

Research Article

Population development of the invasive crab *Hemigrapsus sanguineus* (De Haan, 1853) and its potential native competitor *Carcinus maenas* (Linnaeus, 1758) at Helgoland (North Sea) between 2009 and 2014

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Abstract

The Asian shore crab *Hemigrapsus sanguineus* (De Haan, 1853) has recently established populations in the North Sea and now occurs within the native ranges of the green crab *Carcinus maenas* (Linnaeus, 1758). To determine potential competitive effects and to assess the progress of the invasion, species-specific population characteristics (numerical abundances, biomasses, and size distributions) of the two species around the island of Helgoland (German Bight, southern North Sea) were compared for surveys conducted in 2009 and 2014. Sampling sites were chosen based on accessibility and differed in their topography and wave exposure, which allowed testing for the influence of these factors on the establishment success of *H. sanguineus*. The numerical abundance and biomass of *H. sanguineus* increased markedly and approached those of *C. maenas* in 2014. At a sheltered site, *H. sanguineus* even outnumbered *C. maenas*, whereas the converse was observed at a site exposed to strong winds and waves. Although such contrasting abundance patterns between the native and the introduced shore crab may be the result of direct interference, the dominance of *H. sanguineus* at the sheltered site may also be explained by enhanced larval settling rates caused by odors of conspecifics. The results suggest that the invasion of *H. sanguineus* has not yet reached its equilibrium, and population abundances in the North Sea are expected to further increase in the future.

Key words: biological invasion, alien species, Asian shore crab, European green crab, wind and wave exposure, rocky shore, intertidal ecology, German Bight

Introduction

Non-indigenous species can affect ecosystem structure and functioning in many ways and sometimes drastically. Drastic alterations may ultimately affect human economic interest, ecosystem services, and even human health (Ruiz et al. 2000; Simberloff et al. 2013). Biological invasions are therefore regarded as one of the major threats to biodiversity in the marine realm (Grosholz 2002). Non-native species may compete with native residents for food or space (or both) and often largely displace resident species

by spreading into all available habitats at high population densities (Bax et al. 2003). While biotic interactions are crucial in determining invasion success, environmental characteristics such as temperature regime and wave exposure have repeatedly been shown to limit the spread of non-native species in their new habitats (Pörtner 2002; Hampton and Griffiths 2007; Russel et al. 2008).

On a global scale, brachyuran crabs frequently invade estuarine and marine coastal ecosystems (Brockerhoff and McLay 2011). The European green crab *Carcinus maenas* (Linnaeus, 1758), for example, successfully invaded the Atlantic coast of North

America by 1817. Thereafter, it appeared at many other locations around the world including the Pacific coast of North America and the shores of South Africa and Australia (Carlton and Cohen 2003).

The invasion of the Asian shore crab *Hemigrapsus sanguineus* (De Haan, 1835) along the Atlantic shore of North America in the early 1990s is well documented (McDermott 1998; Ledesma and O'Connor 2001; Lohrer and Whitlatch 2002). After the first specimens were detected in 1988 at Townsend's Inlet, north of the mouth of the Delaware Bay, *H. sanguineus* rapidly spread along the North American east coast. Its present distribution in the USA ranges from Cape Hatteras in North Carolina to the Schoodic Peninsula in Maine (Williams and McDermott 1990; Delaney et al. 2008; Epifanio 2013). In Europe, *H. sanguineus* was first detected in August 1999 in the harbor of Le Havre, France, and shortly afterwards in the Oosterschelde, The Netherlands (Breton et al. 2002). Today, it is distributed from the Contentin Peninsula in France to the German Wadden Sea (Obert et al. 2007; Gothland et al. 2013; Landschoff et al. 2013). Recently, it was reported from the English and western Swedish coasts (Seeley et al. 2015; M. Berggren, Sven Lovén Centre for Marine Sciences – Kristineberg, Fiskebäckskil, Sweden, pers. comm.).

The island of Helgoland is located in the German Bight and represents the only natural hard-bottom habitat in the south-eastern North Sea. The small (1 km²) and relatively remote island is surrounded by an intertidal area of about 0.7 km². As a result, Helgoland provides a unique location to study the dispersal of an invading species and potential competitive processes between an invader and a native ecological equivalent. The intertidal areas around Helgoland are characterized by high biological diversity and the European green crab dominates the crustacean fauna (Reichert and Buchholz 2006). In October 2007, a single male *H. sanguineus* was found on Helgoland (H. Auel, Bremen Marine Ecology, University of Bremen, Bremen, Germany, pers. comm.). In July 2008, *H. sanguineus* was found in low numbers at one site (Scrosati et al. 2011; M. Molis, Alfred Wegener Institute, Bremerhaven, Germany, pers. comm.) and quickly spread over the entire rocky intertidal zone around the island. Currently, *H. sanguineus* is the only non-indigenous brachyuran species with the potential to compete with the native shore crab, *C. maenas*, in the intertidal areas around Helgoland. The Asian shore crab, *Hemigrapsus takanoi* Asakura and Wanatabe, 2005 can also be observed in Helgoland's intertidal area, but has not yet succeeded in establishing a sustainable population (J. Beermann and S. Jungblut, pers. obs.).

On the Atlantic coast of North America, where both species are non-indigenous, several studies have indicated strong competitive interactions between them (e.g. Jensen et al. 2002; Lohrer and Whitlatch 2002; O'Connor 2014). North American *H. sanguineus* were dominant over *C. maenas* in direct competition for food (Jensen et al. 2002). On Helgoland, however, *H. sanguineus* faces an abundant population of *C. maenas* in its native habitat. Being the native species, this may give *C. maenas* a competitive advantage due to enhanced adaptations to local conditions (Dauvin 2009). In the German Wadden Sea the impact of the *Hemigrapsus* species on *C. maenas* seems to be negligible or, if present, seems to be confined to juvenile *C. maenas* (Landschoff et al. 2013). However, populations of *H. sanguineus* may continue to grow, as observed for the Atlantic coast of North America (Kraemer et al. 2007; O'Connor 2014), where green crab populations were negatively affected.

The present study tested for changes in the population abundances and sizes of the alien *H. sanguineus* and the native *C. maenas* between the early phase of its invasion in August 2009 and five years later in August 2014. The unique topography of Helgoland also allowed for the evaluation of the possible influence of key environmental parameters (e.g., exposure to wind and waves) on the abundance and population structure of the two species.

Material and methods

Sampling sites

Four intertidal sampling sites were selected around the island of Helgoland: a northwestern site ("Felswatt"), a northeastern site ("Nordstrand"), a southwestern site ("Kringel"), and a southeastern site ("Augusta Mole") (Figure 1A, Supplementary material Table S1). The northwestern site consisted of a flat rock plateau with few loose stones that were largely covered by the macroalgae *Fucus serratus* Linnaeus, 1753; *Fucus vesiculosus* Linnaeus, 1753 and *Sargassum muticum* Fensholt, 1955. The other three sites were comprised of many small rocks to large immovable boulders lying on top of patches of coarse sand. These hard structures were patchily covered with small- to medium-sized macroalgae such as: *Ulva* spp. Linnaeus, 1753; *Enteromorpha* spp. Link, 1820; *Chondrus crispus* Stackhouse, 1797; and *Mastocarpus stellatus* Guiry, 1984 (Bartsch and Tittley 2004). The northeastern and southwestern sites exhibited a similar slope between the high and low water line. The southeastern site was characterized by a relatively steep slope. For the present study, we quantified the site parameter "wave exposure" on the

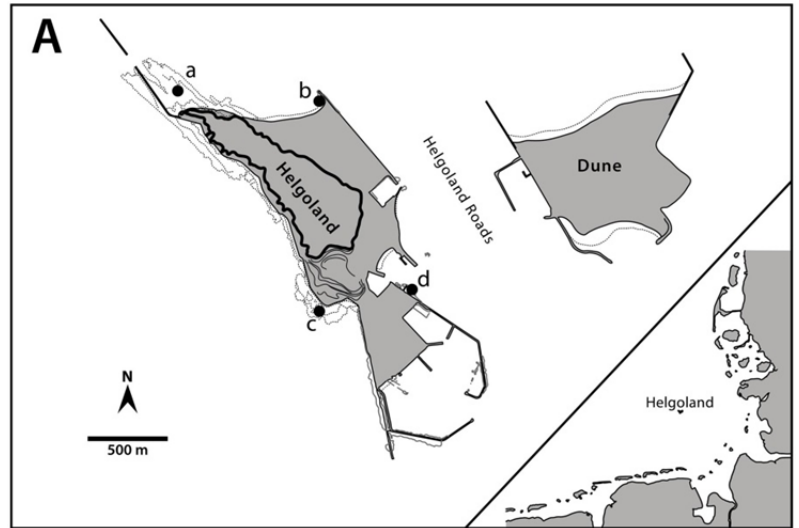
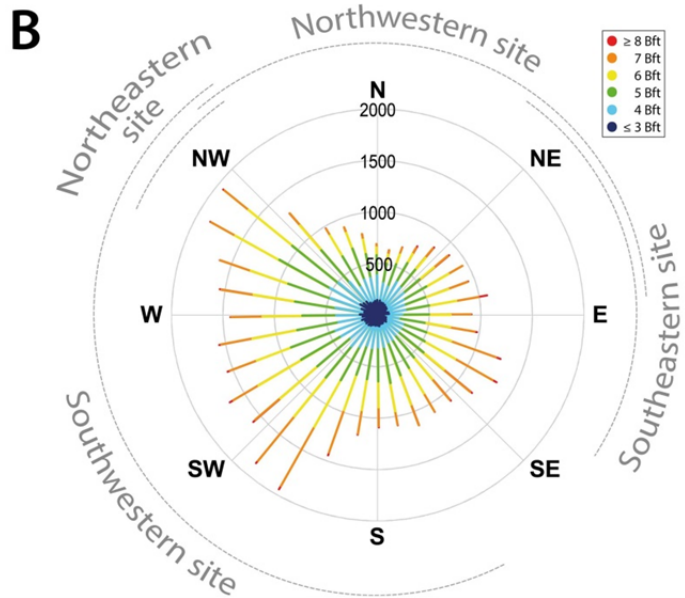


Figure 1. A) The main island of Helgoland with its neighbouring island Dune and their location in the German Bight (southeastern North Sea). Sampling sites are indicated by black circles: a) Northwestern site, b) Northeastern site, c) Southwestern site, d) Southeastern site. Finer lines indicate the intertidal areas. B) Wind exposure of sampling sites around the island of Helgoland. The upright central scale shows the cumulative number of hours with certain mean wind forces per 10° wind direction interval (specified in Beaufort (Bft) and different colours). Outer dashed lines indicate the assigned wind directions of the sampled locations according to their openness to the sea. Classified ranges therefore represent the sites' exposure to multi-directed exposure to wind and waves.



basis of openness and shape of the respective site to the sea in combination with local wind data from 2009 to 2014 (Burrows et al. 2008 and references therein; wind data derived from the webpage of the German Weather Service DWD, <http://www.dwd.de>).

Sampling procedure

Each of the four sites was sampled at low tide around noon on four consecutive days in August 2009 and in August 2014. Samples were taken along defined transects from the low- to the high-water line at three shore levels: close to the high-tide line (high-level), in the middle of the *Fucus* zone (mid-

level), and close to the low-tide line in the lower *Fucus* zone (low-level) (Reichert and Buchholz 2006). In each zone, four quadrats of 0.25 m² were randomly deployed (3 × 4 = 12 samples per site in total) and all decapod crabs with carapace widths ≥ 5 mm were collected. If necessary, the algal cover was removed, all stones in the quadrat were lifted, and any crabs captured. Within each zone, the replicated quadrats were placed 2 m to 5 m apart. As the intertidal area of Helgoland is dominated by large immovable boulders, the chosen quadrat size allowed for sampling in the narrow areas between the boulders. Additionally, a small quadrat ensured that all crabs could be caught by a single person.

In the laboratory, all collected crabs were counted, sex determined, females were checked for eggs, and carapace widths (CW) were measured (using Vernier calipers). Only very few individuals of *H. takanoi*, the edible crab *Cancer pagurus* Linnaeus, 1758 and the bristly crab *Pilumnus hirtellus* (Linnaeus, 1761) were detected. These species were not considered in any further analyses, because they were of minor importance for the focus of the present study.

Statistical analyses

Abundance and biomass

To calculate biomass (fresh mass) for *C. maenas* and *H. sanguineus*, we established carapace width to biomass regression relationships using animals collected in October 2014. Carapace width was measured to the nearest 0.5 mm. Individuals were then blotted for approximately 10 s with tissue paper and weighed (nearest mg) on an electronic scale ($n = 86$ for *C. maenas* and $n = 102$ for *H. sanguineus*). The best-fitting statistical relationships were the polynomial functions:

$$y = -0.01172x + 0.002300x^2 + 0.0001759x^3$$

($R^2 = 0.995$) for *C. maenas*;

$$y = -0.07253x + 0.009637x^2 + 0.0001775x^3$$

($R^2 = 0.981$) for *H. sanguineus*.

Where y is wet mass in mg and x is carapace width in mm. From these relationships, crab biomass per species and site was calculated.

To test for the effects of “species”, “year”, “site” and “shore level” on numerical abundance and biomass of the crabs, linear models were applied. Two sequential model approaches were conducted to avoid over-parameterization in a single model containing all the factors listed above. In the first approach (for abundance and biomass separately), a model was run that included the fully crossed (fixed) effects factors: “species” (*H. sanguineus* and *C. maenas*), “year” (2009 and 2014) and “site” (northwestern, northeastern, southwestern and southeastern). In the second set of models, we selected only those sites, for which the previous analyses revealed significant results. The new analyses were then run separately for these locations and included the factor “shore level” (low, mid and high) instead of “site”.

The abundance data were tested using a generalized linear model (GLM) with Poisson distributed error term and log-link function. A quasi-Poisson correction was applied to account for unexplained variance in the model (i.e. over dispersion in the data). Biomass data were analyzed by applying

linear models (LM) with a Gaussian error term. Prior to the latter analyses, the data were log-transformed to meet the assumptions of normal distribution and homogeneous variances of the residuals.

All models were fitted in R, version 3.2.0 (R Development Core Team 2015), using the generic functions “lm” and “glm”. Graphs were produced with the software GraphPad Prism (version 5.03). For all models, the following diagnostics of model stability were examined: Cook’s distance, leverage (Quinn and Keough 2002), and dfbetas (Cohen and Cohen 2008). For the latter, data points were excluded one by one from the data sets and the derived estimates were compared with those obtained from the models based on all data points. Overall, the checks (Cook’s distance and leverage) confirmed that no influential cases were present. When checking the dfbetas, however, some influential deviations in each of the models were detected. This instability was due to the low numbers of replicates and was therefore assumed to be negligible. Nonetheless, interpretation and discussion of the results were performed with caution.

For the first-approach models, the significances of the interaction terms and main factors were established with likelihood ratio tests (LRT) using the R function “anova” with the argument “test” set to “Chisq” (for abundance data) and “F” (for biomass data), respectively. We compared the deviances of the respective full models with those of the corresponding reduced models not comprising the respective factor and/or term of interest. Pairwise post-hoc comparisons were run to test for individual differences between factor levels. We accounted for multiple testing with a Bonferroni correction of the alpha level. In fact, for the abundance and biomass analyses, we corrected for 15 analyses that were re-run with relevelled intercepts for pairwise comparisons in the outputs. This resulted in a reduced alpha level of $\alpha = 0.0033$. For all second-approach models, we established the significances of the full models by testing them against the respective null models (with LRTs). Because of low numbers of replicates in these analyses ($n = 4$), we refrained from going into further statistical analyses and chose to interpret the results on a descriptive basis, depending on the significance of the full models.

Size distribution

To test for possible differences between the distributions of size classes of the two crab species at the respective sites between 2009 and 2014, individual Pearson’s Chi-squared tests were conducted. Where counts of crabs for a certain size class were

Table 1. Numbers of *Hemigrapsus sanguineus* females, numbers of ovigerous (ovig.) females, and percentage of ovigerous females per site around the island of Helgoland, German Bight (southern North Sea) in 2009 and 2014.

Site	2009			2014		
	total	ovig.	ovig. (%)	total	ovig.	ovig. (%)
Northwest	0	0	0	4	1	25.0
Northeast	12	0	0	59	26	44.1
Southwest	14	2	14.3	27	10	37.0
Southeast	3	1	33.3	15	4	26.6

≤ 5 , the p-values were estimated based on 50,000 replicated simulations. Size classes were defined in 5 mm intervals, ranging from 5–9.5 mm CW as the smallest size class and > 35 mm CW as the largest size class. To identify the size classes responsible for a significant difference between the two distributions, confidence intervals (CI) for each size class per year were calculated (Crow and Gardner 1959). Where confidence intervals for a specific size class did not overlap, the difference between the respective years was considered significant. All χ^2 tests were calculated using R, version 3.2.0 (R Development Core Team 2015). Images were produced with the Software Graph Pad Prism (version 5.03).

Results

Exposure

Wind exposure data for each of the sites (Figure 1B) indicated that the southwestern site experienced remarkably higher wind exposure, resulting in higher wave action and turbulence.

Abundance

Female *H. sanguineus*, including those carrying eggs, were present in both years (Table 1). The percentage of ovigerous females was higher at three of the four sites in 2014 compared to 2009.

The results of the “first approach model” revealed that the numerical abundances of *C. maenas* and *H. sanguineus* varied between the two years for sampling sites around the island of Helgoland (LRT_{species*year*location}: df = 3, $\chi^2 = 35.475$, $p = 0.018$). In the northwestern intertidal (Figure 2A), the abundances of both crab species did not differ significantly between the two years. In both years, however, *C. maenas* was more abundant than *H. sanguineus* (9.6 and 6.5 ind./0.25 m² for *C. maenas* and 0.1 and 0.8 ind./0.25 m² for *H. sanguineus* in 2009 and 2014, respectively). At the northeastern site (Figure 2B), a decrease in abundance of *C. maenas* from 2009 (6.9 ind./0.25 m²) to 2014

(3.6 ind./0.25 m²) was observed, but this was not statistically significant, whereas a pronounced increase in abundance from 3.8 to 10.1 ind./0.25 m² was found for *H. sanguineus*. Accordingly, in 2009 the abundances of *C. maenas* were slightly higher than those of *H. sanguineus*. However in 2014 the inverse was observed with abundances of *H. sanguineus* being significantly higher than those of *C. maenas* (10.1 vs. 3.6 ind./0.25 m²). The abundance of *C. maenas* at the southwestern site (Figure 2C) nearly doubled from 7.9 ind./0.25 m² in 2009 to 14.8 ind./0.25 m² in 2014. No clear difference was detected for *H. sanguineus* (3.4 and 4.8 ind./0.25 m² in 2009 and 2014, respectively). Abundances of *C. maenas* were generally higher than those of *H. sanguineus* in both years. This pattern was even more pronounced in 2014 than in 2009. At the southeastern site (Figure 2D) no significant differences between the abundances of *C. maenas* or *H. sanguineus* were detected between species and years. These abundances ranged between 1.9 and 4.3 ind./0.25 m².

Biomass

Similar to the abundance data, the analyses revealed a significant three-way interaction in the “first approach model” for the biomass data (LRT: $F_{176,3} = 6.479$, $p < 0.001$), indicating that the biomass data of the two species differed between sites and years. At the northwestern site, no significant differences were detected between the years (Figure 2E). Changes in biomass were most pronounced for the northeastern site (Figure 2F), where *C. maenas* clearly decreased in biomass (from 13.6 in 2009 to 5.8 g/0.25 m² in 2014). The biomass of *H. sanguineus* significantly increased (from 0.9 to 22.2 g/0.25 m²). This increase of *H. sanguineus* was also evident at the southwestern site, although it was not significant (2.9 to 9.0 g/0.25 m²; Figure 2G), and no between-year difference was detected for *C. maenas*. At the southeastern site (Figure 2H), *H. sanguineus* showed a significant increase in biomass from 1.0 g/0.25 m² in 2009 to 6.0 g/0.25 m² in 2014, while *C. maenas* biomass did not differ between years.

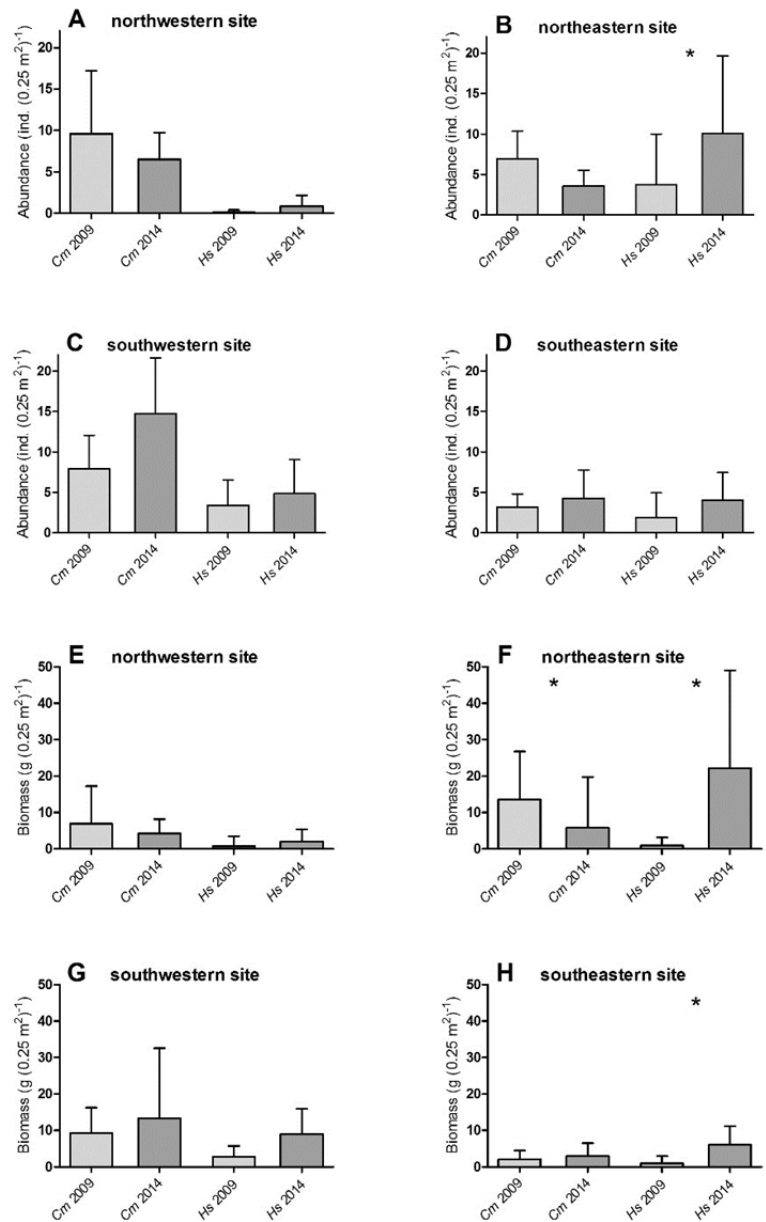


Figure 2. Abundances (A to D) and biomasses (E to H) of *Carcinus maenas* (Cm) and *Hemigrapsus sanguineus* (Hs) in 2009 (light grey bars) and 2014 (dark grey bars) at the sampling sites around the island of Helgoland, German Bight (southern North Sea) (means + SD are presented; Supplementary material Table S2). Asterisks indicate significant inter-annual differences per species.

Size distributions

The size distribution of *Carcinus maenas* differed significantly between years at three of four sites (Figure 3A to D). At the northeastern site, individuals of the size classes “10 to 14.5 mm CW” and “15 to 19.5 mm CW” were most numerous in 2009 (Figure 3B), while in 2014 most individuals belonged to the smallest size class “5 to 9.5 mm CW”. At the two southern sites, no size class was dominant in 2009, but in 2014 most of the indi-

viduals belonged to the size class of “5 to 9.5 mm CW” (Figure 3C and D).

Similar to *C. maenas*, the size distribution of *H. sanguineus* differed significantly between the two years (Figure 3E to H). At the northeastern site significantly more individuals occurred in the size classes between 10 and 24.5 mm CW in 2014 than in 2009. Similar patterns were observed at the southwestern site for the size class “15 to 19.5 mm CW” and at the southeastern site for the size classes between 10 and 19.5 mm CW (Figure 3F, G and H).

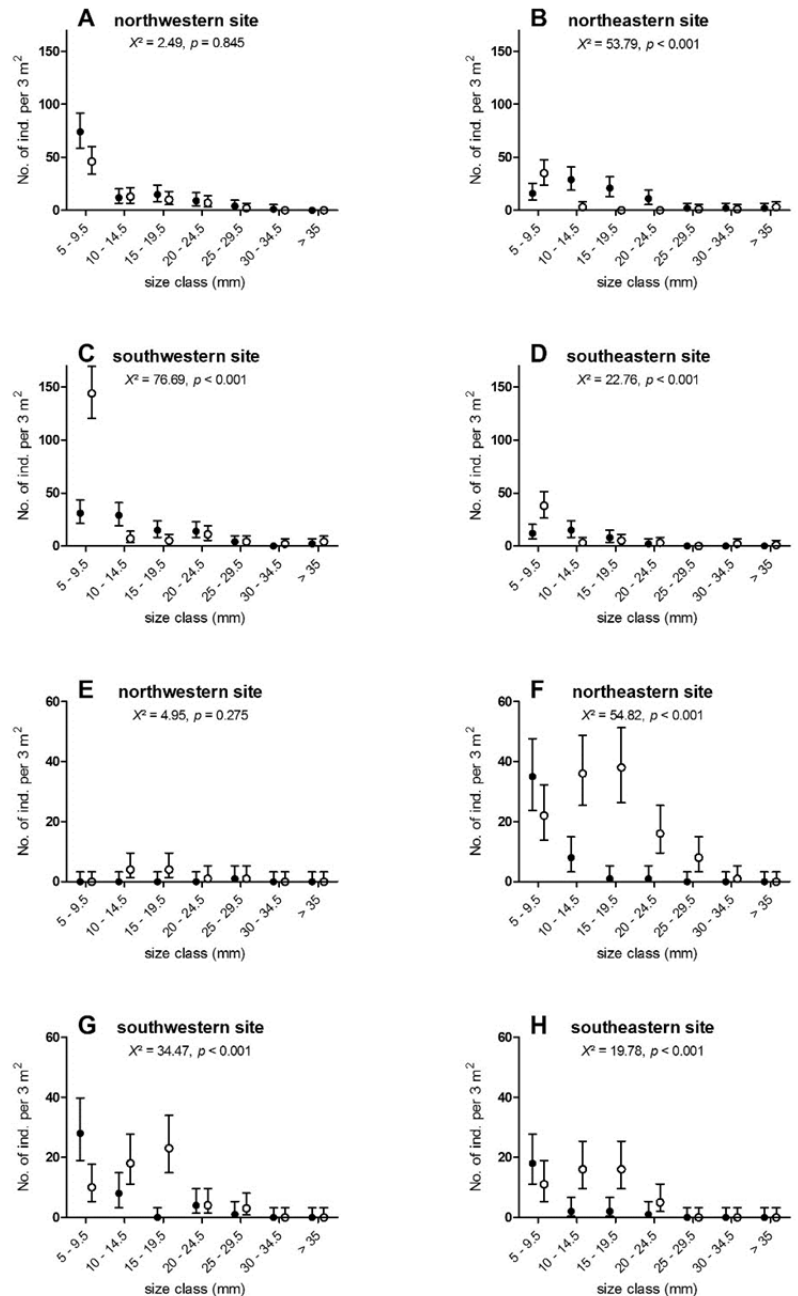


Figure 3. Size frequency distributions of *Carcinus maenas* (A to D) and *H. sanguineus* (E to H) at the different sampling sites around the island of Helgoland, German Bight (southern North Sea) in 2009 (filled circles) and 2014 (open circles) (total number \pm confidence intervals; Supplementary material Table S2). At each site, all 12 samples were pooled, adding up to total of 3 m². Inter-annual comparisons for each size class were significant, when confidence intervals did not overlap.

Abundance and biomass at different shore levels

The southwestern and the northeastern sites exhibited significant differences in the “first approach models” for crab abundances and biomasses. When evaluating the shore level effects (“second approach models”), the abundance of *C. maenas* increased in all three shore levels from 2009 (range of 5.5 to 12.5 ind./0.25 m²) to 2014 (range of 10.5 to 21.0 ind./0.25 m²)

at the southwestern site (LRT_{full model}: df = 11, χ^2 = 181.71, p < 0.001, Figure 4A). In contrast, *H. sanguineus* showed minor increases in abundance at all shore levels, being less abundant than *C. maenas* in all zones and in both years (Figure 4A). At the northeastern site (LRT_{full model}: df = 11, χ^2 = 178.36, p < 0.001, Figure 4B), *H. sanguineus* clearly increased in abundance at the high shore level from 0.8 ind./0.25 m² in 2009 to 3.5 ind./0.25 m² in 2014. At

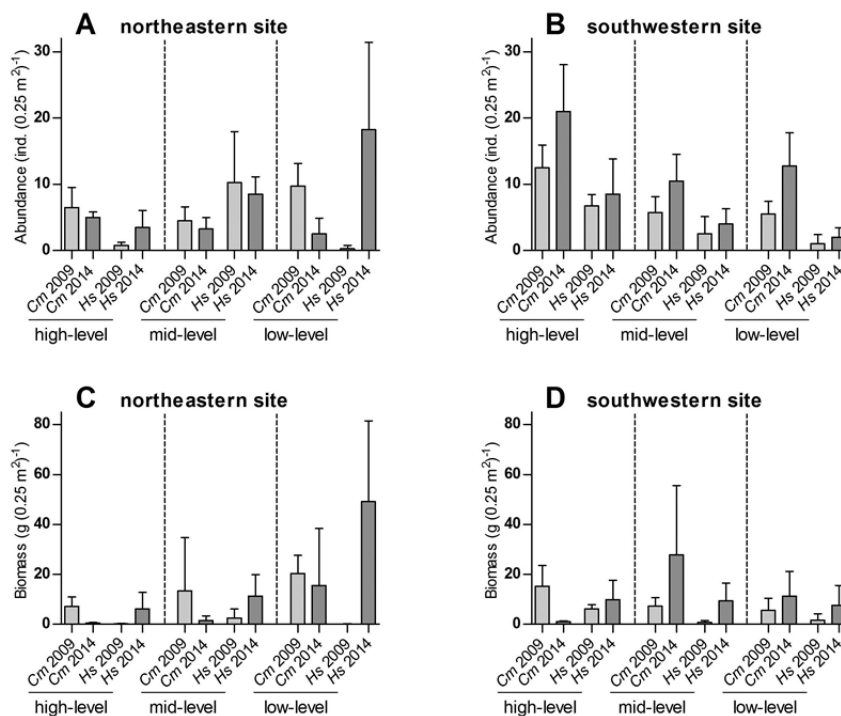


Figure 4. Abundances (A and B) and biomasses (C and D) of *Carcinus maenas* (Cm) and *Hemigrapsus sanguineus* (Hs) in 2009 (light grey bars) and 2014 (dark grey bars) at different intertidal shore levels at selected sites (see text) around the island of Helgoland, German Bight (southern North Sea) (means + SD are presented; Supplementary material Table S2).

the mid-level, no changes in abundance were observed. In both years, *H. sanguineus* was significantly more abundant than *C. maenas* (4.5 and 3.3 ind./0.25 m² for *C. maenas* and 10.3 and 8.5 ind./0.25 m² for *H. sanguineus*). The lower shore level was subject to the largest changes in abundance. From 2009 to 2014, numbers of *C. maenas* decreased significantly from 9.8 to 2.5 ind./0.25 m², whereas those of *H. sanguineus* markedly increased from 0.3 to 18.3 ind./0.25 m².

Similar to the numerical abundance data, the “second approach models” revealed significant three-way interactions for biomasses at the southwestern and the northeastern sites (LRT: $F_{36,11} = 4.392$, $p < 0.001$ and LRT: $F_{36,11} = 6.699$, $p < 0.001$, respectively). At the southwestern site, the biomass of *C. maenas* strongly decreased at the high shore level from 15.1 in 2009 to 1.0 g/0.25 m² in 2014 (Figure 4C). In contrast, the biomass of *C. maenas* increased up to threefold at the other levels. The biomass of *H. sanguineus* increased at all three shore levels from 2009 to 2014. Increases between years were most pronounced at the mid and low-levels with increases from 0.7 to 9.4 and from 1.5 to 7.6 ind./0.25 m², respectively. At the northeastern site, biomasses of *C. maenas* decreased between years at the high- and the mid-shore levels from 7.2 to 0.5 g/0.25 m² and from 13.4 to 1.4 g/0.25 m², respectively. The biomass of *H. sanguineus* increased from 0.2 to 6.2

and from 2.5 to 11.2 g/0.25 m², respectively (Figure 4D). At the lower shore level *C. maenas* biomass did not differ substantially between the years (20.3 and 15.6 g/0.25m²), whereas *H. sanguineus* showed a dramatic increase from 0.1 to 49.1 g/0.25 m².

Discussion

Invasion status of Hemigrapsus sanguineus

Numerical abundance and biomass of the invasive Asian shore crab *Hemigrapsus sanguineus* clearly increased around Helgoland from 2009 to 2014 and reached similar levels to those of the native green shore crab *Carcinus maenas*. During this period, *H. sanguineus* and *C. maenas* were the dominant decapod crustaceans in the intertidal of Helgoland. Population densities of *H. sanguineus* reached up to 144 ind./m² (36 ind./0.25 m²) at the sheltered northeastern site, which represented a new maximum along European coasts. In North America, where *H. sanguineus* appeared in the late 1980s, population densities can be even higher with up to 305 ind./m² in Long Island Sound (Kraemer et al. 2007). Along the NW Atlantic coasts, increased abundance of *H. sanguineus* was accompanied by decreased numbers of *C. maenas*, as well as of several other species of panopeid brachyurans (Kraemer et al. 2007; O’Connor 2014). For the European coasts, this suggests that

the abundance of *H. sanguineus* has not reached its maximum.

O'Connor (2014) separated the invasion process of *H. sanguineus* in Massachusetts into early, middle, and late phases. These phases were characterized by numerical dominance of local species, similar abundances, and numerical dominance of the invader species, respectively. Accordingly, the invasion at Helgoland is in the "middle phase", because the populations of *H. sanguineus* and the native *C. maenas* are of similar size. Alternatively, the possible expansion model for introduced species (Boudouresque et al. 2005) categorizes the phases after the new arrival of a species as "naturalization", "expansion phase" and "persistence phase". The presence of ovigerous *H. sanguineus* females in 2009 indicated that the species was naturalized around the island of Helgoland. The clear increase in abundance of *H. sanguineus* between 2009 and 2014 suggests that the population has moved into the "expansion phase". Further monitoring of the population would be necessary to evaluate, whether the species will attain a stable population size around Helgoland or if its population development will follow the "boom and bust model" (Williamson 1996).

The invasion success of *H. sanguineus* in Europe may partly be due to its ability to dominate *C. maenas* in several ways. In the eastern USA, for example, *H. sanguineus* has been reported to prey on *C. maenas* to a much higher degree than the opposite, especially at the higher densities of *H. sanguineus* (Lohrer and Whitlatch 2002; Griffen and Byers 2006; Griffen and Williamson 2008). While intraspecific aggression was observed to be comparably low in *H. sanguineus* (Griffen 2006), feeding rates of adult *C. maenas* were already negatively affected by the presence of *H. sanguineus* (Griffen et al. 2008). The feeding behavior of *H. sanguineus*, however, was not affected by the presence of its presumed competitor. Nevertheless, in direct competition for food, *C. maenas* of similar mass can be superior over *H. sanguineus* (Jensen et al. 2002; MacDonald et al. 2007). In direct competition for shelter, *C. maenas* was displaced by *H. sanguineus* along the coast of New England, resulting in a higher risk of predation for the green crabs (Jensen et al. 2002). Intra-guild predation of *H. sanguineus* upon *C. maenas* as well as a higher predation risk of *C. maenas* may therefore also explain the rapid increase of the *H. sanguineus* population around Helgoland. In contrast to *H. sanguineus*, *C. maenas* also inhabits the subtidal areas around Helgoland and this potential refuge may supply the intertidal areas with green crab juveniles. Thus, it seems unlikely that the intertidal population of *C. maenas* will severely suffer from the *H. sanguineus* invasion.

Hemigrapsus sanguineus does not appear to be a common prey for seagulls in the Helgoland area. The piers and jetties around the island frequently show residues and carapaces of the edible crab *C. pagurus*, *C. maenas*, and the great spider crab *Hyas araneus* (Linnaeus, 1758). However, no body parts of *H. sanguineus* have been detected to date (S. Jungblut and J. Beermann, pers. obs.). This is consistent with *H. sanguineus* being a cryptic species that is seldom observed outside of cover during daylight hours.

Size distributions

The size distributions of *H. sanguineus* and *C. maenas* differed significantly between 2009 and 2014 among three of the four locations around Helgoland. Individuals of *H. sanguineus* were on average larger (10 to 19.5 mm CW) in 2014, whereas *C. maenas* were smaller. In fact, *C. maenas* showed a major recruitment event in 2014 resulting in high numbers of individuals in the smallest size class (5–9.5 mm CW). These very young specimens may have influenced the density measurements to a certain extent. The observed size patterns of *C. maenas* in August 2014 were similar to those reported for this species in the eastern USA during the "middle phase" of the *H. sanguineus* invasion (Stephenson et al. 2009; O'Connor 2014). In addition to the observed shift in numerical abundance, this further supports the hypothesis that the *H. sanguineus* invasion at Helgoland has entered the "middle phase" (*sensu* O'Connor 2014) or "expansion phase" (*sensu* Boudouresque et al. 2005).

Influence of habitat and wave exposure

The densities of *H. sanguineus* at the northwestern site were comparatively low, which may be explained by the habitat structure. The northwestern site is mainly characterized by a rock plateau with boulders and cobbles. The habitats of the remaining three sites are based on coarse sands. This is consistent with previous reports that cobbles on coarse sands seem to be the preferred habitat of *H. sanguineus* in Europe (Dauvin 2009; Dauvin et al. 2009; Gittenberger et al. 2010; van den Brink et al. 2012; Landschoff et al. 2013). The generally low abundances of a non-native congener, *H. takanoi*, may be due to the lack of its preferred habitat type of muddy sediments around Helgoland (Dauvin et al. 2009; Gothland et al. 2014).

At the southeastern site, only a slight increase in biomass of *H. sanguineus* was detected from 2009 to 2014. Abundance and size distribution of *H. sanguineus* and *C. maenas* remained similar. Population growth in many decapod crustaceans is often limited by

available shelter (see van den Brink et al. 2012 and references therein). The populations of both species may have reached a local carrying capacity situation at this relatively narrow and bordered site and that may currently prevent *H. sanguineus* from increasing in abundance.

Although the southwestern and the northeastern sites showed a similar habitat structure and composition, they strongly differed with respect to wind exposure and, thus, wave action. The strongly exposed southwestern site seemed to be beneficial to *C. maenas*, whereas *H. sanguineus* was highly successful at the sheltered northeastern site. This pattern may partly be explained by the behavior of the megalopa larvae of the two species. Unlike *C. maenas*, megalopae of *H. sanguineus* respond positively to odors of adult and juvenile conspecifics (and even to odors of adult *C. maenas*) with a higher molting and thus higher settlement rate (Zeng et al. 1997; Kopin et al. 2001; O'Connor 2007; Anderson and Epifanio 2009; Anderson et al. 2010; O'Connor and Judge 2010). The resulting "gregarious settlement" of megalopae and/or juveniles would facilitate the establishment of larger populations at more sheltered sites, where odors likely persist longer in the water (Kopin et al. 2001; Steinberg et al. 2007; Anderson and Epifanio 2009; Anderson and Epifanio 2010).

Around the island of Helgoland, *H. sanguineus* was most abundant at the sheltered northeastern site. In contrast, in most other studies, *H. sanguineus* inhabited moderately to very exposed coasts and habitats with high hydrodynamic activity (Fukui 1988; Lohrer et al. 2000b; Dauvin 2009; Dauvin et al. 2009; van den Brink et al. 2012). However, similar to the current findings at Helgoland, O'Connor (2014) detected higher densities of *H. sanguineus* at a more sheltered site in Narragansett Bay as opposed to more exposed sites along the outer coast of Massachusetts. The whole island of Helgoland may be regarded as highly hydrodynamic, due to its relatively remote location in the center of the German Bight. However, even in a generally high-hydrodynamic location, more sheltered sites may act as stepping-stones for *H. sanguineus* during its invasion process.

Effects at different tidal levels

At the highly exposed southwestern site, abundances of *H. sanguineus* decreased from higher to lower tidal levels, whereas at the sheltered northeastern location, this pattern was reversed. The intertidal vertical distribution of *H. sanguineus* has repeatedly been a matter of discussion. Previous studies have revealed no clear patterns, some investigations have

even produced contrasting results (Lohrer et al. 2000a, b; Lohrer and Whitlatch 2002). Lohrer et al. (2000a) therefore suggested that the vertical distribution of *H. sanguineus* may be predetermined by the structural complexity of the habitat (i.e. available shelter) rather than by tidal height. Although structural habitat complexity was not directly measured in the present study, overall habitat structures in the different tidal heights were similar between the two sites. The observed vertical distribution patterns may therefore result from the different degrees of wave exposure, although other factors, e.g. behavior, mortality or recruitment, may also be relevant (Crowe and Underwood 1998).

Conclusions

Differences in numerical abundance, biomass, and size distribution of the two crab species between the four sampling sites around Helgoland are probably caused by species-specific habitat preferences. The observed patterns may also partly result from different degrees of wave exposure, promoting the recruitment of *H. sanguineus* megalopae in sheltered areas. The current findings resemble the "mid-phase" invasion status of *H. sanguineus* in North America, where *H. sanguineus* and *C. maenas* are both non-indigenous species. The invasion process of *H. sanguineus* around Helgoland seems to be still ongoing. As a consequence, reported interspecific competition for shelter and direct interference competition or even intra-guild predation between *H. sanguineus* and *C. maenas* will likely increase in the future, potentially revealing clearer competitive and predator-prey interactions. The warming due to climate change is up to four times higher in the North Sea than the global average (Belkin 2009). In addition, the increasing anthropogenic influences in coastal areas can cause severe habitat alterations (Bulleri and Chapman 2010). Both factors have the potential to change competitive relationships in favor of non-indigenous species (Byers 2002). Invasion progression of *H. sanguineus* and possible effects on the native *C. maenas* population are thus still difficult to predict.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Sampling locations.

Table S2. Numbers and carapace widths of *C. maenas* and *H. sanguineus* sampled around Helgoland.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2017/Supplements/AI_2017_Jungblut_et_al_Supplement.xlsx