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Recruitment patterns, low cannibalism and reduced interspecific predation contribute to high invasion success of two Pacific crabs in northwestern Europe

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ABSTRACT

Life-history traits and interactions with native species play an important role for the successful establishment of non-native species in new habitats. We investigated the recent successful invasion of the Pacific crabs *Hemigrapsus takanoi* and *H. sanguineus* to the southeastern North Sea coast with respect to their recruitment patterns, as well as interactions of juvenile with sub-adult individuals among the Pacific crabs and with native shore crabs *Carcinus maenas*. A field survey of juvenile native and introduced crab abundances (carapace width 1.4–10 mm) was conducted in the northern Wadden Sea, spanning 24 months from 2014 to 2016. The survey revealed different seasonal recruitment patterns of native *C. maenas* and both introduced *Hemigrapsus* species. Native shore crabs showed a single recruitment peak from June to July, while *Hemigrapsus* spp. mainly recruited from August to early September, but recruits occurred in low densities throughout the winter until the end of the following spring season. Field experiments on the effects of larger crabs on the recruitment intensity showed that recruitment of *H. takanoi* was enhanced by the presence of larger congeners, but remained unaffected by larger *C. maenas*. Recruitment of juvenile *C. maenas*, by contrast, was reduced by the presence of larger *Hemigrapsus* spp. Additional laboratory experiments revealed high rates of cannibalism on newly recruited *C. maenas* by subadult conspecifics as well as strong predation by larger *Hemigrapsus* spp. In contrast, newly recruited *Hemigrapsus* spp. had a much lower risk of being preyed on by subadult conspecifics and native shore crabs. Our results suggest that the timing of recruitment in combination with low intraspecific competition and reduced predation pressure by native shore crabs are crucial for the rapid and ongoing establishment of *Hemigrapsus* spp. in the Wadden Sea.

1. Introduction

Worldwide, marine ecosystems are invaded by a continuously rising number of non-native species, which is in particular true for coastal and estuarine habitats (Gollasch, 2006; Ruiz et al., 1997; Williams and Grosholz, 2008). The establishment of non-native species can profoundly affect species communities in invaded environments, driven by direct and indirect interactions between native and non-native species (Buschbaum et al., 2016; Edelist et al., 2013; Grosholz et al., 2000; Jensen et al., 2002; Levin et al., 2002; Reise et al., 2017). Life-history traits, especially traits related to reproduction (Bremner, 2008; Lockwood et al., 2005), and niche allocation processes (Herborg et al., 2007; Peterson, 2003) are assumed to play an important role for the successful establishment and spread of non-native species. Detailed knowledge of the ecology and life-history of non-native species substantially contributes to the understanding of underlying processes of successful bio-invasions, and can also allow projections on possible effects of newly arrived species on native communities. For example, high fecundity and the duration and timing of reproduction periods have been attributed to invasion success in plants (Gerlach and Rice, 2003; Rejmanek and Richardson, 1996) as well as freshwater fish

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(Olden et al., 2006), crayfish (Chucholl, 2012) and gammarids (Grabowski et al., 2007; Pöckl, 2009).

In European coastal waters, the northwestern Pacific Brush-clawed shore crab *Hemigrapsus takanoi* Asakura and Watanabe 2005 and the Asian shore crab *Hemigrapsus sanguineus* (de Haan, 1835), are among the most recent successfully established non-native species. *Hemigrapsus takanoi* was for the first time reported from a ship's hull in Bremerhaven, Germany, in 1993 (Gollasch, 1999) and from the Bay of Biscay coast at La Rochelle, France, in 1994 (Noël et al., 1997). Initially identified as *H. penicillatus*, all populations of Brush-clawed shore crabs in Europe have later been assigned to the newly described *H. takanoi* (Asakura and Watanabe, 2005; Yamasaki et al., 2011). Within two years, this species had extended its range from northern Spain to southern Brittany (Noël et al., 1997). In 1999, it was reported from Le Havre at the French coast of the English Channel (Breton et al., 2002) and in 2000 from the Dutch Delta (Wolff, 2005). In 2006, it was found in the Dutch part of the Wadden Sea (Gittenberger et al., 2010), one year later also on the coast of Lower Saxony, Germany (Obert et al., 2007) and by 2009, it had reached the Sylt-Rømø-Bight between Germany and Denmark in the northern part of the Wadden Sea (Landschoff et al., 2013), thus currently occurring along 2200 km of the European Atlantic and North Sea coastline. Recently, it has also been reported from Great Britain (Ashelby et al., 2017; Wood et al., 2015) and the southwestern Baltic Sea (Geburzi et al., 2015).

Hemigrapsus sanguineus was first recorded at Le Havre and in the Dutch Delta system in 1999 (Breton et al., 2002; Wolff, 2005), spreading along the French, Belgian and Dutch coast of the English Channel and the southern North Sea in the following years (Dauvin and Dufossé, 2011; Gothland et al., 2013; Kerckhof et al., 2007; Wolff, 2005). It reached the Dutch Wadden Sea in 2004 (Gittenberger et al., 2010), German waters in 2006 (Obert et al., 2007) and occurred along the whole German Wadden Sea Coast and on the island of Helgoland in the German Bight by 2009 (Jungblut et al., 2017; Landschoff et al., 2013). In 2012, it was also reported from the Danish Wadden Sea islands Rømø and Fanø (pers. observation) and recently also from Great Britain (Seeley et al., 2015). On the Atlantic coast of North America, *H. sanguineus* was initially reported as an invasive species in 1988 at the mouth of Delaware Bay (McDermott, 1998) and is currently distributed in the United States from South Carolina to Maine (Epifanio, 2013).

The Wadden Sea as the coastal area of the southeastern North Sea is dominated by unstable sediments, and oyster and mussel reefs are the only naturally occurring extensive hard-bottom substrates. While comparatively species-poor, the proportion of non-native species is high, as reflected by over 60 non-native macrobenthic species alone (Buschbaum et al., 2012; Reise et al., 2010). The native decapod crustacean fauna of the Wadden Sea is dominated by the European shore crab *Carcinus maenas*, which is very abundant in benthic communities both inter- and subtidally, and itself a globally successful invader of coastal ecosystems (Carlton and Cohen, 2003). The recent arrival of the two *Hemigrapsus* spp. in this ecosystem allows to simultaneously study interactions between native and invasive and two closely related invasive species, as well as the ongoing establishment process.

Several studies reported detrimental effects of growing *Hemigrapsus* populations on *C. maenas* in North America (Kraemer et al., 2007; O'Connor, 2014) and Europe (van den Brink et al., 2012). These can be connected to apparent advantages of *Hemigrapsus* spp. over *C. maenas* in competition for food and shelter (Gothland et al., 2014; Hobbs et al., 2017; Jensen et al., 2002), but also to reduced recruitment success of *C. maenas* as a consequence of predation on early juveniles by *H. sanguineus* (Lohrer and Whitlatch, 2002). Early juvenile crabs are an especially sensitive life stage, as they experience high predation pressure (especially from other decapods) and strongly depend on suitable nursery habitats (Lohrer and Whitlatch, 2002; Moksnes et al., 1998). They usually occur in high densities but only for a relatively short time, and all processes influencing crab recruitment are assumed to cause effects on the population level (Moksnes, 2002).

This study aims to investigate temporal dynamics of the recruitment and early juvenile stages of Asian shore crabs in comparison to European shore crabs, as well as possible competitive interactions affecting early juvenile crabs. The first part of the study comprises regular observations of the abundances of *Hemigrapsus* spp. and *C. maenas* in the intertidal of the northern Wadden Sea between 2014 and 2016, with a special focus on size class distributions and the occurrence of recruitment events. Based on observations of several broods per season regularly occurring in *Hemigrapsus* spp. (Fukui, 1988; McDermott, 1998; van den Brink et al., 2013) while only one brood per season is common for *C. maenas* in the North Sea (Crothers, 1967; Klein Breteler, 1976), differences in reproductive cycling of native and non-native species favouring the establishment of *Hemigrapsus* spp. are hypothesised. To the best of our knowledge, the survey data represent the first temporally highly resolved, perennial dataset of *Hemigrapsus* spp. abundances in their invaded European range.

The second part of the study comprises field and laboratory experiments on the influence of subadult and adult crabs on the recruitment success of juveniles, and intra- (e.g. cannibalism) and interspecific predation pressure on newly settled crabs. The latter is a putatively important interaction in crab populations, shaping distribution patterns and abundances of juveniles (Moksnes et al., 1998). We hypothesize differences in the recruitment success of juveniles in response to larger crabs, as well as differential patterns of predation pressure on early juveniles between *C. maenas* and *Hemigrapsus* spp.

2. Material and methods

2.1. Study area

All field investigations and experiments were carried out in the intertidal zone near the northern part of the island of Sylt in the northern Wadden Sea (Fig. 1). This area is dominated by sedimentary soft-bottom habitats with several mixed beds of native blue mussels (*Mytilus edulis*) and introduced Pacific oysters (*Magallana gigas*, Reise et al., 2017), as well as artificial hard structures (boulder groynes), which provide epibenthic hard-bottom habitats in close proximity to each other. It is particularly in these hard-bottom habitats where both *Hemigrapsus* spp. occur in the Wadden Sea. On Sylt, the first specimen of *Hemigrapsus* spp. were found in 2008 close to harbours at the southern and northern tips of the island (J. Landschoff, K. Reise pers. comm.). In 2011, *Hemigrapsus* spp. were already found in hard-bottom habitats at 12 sites all along the east coast of Sylt, occurring sympatrically at 5 of these sites and always co-occurring with *C. maenas* (Landschoff et al., 2013).

We selected an intertidal mixed oyster-mussel-bed at the northern tip of the island (N 55.028° E 8.434°; 'site A'), dominated by *H. takanoi*, and boulder groynes in that area (N 55.013° E 8.432°; 'site B'), dominated by *H. sanguineus*, as sampling sites for the survey (Fig. 1). At site A, also the field experiment was conducted. Both sites are located between 0.3 and 0.5 m above mean low tide level.

2.2. Survey

To gain insight in temporal variations of recruitment and

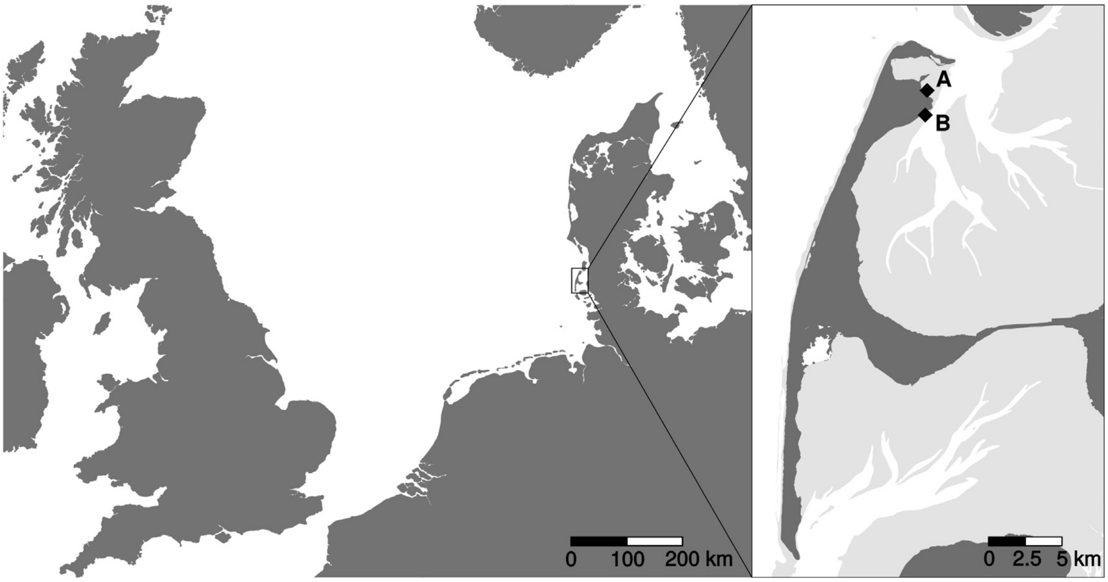

Fig. 1. The island of Sylt and its location in the southeastern North Sea. The two sampling sites (A and B) are located at the northern tip of the island. Light grey areas represent tidal flats.

abundances of juvenile crabs, as well as possible differences in habitat preferences between the three crab species in the Wadden Sea, a quantitative survey was carried out from December 2014 to December 2016. The survey comprised bi-weekly samplings at the sites A and B. Based on the results of a pilot study, both sites were identified as representative habitats for sampling recruiting and juvenile crabs of all three species (Geburzi, 2014).

At each sampling date and site, two samples of 625 cm^2 surface area were taken at low tide by placing a 25 × 25 cm steel frame on the substrate and transferring all substrate and crabs within the frame, including the upper approx. 5 cm of sediment, into plastic buckets. Distance between the two samples was at least 10 m. The samples were transported to the lab and sieved (mesh size 0.5 mm). Remaining crabs in the sieve were identified to species level by using morphological characters. For distinguishing the two *Hemigrapsus* species we followed the characters given in Breton et al. (2002). The carapace width (CW) of each individual was measured to the nearest 0.01 mm with digital callipers. A stereo microscope was used for species determination and measurements when necessary.

2.3. Recruitment experiment

An inclusion-exclusion experiment was conducted in the field during the peak recruitment periods of *C. maenas* and *Hemigrapsus* spp. in summer and autumn 2016 to assess the influence of adult crabs on the recruitment of juveniles. Fully enclosed, cylindrical cages (15 cm diameter, 15 cm height) were constructed of a PVC scaffold and plastic mesh with 3 mm mesh size, which allowed crabs up to 7.5 mm CW to enter the cages (the larger ones by crawling sideways). The following size categories for crabs were defined for this (and the laboratory) experiment: 'recruits' $\leq$ 2 mm CW, 'juveniles' 2.1 mm–7.5 mm CW, which together represent '0-year-crabs', 'subadults' 7.6 mm–9.9 mm CW and 'adults' $\geq$ 10 mm CW.

To provide an attractive substrate for recruiting crabs, the cages were filled with a bottom layer of sand and approximately 4 cm of blue mussels, small oysters and empty shells which were taken from the surrounding area and cleaned thoroughly under running fresh water to remove any crabs. The cages were placed in a flow-through seawater tank for about 36 h to allow the mussels to settle and to produce byssus threads for mutual attachment, which resulted in a natural matrix of mussels, oysters and dead shell material. The experimental setup consisted of five treatments, with six replicates each. Inclusion cages were stocked with (1) nine *C. maenas* (ranging from 14.7 to 25.6 mm CW), (2) nine *H. takanoi* (ranging from 10.1 to 16.4 mm CW) or (3) nine *H. sanguineus* (ranging from 10.0 to 16.1 mm CW), respectively. Predator densities in the cages correspond to maximum densities of *Hemigrapsus* spp. in this part of the Wadden Sea, which reach up to 600 crabs m^{-2} (pers. observation, numbers include all crabs $\geq$5 mm CW). Exclusion cages without any crabs served as (4) control treatment to assess the recruitment of 0-year crabs without predation. Open 'cages', consisting of a cage bottom and a 5 cm high mesh ring filled with substrate were used as (5) cage-control treatment to assess natural levels of predation on recruiting crabs at the experimental site.

The closed and open cages were deployed at low tide on the tidal flat along the edge of the oyster-mussel-bed, using iron rods (30 cm length) for fixation. Treatments were arranged in random order and a distance of at least 2 m was kept between the cages to ensure independency of the experimental units. At the chosen site, *H. takanoi* is the dominating *Hemigrapsus* species while *H. sanguineus* only occurs in comparatively low densities (Geburzi, 2014). The experiment was conducted in two runs (subsequently referred to as 'run A' and 'run B') during the peak recruitment periods of *C. maenas* and *Hemigrapsus* spp., as inferred from the survey data. The experiment runs were set up 3 July 2016 and 8 September 2016 for 53 and 49 days, respectively. During the experimental period the cages were controlled once a week to check the experimental set-up and to remove drifting macroalgae covering the mesh. At the end of the experiment, the cages were transported to the laboratory and their contents were sieved over a 0.5 mm mesh. All crabs that had recruited to the cages were determined to species level using a stereo microscope and measured to the nearest 0.01 mm with digital callipers. Additionally, the number of surviving predators in the inclusion cages was noted.

2.4. Predation experiment

To assess predation pressure and cannibalism exerted by subadults on newly settled crabs (recruits), a lab experiment was conducted. Cylindrical glass bowls (9.5 cm diameter, 8.0 cm height) were filled with 200 mL filtered seawater and equipped with a thin layer of fine sand and a mussel valve (approx. 20 mm length) as substrate and shelter. Each glass bowl was stocked with six recruits of either *C. maenas*, *H. takanoi* or *H. sanguineus* (CW 1.5–1.8 mm). They were collected in the field 1–4 d prior to the experiment and kept in flow-through aquaria until the experiment started. The bowls were randomly assigned to one out of four treatments, with six replicates each. Treatments were as follows (1) one subadult male *C. maenas* (CW 9.12 ± 0.65 mm), (2) one subadult male *H. takanoi* (CW 7.81 ± 0.85 mm) and (3) one subadult male *H. sanguineus* (CW 7.80 ± 0.36 mm) per bowl as predator, and (4) no predator as a control to assess natural background mortality during the course of the experiment. The difference in CW between *Carcinus* and *Hemigrapsus* predators was chosen to take into account the relatively smaller chelae of *C. maenas* compared to *Hemigrapsus* spp. (compare Payne and Kraemer, 2013). All predators were starved for 24 h prior to the experiment to standardize hunger levels. The experiment was conducted in a climate chamber under constant temperature (15 °C) and natural light/dark cycle. The experiment ran over 12 h and the number of surviving recruits was controlled hourly and noted for each bowl. As newly settled *Carcinus* and *Hemigrapsus* did not occur at the same time, the experiment had to be conducted in separate runs for *C. maenas* (25 June 2016) and *Hemigrapsus* spp. (24 October 2016) as prey, respectively. However, the results were considered comparable with each other since both runs were conducted under the same lab conditions.

2.5. Data analysis

For the analysis of the survey data, in a first step actual size classes representing moult stages were determined from the size-frequency distributions of each species. Recognition of the moult stages and estimation of mean size and standard deviation for each stage was performed using Bhattacharya's method (Bhattacharya, 1967) implemented in FiSAT II software, version 1.2.2 (Gayanilo et al., 2005) (decomposition of size-frequency distributions is shown in Appendix 1). Size ranges for the stages were then determined by calculating the interception points of the probability density functions of neighbouring modal groups. The ranges were subsequently used to calculate size-class specific abundances (individuals m^{-2}) for each sampling date and site with the two samples per site pooled. Graphical output was produced with R, version 3.3.3 (R Core Team, 2017) and the additional package ‘ggplot2’ (Wickham, 2009).

The recruitment data were analysed by fitting a generalised linear model (GLM) with ‘species’ (*Carcinus* and *Hemigrapsus*) and ‘treatment’ (exclusion, open, *C. maenas* inclusion, *H. takanoi* inclusion and *H. sanguineus* inclusion) as predictor variables, and the counts of 0-year crabs as response variable. The model was fitted with a negative binomial error term and a log-link function, accounting for overdispersion and aggregation in the data as a source of unexplained variance in the model. The analysis was performed with R, version 3.3.3, using the function ‘glm.nb’ provided with the ‘MASS’ package (Venables and Ripley, 2002), and the ‘ggplot2’ package was used for graphical output.

For the analysis of the predation experiment, a Kaplan-Meyer estimator of survival probability was calculated for each predator-prey combination. An asymptotic log-rank test was performed to detect overall differences of survival probabilities between species, and pairwise log-rank tests were subsequently performed for relevant predator-prey combinations. To correct for multiple testing in the pairwise comparisons, the p-values were adjusted using Holm's sequential Bonferroni correction. The survival analysis was performed with R, version 3.3.3, using the ‘survival’ package (Therneau, 2015), and the ‘survminer’ package (Kassambara and Kosinski, 2017) for plotting the survival curves.

3. Results

3.1. Survey

Over the two years of survey between December 2014 and December 2016, a total number of 2′073 *Carcinus maenas*, 4′566 *H. takanoi* and 4′193 *Hemigrapsus sanguineus* ≤ 10 mm CW were sampled and measured. From the size-frequency distributions, mean sizes and size ranges for the first five juvenile moult stages of each species were estimated (Table 1), subsequently referred to as C-1 to C-5. All individuals of each species from the 6th moult stage to 10 mm CW were pooled into a single size class (referred to as C-6), as individual numbers and separation indices were too low to define reliable size ranges for further moult stages. Mean CW of C-1 *C. maenas* (1.41 mm) is considerably smaller compared to *H. takanoi* (1.68 mm) and *H. sanguineus* (1.89 mm). The size difference between *C. maenas* and *H. takanoi* decreases with subsequent moults and approximately equals out from C-3 on, but it remains about the same between *C. maenas* and *H. sanguineus*.

The survey data revealed differing patterns of the three species in the occurrence and abundances of recruiting (C-1) and juvenile crabs at the two sampling sites. In general, lower densities of crabs were recorded on the oyster reef (site A) compared to the boulder groynes (site B) which is reflected in the total number of crabs in both habitats (3′632 at site A, 7′200 at site B). The recruitment of *C. maenas* at both sites started mid June and ended early September in 2015 and mid July in 2016, respectively (Figs. 2 and 3). The maximum density of C-1 *C. maenas* was 792 ± 104 individuals m^{-2} (mean ± SE), recorded at site B on 4 July 2016. Outside the well-defined recruitment period, no C-1 *C. maenas* were found in the samples. Density peaks of subsequent size classes of *C. maenas* were delayed by about two weeks compared to the preceding size class, and densities continuously decreased from C-1 to C-5, depicting growth and mortality between the moult stages. C-6 *C. maenas* were recorded year-round in low densities at both sites, with slightly higher densities observed from late summer to early winter.

Considering the spatial distribution patterns, *H. takanoi* dominates at site A (Fig. 2), while *H. sanguineus* dominates at site B, however densities of C-4 and C-5 *H. takanoi* were similar to *H. sanguineus* from autumn to spring (Fig. 3). Recruitment of both *Hemigrapsus* species peaks at the same time in late August/early

Table 1
Mean (estimated by Bhattacharya's method), minimum and maximum carapace width [mm] of juvenile *C. maenas*, *H. takanoi* and *H. sanguineus*. Size classes C-1 to C-5 represent actual moult stages, size class C-6 pools all individuals from the 6th moult stage to 10 mm CW.

Size class	*C. maenas*			*H. takanoi*			*H. sanguineus*		
	mean	min	max	mean	min	max	mean	min	max
C-1	1.41	1.22	1.62	1.68	1.34	1.87	1.89	1.43	2.10
C-2	1.88	1.62	2.13	2.10	1.87	2.34	2.32	2.10	2.54
C-3	2.49	2.13	2.85	2.58	2.34	2.84	2.80	2.54	3.12
C-4	3.11	2.85	3.35	3.10	2.84	3.36	3.40	3.12	3.75
C-5	3.61	3.35	3.91	3.76	3.36	4.30	4.33	3.75	4.76
C-6	–	3.91	10.00	–	4.30	10.00	–	4.76	10.00

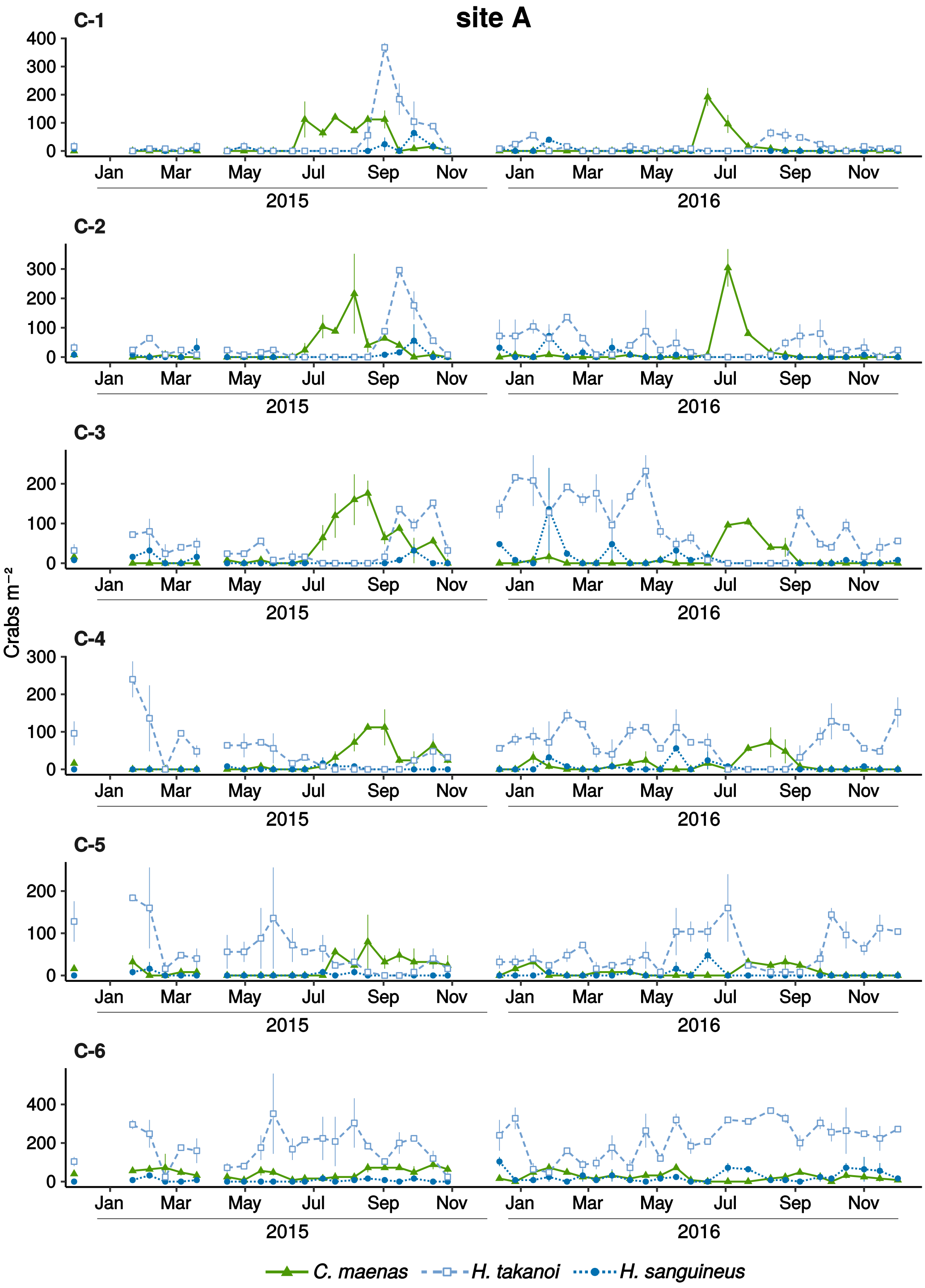

Fig. 2. Mean densities ± SE of juvenile crabs on an intertidal oyster-mussel-bed (site A) between Dec 2014 and Dec 2016, based on bi-weekly samplings. Numbers C1 - C6 refer to size classes (see Table 1 for details). Green, solid: *C. maenas*, light blue, dashed: *H. takanoi*, dark blue, dotted: *H. sanguineus*. Gaps in the data are caused by samplings that had to be cancelled due to high water levels. Note different y-axis ranges. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

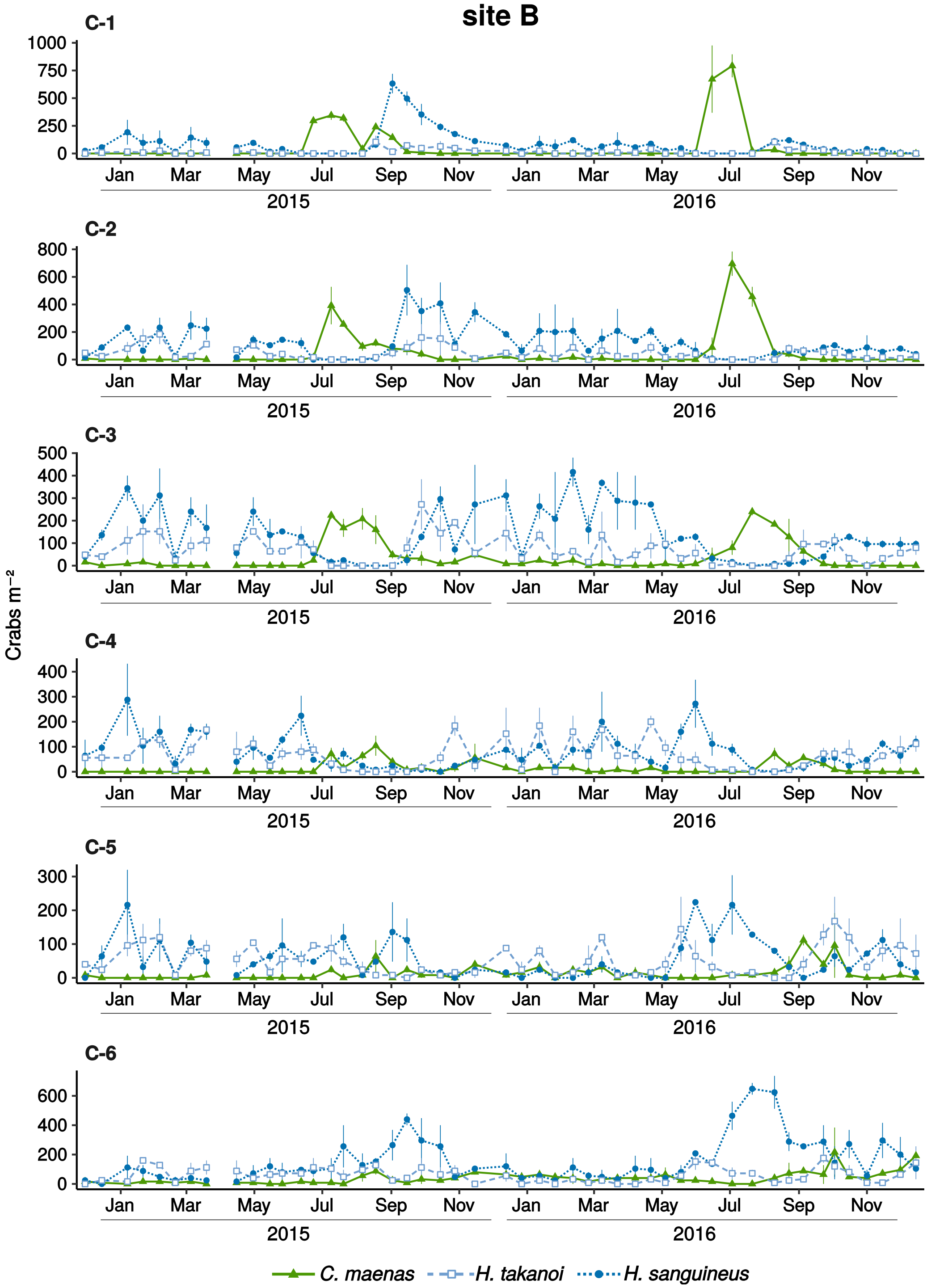

Fig. 3. Mean densities ± SE of juvenile crabs on intertidal boulder groynes (site B) between Dec 2014 and Dec 2016, based on bi-weekly samplings. Numbers C1 - C6 refer to size classes (see Table 1 for details). Green, solid: *C. maenas*, light blue, dashed: *H. takanoi*, dark blue, dotted: *H. sanguineus*. Gaps in the data are caused by samplings that had to be cancelled due to high water levels. Note different y-axis ranges. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

September. Maximum C-1 densities were 368 ± 16 individuals m^{-2} for *H. takanoi* and 632 ± 88 individuals m^{-2} for *H. sanguineus*, recorded on 3 September 2015, at site A and B, respectively. Intensity of recruitment of both *Hemigrapsus* species was much lower in 2016 compared to 2015, thus showing an opposing trend with *C. maenas.* Moulting stage C-1 of *Hemigrapsus* spp. also occurred throughout the winter months, with *H. sanguineus* regularly reaching densities around 100 individuals m^{-2} (Fig. 3). In both years however, the density of C-1 *Hemigrapsus* spp. dropped to zero at the beginning of the *C. maenas* recruitment period. Densities of subsequent size-classes of *Hemigrapsus* spp. increased as well time-delayed compared to the preceding size-class. Constantly high densities of C-2 and C-3 from October to May indicate a low mortality and slow growth of *Hemigrapsus* juveniles over the winter months. Densities of C-4 to C-6 increase towards the spring and summer, reaching a maximum coinciding with the recruitment period of *C. maenas.*

3.2. Recruitment experiment

Recruitment of *H. sanguineus* was as expected very low at the experimental site, because it is not the preferred habitat for this species (one and three crabs were found among all cages in run A and B, respectively). Therefore, only the recruitment of *H. takanoi* and *C. maenas* are compared in the following.

The results of the GLM revealed that recruitment of 0-year crabs differed significantly between the two species ($LRT_{species}$: df = 1, $\chi^2 = 29.68$, $p < 0.0001$). Recruitment of *C. maenas* during run A (July to early August 2016, main settlement period for *C. maenas*) was higher (17.0 ± 1.2 ind. $cage^{-1}$, all values given as mean ± SE) than of *H. takanoi* (8.9 ± 1.2 ind. $cage^{-1}$) during run B (September to mid October 2016, main settlement period for *Hemigrapsus* ssp.), which may reflect the generally low ambient recruitment of *Hemigrapsus* spp. in 2016 (see section ‘3.1. Survey’). Furthermore, the recruitment of 0-year crabs varied for different species-treatment combinations ($LRT_{species*treatment}$: df = 4, $\chi^2 = 22.86$, $p \leq 0.001$). This variation was mainly driven by contrasting recruitment patterns between the two *Hemigrapsus*-inclusion treatments and the three other treatments (Fig. 4). Recruitment of 0-year *C. maenas* was almost equal in the exclusion (18.8 ± 1.9 ind. $cage^{-1}$) and *C. maenas*-inclusion treatments (19.8 ± 3.3 ind./cage) and in the open cages (19.3 ± 2.1 ind. $cage^{-1}$). However, it was reduced in the *H. takanoi*- (15.7 ± 2.8 ind. $cage^{-1}$) and even more the *H. sanguineus*-inclusion treatments (11.1 ± 1.3 ind. $cage^{-1}$) (Fig. 4 A). On the contrary, recruitment of 0-year *H. takanoi* was increased in the two *Hemigrapsus*-inclusion treatments (13.7 ± 2.8 ind. $cage^{-1}$ for *H. takanoi* inclusion and 11.8 ± 3.1 ind. $cage^{-1}$ for *H. sanguineus* inclusion) compared to the exclusion treatment (6.5 ± 1.6 ind. $cage^{-1}$) and open cages (8.2 ± 3.2 ind. $cage^{-1}$), while recruitment to *C. maenas*-inclusion cages was slightly lower compared to the exclusion control group (4.3 ± 1.4 ind. $cage^{-1}$) (Fig. 4 B).

Colonisation of the open cages by crabs >7.5 mm CW differed between species. It was 0.2 ± 0.4 ind. $cage^{-1}$ for *H. sanguineus* and 3.6 ± 2.2 ind. $cage^{-1}$ for *H. takanoi.* Both densities were consistent with their ambient densities at this site (pers. observation). Numbers of *C. maenas* in the open cages were 2.7 ± 2.9 ind. $cage^{-1}$. The cage design effectively prevented the colonisation of crabs >7.5 mm CW to the exclusion and inclusion cages, and no additional crabs could be found at the end of the experiment. Mean survival of predator crabs in the inclusion cages (n = 9 at the beginning of the experiment) was 2.2/4.5 for *C. maenas* (run A and B, respectively), 5.5/7.5 for *H. takanoi* and 8.7/8.3 for *H. sanguineus*.

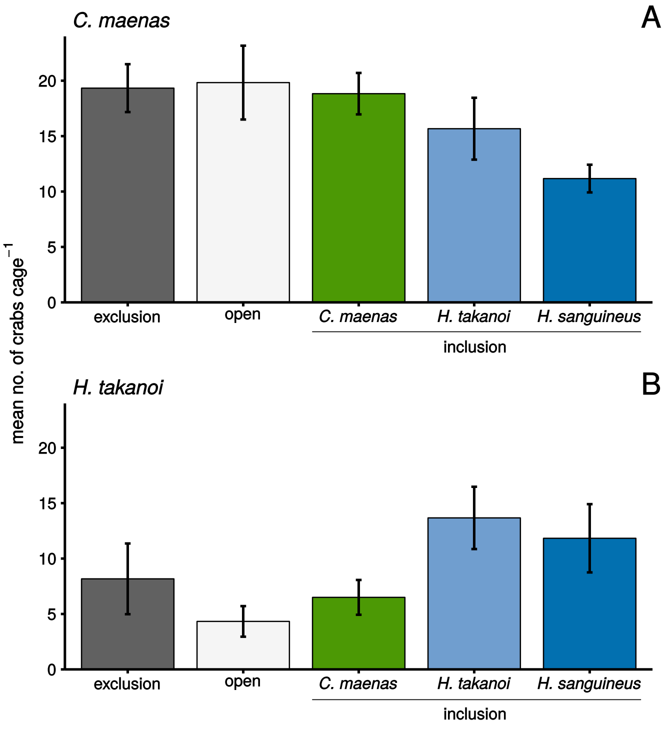

Fig. 4. Response of 0-year *C. maenas* (A) and *H. takanoi* (B) to the presence of adult crabs in the field experiments. Data are mean numbers ±SE of crabs ≤7.5 mm CW $cage^{-1}$ for the different treatments. Number of cages per treatment n = 6. *H. sanguineus* was neglected in the analysis because of extremely low recruitment at the experimental site.

3.3. Predation experiment

The survival probability of newly settled crabs differed significantly between treatments (e.g. predator species) among species (asymptotic log-rank test: df = 3, $\chi^2 = 176.28$, $p < 0.0001$; Fig. 5). Newly settled *C. maenas* had a significantly lower survival probability when confronted to conspecific subadults compared to either *Hemigrapsus* species as predator (Log-rank tests: df = 1, $\chi^2 = 21.5$, adjusted $p \leq 0.0001$ for *H. takanoi* and df = 1, $\chi^2 = 14.7$, adjusted $p = 0.0014$ for *H. sanguineus*; Fig. 5 A). For *Carcinus* recruits, the effects of cannibalism are therefore higher than predation by both *Hemigrapsus* species.

Survival probabilities of newly settled *Hemigrapsus* spp. when confronted with a subadult conspecific were almost equal or only slightly reduced compared to the control treatments without conspecific predator (Fig. 5 B, C). This indicates a strong difference in the tendency to cannibalistic behaviour between *C. maenas* and *Hemigrapsus* spp. The survival probabilities of *Hemigrapsus* recruits were reduced to about 0.3 with *C. maenas* as predator, which was significantly higher than those of *C. maenas* recruits (survival probability < 0.1) with *C. maenas* as predator (Log-rank tests: df = 1,$\chi^2 = 22.5$, adjusted $p \leq 0.0001$ for *H. takanoi* and df = 1, $\chi^2 = 23.5$, adjusted $p \leq 0.0001$ for *H. sanguineus*). The survival probabilities of *Hemigrapsus* recruits were, however, in the range of *C. maenas* survival probabilities with *Hemigrapsus* spp. as predators. Both *Hemigrapsus* species slightly reduced the survival of each other's juveniles, but survival probabilities of these predator-prey-combinations did not differ significantly from the same-species combinations (Fig. 5 B, C). Detailed statistical results for all pairwise comparisons are given in Appendix 2. Mortality of newly

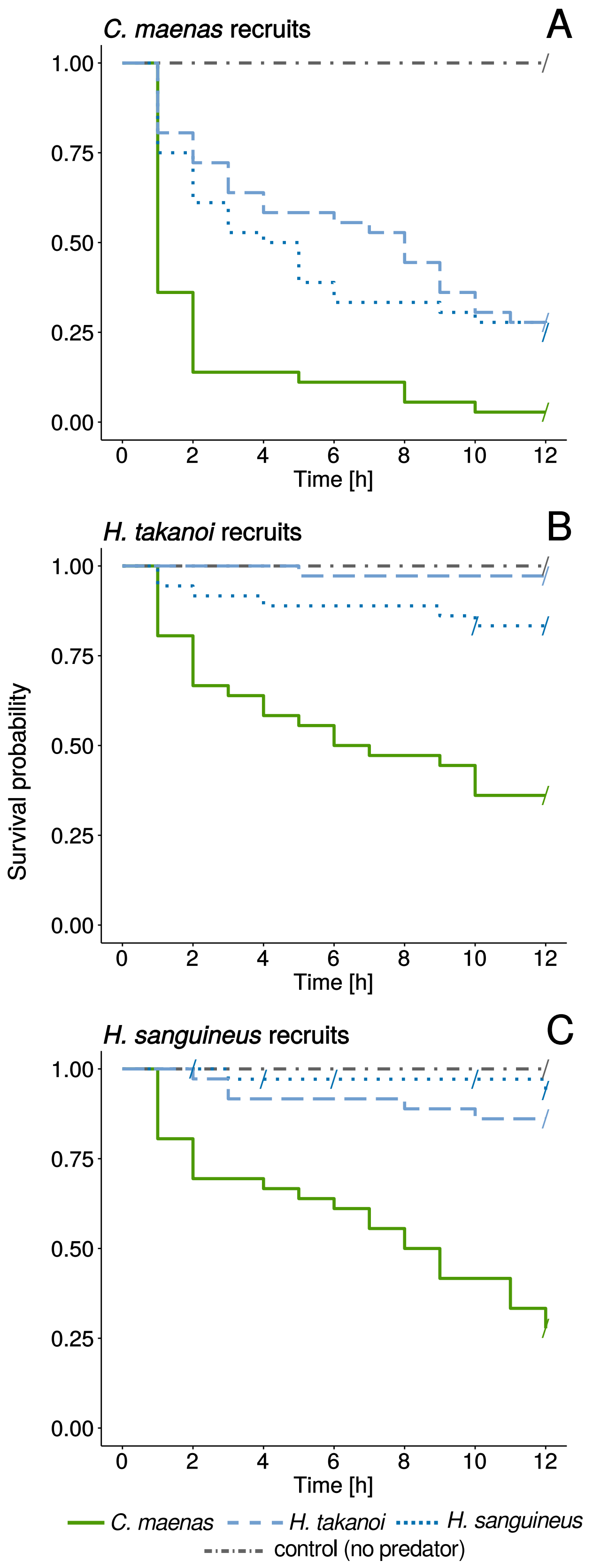

Fig. 5. Survival probabilities of recruits (1.5–1.8 mm CW) of *C. maenas* (A), *H. takanoi* (B) and *H. sanguineus* (C) (6 recruits per replicate [n = 6] per species) over 12 h, when paired with subadult (7.8–9.1 mm CW) *C. maenas* (green, solid lines), *H. takanoi* (light blue, dashed lines), *H. sanguineus* (dark blue, dotted lines) as predators, or no predator (grey, dot-dashed lines). Slashes (/) indicate censored data, i.e. recruits which from died other reasons than predation during the experiment. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

settled crabs in the control treatments was very low during the experiment, as only one *H. takanoi* was found dead at the last control. Thus, any differences in survival of newly settled crabs could be attributed to predation by subadults.

4. Discussion

This study revealed differential seasonal and spatial patterns of recruit and juvenile occurrence between invasive (*Hemigrapsus* spp.) and native (*Carcinus maenas*) crabs in the Wadden Sea. It furthermore revealed differential inter- and intraspecific effects of adult/subadult crabs on the recruitment of juveniles, particularly by differing levels of predation and cannibalism. The combined results describe important factors for the invasion success of *Hemigrapsus* spp.

4.1. Recruitment patterns of native C. maenas and introduced Hemigrapsus spp.

We detected a temporal shift of recruitment peaks between *C. maenas* and *Hemigrapsus* spp. The European shore crab *Carcinus maenas* shows a well defined recruitment period of 3 months at most with peak densities of C-1 individuals in early July, whereas no C-1 individuals were present at other times of the year. This is in accordance with earlier observations and the fact that *C. maenas* females only produce one brood per season in these latitudes (Crothers, 1967; Dawirs, 1985; Naylor, 1962). The recruitment of *H. takanoi* and *H. sanguineus*, by contrast, begins in August and peaks late August to mid September. The onset of juvenile recruitment is in accordance with data for *H. sanguineus* and *H. penicillatus* from their native range (Fukui, 1988; Pillay and Ono, 1978). After the density peak in late summer, *Hemigrapsus* recruitment decreases, but C-1 individuals occur in the intertidal zone in lower densities until January (*H. takanoi*, site A) or even April/May of the following year (*H. sanguineus*, site B). It is, however, unlikely that *Hemigrapsus* actually recruits during the winter months, as ovarian, egg and larval development are strongly temperature-dependent and appear to be extremely prolonged at water temperatures below 15 °C (Epifanio, 2013; van den Brink et al., 2013). The observed pattern might rather result from crabs which recruited in late autumn and overwintered in the intertidal at C-1 stage, with the long intermoult duration being as well a consequence of low temperatures (see Leffler, 1972). The still considerably extended recruitment periods of *Hemigrapsus* spp. could be an advantageous strategy to compensate for short periods of unfavourable conditions in variable environments, or to avoid strong density-dependent intraspecific competition. On the other hand, the short period of massive recruitment in *C. maenas* might reflect a strategy to reduce the risk of predation for recruiting crabs. Interestingly, densities of C-1 *Hemigrapsus* drop to zero almost exactly at the time when *C. maenas* recruitment starts. Predation or expulsion by *C. maenas* is most likely not the cause of this decline, as in this case, at least some C-1 *Hemigrapsus* would be expected to survive/remain at the site. Whether the observed pattern is coincidentally caused by the natural rhythm of *Hemigrapsus* recruitment, or actually a reaction of *Hemigrapsus* to the high recruitment rates of *C. maenas*, needs further investigation. Besides a migration of juvenile *Hemigrapsus* to a different (micro-)habitat, also chemical cues affecting the timing and duration of larval release, larval development and metamorphosis may be responsible for the observed temporal pattern. For example, exudates released by conspecifics and other crab species play an important role in these processes, in particular on the 'time to moult' of the megalopa (Forward et al., 2001; Kopin et al., 2001; O'Connor, 2007).

Overall, the shifted recruitment periods indicate temporal niche segregation between the early juvenile stages of *C. maenas* and *Hemigrapsus* spp., by which direct competition for resources (e.g. food, shelter) is avoided. The differential timing of recruitment – and ultimately reproduction – may thus considerably facilitate the establishment of the non-native species, particularly in the initial phase of introduction, when *Hemigrapsus* abundances were still low. Similarly, differential timing of recruitment of *C. maenas* compared to native crabs is assumed to have facilitated its establishment as non-native species in Australia (Garside et al., 2015). As *C. maenas* has been shown to be inferior to same-sized *H. sanguineus* when competing for food and shelter (Jensen et al., 2002), the different recruitment periods can also be beneficial for the native species, especially when considering the size advantage of C-1 *Hemigrapsus* spp. over *C. maenas*. An earlier recruitment of *Hemigrapsus*, before *C. maenas*, can be assumed in this context to be even more advantageous for *Hemigrapsus*, and to potentially increase competitive pressure on *C. maenas* recruits. However, this could be prevented by too low water temperatures in spring which don't allow for earlier development of *Hemigrapsus* eggs and larvae. The apparent difference in recruitment site preference between *H. takanoi* (mussel-oyster-reef) and *H. sanguineus* (boulder groyne) coincides well their differing habitat preferences, with *H. sanguineus* dominating in rockier habitats with higher wave exposure, while *H. takanoi* dominates in muddier, more sheltered habitats (Dauvin, 2009; Landschoff et al., 2013; Mingkid et al., 2006). The fact that these differences in site preference are already pronounced at the C-1 stage, points to a pre-settlement process as the underlying mechanism. This spatial niche segregation into different microhabitats appears to be very effective as it even occurred within a few meters distance between the windward and lee side of a longshore boulder groyne (Geburzi, 2014). It likely plays an important role for the sympatrical spread of the two *Hemigrapsus* species, as it reduces competition for food and space especially among recruits and early juvenile stages which occur in high abundances at the same time.

Growth patterns and temporal variation of densities of subsequent size classes C-2 to C-6 differ as well between *C. maenas* and *Hemigrapsus* spp. Density peaks of *C. maenas* C-2 to C-5 are delayed by about 2 weeks compared to the preceding class, reflecting regular moult intervals for about the first 2 months after recruitment. The occurrence of early juvenile *C. maenas* at the sampling sites is mostly restricted to 3–4 months following the recruitment peak and characterised by a sharp decline in density between consecutive size classes. Besides the possibility of high mortality due to strong predation pressure (Moksnes et al., 1998), these observations may also reflect size-dependent habitat shifts and migrations, as they were described by Thiel and Dernedde (1994). As they grow bigger, juvenile *C. maenas* emigrate from the mussel beds and clumps to adjacent sand flats and later to subtidal areas. Our survey data indicate emigration of juvenile *C. maenas* in early autumn, which is much earlier than before the arrival of *Hemigrapsus* spp. in the Wadden Sea, when it occurred only in late autumn (Beukema, 1991; Thiel and Dernedde, 1994). This could be a direct effect of the presence of *Hemigrapsus* spp. as a new competitor/predator, mitigating the beneficial effects of staying in the mussel beds (compare Griffen and Riley, 2015).

The data reflect well that *H. takanoi* and *H. sanguineus* are predominantly intertidal species in all stages after metamorphosis (Landschoff et al., 2013; Lohrer et al., 2000; Noël et al., 1997; van den Brink et al., 2012). Early *Hemigrapsus* juveniles (C-2 to C-5) occur year-round in higher densities than *C. maenas*, except for the peak periods of the respective *C. maenas* size class. Slowly decreasing densities of C-2 from September to May while at the same time densities of C-3 and C-4 show an increasing trend, suggest that the youngest *Hemigrapsus* cohorts still moult during the winter months, though with very long moult intervals. With rising water temperatures in spring and summer, moult intervals apparently become shorter and moult synchronises, as rising temperatures accelerate growth, while the overall length of moulting intervals increases from stage to stage (Dawirs, 1985; Klein Breteler, 1975). This leads to pronounced density peaks of late juvenile *Hemigrapsus* (C-5 and C-6) between May and August, coinciding with the recruitment period of *C. maenas*. This pattern may have implications for *C. maenas*, as high densities of a new putative competitor/predator in an important recruitment habitat (Moksnes, 2002; Moksnes et al., 1998) could negatively affect the recruitment success of the native species (see below).

4.2. Intra- and interspecific effects on crab recruitment

The results of the field caging experiment indicate differential intra- and interspecific influences of the presence of larger crabs on the recruitment of juvenile *C. maenas* and *H. takanoi*. No direct conclusions can be drawn about *H. sanguineus*, as they recruit only in very low numbers at the experimental site, but effects are assumed to be similar to *H. takanoi* considering their similar size and behaviour.

Both *Hemigrapsus* species substantially reduced the recruitment of *C. maenas* juveniles compared to the control treatment excluding larger crabs, in case of *H. sanguineus* by almost 50%. However, no effect on native shore crab recruitment was detected in the *C. maenas*-inclusion treatment. A possible explanation for the slightly surprising lack of an effect in this treatment, which strongly contrasts the results of the corresponding treatment in the predation experiment (see below), might be the low survival of *C. maenas* predators in the cages. The low survival could be caused by cannibalism between the predators due to their very high initial density, which in turn reduced density-dependent effects of the larger *C. maenas* on conspecific recruits. The recruitment of *H. takanoi*, by contrast, was strongly enhanced by the presence of larger crabs of both *Hemigrapsus* species, and slightly, though not significantly, reduced by the presence of larger *C. maenas*. These findings are partly congruent with a similar experimental study at the U.S. east coast, also reporting a reduced recruitment of *C. maenas* when *H. sanguineus* was present (Lohrer and Whitlatch, 2002). However, no positive effect of *H. sanguineus* on conspecific recruitment was observed in that study. The reduced *C. maenas* recruitment to *Hemigrapsus*-inclusion cages could be explained by either increased predation by *Hemigrapsus* spp. or an avoidance of *C. maenas* recruits based on chemical cues. The latter possibility is considered less likely as it would presume *C. maenas* to have 'learned' to distinguish and avoid chemical cues released by *Hemigrapsus* spp. within just a few years of coexistence. The enhanced recruitment of *H. takanoi* to *Hemigrapsus*-inclusion cages on the other hand indicates a positive response of *H. takanoi* to conspecific/congeneric cues. Such effects were already described for *H. sanguineus* (Kopin et al., 2001; O'Connor, 2007), as well as several other crab species (reviewed in Forward et al., 2001). In summary, the results show that the presence of (sub)adult *Hemigrapsus* spp. enhances the recruitment of conspecifics/congeners while at the same time it impairs the recruitment of *C. maenas*. Thus, these processes reveal interactions between non-native and native crabs that may substantially contribute to the success of *Hemigrapsus* spp. in the southeastern North Sea.

The results of the predation experiment reveal different levels of predation and cannibalism on newly recruited crabs as an additional factor facilitating the establishment of the newly arrived *Hemigrapsus* spp. Subadults of *C. maenas* showed a generally higher tendency to prey on new recruits compared to subadult *Hemigrapsus*, and their predation pressure was highest on conspecifics

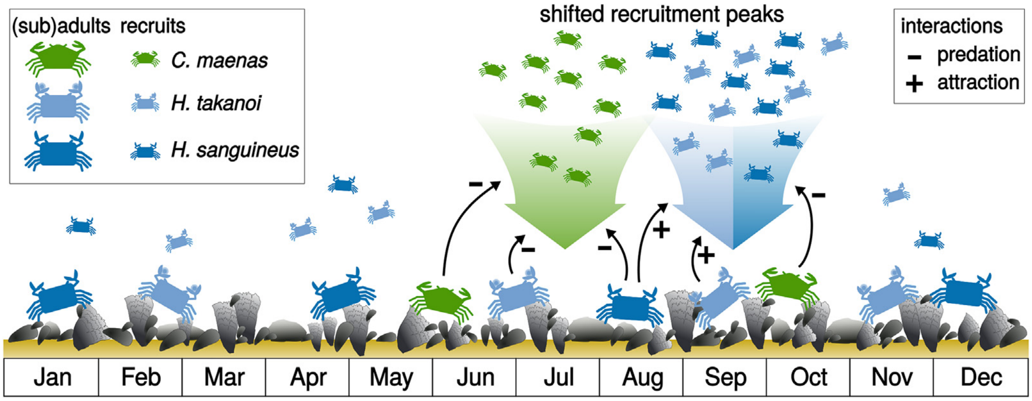

Fig. 6. Schematic illustration of processes and patterns shaping densities and interactions of native and invasive crabs in the Wadden Sea intertidal. Peak periods of juvenile recruitment are temporally shifted between *C. maenas* and *Hemigrapsus* spp. and no *Hemigrapsus* recruitment occurs during *C. maenas* recruitment peaks. From late autumn to early spring, only *Hemigrapsus* spp. are present in the intertidal. *C. maenas* (sub)adults prey on recruiting conspecifics as well as *Hemigrapsus* spp., while *Hemigrapsus* (sub)adults prey only on *C. maenas* recruits, but enhance *Hemigrapsus* recruitment (black arrows).

(i.e. cannibalism). This distinct tendency to cannibalism is well described for *C. maenas* and considered an important factor for recruitment success and regulation of population density in this species (e.g. Almeida et al., 2011; Moksnes, 2004; Moksnes et al., 1998). In contrast, subadult *Hemigrapsus* showed almost no cannibalism and only very low rates of intra-genus predation, while their predation pressure on *C. maneas* recruits was as high as vice versa. Griffen et al. (2015) already reported low rates of cannibalism in *H. sanguineus*, which is also the case for *H. takanoi*, as our results show. The establishment of *Hemigrapsus* spp. in the Wadden Sea intertidal thus added two new species preying on *C. maenas* recruits, while *C. maenas* is the only crustacean predator of *Hemigrapsus* recruits. The asymmetry of the predator-prey relationship between the three species might be even more pronounced in the field, as the density maxima of subadult *Hemigrapsus* on the oyster reef and boulder groynes occur around the peak periods of *C. maenas* recruitment. On the other hand, densities of subadult *C. maenas* only slightly increase during peak recruitment of *Hemigrapsus* spp.

The experimental setup was of course a simplification of the natural conditions, as it did neither include variations in predator and prey densities, nor different levels of habitat complexity, nor alternative food sources, all of which influencing the predation risk for crab recruits (Almeida et al., 2011; Lohrer and Whitlatch, 2002; Moksnes et al., 1998). These factors might also explain why no reduction of *C. maenas* recruitment in *C. maenas* inclusion treatments was observed in the field experiment, probably along with the higher mortality of *C. maenas* predators (see above). Nevertheless, as the conditions were equal for all three species, the experiment provides comparable results for background levels of cannibalism and predation. The lack of juvenile cannibalism in *Hemigrapsus* spp. probably is of great importance for their invasion success, as it allows them to tolerate high densities of several cohorts in the same habitat. This result also complements the recently described high conspecific tolerance among similar-sized adult *H. sanguineus* in suitable habitats (Hobbs et al., 2017).

4.3. Conclusions

The data presented in this study show that timing of recruitment as well as direct (predation/cannibalism) and possibly also indirect (chemical cues) interactions of recruiting crabs contribute to the high invasion success of *H. takanoi* and *H. sanguineus* in the Wadden Sea. The presence of *Hemigrapsus* at a site enhances the recruitment of juveniles, leading to a positive feedback on crab densities in suitable habitats once they are occupied (Fig. 6). Low rates of cannibalism positively affect the maintenance of high population densities (but see Griffen et al., 2015 for effects of cannibalism in a dense *H. sanguineus* population). Among recruiting crabs, temporal niche segregation (between *C. maenas* and *Hemigrapsus* spp., Fig. 6) and spatial niche segregation (between *H. takanoi* and *H. sanguineus*) may strongly reduce competition for resources. Increased predation pressure by subadult *Hemigrapsus* on recruiting *C. maenas* may further reduce competition for subsequently recruiting *Hemigrapsus* spp.

In the long run, it seems possible that *Hemigrapsus* spp. could take over the role as the dominant crab species in intertidal hard-bottom habitats in the Wadden Sea (Lohrer and Whitlatch, 2002; van den Brink et al., 2012). However, the spread of *Hemigrapsus* will most likely not threaten the *C. maenas* population on a Wadden Sea-wide scale, as large parts of its adult population live subtidally and will provide a stable source of recruitment to the intertidal, where recruits and juveniles also use other habitats such as seagrass beds as nursery ground (Landschoff et al., 2013; Moksnes et al., 1998), a habitat in which *Hemigrapsus* currently does not occur. Finally, the results of this study highlight the need to consider life-history traits in combination with interactions among juvenile stages in order to gain insight in the establishment and spread as well as potential impacts of marine non-native species.

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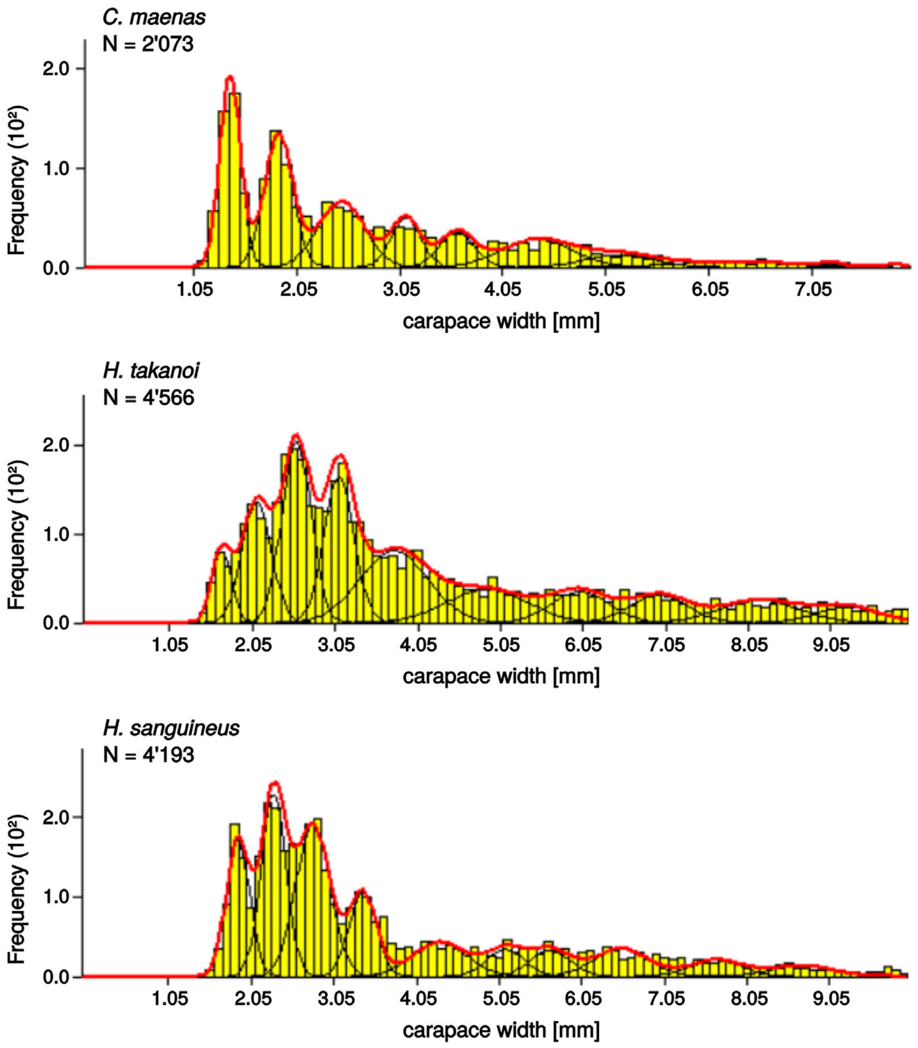
Appendix



Appendix 1. Decomposition of the size-frequency distributions of *C. maenas* (top), *H. takanoi* (middle) and *H. sanguineus* (bottom) by the Bhattacharya method for the 2014–2016 survey data.

Appendix 2
Detailed results of all pairwise Log-rank tests from the predation experiment. Provided are test statistics (χ^2), 'raw' p-values and adjusted p-values (Holm's sequential Bonferroni method) for combinations of recruit species and treatment (i.e. predator species) pairs as given in the first 4 columns of the table. For all tests df = 1. Treatment codes: C – subadult *C. maenas*, S – subadult *H. sanguineus*, T – subadult *H. takanoi*.

Tested combination				χ^2	Raw p-value	Adj. p-value
Recruits	Treatment	Recruits	Treatment			
C. maenas	– C	*C. maenas*	– S	14.7	0.00012	0.0014***
			– T	21.5	<0.0001	<0.0001***
		H. sanguineus	– C	23.5	<0.0001	<0.0001***
			– S	74.6	<0.0001	<0.0001***
		H. takanoi	– C	22.5	<0.0001	<0.0001***
			– T	75.9	<0.0001	<0.0001***
C. maenas	– S	*C. maenas*	– T	0.5	0.48	1
		H. sanguineus	– C	0.8	0.36	1
			– S	37.9	<0.0001	<0.0001***
		H. takanoi	– S	25.8	<0.0001	<0.0001***
C. maenas	– T	*H. sanguineus*	– T	22.4	<0.0001	<0.0001***

Appendix 2 (*continued*)

Tested combination				χ^2	Raw p-value	Adj. p-value
Recruits	Treatment	Recruits	Treatment			
		H. takanoi	− C	0.2	0.63	1
			− T	32.3	<0.0001	<0.0001***
H. sanguineus	− C	*H. sanguineus*	− S	33.5	<0.0001	<0.0001***
			− T	25.2	<0.0001	<0.0001***
		H. takanoi	− C	0.1	0.77	1
H. sanguineus	− S	*H. sanguineus*	− T	1.3	0.26	1
		H. takanoi	− S	2.1	0.14	1
			− T	0.4	0.52	1
H. sanguineus	− T	*H. takanoi*	− S	0.1	0.72	1
			− T	2.9	0.09	0.81
H. takanoi	− C	*H. takanoi*	− S	16.9	<0.0001	0.0005***
			− T	31.1	<0.0001	<0.0001***
H. takanoi	− S	*H. takanoi*	− T	3.9	0.05	0.47

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