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Research article

Recent expansion of two invasive crabs species *Hemigrapsus sanguineus* (de Haan, 1835) and *H. takanoi* Asakura and Watanabe 2005 along the Opal Coast, France

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Abstract

Nowadays, invasions of invertebrate species in coastal ecosystems have become an ineluctable and irreversible phenomenon. The recent introduction of two western pacific crustacean decapods—the Asian shore crab, *Hemigrapsus sanguineus*, and the brush-clawed shore crab, *Hemigrapsus takanoi*—along the French coast has revealed the problematic effects that invasive species can have on biodiversity and also the competition that invasive species represent for native crab species. This study describes the distribution and abundance of both *Hemigrapsus* species along the Opal coast on the French side of the Dover Strait in spring 2008. Both species occupy habitats similar to that of the green crab, *Carcinus maenas*. However, the habitats colonised by the two species are clearly segregated: low hydrodynamic muddy habitats for *H. takanoi* and high hydrodynamic habitats with fine and medium sands for *H. sanguineus*. Both species can live in sympatry in harbours. In spring 2008, the maximum density outside Dunkirk harbour was 12 ind.m^{-2} for *H. sanguineus*, and inside Dunkirk harbour, the maximum density was 60 ind.m^{-2} for *H. takanoi*. In this location, *H. takanoi* dominated *C. maenas* significantly. No ovigerous females of either invasive species were found during the spring. Both species have high colonisation potential, ranging from south of the Bay of Biscay to Germany for *H. takanoi* and from the western part of the English Channel to Germany for *H. sanguineus*.

Key words: invasive marine species, crab, Crustacea, Decapoda, *Hemigrapsus sanguineus*, *Hemigrapsus takanoi*, *Carcinus maenas*, English Channel, North Sea, competition

Introduction

Among the most recent brachyuran species to have colonised the French Atlantic coastline are two Asian crabs from the genus *Hemigrapsus* (superfamily Grapsoidea). The brush-clawed shore crab *H. takanoi* Asakura and Watanabe, 2005 (Figure 1) was initially identified as *H. penicillatus* (de Haan, 1835) and first recorded in 1994 at La Rochelle on the Atlantic coast of France (Noël et al. 1997). This species was subsequently reported from the harbour at Le Havre in 1999 on the French side of the English Channel (Breton et al. 2002). In the same year (1999), the Asian shore crab *H. sanguineus* (de Haan, 1835) (Figure 2) was also discovered in Le Havre (Breton et al. 2002). *Hemigrapsus sanguineus* was later observed along the Opal Coast during the autumn of 2005 in the intertidal zone at Wimereux near the Wimereux Marine Station (M. Priem, personal communication). During a scuba dive in autumn 2006 *H. takanoi* was found in one of the Dunkirk harbour basins (Y. Müller personal communication).

The aims of this study are to present the geographical distribution of both invasive species in the intertidal zone of the Opal coast from the eulittoral zone to evaluate the density of both species in this area, and to estimate the possible competition represented by both non-native species of *Hemigrapsus* for the native common shore crab, *Carcinus maenas* (Linnaeus, 1758). The known distribution of both exotic species in European waters as of July 2008 is also presented.

Figure 1. *Hemigrapsus takanoi* male collected on Dunkirk harbour on 11 April 2008 (Photograph by A. Tous Rius)

Figure 2. *Hemigrapsus sanguineus* male collected on Wimereux 'Fort de Croy' on 5 May 2008 (Photograph by A. Tous Rius)

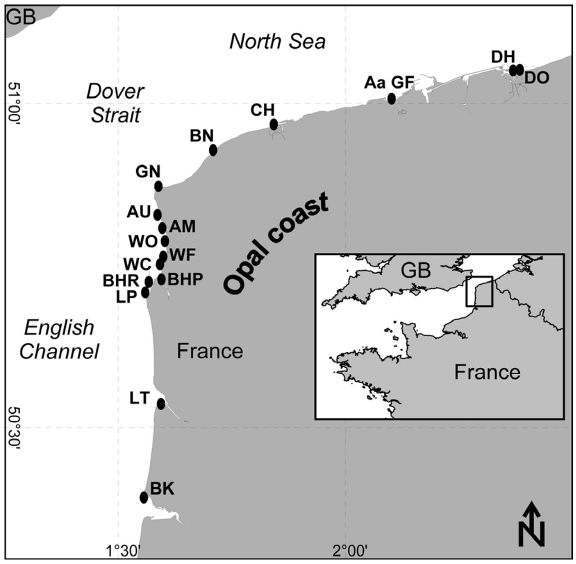

Figure 3. Location of the 16 sites that were sampled along the Opal coast in April-May 2008 (see Table 1 for the abbreviations of the sampled locations)

Material and Methods

Field site

The 160 km of the French side of the eastern English Channel from the Authie estuary in the south to the Belgian border in the southern North Sea is know as the Opal Coast (Figure 3). This coastline is characterised by a succession of sand dunes and rocky shores, extending from Boulogne-sur-mer to Gris Nez Cape and around Blanc Nez Cape. Hard substratum with dykes and boulders are also found at the estuaries of the Authie, Canche and Aa, and in the three main harbours of the region: Boulogne-sur-mer, Calais and Dunkirk. All these potential favourable crab habitats were sampled at the beginning of the spring 2008, from 3 April to 6 May.

Sampling procedure

At each of the 16 sampled sites shown in Figure 3, the crabs collected were found under 3 × 30 boulders in the eulittoral zone (approx. upper, middle and lower) for a total of 270 boulders per site. Although the middle of the eulittoral zone was always sampled at each site, it was not always possible to sample all three parts due to a lack of boulders (Table 1). Depending on the number of boulders at each site, between one and five series of 30 boulders were turned over, with the total number turned over varying between 30 and 270.

In the areas where *Hemigrapsus* species were present in abundance, an estimation of the species density was made based on a 1 m^2 quadrat, with six replicates being done at each site (except outside Dunkirk harbour, where only three replicates were sampled) (Table 2). The densities of the crabs were also estimated in sub-quadrats of 0.25 m^2 in four sites on three square meters at each site, for a total of 12 sub-quadrats (Table 3). Rocks and boulders were turned over to collect the crabs; in some cases, it was also necessary to extract the crabs from the burrows that they had excavated.

Table 1. Main sampling characteristics of the three shore crabs; *Carcinus maenas*, *Hemigrapsus sanguineus* and *H. takanoi*—collected at the 16 Opal coast sites (upper, middle and lower eulittoral zones) on sampling dates during spring 2008. Mean number under 30 boulders ± Standard Deviation. See Figure 1 for the site locations

Sites locations names and abbreviations (in bold), coordinates and sampling dates	N. boulders	Total number of crabs collected	*C. maenas*	*H. sanguineus*	*H. takanoi*
Berck – Authie **BK** (50°23'36"N, 1°33'27"E); 09/04/2008)	4 × 30	222	55.25 ± 5.12	0.25 ± 0.5	-
Le Touquet – Canche **LT** (50°32'12"N, 1°35'38"E; 09/04/2008)	3 × 30	80	26.68 ± 9.87	-	-
Le Portel **LP** (04/04/2008)	9 × 30	180	17.78 ± 14.98	2.22 ± 3.27	-
Upper (50°42'28"N, 1°33'34"E)	3 × 30	99	28.67 ± 21.73	4.33 ± 4.93	-
Mid (50°42'29"N, 1°33'36"E)	3 × 30	42	11.67 ± 10.41	2.33 ± 2.08	-
Lower (50°42'30"N, 1°33'40"E)	3 × 30	39	13.00 ± 7.00	-	-
Boulogne Harbour (R) **BHR** (50°43'29"N, 1°34'02"E; 24/04/2008)	2 × 30	29	10.5 ± 0.71	4.00 ±5.65	-
Boulogne Harbour (P) **BHP** (50°43'41"N, 1°35'49"E; 24/04/2008)	4 × 30	168	11.25 ± 3.50	0.75 ± 1.50	30.00±19.4
Wimereux Créche **WC** (07/04/2008)	9 × 30	82	6.67 ± 3.35	2.44 ± 2.30	-
Upper (50°45'01"N, 1°35'49"E)	3 × 30	21	4.33 ± 3.21	2.67 ± 3.06	-
Mid (50°45'06"N, 1°35'27"E)	3 × 30	30	8.33 ± 3.05	1.67 ± 2.08	-
Lower (50°45'06"N, 1°35'26"E)	3 × 30	30	7.33 ± 3.51	2.67 ± 2.52	-
Wimereux 'Fort de Croy' **WF** (50°45'02"N, 1°35'41"E; 05/04/2008)	3 × 30	141	18.00 ± 9.54	29.00 ±15.87	-
Wimereux 'Pointe aux Oies' **WO** (03/04/2008)	9 ×30	178	13.44 ± 8.37	6.55 ± 4.59	-
Upper (50°47'15"N, 1°36'10"E)	3 × 30	28	7.33± 1.53	1.67 ± 1.15	-
Mid (50°47'13"N, 1°36'05"E)	3 × 30	58	9.00 ± 6.08	10.33 ± 5.77	-
Lower (50°47'13"N, 1°36'02"E)	3 × 30	92	23.67 ± 1.53	7.00 ± 0.00	-
Ambleteuse **AM** (03/04/2008)	9 × 30	90	4.44 ± 4.90	4.67 ± 7.33	-
Upper (50°48'26"N, 1°35'49"E)	3 × 30	2	0.67 ± 0.58	-	-
Mid (50°48'11"N, 1°35'55"E)	3 × 30	36	3.33 ± 3.21	8.67 ± 12.50	-
Lower (50°48'08"N, 1°35'51"E)	3 × 30	52	12.67 ± 6.81	4.67 ± 3.21	-
Audresselles **AU** (10/04/2008)	9 × 30	50	4.17 ± 3.06	4.17 ± 5.23	-
Mid (50°49'51"N, 1°35'19"E)	3 × 30	35	3.33 ± 3.06	8.33 ± 4.04	-
Lower (50°49'38"N, 1°35'11"E)	3 × 30	15	5.00 ± 3.46	-	-
Gris Nez Cape **GN** (08/04/2008)	9 x 30	59	1.33 ± 1.33	4.00 ± 6.67	-
Upper (50°52'19"N, 1°35'19"E)	3 x 30	16	0.33 ± 0.58	1.33 ± 1.53	-
Mid (50°52'20"N, 1°35'15"E)	3 × 30	35	1.00 ± 0.00	10.67 ± 8.62	-
Lower (50°52'23"N, 1°35'18"E)	3 × 30	8	2.67 ± 1.53	-	-
Blanc Nez Cape **BN** (50°55'41"N, 1°42'31"E; 10/04/2008)	4 × 30	7	0.75 ± 0.96	1.00 ± 1.15	-
Calais Harbour **CH** (50°58'03"N, 1°50'31"E; 10/04/2008)	1 × 30	15	12	1	2
Grand Fort Philippe – **AaGF** (51°00'30"N, 2°06'01"E; 21/04/2008)	5 × 30	83	4.4 ± 2.40	-	12.2 ± 8.92
Dunkirk outside Harbour **DO** (51°03'03"N, 2°22'03"E; 11/04/2008)	2 × 30	76	4.50 ± 4.94	31.5 ± 13.44	2.00 ± 2.83
Dunkirk Harbour **DH** (51°03'03"N, 2°22'16"E; 06/05/2008)	3 × 30	297	17 ± 4.36	2.33 ± 1.15	73.00±21.66

Laboratory observations

The collected crabs were identified, counted and sexed. Then the carapace width (CW) was measured between the third antero-lateral teeth (Delaney et al. 2008). The class-size histograms were constructed in 1 mm classes.

Statistical analyses

A variety of tests were used to examine different hypotheses (H0 & H1).

A χ^2 test (Scherrer 1984) was used to verify the existence of a distribution pattern:

- H0: there is no distribution pattern, and the distributions of the three shore crabs are identical along the Opal coast.
- H1: there is a shore crab distribution pattern along the Opal coast.

A Wilcoxon-Man-Whitney test (U_{wmw}) was used to test the origin of the distribution pattern if such a pattern existed:

- H0: there was no latitudinal distribution pattern for the three shore crabs.
- H1: there was a latitudinal (North/South) distribution pattern for the three shore crabs.

A Kruskall-Wallis test (KW) (Scherrer 1984) was used to examine the distribution of *H. sanguineus* in the eulittoral zone (upper, mid and lower).

- H0: there was no difference between the three distributions of the shore crabs.
- H1: there was a preference in the Asian shore crab distribution (n > 5 and K>2, where n= number of individuals and K= number of samples).

A Post Hoc test was done *a posteriori* to see whether one sub-zone was more colonised that the others. The test consisted of paired comparison of the upper and middle parts and the upper and lower parts of the eulittoral zone.

- H0: the abundances were similar.
- H1: the abundances were significantly different (Student test).

A χ^2 test was used to analyse the difference in density (n.ind.m^{-2}) at the five sites where the density was estimated.

- H0: the densities of the three shore crabs were similar in all five sites.
- H1: there was a significant difference between the densities of the five sites.

An equal distribution test (d^2) was also performed to test the equi-probability of the samples.

- H0: there was similar chance of sampling all three species.
- H1: one species was dominant.

Results

Presence of both Hemigrapsus species along the Opal coast

Table 1 presents the results of the spring sampling (April-May 2008) along the Opal coast from Berk in the south to Dunkirk in the north (Figure 1). *Hemigrapsus takanoi* was found only in the harbours and at the mouth of the Aa estuary, Grand Port Philippe. The maximal abundance was in the Boulogne-sur-mer and Dunkirk harbours, with means of 30 and 73 individuals under 30 boulders respectively. *Hemigrapsus sanguineus* was more extensively distributed, being recorded at 14 of the 16 prospected sites. This species was absent at two sites: in a low salinity zone in the Canche estuary, Touquet and in a muddy zone heavily colonised by *H. takanoi* at Grand Fort Philippe (GF). Despite this extensive distribution, the abundance of *H. sanguineus* was important in only two sites: Wimereux Fort de Croy (WF) and Outer Dunkirk harbour (ODH), where the mean abundances were 29 and 31.5 individuals under 30 boulders respectively. Distributions of *H. sanguineus* and *Carcinus maenas* were not homogeneous and depended on the sites sampled (χ^2, $p < 0.05$). The proportion of *H. sanguineus* was higher in the sites located to the north of Boulogne-sur-mer (U_{wmw}, $p < 0.05$), while the proportion of *C. maenas* was higher in the sites located to the south of Boulogne-sur-mer where the other shore crabs were absent or rare (U_{wmw}, $p < 0.05$).

Sex-ratio

Among the 2,395 crabs collected during the sampling period (Table 1), 1584 = *C. maneas*, 427 = *H. takanoi* and 384 = *H. sanguineus*. No ovigerous females were found for any *Hemigrapsus* species, and only 13 of the 588 *C. maenas* females recorded carried eggs. The sex ratios (number of males/number of females) were respectively 1.69 for *C. maenas*, 0.96 for *H. takanoi* and 1.31 for *H. sanguineus*.

Class size

The frequency distributions of the male and female 1.0 mm carapace width (CW) classes (Figure 4) indicate a larger extended size class for *C. maenas* than for the two other species. The smallest *C. maenas* male was 4 mm, while the smallest female was 3 mm; the largest male was 47.5 mm, and the largest female was 45 mm. Most of the male and female sizes were similar, ranging from 9 to 25 mm (mean size about 16-17 mm) (Figure 4A). The smallest *H. takanoi* (male and female) was 7 mm, while the largest female was 20 mm and the largest male was 25 mm. Most of the males and females were similar in size, ranging from 9 to 19 mm (mean size about 12-13 mm) (Figure 4B). For the third species, *H. sanguineus*, the smallest male was 4 mm and the largest, 26 mm; the smallest female was 9 mm and the largest, 27 mm. Most of the males and females were similar in size, ranging from 9 to 20 mm (mean size about 12-13 mm) (Figure 4C).

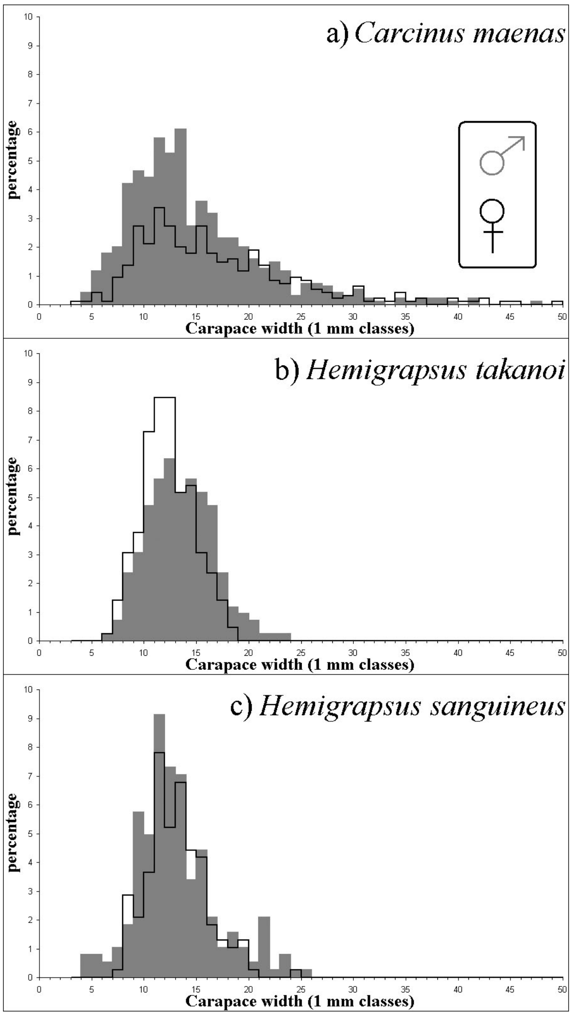

Figure 4. Frequency distribution of carapace-width (1 mm classes) of all species collected under boulders at the 16 sites sampled in April-May 2008: (a) *Carcinus maenas*, (b) *Hemigrapsus takanoi* and (c) *Hemigrapsus sanguineus*

Distribution of Hemigrapsus sanguineus in the littoral zone

The distribution of *H. sanguineus* crabs in the intertidal zone (eulittoral) was analyzed for the abundant specimens collected under 3 × 30 boulders (upper, middle and lower parts of the eulittoral) at six sites: Le Portel (LP), Wimereux Crèche (WC), Wimereux 'Pointe aux Oies' (WO), Ambleteuse (AM), Audreuselles (AU) and cape Gris Nez (GN) (Table 1). Statistical tests revealed that the distribution of *H. sanguineus* was not similar in the three part of the eulittoral (KW, $p < 0.01$) and that the abundance of the species in the mid-eulittoral was significantly higher than those found in the upper and lower part of the eulittoral (Post Hoc test, $p < 0.01$). There was no significant difference between the estimated abundances for the upper and the lower eulittoral. In addition, no specimens of this species were collected in the upper eulittoral at AM, and none were found in the lower eulittoral at LP and GN.

Density of the three shore crabs

The densities of the three species of shore crabs were estimated at the five sites where the abundances of both *Hemigrapsus* species were significant [i.e., Boulogne-sur-mer Harbour (BHP), Wimereux Fort de Croy (WF), Grand Fort Philippe (GF), Outer Dunkirk Harbour (ODH) and Dunkirk Harbour (DH)] (Table 2). The density of *C. maenas* varied between 5.8 and 14.3 ind.m^{-2}, while that of *H. sanguineus* varied between 0.7 to 12.0 ind.m^{-2}. The density of *H. takanoi* was higher, varying from 12.1 to 60.2 ind.m^{-2}. At WF and ODH, *H. sanguineus* dominated *C. maenas* significantly (d^2, $p < 0.01$); at GF and DH, *H. takanoi* dominated *H. sanguineus* and *C. maneas* significantly (d^2, $p < 0.01$); and at BHP, *C. maenas* dominated *H. takanoi* (d^2, $p < 0.01$). In April-May 2008, there was no significant difference in the sizes of the *H. sanguineus* males and females sampled at WF and ODH and between the male and female *H. takanoi* sampled at BHP, GF and DH.

Table 2. Density (number of individuals per square meter) of the three shore crabs: *Carcinus maenas* (***CM***), *Hemigrapsus sanguineus* (***HS***) and *H. takanoi* (***HT***), estimated at five Opal coast sites during spring 2008. N.m^2 (number of quadrats used to estimate the density). Mean ± Standard Deviation. See Figure 1 for the site locations, Table 1 for site names

Sites	N. m²	***CM***	***HS***	***HT***
BHP	6	14.33±7.06	-	12.17±5.84
WF	6	5.83±5.00	11.17±5.04	-
AaGF	6	7.83±6.24	-	15.00±5.21
DO	3	7.33±1.16	12.00±5.00	-
DH	6	6.17±3.31	0.67±0.82	60.17±21.28

Table 3. Number of ind.0.25m^{-2} in 12 sub-quadrats of the three shore crabs: *Carcinus maenas* (***CM***), *Hemigrapsus sanguineus* (***HS***) and *H. takanoi* (***HT***), estimated at 5 Opal coast sites during spring 2008. SQ*ij*: sub-quadrat, where *i* is the numbering of quadrat and *j* that of the sub-quadrat. See Figure 1 and Table 2 for the site locations and names

Sites	***CM***	***HS***	***HT***
BHP			
SQ11	1	-	2
SQ12	1	-	1
SQ13	2	-	6
SQ14	2	-	3
SQ21	6	-	6
SQ22	2	-	1
SQ23	4	-	4
SQ24	6	-	2
SQ31	6	-	4
SQ32	6	-	0
SQ33	9	-	2
SQ34	3	-	0
WF			
SQ11	0	4	-
SQ12	0	1	-
SQ13	1	5	-
SQ14	0	3	-
SQ21	0	2	-
SQ22	2	1	-
SQ23	3	1	-
SQ24	0	0	-
SQ31	0	2	-
SQ32	2	0	-
SQ33	3	3	-
SQ34	6	1	-
Aa GF			
SQ11	3	-	4
SQ12	5	-	4
SQ13	3	-	3
SQ14	2	-	7
SQ21	2	-	2
SQ22	1	-	0
SQ23	2	-	10
SQ24	1	-	5
SQ31	2	-	1
SQ32	3	-	7
SQ33	2	-	5
SQ34	1	-	9
DH			
SQ11	1	-	6
SQ12	0	-	2
SQ13	6	-	9
SQ14	0	-	4
SQ21	0	-	31
SQ22	1	-	16
SQ23	4	-	12
SQ24	2	-	13
SQ31	1	-	15
SQ32	1	-	20
SQ33	1	-	12
SQ34	1	-	35

For four sites (BHP, WF, GF and DH), 0.25 m^2 sub-quadrats were sampled to identify the respective densities of the three shore crabs (Table 3). For three of the four sites (BHP, WF and GF), there was no significant dominance of the non-indigenous species *Hemigrapus* over *C. maenas*. However, at DH, *H. takanoi* dominated *C. maneas* significantly (d^2, $p < 0.01$). In fact, of all the sites sampled along the Opal coast in spring 2008, this site had the highest density of *H. takanoi* (Table 2).

Discussion

Hemigrapsus takanoi and *H. sanguineus* are presumed to have been introduced along the European coast by larvae released from ballast water (Noël et al. 1997; Gollasch 1999; Breton et al. 2002). By April-May 2008, respectively two and three years after the first observations in the Opal coast, both species are now common in all this area.

At the five sites where crab densities were estimated (i.e., BHP, WF, GF, ODH and DH), the sediment particle size distribution was analyzed by dry-sieving the sediment through a stack of Wentworth-grade sieves using the Buchanan technique. Percentages were calculated for each of five sediment types, defined according to grain size: gravel (> 2000 µm), coarse sand (500-2000 µm), medium sand (200-500 µm), fine sand (63-200 µm) and silt/clay (< 63 µm) (Table 4). Both *Hemigrapsus* habitats showed a bimodal distribution, with medium sand and gravel for *H. takanoi* and fine sand and gravel for *H. sanguineus*. The proportion of fine sand was higher at WF than at ODH, and the proportion of silt-clay was higher at GF than at any other site, particularly DH. There is a segregation of the habitats colonised by the two non-indigenous species: *H. takanoi* tends to occupy low hydrodynamic habitats with mud, while *H. sanguineus* tends towards high hydrodynamic habitats with fine and medium sands. Usually, both species can live in sympatry in the habitats favoured by *H. takanoi*, though at Grand Fort Philippe (Aa estuary), no *H. sanguineus* were sampled with *H. takanoi*.

Hemigrapsus takanoi: habitat and distribution

Hemigrapsus takanoi was found in low hydrodynamic zones, such as the Aa estuary and the harbours at Boulogne-sur-mer and Dunkirk, where abundant populations existed under the boulders covering the soft-bottom composed of gravel, medium sand and mud. In Calais harbour, only two specimens were found, but the area sampled (lower eulittoral) had few boulders and thus the habitat appeared unfavourable for crabs. Class-sizes in colonised sites were similar, probably indicating the synchronous colonisation of this non-indigenous species in favourable habitats along the Opal coast. The sex-ratio (≈ 1) was similar to the one reported by Noël et al. (1997) for the French Atlantic coast, but the largest specimens found along the Opal coast were smaller than those found on the French Atlantic coast: 25 mm vs. 28 mm for the males and 20 mm vs. 23 mm for the females respectively. In the Netherlands, the biggest males of *H. takanoi* are found below tide marks, at least in some localities (C. d'Udekem d'Acoz, personal communication).

Since its first recorded sighting at La Rochelle on French Atlantic coast in 1994 (Noël et al. 1997), the species has been reported along the coast of the Bay of Biscay from Laredo in Spain

Table 4. Main characteristics of the sediment in five sites: Boulogne harbour (BHP), Grand Fort Philippe – Aa (GF), Dunkirk harbour (DH), Wimereux Fort de Croy (WF) and outer Dunkirk harbour (ODH). Mean ± Standard Deviation

	BHP	GF	DH	Mean sediment-size for *H. takanoi* habitat	WF	DO	Mean sediment-size for *H. sanguineus* habitat
Silt-clay (< 63 µm)	4.95	10.85	2.00	4.50 ± 4.51	0.75	1.89	1.32 ± 0.81
Fine sand (63-200 µm)	5.82	5.54	17.51	9.62 ± 6.83	15.22	44.05	29.63 ± 20.38
Medium sand (200-500 µm)	29.73	17.97	17.60	21.78 ± 6.90	30.77	9.02	19.90 ± 15.38
Coarse sand (500-2000 µm)	11.00	3.64	9.55	8.06 ± 3.90	16.93	11.03	13.98 ± 4.17
Gravel (> 2000 µm)	48.50	62.00	43.75	51.42 ± 9.47	36.33	34.01	35.17 ± 1.64

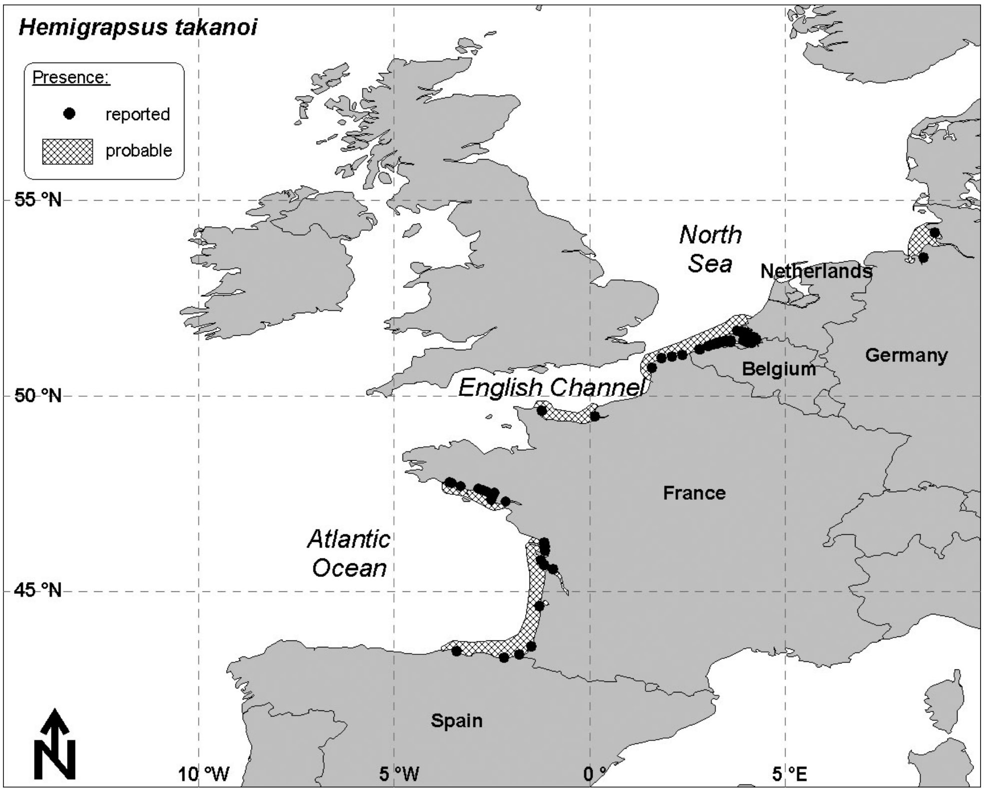

Figure 5. Distribution of *Hemigrapsus takanoi* along the north-eastern Atlantic coast from its introduction in Europe in 1994 to July 2008 (see text and Annex 1 for the reported locations)

and north of the Bay of Biscay (Loire Atlantique and Morbihan (Noël et al. 1997; Noël and Gruet 2008). Breton et al. (2002) reported its presence in Le Havre harbour during 1999. In August 2008, one adult male was sampled at Saint-Vaast-La-Houge in the Bay of Seine (Dauvin 2009). Apart from the Opal coast, which is the southern limit of its presence in the North Sea (Figure 5), *H. takanoi* is now common along the coasts of Belgium (Dumoulin 2004; d'Udekem d'Acoz 2006; Nuyttens et al. 2006) and the Netherlands (Nijland 2000; Nijland and Beekman 2000; Nijland 2000; Faasse et al. 2002; d'Udekem d'Acoz and Faasse 2002; Dumoulin 2004). It has been observed in Germany since August 1993, first in the Bremerhaven harbour in the hull fouling of a commercial vessel (Gollasch 1999) and later in Lower Saxony at Norddeich (Obert et al. 2007) (Figure 5). For the time being, this species has not been reported from the English coast and in France from the south of Brittany to the western part of the Bay of Seine, in spite of favourable habitats in harbours, such as Brest and Saint-Malo, and in many small estuaries around the Brittany. However *H. takanoi* is present along approximately 1,000 km of coastline, ranging from the western part of the Bay of Seine in France to Lower Saxony in Germany.

Along the Atlantic coast, the maximum density of *H. takanoi* in the 1990s was 20 ind.m^{-2} (Noël et al. 1997), and 5 ind.m^{-2} in the Osterscheldt, Netherlands during September 2000 (Nijland 2000). In spring 2008, only two years after its first observation in Dunkirk harbour its density reached 60 ind.m^{-2}, five times higher than the density of its congeneric species *H. sanguineus* (maximum 12 ind.m^{-2}). This shows the high colonisation potential of this non-indigenous species, which can produce up to 50,000 eggs three to four times during the spawning season (McDermott 1998a). Since no ovigerous female was found during the spring sampling period, the spawning period must start later in the summer, as with *H. sanguineus*. Spawning period begins in May in the Bay of Biscay (Noël et al. 1997).

Hemigrapsus sanguineus: habitat and distribution

Hemigrapsus sanguineus was found in abundance on the rocky shores of the Opal coast from the Alprech Cape to the Gris Nez Cape (Figure 3) under the boulders on soft-bottoms composed mainly of fine sand and gravel. The entire eulittoral zone appeared to be colonised, but during the spring sampling period (April-May), the mid-eulittoral was the preferred habitat of this Asian shore crab. This is in agreement with the observations of C. d'Udekem d'Acoz (personal communication) in the Eastern Scheldt, the Netherlands. In that area, *H. sanguineus* was found rather high on the shore and not on the lowest part of the shore. On the other hand, *H. takanoi* is spread on most on the shore and is also found below tide marks. However the high limestone cliffs such as the Cape Blanc Nez with its flint boulders and mobile coarse sand due to high hydrodynamics, was unfavourable for this non-indigenous crabs; only four *H. sanguineus* specimens were found under the 90 boulders at Cape Blanc Nez. Outside the rocky section of the Opal coast (Figure 3), boulders were only present along the estuary dykes, at Authie, Canche and Aa, and the three main harbours at Boulogne-sur-mer, Calais and Dunkirk. Although such habitats appear to be favourable for *H. sanguineus*, only one individual was found at Berk on the Authie estuary to the south of Boulogne-sur-mer. None were found at the mouth of the Canche estuary, probably due to the low salinity in the zone sampled.

The spring distribution along the Opal coast, with the highest abundances occurring in the mid-eulittoral, was comparable to those reported from along the North American coast, but the species was also observed in the subtidal zone during winter period (Kraemer et al. 2007). *Hemigrapsus sanguineus* can survive in various biotopes including artificial structures, mussel beds and oyster reefs; however it is usually found under the shelter of rocks, shells and other debris on tidal flats (McDermott 1991, 1998a, b; Ahl and Moss 1999; Williams and McDermott 1990). Furthermore, *H. sanguineus* is able to tolerate a wide range of salinities and temperatures, as well as the damp conditions in the upper intertidal regions (Benson 2005). In Tanaba Bay, the recruitment of juveniles was evident in the upper and mid-eulittoral, with the larger individuals migrating to the lower eulittoral (Lohrer et al. 2000).

Class sizes were similar in the colonised sites of the Opal coast. Nevertheless, the maximal CW observed (26 mm for the males and 27 mm for the females) were smaller than those reported along the Atlantic coast of the United States,

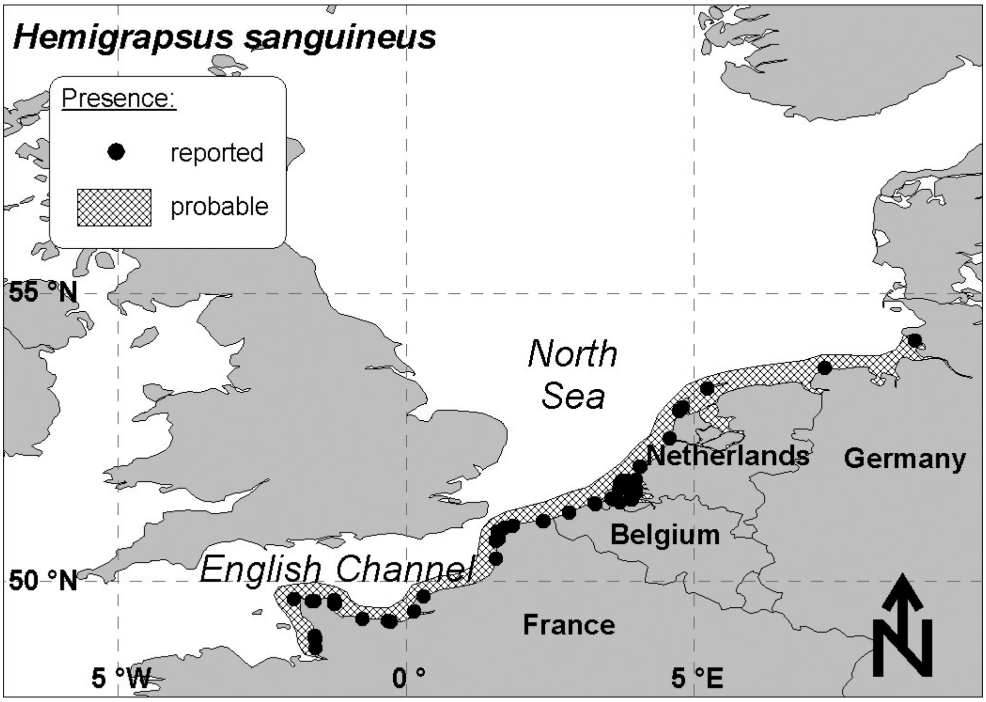

Figure 6. Distribution of *Hemigrapsus sanguineus* in the English Channel and the southern part of the North Sea from its introduction in Europe in 1999 to July 2008 (see text and Annex 1 for the reported locations)

where the sizes reached 43 mm for the males and 36 mm for the females (McDermott 1998a), and smaller than those observed in the Cotentin (French side of the English Channel) during the summer 2008 (34 mm for the males and 31 mm for the females) (Dauvin 2009).

Figure 6 shows the current known distribution of *H. sanguineus* for the northeastern European coast. They are present over approximately 1,100 km, including the coasts of the western part of the Channel (Dauvin 2009), the Bay of Seine (Breton et al. 2002; P. Hacquebart personal communication), the eastern part of the Channel (this study and F. Durand, personal communication), Belgium (Breton et al. 2002; Kerckhof et al. 2007), the Netherlands (Nijland and Beckman 2000; d'Udekem d'Acoz and Faasse 2002; Faasse 2004; Campbell and Nijland 2004; Nijland and Faasse 2005; Nuyttens et al. 2006; d'Udekem d'Acoz 2006) and Germany (Obert et al. 2007). This species has been recorded in the Mediterranean Sea only once, in August 2001 in the northern Adriatic (Schubart 2003).

Hemigrapsus sanguineus was observed for the first time in 1988 at Cape May, New Jersey, United States (Williams and McDermott 1990). By 2008, it had colonised the entire temperate zone from North Carolina to Maine (McDermott 1998b, 2000; Delaney et al. 2008). The colonised habitats are varied littoral zones, estuaries and/or mudflats that have rocks, boulders and shells (McDermott 1991, 1998b; Ahl and Moss 1999; Williams and McDermott 1990; Gerard et al. 1999; Jensen et al. 2002; Brousseau et al. 2003; Kraemer et al. 2007; Delaney et al. 2008). The maximum densities on the United States coast were those reported by McDermott (1998b) for the site 'Townsends and Hereford Inlets' in New Jersey, where the density was 320 ind.m^{-2}, and by Kraemer et al. (2007) for a site in western Long Island Sound in 2001-2002, where the density was 350 ind.m^{-2}. Other densities over 100 ind.m^{-2} have been reported along this coast: 150 ind.m^{-2} on Long Island (Brousseau et al. 2003) and 190 ind.m^{-2} at Demerest Lloyd State Park in Massachusetts (Jensen et al. 2002). Still, for 52 sites along a 725 km coastal transect from New Jersey to Maine, Delaney et al. (2008) reported a lower density in August 2005, with a maximum of about 44 ind.m^{-2} in the south of the transect and a total absence of this species in the northern part of transect as far as 43°48.5'N latitude. It is possible that, after a phase of intense colonisation, the density declined. In the western part of Long Island Sound estuary, Kraemer et al. (2007) recorded a reduction of the mean density from about 120 ind.m^{-2} in the period 1998-2001 to 80 ind.m^{-2} in the period 2002-2005.

This probably indicates that the Opal coast population, with its maximal density of 12 ind.m^{-2}, is just beginning its colonisation and that the maximum of density will be reached only in several years. Similar abundances, around 10, were also observed by Dauvin during summer 2008 in northern Cotentin (English Channel) (Dauvin 2009). Like *H. takanoi*, *H. sanguineus* shows a high colonisation potential. This species can produce up to 40,000 eggs several times during the spawning season (McDermott 1998a). No ovigerous females were found during the spring period. The spawning period apparently starts later in the summer: 72.5 % of females found in northern Cotentin in the summer of 2008 in temperature conditions similar to the Opal coast were ovigerous. The sex-ratio (1.31) was similar that the one reported by McDermott (1998b) for the Atlantic coast of the United States (1.23), with the number of males higher the number of the females.

Competition with Carcinus maenas

When *H. sanguineus* occur in high densities, this species can play an important role in restructuring the prey communities in intertidal habitats because they have the potential to affect populations of native species such as crab, fish, and shellfish by disrupting the food web (Brousseau et al. 2001). Specifically, this Asian species occupies habitats similar to the common shore crab *Carcinus maenas*, but along the American coast, it also competes with larger species, like the blue crab *Callinectes sapidus* Rathbun, 1896 and the rock crab *Cancer irroratus* Say, 1817 (Gerard et al. 1999; Tyrell and Hariis 1999; Jensen et al. 2002). *Carcinus maenas* has been reported to reduce feeding when *H. sanguineus* is present (Griffen and Byers 2006). Nevertheless, MacDonald et al. (2007) has shown that *C. maenas* is better than *H. sanguineus* at obtaining food, probably because it is the fastest at finding and consuming the food, as has been shown experimentally by De Graff and Tyrell (2004).

According to Jensen et al. (2002), *C. maenas* has become uncommon under rocks in some areas from the east coast of North America since the arrival of *H. sanguineus*. These authors demonstrated that the number of *C. maenas* juveniles under rocks is drastically reduced in the presence of *H. sanguineus*, compared to areas when the two species do not overlap. C. d'Udekem d'Acoz (personal communication) has observed a drastic reduction in the number of juvenile *C. maenas* in some Dutch shore with a very high density of *H. takanoi*. Only 20% of *C. maenas* juveniles in the study of Jensen et al. (2002) being found under rocks in areas occupied by *Hemigrapsus*. Similarly, in their New Jersey to Maine transect, Delaney et al. (2008) observed the absence or low density of *C. maenas* in the areas colonised by *H. sanguineus*, and conversely higher abundances of *C. maenas* where *H. sanguineus* was absent. A similar pattern was observed for the Opal Coast, with a dominance of *C. maenas* south of Boulogne-sur-mer in an area weakly colonised by both non-indigenous *Hemigrapsus* species. For the moment, no competition has been found between the two non-indigenous species. But in the Dunkirk harbour, *H. takanoi* dominated the native shore crab *C. maenas* significantly; this site had the highest density of crabs in the spring of 2008 (60 ind.m^{-2}).

Future distribution and possible impact of Hemigrapsus species along the European coasts

The reproductive output of *H. sanguineus* is important: mature females may have 3-4 clutches per breeding season, with a mean clutch size of 15,000 and a maximum of at least 40,000-50,000 eggs per crab, but the number of these eggs which hatched and the larval survival in the filed remain unknown (McDermott 1998b; Gerard et al. 1999). Planktonic larval stages, which last for about a month under optimal temperature and salinity conditions (Epifanio et al. 1998), vary in relation to the sea temperature, from 16 days at 25°C to 55 days at 15°C, thus providing an efficient mechanism for dispersal. This long larval dispersal phase could be favourable to the propagation of the species in the Channel and the North Sea under a megatidal regime that ensures efficient larval dispersal (Ellien et al. 2000).

For both non-indigenous *Hemigrapsus* species, it is hypothesized that they have probably dispersed from the Netherlands and Belgium populations which were being introduced with ballast water (Gollasch 1999). This road of colonization from the North Sea to the eastern part of the English Channel was well illustrated for the introductive razor clam *Ensis directus* (Conrad, 1843). Since the first specimens were found in 1979 near the mouth of the river Elbe in the German Bight, its extension in the North-European waters was rapid (Dauvin et al. 2007). Its progression in the eastern Channel appears to move in the opposite direction of the residual tidal transport and its distribution reaches nowadays the eastern Bay of Seine (Dauvin et al. 2007). The late colonization of Berk site which is the southwards and the most distant from Belgium reinforces this hypothesis on North Sea origin of the *Hemigrapsus* species along the Opal Coast.

In Japanese waters, the growth and maturation of these *Hemigrapsus* is rapid. Newly settled juveniles have a mean carapace width around 2 mm but reach 20 mm in about two years (Fukui 1988). The crabs become reproductively mature at this age and, although growth is slower in mature crabs, they can reach a maximum carapace width of 40 mm, corresponding to a maximum lifespan of around eight years. This old age was probably exceptional and more of the adult specimen could be life more than 2 years (C. d'Udekemn d'Acoz, personal communication). Ledesma and O'Connor (2001) and McDermott (1998a) have suggested that the length of the reproductive period of *H. sanguineus* is related to latitude and therefore to water temperature. In southern parts of Japan, the breeding season is 8 months long (Fukui 1988), whereas in northern Japan, it lasts three months (Takahashi et al. 1985 in McDermott 1998a).

Although McDermott (1998a) reported that breeding occurred through September at Gooseberry in Buzzards Bay, ovigerous females were found only until early August in Sandwich in Cape Cod Bay. In New Jersey, ovigerous females were observed from June to August, with some of them producing at least two broods during the summer. In New Jersey, the smallest female was 12.1 mm and the largest was 35.8 mm. It is probable that this smallest female was only one year old, given that during the July-August 2008 observations in northern Cotentin (the French coast of the English Channel), the smallest female was 13 mm and the largest was 31 mm, whereas the largest male was 34 mm (Dauvin 2009).

In the Western Pacific, the distribution of *H. sanguineus* ranges from ~20° to 50°N latitude, including the coasts of Hong Kong, Taiwan and Japan and the Pacific coast of China and Korea (McDermott 1998a). On the eastern coast of the United States, this species has been present from North Carolina to Maine ~ 34° to 43°N (McDermott 1998b; Delaney et al. 2008). On the European coast, the latitude ranges today from ~ 49° to 54°N, but the northern limit can extend northwards to ~ 60-65°N due to the warmer temperatures along the north-eastern European coast in relation to the North Atlantic drift. In the future, *H. sanguineus* may also extend its European distribution southwards to north-eastern Africa, thus invading the entire Mediterranean, where it could be in competition with a common native Grapsinae crab *Pachygrapsus marmoratus* (J.C. Fabricius 1787).

It is also possible that the second species *H. takanoi* will increase its latitudinal distribution considerably in the European waters, as *H. sanguineus* will likely do to the south and northwards ~ 60-65°N in relation to the North Atlantic drift. But the preferred harbour habitats of *H. takanoi* have poorly diversified benthic communities due to the confined environment and the organic and metallic pollutions that eliminate sensitive species. This could well be the best location to examine its competition with *C. maenas*, which appears to be abundant in the muddy sediment under boulders.

In the future it may be necessary to survey: i) the geographical extension of both *Hemigrapsus* species along the European coast, especially in the UK; ii) the increase of the established populations along the Opal Coast, particularly *H. sanguineus*, which is known to produce chemical cues that promote gregarious settlement and encourage rapid population increases in colonised areas (Kopin et al. 2001; O'Connor 2007); iii) the competition with intertidal crabs, not only with *C. maenas* but also with those with an intertidal juvenile phase that have commercial value, such as *Cancer pagurus* and *Necora puber* (L., 1767); iv) the possible consumption of *Hemigrapsus* by top level predators; i.e. Kim and O'Connor (2007) found that *H. sanguineus* megalops can be consumed by the killifish, *Fundulus majalis* (Walbaum, 1792); and v) the potential effect of predation on wild intertidal *Mytilus edulis* (L., 1758) populations and the *Mytilus edulis* and *Crassostrea gigas* cultivated in shellfish farms. Shellfish production is highly developed along the French Atlantic coast and is essential for the coastal economy. In fact, if *H. sanguineus* migrated to deeper waters during the winter, it could present a threat to these mussel and oyster farms. But due to the low temperature, its metabolism will slow down and the predation will be reduced.

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Annex 1
Published records of invasive species crabs, *Hemigrapsus sanguineus* and *Hemigrapsus takanoi* (along the north-eastern Atlantic coast)

Species	Location	Geographic coordinates		Record date	Reference
		Latitude	Longitude		
Hemigrapsus sanguineus	Granville outside harbour (Cotentin, France)	48°49'58"N	1°36'28"W	29/07/2008	Dauvin 2009
	Agon-Coutainville (Cotentin, France)	49°01'29"N	1°36'01"W	17/08/2008	Dauvin 2009
	Blainville sur mer (Cotentin, France)	49°03'33"N	1°36'47"W	12/07/2008	Dauvin 2009
	Gonneville (Cotentin, France)	49°04'57"N	1°36'43"W	02/08/2008	Dauvin 2009
	Goury (Cotentin, France)	49°42'53"N	1°56'45"W	05/08/2008	Dauvin 2009
	Querqueville (Cotentin, France)	49°40'08"N	1°40'47"W	12/08/2008	Dauvin 2009
	Salines (Cotentin, France)	49°39'28"N	1°38'45"W	05/08/2008	Dauvin 2009
	Gatteville-Phare (Cotentin, France)	49°41'44"N	1°15'56"W	11/08/2008	Dauvin 2009
	Saint-Vaast (Cotentin, France)	49°35'34"N	1°15'48"W	11/08/2008	Dauvin 2009
	La Hougue (Cotentin, France)	49°34'30"N	1°16'18"W	11/08/2008	Dauvin 2009
	Le Havre harbour (Bay of Seine, France): • the Môle Central • the Canal Central Maritime	49°29'11"N	0°06'23"E	29/08/1999 24/10/1999	Breton et al. 2002
	Knokke Heist, Nieuwpoort (Belgium)	51°21'07"N	3°17'42"E	2006	Kerckhof et al. 2007
	Knokke Heist, Duinbergen (Belgium)	51°20'44"N	3°15'35"E	20/07/2006	d'Udekem d'Acoz 2006
	Knokke Heist, Albertstrand (Belgium)	51°20'50"N	3°16'29"E	21/07/2006	d'Udekem d'Acoz 2006
	Estuary "Oosterchelde", Schelphoek (Netherlands)	51°41'26"N	3°49'03"E	21 and 23/08/1999	Breton et al. 2002
	Hoek van Holland (Netherlands)	51°58'35"N	4°07'56"E	04/2004	Campbell and Nijland 2004, Faasse 2004
	Delta area in the south-west of the Netherlands	51°51'18"N	4°02'50"E	1999 and 2004	d'Udekem d'Acoz and Faasse 2002, Faasse 2004
	Nieuwpoort-Bad (Netherlands)	51°09'14"N	2°42'23"E	2006	Nuyttens et al. 2006
	Lower Saxony on the island of Norderney (Germany)	53°42'31"N	7°08'51"E	29/11/2007	Obert et al. 2007
	Schleswig-Holstein (Germany)	54°30'57"N	9°34'09"E	End 2006	Obert et al. 2007
Hemigrapsus takanoi	Laredo (Spain)	43°24'43"N	3°24'40"W	1997	Noël et al. 1997
	Barzan: «beach» (Gironde estuary, France)	45°30'47"N	0°52'16"W	unknown	Noël and Gruet 2008
	Meschers-sur-Gironde: « Plage des Nonnes, Carrières de Meschers» (Gironde estuary, France)	45°33'24"N	0°57'39"W	28/10/2003	Noël and Gruet 2008
	Saint-Georges-de-Didonne: « Ile aux Mouettes » (Gironde estuary, France)	45°36'19"N	1°00'48"W	29/10/2003	Noël and Gruet 2008
	Vaux-sur-Mer: « Nauzan » (Gironde estuary, France)	45°38'05"N	1°04'36"W	30/10/2003	Noël and Gruet 2008
	Saint-Palais-sur-Mer: « Nauzan North » (Gironde estuary, France)	45°38'21"N	1°05'33"W	30/10/2003	Noël and Gruet 2008
	La Rochelle (Vendée coast, France)	46°35'20"N	1°09'36"W	1994	Noël et al. 1997
	Sainte-Radégonde-des-Noyers: « Sèvre-Niortaise estuary » (Vendée coast, France)	46°18'16"N	1°08'39"W	08/10/2005	Noël and Gruet 2008
	L'Aiguillon-sur-Mer: « Lay estuary and harbour » (Vendée coast, France)	46°18'47"N	1°20'04"W	08/10/2005	Noël and Gruet 2008
	Talmont-Saint-Hilaire: Payré estuary and Guittière harbour (Vendée coast, France)	46°25'29"N	1°35'45"W	08/10/2005	Noël and Gruet 2008

Annex 1 (continued)

Species	Location	Geographic coordinates		Record date	Reference
		Latitude	Longitude		
Hemigrapsus takanoi	Les Sables-d'Olonne: « Bassin des Chasses » and Olona harbour (Vendée coast, France)	46°29'25"N	1°46'37"W	09/10/2005	Noël and Gruet 2008
	Brem-sur-Mer:« Etier et marais de la Gachère » (Vendée coast, France)	46°36'03"N	1°51'34"W	09/10/2005	Noël and Gruet 2008
	Saint-Gilles-Croix de Vie: « Estuaire de la Vie » (Vendée coast, France)	46°41'49"N	1°56'49"W	09/10/2005	Noël and Gruet 2008
	Saint-Gilles-Croix de Vie: « harbour» (Vendée coast, France)	46°41'36"N	1°56'19"W	02/02/2007	Noël and Gruet 2008
	La Barre-de-Monts: « Etier et baie de Bourgneuf » (Vendée coast, France)	46°53'33"N	2°08'17"W	09/10/2005	Noël and Gruet 2008
	Beauvoir-sur-Mer: « Port du Bec et étier » (Vendée coast, France)	46°56'15"N	2°04'20"W	09/10/2005	Noël and Gruet 2008
	Barbâtre: « La Berche, île de Noirmoutier » (Vendée coast, France)	46°56'29"N	2°11'15"W	17/11/2005	Noël and Gruet 2008
	Bouin: « Port des Champs » (Vendée coast, France)	46°58'09"N	2°02'00"W	19/10/2005	Noël and Gruet 2008
	Bouin: « Port des Brochets » (Vendée coast, France)	46°58'17"N	2°02'26"W	9/10/2005	Noël and Gruet 2008
	Pornic: « harbour » (Atlantic coast, France)	47°07'58"N	2°06'14"W	19/10/2005	Noël and Gruet 2008
	Paimboeuf: « Loire estuary » (Atlantic coast, France)	47°17'27"N	2°02'01"W	09/10/2005	Noël and Gruet 2008
	Guérande: « Traict du Croisic, Sissable » (Atlantic coast, France)	47°18'13"N	2°29'14"W	03/01/2006	Noël and Gruet 2008
	Assérac: « Pointe de Pen Bé » (Atlantic coast, France)	47°25'24"N	2°27'29"W	03/01/2006	Noël and Gruet 2008
	Camöel: « Vilaine estuary » (Morbihan and Finistere coast, France)	47°30'08"N	2°23'43"W	24/10/2005	Noël and Gruet 2008
	Pénerf: « Harbour » (Morbihan and Finistere coast, France)	47°30'31"N	2°37'48"W	03/05/2006	Noël and Gruet 2008
	Larmor-Baden: « Golfe du Morbihan, Pen En Toul » (Morbihan and Finistere coast, France)	47°34'57"N	2°37'48"W	03/05/2006	Noël and Gruet 2008
	Belz : « Rivière d'Etel, Saint Cado » (Morbihan and Finistere coast, France)	47°41'08"N	3°11'14"W	09/2007	Noël and Gruet 2008
	Locmiquélic: « Blavet estuary» (Morbihan and Finistere coast, France)	47°43'37"N	3°20'46"W	2007	Noël and Gruet 2008
	Lorient: « Aval de l'Etang du Ter » (Morbihan and Finistere coast, France)	47°43'31"N	3°22'20"W	2007	Noël and Gruet 2008
	Saint-Vaast-La-Houge (Cotentin, France)	49°35'34"N	1°15'48"W	11/08/2008	Dauvin 2009
	Le Havre harbour: « the Môle Central » (Bay of Seine, France)	49°29'11"N	0°06'23"E	29/08/1999	Breton et al.2002
	Knokke Heist, Albertstrand (Belgium)	51°20'50"N	3°16'28"E	21/07/2006	d'Udekem d'Acoz 2006
	Nieuwpoort-Bad (Netherlands)	51°09'14"N	2°42'23"E	2006	Nuyttens et al. 2006
	Sas van Goes (Netherlands)	51°19'58"N	3°49'51"E	19/03/2000, 21/04/2000, 09/2000	Nijland 2000, Nijland and Beekman 2000
	Bremerhaven harbour (Germany)	53°38'35"N	8°32'54"E	08/1993	Gollash 1999
	The tidal zone near Norddeich (Germany)	54°13'10"N	8°49'50"E	02/12/2007	Obert et al.2007