

Research Article

Globalization pressure and habitat change: Pacific rocky shore crabs invade armored shorelines in the Atlantic Wadden Sea

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Abstract

Two Northwest Pacific crabs have almost simultaneously invaded Northeast Atlantic shores. In the Wadden Sea, *Hemigrapsus sanguineus* and *H. takanoi* have become established on artificial-boulder shorelines. Peak densities of >100 crabs (>5 mm carapace width) per m² were attained within 2–3 years of arrival. The invaders segregated by microhabitat, with *H. sanguineus* dominant on exposed shores and *H. takanoi* dominant on sheltered shores as well as colonizing beds of mussels and oysters on mudflats. A field experiment indicated *H. sanguineus* displaced juvenile native shore crabs *Carcinus maenas* from beneath-boulder substrate. However, this displacement appeared restricted to armored shorelines, with little to no effect on large populations of *C. maenas* that occur widely in shallow, soft bottom, habitats of the coastal zone of the North Sea.

Key words: invasive marine species; artificial shores; *Hemigrapsus*; *Carcinus*; competition

Introduction

The current level of global trade has resulted in levels of unintended species introductions many times greater than the rate of natural dispersal (Davis 2009; Simberloff 2009). In particular, transoceanic shipping with ever larger and faster vessels as well as the global practice of transferring aquaculture organisms are responsible for an influx of nonnative coastal species, confronting native species with a broad array of potential competitors (Briggs 2012). The outcome may not only depend on the alien species' inherent invasiveness but may also vary with changes in receiving ecosystems such as species extinctions, state of eutrophication and pollution, climate warming, or habitat fragmentation and transformation (Mooney et al. 2005; Reise et al. 2006; Sax et al. 2005). We here describe a case where coastal-habitat alteration virtually paved the way for successful invasions of two nonnative species.

The Wadden Sea is a coastal region of the North Sea that includes the planet's largest area of coherent intertidal mud and sand flats and also supports but one common native brachyuran crab, *Carcinus maenas* (L., 1758) (Reise 1985; Reise et al. 2010). At present, at least 66 introduced nonnative macrobenthic species have become established in the Wadden Sea (Buschbaum et al. 2012). Most have immigrated into the Wadden Sea after being first introduced elsewhere on the European Atlantic coast. This study focused on two Asian shore crabs: *Hemigrapsus takanoi* Asakura and Watanabe, 2005 (separated from *H. penicillatus* since 2005) and *H. sanguineus* (de Haan, 1835). The rapid spread of these two species in the Wadden Sea is described in this paper. Because they can cling tightly to surfaces and tend to hide in narrow crevices, these grapsid crabs are able to travel on ship trunks, in anchor boxes, on ropes, or inside ballast water systems.

The anthropogenic spread of brachyuran crabs has occurred on a global scale. The Asian shore crab *H. sanguineus* invaded the east coast of North America (McDermott 1998) in the mid-1980s, and the closely related *H. takanoi* and *H. sanguineus* have been present on the Atlantic coast of France and the Dutch Delta area since the 1990s (Noël et al. 1997; Breton et al. 2002). The native European *C. maenas* was first introduced to the Atlantic coast of North America and later, introduced to the Pacific coast of North America, South America, South Australia, and Tasmania. As well, hybrids of *C. maenas* and the Mediterranean *C. aestuarii* are now found in South Africa and Japan (Carlton and Cohen 2003; Darling et al. 2008).

Hemigrapsus takanoi, originally identified as *H. penicillatus* but shown to be *H. takanoi* by Yamasaki et al. (2011), was found at La Rochelle in France in 1994 (Noël et al. 1997), by 1997 had already spread about 1000 km further north to Le Havre (Breton et al. 2002), and in 2000 was detected about 400 km further east at several sites in the Dutch Delta area (Nijland and Beekman 2000; Wolff 2005). Since 2006, *H. takanoi* has been present in the Dutch Wadden Sea (Gittenberger et al. 2010) and reported from the German Wadden Sea since 2007 (Obert et al. 2007). The current distribution is from the Bay of Biscay to the North Sea albeit with some gaps in between (see maps in Dauvin et al. 2009 and Dauvin and Delhay 2010). These gaps may be an indication of multiple independent introductions, or suggest spread via hitchhiking on ships and with oyster transports rather than the continuous distribution expected if the vector of spread were the long-shore drift of pelagic larvae. Furthermore, Gollasch (1999) found *H. penicillatus* (now regarded as *H. takanoi*) in the hull fouling of a ship in Bremerhaven in 1993 (Germany), an area that at the time lacked an established population of the species. This observation is consistent with the hypothesis of dispersal by ships along coasts, and may explain a range of >2000 km occupied in less than two decades.

Hemigrapsus sanguineus was first found, together with *H. takanoi*, at Le Havre in 1999 (Breton et al. 2002) and in the Dutch Delta area (d'Udekem d'Acoz and Faasse 2002; Nijland and Faasse 2005; Wolff 2005). The first record for the Dutch Wadden Sea is from 2004 (Gittenberger et al. 2010) and for the German Wadden Sea from 2006 (Obert et al. 2007). Dauvin et al. (2009) and Dauvin and Dufossé

(2011) indicate there is a continuous range from Mount Saint-Michel Bay to the Wadden Sea. Again, one may wonder whether a spread of over >1000 km in <10 years was achieved by long-shore transport of larvae from a single site of introduction, by multiple introductions, or by hitchhiking with vessels along the coast. Isolated records from ports in the Mediterranean Sea (Schubart 2003) and the Black Sea (Micu et al. 2010), as well as the remarkable tandem invasion of the two grapsid species from France to Germany, suggest that the range expansion in Europe was partly due to shipping vectors and not entirely due to larval dispersal. To date, neither grapsid species has been reported from the British Isles, except *H. sanguineus* in the Channel Islands (J-C. Dauvin, Univ. Lille Nord de France, pers. com.).

The European Wadden Sea is a sedimentary environment devoid of natural rocky shores (Reise et al. 2010). At first, wooden structures were used to protect shorelines from erosion but in the 19th century hard coastal defenses became fashionable and were standard in the 20th century (Reise 2005). This wide introduction of an artificial habitat may not only have affected some native species adapted to soft shorelines and widened spatial niches of some other native species, but serves as a prerequisite for rocky shore species to invade. These structures constitute a major structural change making a recipient region more susceptible to native invaders from adjacent regions that have rocky coasts as well as introduced alien species that have evolved to live in rocky shoreline habitat. We here examine how this conversion to armored coastline may explain the rapid invasion of two introduced species.

In the Wadden Sea, invading *Hemigrapsus* spp. only need to contend with the native shore crab *C. maenas*. This native species occupies a key position in the Wadden Sea food web and attains high densities, especially in seagrass beds and mussel beds (Beukema 1991; Klein-Breteler 1976; Reise 1985; Scherer and Reise 1981). Juvenile *C. maenas* inhabit the intertidal zone while some adults migrate with the tides between intertidal and subtidal zones and others remain permanently subtidal. The main goal of this study was to evaluate how *C. maenas* in its native habitat responded to establishment of two Pacific invasive species.

Carcinus maenas first arrived on the eastern coast of North America about 200 years ago and there were local declines in its abundance when

H. sanguineus arrived about 25 years ago (Lohrer and Whitlatch 2002). Likewise in France, the native *C. maenas* declined at some sites where *Hemigrapsus* spp. invaded (Dauvin et al. 2009). To further study this interaction between the three species, we conducted rapid surveys in the Wadden Sea; carried out quantitative assessments of shore crab abundance around the island of Sylt to detect habitat preferences and spatial overlap among species; and used an *in situ* field experiment to examine the interaction between *H. sanguineus* and *C. maenas* in boulder patches.

Materials and methods

Sampling

From 2007 onwards, several sites in the Wadden Sea were qualitatively searched for *Hemigrapsus* spp. with priority given to armored shore lines, mussel (*Mytilus edulis*) beds, and oyster beds (*Crassostrea gigas*). A systematic assessment on introduced alien species was performed during August to October, 2009 to 2011, on boulder shorelines of 8 port localities located on the German Wadden Sea coast (Figure 1). This sampling method is described in detail by Buschbaum et al. (2012).

A quantitative survey was carried out at 13 sites along the shores of the island of Sylt in May-June 2011 (Figure 2). We omitted the upper tidal zone (no crabs) and spread replicates between mid and low tide level at random. At each site, 4 to 12 replicates of 1 m² or 0.25 m² were sampled by hand, by turning over boulders and rubble, and by raking the upper layer of sediment to a depth of 5 cm. The smaller sample area was applied at mussel and oyster beds. Crabs <5 mm carapace width (CW) were not counted. Searching by hand was compared to sieving with a mesh of 5 mm and searching sieve residues in the lab at a mussel bed with 6 replicates for each method (site S13 in Figure 2 and Table 2). The hand survey yielded on average 23 adult *Hemigrapsus* spp. m⁻² compared with an average of 19 adults m⁻² by sieving, confirming the suitability of the hand survey for collecting adults. In contrast, for juvenile *C. maenas*, the averages were 26 and 49 m⁻² for the hand and sieve method, respectively, which indicates the abundance of juvenile shore crabs was underestimated in mussel-bed habitat.

At sites S12, S13 and S14 (Figure 2 and Table 2), hand sampling in 2010 was performed within

a ring made of flexible mesh wire (5 mm mesh) enclosing an area of 963 cm². At each site, 20 replicates were taken at random with the condition that the boulders fit into the ring. Mussels including the upper layer of sediment were washed over a 1-mm mesh sieve.

One site with brushwood groins was investigated but quantification of abundances was impossible without illegally dismantling the structures; therefore, the results for this site represent presence/absence data. In the shallow subtidal zone at the northern tip of Sylt, a total of 16 hauls with an oyster dredge (wrought iron blade of 1 m in length and mesh size of the bag 10 mm; haul duration of 15 min each) were taken in 2010 and 2011 and sampled qualitatively on board (for further details of sampling see Buhs and Reise 1997).

Field experiment

Boulders were removed from a revetment at the seaside of the Wadden Sea Station Sylt in List (sites S12 and S13 in Figure 2) and carried 100 m onto an adjacent sand flat at mid tide level, where 12 patches of 0.25 m² were each covered with 10 to 15 boulders. Patches were arranged in a rectangular 3×4 matrix with a distance of 6 m to the nearest patch. *H. sanguineus* were collected at the revetment. On 23 June 2011, every other patch was stocked with 12 to 16 male and female crabs ranging from 5 to 34 mm carapace width (CW) in size. After 4 d, the patches were sampled by hand at low tide for *H. sanguineus* and *C. maenas*, which were counted and carapace width measured. We tested for differences with the 2-sided Mann-Whitney-U-test.

Species identification

We followed Breton et al. (2002) and Asakura and Watanabe (2005) to distinguish the two grapsid species. In the field, also coloration patterns were used. *H. sanguineus* has a mottled carapace with legs conspicuously dark ringed and with dark bristles. The carapace of *H. takanoi* is more evenly dark brownish-green and has small light hairs at legs and claws. However, individuals <8 mm CW are difficult to identify in the field. Specimens collected during quantitative surveys were all measured in the lab, and there the smallest individuals were inspected under a stereo microscope, looking at the suborbital crest (see Figure 3 in Breton et al. 2002).

Figure 1. Records of *Hemigrapsus sanguineus* and *H. takanoi* in the Dutch Wadden Sea in 2009 (after Gittenberger et al. 2010) and German Wadden Sea including the Danish Island of Rømø in 2007–2011. No. 1 to 8 refer to locations listed in Table 1. Light grey indicates tidal flats.

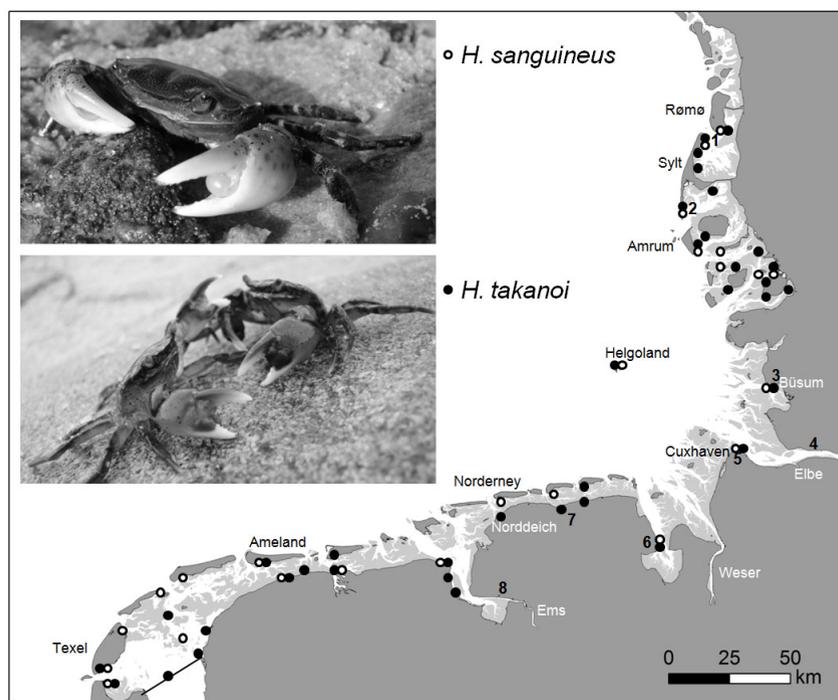


Table 1. Rare (≤ 3 crabs after 15 min of search) and abundant occurrence of *Hemigrapsus sanguineus* (s, S), *H. takanoi* (t, T) and *Eriocheir sinensis* (e, E) at armored shorelines in the German Wadden Sea from 2009 to 2011, sampled in rapid assessment surveys on alien species. Lower case letters refer to rare and upper case letters to abundant crabs, respectively. For locations see numbers in Figure 1.

Site	Habitat	salinity	2009	2010	2011
1 List (Sylt)	Revetment, boulders, sandy	30-31	S, t	S, t	S, t
2 Hörnum (Sylt)	Revetment, boulders, sandy	30	S	S, t	S, t
3 Büsum	Port, boulders, muddy	24-25	s	t	t, e
4 Brunsbüttel	Revetment, boulders, muddy	6-10	E	E	E
5 Cuxhaven	Revetment, boulders, sand and mud	18-20	s, t	t	s, T, e
6 Wilhelmshaven	Revetment, boulders, mud	30	s, t	t	t
7 Bengersiel	Revetment, boulders, muddy	30	s, T	T	T
8 Emden	Port, boulders, muddy	10-17			

Results

Time line and distribution

The invasion of the Wadden Sea by both species of *Hemigrapsus* occurred at about the same time, and spread rapidly from west to east (Figure 1). According to Gittenberger et al. (2010), *H. sanguineus* was first collected in the western (Dutch) Wadden Sea in 2004 (Gittenberger et al. 2010) and two specimens were collected in the northern Wadden Sea in 2006 (Holmer Siel, collected by B. Kreutz, G. Meurs, Multimar Tönning, Germany, pers. com.). In 2007, it was found at two other sites (Amrum and Norderney;

R. Borcharding, Schutzstation Wattenmeer, Husum, Germany, pers. com.; Obert et al. 2007) and, in 2008, at an additional six sites, including the offshore island of Helgoland (M. Molis, AWI-Helgoland, Germany, pers. com.). Since 2009, almost the entire German Wadden Sea had been invaded. Similarly, *H. takanoi* was detected first in the Dutch Wadden Sea in 2006 (Gittenberger et al. 2010), and in 2007 at Norddeich (Obert et al. 2007) and Büsum (R. Borcharding, pers. com.) (Figure 1). By 2009, it was found throughout this range at shores with boulders for coastal defense and beds of mussel or oyster (pers obs; H. Büttger, BioConsult, Husum, Germany, pers. com.).

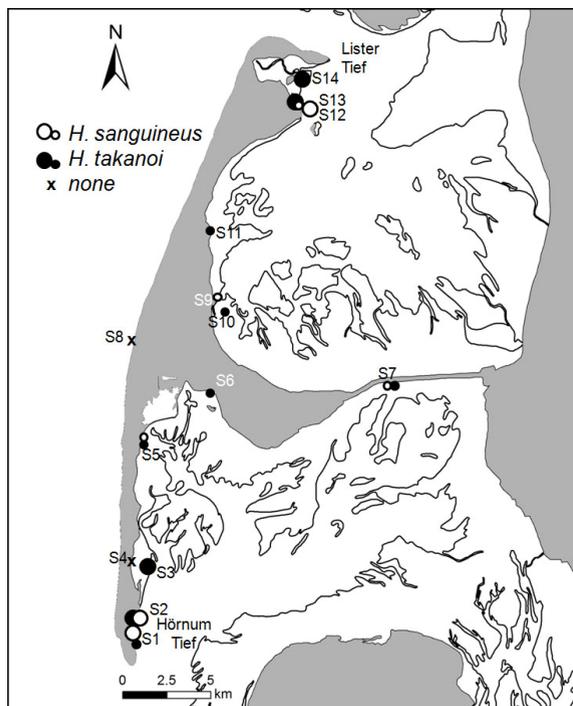


Figure 2. Occurrence of *H. sanguineus* and *H. takanoi* at selected sites around the Island of Sylt in 2011. Large circle refers to ≥ 40 crabs m^{-2} in *H. sanguineus* and large filled circles to ≥ 3 crabs m^{-2} in *H. takanoi*. Small symbols refer to lower abundances. For no. S1-14 see Table 2. Lines between island and mainland indicate mean low tide.

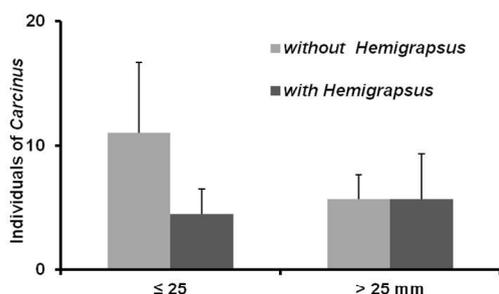


Figure 3. Four days after establishing patches of boulders with and without *Hemigrapsus sanguineus* in June 2011, significantly ($p < 0.01$) more juvenile (≤ 25 mm carapace width) *Carcinus maenas* took low tide refuge under boulders initially free of *H. sanguineus* than under boulders stocked with 12 to 16 grapsid crabs, while larger *C. maenas* hiding under these boulders made no difference between treatments ($p = 0.59$; Mann-Whitney-U-test, 2-sided, $n=6$). Column height indicates mean number of shore crabs and vertical lines positive standard deviation.

Hemigrapsus sanguineus apparently colonized some sites first but was later completely displaced by *H. takanoi* (Table 1). At Büsum, Cuxhaven, Wilhelmshaven and Benersiel (No. 3, 5, 6 and 7 in Figure 1) the two species collected together in 2009 but in 2010 and 2011 *H. sanguineus* had become rare or not detected at these relatively sheltered sites along the mainland shores. Should this be a general finding, it could produce a pattern where *H. sanguineus* tends to dominate along island shores and *H. takanoi* dominates along mainland shores. Two estuarine sites with low salinity (No. 4 and 8 in Figure 1) were devoid of *Hemigrapsus* spp. In the Elbe estuary, however, another invasive grapsid (Chinese mitten crab *Eriocheir sinensis* H. Milne Edwards, 1853) was abundant. All sites occupied by *Hemigrapsus* spp. in 2009 were still occupied in 2011.

At the leeward side of the Island of Sylt, *Hemigrapsus* was recorded at 11 sites: at 2 sites only *H. sanguineus* was detected; at 4 sites only *H. takanoi* was detected; and both species were present in the remaining 5 sites (Figure 2). Both species were absent from sandy beaches, salt marshes, sediment flats, and from dredge hauls in the subtidal zone. Both species were found underneath boulders and at brushwood groins, and *H. takanoi* was also found in mussel and oyster beds. The native *C. maenas* occurred at all sites where the invasive grapsid crabs were found. Sampling with an oyster dredge for *Hemigrapsus* spp. in the shallow subtidal of the List tidal basin was in vain, while adult *C. maenas* was common in these dredge hauls.

Size and abundance

Quantitative sampling focused on individuals > 5 mm CW along the shores of the island of Sylt (Table 2). Of these, *H. sanguineus* was on average slightly larger (15.8 ± 4.5 mm CW; $n = 799$) than *H. takanoi* (14.8 ± 4.3 mm CW; $n = 121$) but, in both species, the largest males were 34 mm CW. Both grapsid species had their highest densities near port locations at the northern and southern end of the island. While the highest abundance of *H. takanoi* was 18 crabs per m^2 among mussels behind a revetment, that of *H. sanguineus* was up to 100 crabs per m^2 underneath boulders. Standard deviation among replicate samples was high, indicating a tendency to aggregate under suitable boulders during low

Table 2. Abundance (crabs $> 5 \text{ mm m}^{-2} \pm$ standard error; 4 to 12 replicate samples) along the shores of the Island of Sylt in the northern Wadden Sea in May/June 2011. For site no. see Figure 2, (p) = present but not quantified.

Site and type of shore habitat (number of replicates)	<i>H. sanguineus</i>	<i>H. takanoi</i>	<i>C. maenas</i>
S1 Seawall with boulders (6)	100.0 \pm 21.1	0.7 \pm 0.7	10.0 \pm 2.7
S2 Boulders with mussels (5)	40.0 \pm 7.8	12.8 \pm 3.4	55.2 \pm 9.9
S3 Oyster bed with mussels (6)	0	5.3 \pm 2.2	48.7 \pm 4.3
S4 Lower salt marsh (6)	0	0	2.3 \pm 1.9
S5 Boulders, rubble, muddy sand (6)	0.2 \pm 0.2	0.3 \pm 0.2	6.2 \pm 1.2
S6 Boulders on mud (6)	0	0	3.2 \pm 1.3
S7 Boulders, brushwood groins, mud (4)	0.8 \pm 0.8	2.0 \pm 1.7	7.5 \pm 1.2
S8 Exposed sandy beach with groin	0	0	(p)
S9 Boulders, rubble, muddy sand (6)	1.5 \pm 0.4	0	21.8 \pm 5.0
S10 Oyster bed with mussels (6)	0	1.3 \pm 0.8	46.0 \pm 11.2
S11 Brushwood groins, mud	0	(p)	(p)
S12 Revetment with boulders, sand (6)	62.7 \pm 9.1	0	26.0 \pm 3.4
S13 Mussel bed sheltered by revetment (12)	3.3 \pm 1.2	18.0 \pm 4.6	37.7 \pm 6.7
S14 Oyster bed with mussels (8)	0	3.0 \pm 1.5	20.0 \pm 3.5

Table 3. Abundance (crabs $> 5 \text{ mm m}^{-2} \pm$ standard error; 6 to 20 replicate (n) samples) at sandy shore defended with boulders at Wadden Sea Station Sylt (site S12 in Figure 2), a nearby mussel bed (site S13) and an oyster bed with mussels in Königshafen (site S14).

Underneath boulders	Sept. 2010 n=20	Dec. 2010 n=20	June 2011 n=6
<i>Hemigrapsus sanguineus</i>	54 \pm 10	166 \pm 47	63 \pm 9
<i>Carcinus maenas</i> juveniles	43 \pm 7	41 \pm 11	26 \pm 3
Mussel bed behind revetment	Oct. 2010 n=20		June 2011 n=12
<i>Hemigrapsus sanguineus</i>	1 \pm 1		3 \pm 1
<i>Hemigrapsus takanoi</i>	17 \pm 4		18 \pm 5
<i>Carcinus maenas</i> juveniles	158 \pm 18		38 \pm 7
Oyster bed with mussels	Oct. 2010 n=20		May 2011 n=8
<i>Hemigrapsus takanoi</i>	3 \pm 2		3 \pm 1
<i>Cracinus maenas</i> juveniles	110 \pm 13		20 \pm 4

tide. Juvenile *C. maenas* were more widespread than *Hemigrapsus* spp. but showed a similar preference for boulder shores and for mussel/oyster beds. Highest abundance, about 55 crabs per m^2 , was observed under boulders encrusted with many mussels. The lowest abundance of *C. maenas* (site S1) corresponded to the site of highest abundance of *H. sanguineus* (Table 2).

Abundance estimates from three sites varied between sample dates with no discernable pattern (Table 3). The highest density observed was for *H. sanguineus* with 166 crabs per m^2 underneath boulders compared to 158 crabs per m^2 for juvenile *C. maenas* in a mussel bed.

Field experiment

In the course of 4 days, the experimental patches with boulders were left by 45 of the 88 *H. sanguineus* initially stocked of which only 7 entered the control patches. In contrast, 160 *C. maenas* were had immigrated into the boulder patches, with significantly more crabs of $\leq 25 \text{ mm CW}$ collected from the control patches (those initially without grapsid crabs; Mann-Whitney-U-test, 2-sided, $p < 0.01$). In contrast, *C. maenas* $> 25 \text{ mm}$ (up to 60 mm) were collected from stocked and control patches equally (Figure 3).

Discussion

In < 20 years, *Hemigrapsus takanoi* and *H. sanguineus* have spread to >2000 km of coastal habitat in Western Europe. In the otherwise soft sediment habitats of the Wadden Sea, high abundances were quickly achieved at artificial boulder shores. The large-scale transformation of natural soft-sediment shores into rock and boulder armored shores may be regarded as an “invitation” to species pre-adapted to this kind of artificial habitat. The native *C. maenas* had the advantage to be there first and mostly uses artificial boulder shores as a nursery (pers. obs.). Since the arrival of the Asian shore crabs, the native shore crab has to share this habitat with the two invaders. We suggest that it was the combination of intensified transoceanic shipping and the presence of a suitable anthropogenic habitat in the recipient coastal region that made this invasion success not only possible but also likely to happen. In natural habitats of the Wadden Sea, the native shore crab prevails in most of the habitat; however, it may be displaced by the alien species in the artificial shoreline habitat.

Habitats

In their native range, *H. takanoi* and *H. sanguineus* typically occupy the rocky intertidal zone underneath boulders (Asakura and Watanabe 2005; Lohrer et al. 2000). Although the Wadden Sea is originally an entirely soft-sediment environment, there has been widespread construction of hard coastal defenses in place of natural shoreline, and this can only increase with the expected rise in sea level (Reise 2005). Since the early 1900s, huge amounts of boulders have been dumped at exposed and sheltered shores, at the seaward foot of dikes, and at revetments and jetties. The grapsid crabs might not have been able to invade the Wadden Sea had this artificial habitat not been present as a gateway.

Earlier work suggests there is microhabitat segregation between *H. takanoi* and *H. sanguineus* with the former occurring beneath boulders of sheltered muddy shores and the latter beneath boulders on exposed and sandy shores (Dauvin et al. 2009; Gittenberger et al. 2010). Our observations support these findings. Interestingly, a parallel pattern evolved at the Pacific coast of North America among the native grapsids with *H. oregonensis* dwelling beneath rocks on mud and *H. nudus* beneath rocks on

sand (Steinberg and Epifanio 2011). *H. takanoi* and *H. sanguineus* may occur together in high densities, i.e., at Dunkirk harbor (France) in April 2010 (J-C. Dauvin, Univ. Lille Nord de France, pers. communication), however, we never observed high abundances of both species at the same site, and noted that four sheltered sites were initially invaded by *H. sanguineus* and subsequently were abandoned while *H. takanoi* prevailed, suggesting competitive displacement. In the Oosterschelde tidal bay, part of the Dutch delta area, *H. takanoi* dominated under hard substrates along the shore, while *H. sanguineus* took over at the exposed storm surge barrier (Van den Brink et al. 2012).

In mixed oyster/mussel beds at some distance from the shore on intertidal flats and near low tide line, we encountered *H. takanoi* but not *H. sanguineus*. These beds accumulate silt and mud, and thus correspond to the sheltered type of boulder shores. Oysters and mussels offer plenty of shelter, however, abundance of *H. takanoi* remained low compared to some boulder shores we investigated, i.e., Cuxhaven and Bengersiel. We observed that mussel beds without, or with very few oysters, served the crabs just as well as oyster beds. Sediment flats without such epibenthic structures were devoid of *H. takanoi*. None were found in salt marshes or intertidal seagrass beds.

In addition to hydrodynamics and substrate type, the two species appear to have different salinity tolerances. *H. takanoi* is found at locations with a salinity as low as 9 to 12 (Gittenberger et al. 2010; Soors et al. 2010) while *H. sanguineus* is only found at locations with a salinity of ≥ 19 (Gittenberger et al. 2010). Ledesma and O'Connor (2001) suggested an optimal range of 24–35 for adult *H. sanguineus* and, under experimental conditions, larvae did not survive below salinity of 25 (Epifanio et al. 1998). Except for estuaries and sluices, salinity seems appropriate for both species throughout the Wadden Sea, however, the invading crab species may segregate not only with respect to sediment type but also along the salinity gradient. Consistent with published work, neither Asian shore crab was found in the Elbe estuary at salinities of 6 to 10; however, large numbers of another grapsid crab from Asia, *Eriocheir sinensis*, was found at these sites.

Stephenson et al. (2009) studied the spread of *H. sanguineus* along the coast of Maine and suggest a barrier exists where mean summer temperatures are below 13°C. Assuming the

same threshold, one if not both alien *Hemigrapsus* species could spread northward into the Limfjord and Skagerrak-Kattegat region. Winter temperatures do not appear to be a barrier because, *Hemigrapsus* spp. in the northern Wadden Sea have survived three winters in a row (2010 to 2012) in which ice covered the shore and water temperatures dropped to -2°C . *H. sanguineus* aggregated, slowly crawling, even with ovigerous females, under boulders at low tide level (pers. obs.). Due to their wide temperature tolerance, the continuing northward spread of the hemigrapsids in Europe may not be related to the recent increases in summer and winter temperatures (Wiltshire and Manly 2004; MacKenzie and Schiedek 2007), in contrast to the case for the spread of other nonnative introduced species such as the Pacific oyster (Diederich et al. 2005; Nehls et al. 2006), the American slipper limpet (Thieltges et al. 2004; Nehls et al. 2006) and an Australasian barnacle (Witte et al. 2010). Thus, the tandem invasion of *H. takanoi* and *H. sanguineus* may not reverse if it becomes cooler again.

Phase of invasion

Invasions of introduced species often begin with a lag phase before advancing into exponential population growth, which after some years of very high densities may turn into decline during the accommodation phase (Reise et al. 2006). Virtually no lag phase was observed in the *Hemigrapsus* spp. invading the Wadden Sea. Within 2 to 3 years, high numbers of grapsid crabs were found almost everywhere that there was suitable habitat.

Obtaining quantitative abundance estimates for grapsid crabs can be difficult and to some extent depends on the alertness of the investigator and on habitat structure. In our case, some small crabs will always be overlooked, and we adopted a lower size limit of 5 mm CW to save time and avoid biased data on smaller crabs. As well, direct comparisons to other studies must be made carefully due to variation in sizes considered and differences in sampling techniques. However, in most studies, the crabs tended to be in a size range of 10 to 25 mm CW (i.e., Dauvin 2009; Dauvin and Dufossé 2011; McDermott 1998; Stephenson et al. 2009; this study), and for this size range the abundance data may be fairly comparable. Van den Brink et al. (2012) reported abundance data from a general benthic monitoring with box corer in soft-

sediments in the Dutch delta area, with generally low abundances of *C. maenas* and from 2004 onwards also on *H. takanoi*. Only for the latter there was a high abundance estimate of 79 m^{-2} at one locality in 2010.

Mean abundance of *Hemigrapsus* spp. at the island of Sylt in 2011 was 46 crabs m^{-2} , which is comparable to the 33 crabs m^{-2} reported for boulder shores in northern France (Dauvin and Dufossé 2011) but is 3 to 4 times lower than densities of *H. sanguineus* from New England shores south of Maine (i.e., Jensen et al. 2002; Kraemer et al. 2007; McDermott 1998; O'Connor 2001). Thus, the abundance peak for the current Asian shore crab invasion event in Europe may still be ahead.

Receptive shores

Underneath boulders placed for coastal shoreline defense, the invasive *Hemigrapsus* spp. met high densities of juveniles of native *C. maenas* and partially displaced them. However, high juvenile densities of *C. maenas* also occur in the extensive intertidal seagrass beds during summer (Scherer and Reise 1981) and clumps of mussels in autumn (Thiel and Dornedde 1994). Most of the adult *C. maenas* perform tidal migrations and stay subtidal during low tide while some migrate offshore, too far away to visit the intertidal zone regularly (Klein-Breteler 1976; Reise and Bartsch 1990). At present, it is rather unlikely that *Hemigrapsus* spp. exert a significant effect on the total population size of *C. maenas* in the Wadden Sea. Low abundance of *H. takanoi* at mussel and oyster beds may be due to adult *C. maenas* being present when the tide is in, presumably preying on the much smaller grapsids. This situation resembles large *Callinectes sapidus* preventing the establishment of *C. maenas* in Chesapeake Bay (DeRivera et al. 2009). In the Dutch delta area, *C. maenas* abundance has declined since the 1990s, and Van den Brink et al. (2012) suggest that this might have facilitated the establishment of *H. takanoi*. Based on their field survey, they postulate that *H. takanoi* may be a strong interference competitor of or predator upon small *C. maenas*. Jensen et al. (2002) found that *H. sanguineus* pushes *C. maenas* out of shelter in a simplified aquarium environment. On the other hand, when competing for common food, *C. maenas* had an advantage over *H. sanguineus* (Jensen et al. 2002; MacDonald et al. 2007).

Our field experiment demonstrated that small *C. maenas* avoided patches of boulders which had been stocked with *H. sanguineus*. This experimental outcome supports observations on decreasing densities of *C. maenas* where *Hemigrapsus* spp. invaded (Jensen et al. 2002; Lohrer and Whitlatch 2002; Kraemer et al. 2007; Griffen and Delaney 2007; Dauvin et al. 2009; Dauvin and Dufossé 2011). We also observed that an unexpectedly low density of *C. maenas* coincided with the location where *H. sanguineus* attained its highest density at Sylt. From such observations and the experiment, we conclude that juvenile *C. maenas* are inferior to *H. sanguineus* at boulder shores. However, considering the heavy loss of experimentally added grapsids within 4 days, the reverse may be the case when large adults of *C. maenas* encounter small grapsids. This needs to be tested in further experiments.

Management

In the near future, there will be three instead of one common species of brachyuran crabs in the Wadden Sea; supplemented by the Chinese *Eriocheir sinensis* commuting between fresh and coastal waters. The natural prevalence of just one native crab is an unusual state compared to most other coastal regions and may be explained by the natural lack of boulder shores or rocky outcrops in the Wadden Sea. This habitat state has been changed by the introduction of hard shores for coastal defense, and therefore it may have been only a question of time until alien crabs invaded given the high availability of potential propagules in shipping vectors.

It is not feasible to remove grapsid crabs from the Wadden Sea if the goal is to maintain the species composition, structure, and functioning of the original ecosystem. However, as the Wadden Sea is under nature protection and has been designated a world heritage site, coastal protection could adopt a more natural approach, i.e., sand nourishments instead of boulders. To prevent waves from undercutting solid walls (Linham and Nicholls 2010), sand replenishments may work better than enhanced stone revetments. This change in strategy is already gaining ground in the Wadden Sea (CPSL 2005; 2010). In some cases, established hard protections may even be covered with sand to improve energy dissipation during storm surges, and at the same time eliminate the preferred habitat of grapsid crabs and other alien rocky

shore species. Sand supply from offshore to inshore areas may further help to improve the coastal sediment balance in the face of sea level rise (Reise 2003). Coastal defense and adaptation to sea level rise, shoreline habitat restoration, and control of alien species invasions may thus go hand in hand.

Conclusions

Transoceanic trade has allowed colonization of the Wadden Sea by *H. takanoi* and *H. sanguineus* and permitted rapid spread once they arrived. Moreover, the transformation of soft-sediment shores into armored shorelines by addition of boulders has turned the otherwise unsuitable Wadden Sea into an almost ideal habitat for these crabs. The partial retreat of the native shore crab from the shores may be displacement by the non-native grapsid crabs. *H. takanoi* and *H. sanguineus* themselves show segregation along a habitat gradient but still only take a fraction of the original habitat niche of the native shore crab *C. maenas*. At boulder shores, *C. maenas* seems to be inferior to *Hemigrapsus* spp. but will likely prevail in the dominant habitat type in the Wadden Sea. Invader control might be achieved should coastal protection measures shift from hard to soft defenses.

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Supplementary material

The following supplementary material is available for this article.

Appendix 1. Records of invasive crabs at armored shorelines in the German Wadden Sea from 2009 to 2011: *Hemigrapsus sanguineus*, *H. takanoi* and *Eriocheir sinensis*.

Appendix 2. Abundance of crabs along shores of the Island of Sylt in the German Wadden Sea in summer 2011: *Hemigrapsus sanguineus*, *H. takanoi* and *Carcinus maenas*, (p) = present but not quantified.

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