities and sex ratios of *H. takanoi* and *C. maenas* to their natural occurrences within oyster reefs and did not find significant differences in the effects on the studied prey species (see *M. edulis* Fig. 4; *A. modestus* and *C. gigas* Fig. 5). However, for consumption rate comparisons between Asian brush-clawed shore crabs and native *C. maenas*, our more controlled laboratory experiments were much more suitable. They revealed that the consumption rate of single *C. maenas* is generally higher than of single *H. takanoi*, but the net effect on the number of consumed prey organisms in the field may be different when considering crab densities on oyster reefs. For example, our comparative experiments on consumption rates of *C. maenas* and *H. takanoi* (see

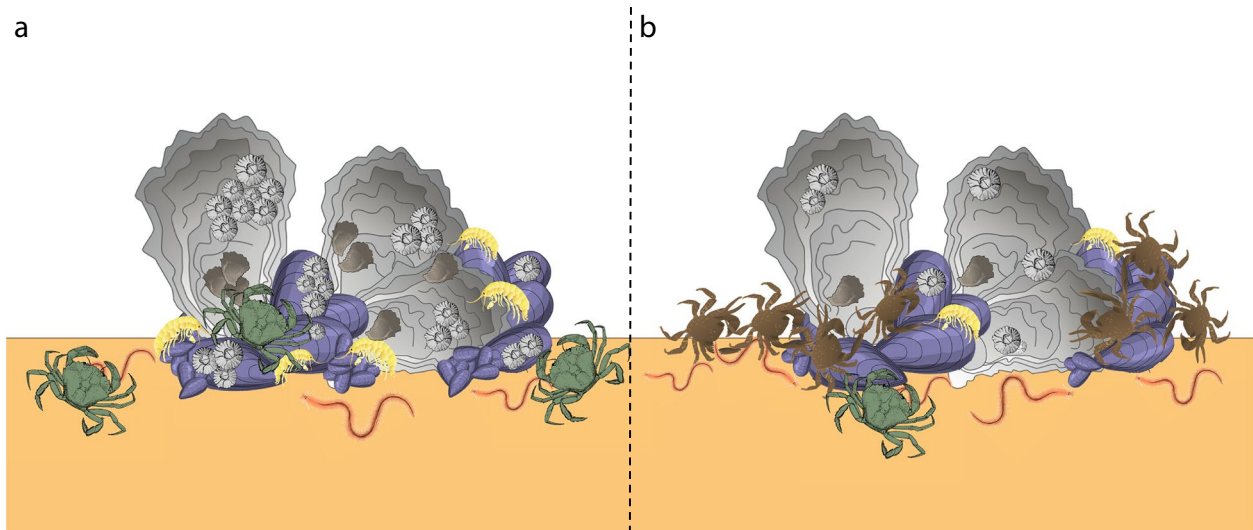


Fig. 11 Schematic illustration of predator-prey interactions and densities of prey organisms in mixed reefs of mussels and oysters before (a) and after the introduction (b) of Asian brush-clawed shore crabs. It is suggested that the establishment and high densities of *Hemigrapsus takanoi* have caused higher predation pressure on epibenthic prey

Fig. 10) revealed that the mean consumption of a single *C. maenas* was about 7 amphipods d^{-1} , which was almost two times higher than 4 amphipods d^{-1} consumed by a single *H. takanoi* (mean of both sexes). Assuming the highest densities found for *C. maenas* (38 individuals m^{-2} in 2011) and *H. takanoi* (248 individuals m^{-2} in 2018), this corresponds to a total consumption of 266 amphipods $m^{-2} d^{-1}$ by *C. maenas* but of 992 amphipods $m^{-2} d^{-1}$ by *H. takanoi*, respectively. A similar pattern was found when considering the habitat building blue mussels as prey. The mean consumption rate of a single *C. maenas* was 27 mussels d^{-1} (see Fig. 10) and about 4.5 times higher than 6 mussels d^{-1} consumed by a single *H. takanoi* (mean of both sexes). This corresponds to a total consumption rate of 1026 mussels $m^{-2} d^{-1}$ by *C. maenas* and 1488 mussels $m^{-2} d^{-1}$ by *H. takanoi*, respectively, when again using the highest densities of both crab species during the study period. In both cases, the total predation pressure of *H. takanoi* is much higher than that of the native *C. maenas*. Although natural consumption rates might be lower, these examples demonstrate how the predation conditions may have changed by the introduction of *H. takanoi* and its successful establishment on oyster reefs in the Wadden Sea (Fig. 11). Whether and to what extent these changed consumption patterns and the cumulative predation pressure of both crab species will affect the habitat and its associated organisms in the long term remains to be investigated.

This study combined a series of small case experiments to provide the most comprehensive overall picture of potential predation effects of the introduced Asian brush-clawed shore crab *H. takanoi* in comparison to the native

organisms such as barnacles, amphipods, as well as juvenile Pacific oysters and blue mussels in mixed reefs of mussels and oysters, while predation pressure on endobenthic polychaetes is reduced due to decreased densities of native *Carcinus maenas*

C. maenas that may explain the current invasion status of the Asian brush-clawed shore crab.

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Declarations

Conflict of interest The authors declare no conflict of interest.

Ethical approval All applicable international, national, and institutional guidelines for animal testing, animal care, and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling were obtained by the authors from the competent authorities. The study is compliant with CBD and Nagoya protocols.

Data availability The datasets generated during and/or analyzed during the current study are submitted to the PANGAEA repository <https://www.pangaea.de/>.

Author contribution AC and CB conceived and designed the research. AC and KW conducted the experiments. AC, CB, and KW analyzed the data. CB and AC wrote the manuscript. All authors read and approved the manuscript.

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