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.
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 known 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 m² 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 m² 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.
Hemigrapsus sanguineus and H. takanoi along the Opal Coast

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°32’32”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 | - |
| Mid (50°42’30”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 (K) 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 | 3.33 ± 3.51 | 1.67 ± 2.08 | - |
| Lower (50°45’06”N, 1°35’40”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 Gies’ 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 | 58 | 9.00 ± 6.08 | 10.33 ± 5.77 | - |
| Mid (50°47’11”N, 1°36’05”E) | 3 × 30 | 36 | 3.33 ± 3.21 | 10.33 ± 5.77 | - |
| Lower (50°47’13”N, 1°36’02”E) | 3 × 30 | 35 | 7.33 ± 3.51 | 2.67 ± 2.52 | - |
| 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 | 21 | 0.67 ± 0.58 | 1.67 ± 1.15 | - |
| 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 × 30 | 59 | 1.33 ± 1.33 | 4.00 ± 6.67 | - |
| Upper (50°52’19”N, 1°35’19”E) | 3 × 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°58’34”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 \( \chi^2 \) test (Schererrer 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 (Uwmw) 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 \textit{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 \( \chi^2 \) 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). \textit{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. \textit{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 \textit{H. takanoi} at Grand Fort Philippe (GF). Despite this extensive distribution, the abundance of \textit{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 \textit{H. sanguineus} and \textit{Carcinus maenas} were not homogeneous and depended on the sites sampled (\( \chi^2, p < 0.05 \)). The proportion of \textit{H. sanguineus} was higher in the sites located to the north of Boulogne-sur-mer (Uwmw, \( p < 0.05 \)), while the proportion of \textit{C. maenas} was higher in the sites located to the south of Boulogne-sur-mer where the other shore crabs were absent or rare (Uwmw, \( p < 0.05 \)).

Sex-ratio

Among the 2,395 crabs collected during the sampling period (Table 1), 1584 = \textit{C. maenas}, 427 = \textit{H. takanoi} and 384 = \textit{H. sanguineus}. No ovigerous females were found for any \textit{Hemigrapsus} species, and only 13 of the 588 \textit{C. maenas} females recorded carried eggs. The sex ratios (number of males/number of females) were respectively 1.69 for \textit{C. maenas}, 0.96 for \textit{H. takanoi} and 1.31 for \textit{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 \textit{C. maenas} than for the two other species. The smallest \textit{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 \textit{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,
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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 (d², p < 0.01); at GF and DH, H. takanoi dominated H. sanguineus and C. maenas significantly (d², p < 0.01); and at BHP, C. maenas dominated H. takanoi (d², 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.m² (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     | 14.3±7.06 | -      | 12.1±5.84 |
| WF    | 6     | 5.8±5.00  | 11.1±5.04 | -     |
| AaGF  | 6     | 7.8±6.24  | -      | 15.0±5.21 |
| DO    | 3     | 7.33±1.16  | 12.0±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. SQij: 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   | 1  | -  | 2  |
| SQ11  | 1  | -  | 1  |
| SQ12  | 2  | -  | 6  |
| 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  | 9  | -  | 0  |
| WF    | 0  | 4  | -  |
| SQ11  | 0  | 1  | -  |
| SQ12  | 1  | 5  | -  |
| SQ13  | 0  | 3  | -  |
| SQ21  | 2  | 2  | -  |
| SQ22  | 2  | 1  | -  |
| SQ23  | 3  | 1  | -  |
| SQ24  | 0  | 0  | -  |
| SQ31  | 0  | 2  | -  |
| SQ32  | 2  | 0  | -  |
| SQ33  | 3  | 3  | -  |
| SQ34  | 6  | 1  | -  |
| Aa GF | 3  | -  | 4  |
| SQ11  | 5  | -  | 4  |
| SQ12  | 3  | -  | 3  |
| SQ13  | 2  | -  | 7  |
| SQ14  | 2  | -  | 2  |
| SQ21  | 1  | -  | 0  |
| SQ22  | 2  | -  | 10 |
| SQ23  | 1  | -  | 5  |
| SQ31  | 3  | -  | 7  |
| SQ32  | 2  | -  | 5  |
| SQ33  | 1  | -  | 9  |
| DH    | 1  | -  | 6  |
| SQ11  | 0  | -  | 2  |
| SQ12  | 6  | -  | 9  |
| SQ13  | 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 m² 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 Hemigrapsus over C. maenas. However, at DH, H. takanoi dominated C. maneas significantly (d², 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 sympathy 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 Croÿ (WF) and outer Dunkirk harbour (ODH). Mean ± Standard Deviation

|                     | BHP | GF  | DH  | WF   | DO   | Mean sediment-size for *H. takanoi* habitat | Mean sediment-size for *H. sanguineus* habitat |
|---------------------|-----|-----|-----|------|------|-------------------------------------------|--------------------------------------------|
| Silt-clay (< 63 µm) | 4.95| 10.85| 2.00| 4.50±4.51| 0.75 | 1.32±0.81                                  |                                            |
| Fine sand (63-200 µm)| 5.82| 5.54| 17.51| 9.62±6.83| 15.22| 29.63±20.38                                |                                            |
| Medium sand (200-500 µm)| 29.73| 17.97| 17.60| 21.78±6.90| 30.77| 19.90±15.38                                |                                            |
| Coarse sand (500-2000 µm)| 11.00| 3.64| 9.55| 8.06±3.90| 16.93| 13.98±4.17                                 |                                            |
| Gravel (> 2000 µm)  | 48.50| 62.00| 43.75| 51.42±9.47| 36.33| 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)
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; 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 ‘Townsend 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 Demarest 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.
has become uncommon under rocks in some
De Graff and Tyrell (2004).
The food, as has been shown experimentally by
H. (2007) has shown that
Byers 2006). Nevertheless, MacDonald et al.

This probably indicates that the Opal coast
population, with its maximal density of 12
ind.m\(^{-2}\), is just beginning its colonisation and
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 spawning 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

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.
Hemigrapsus sanguineus and H. takanoi along the Opal Coast

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’Udekem 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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Hemigrapsus sanguineus and H. takanoi along the Opal Coast
### 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               |
|--------------------------------|-----------------------------------------------|------------------------|-------------|-------------------------|
| *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                             | 49°29’11”N 0°06’23”E  | 29/08/1999  | Breton et al. 2002      |
|                               | • the Canal Central Maritime                   |                        | 24/10/1999  |                         |
|                               | 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 “Oosterschelde”, Schelphoek (Netherlands) | 51°41’26”N 3°49’03”E  | 21 and     | 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    | 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 estuary, 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          |
|-----------------------|---------------------------------------------------------------------------|------------------------|-------------|-------------------|
| *Hemigrapsus sanguineus* and *H. takanoi* along the Opal Coast |                                                                          |                        |              |                  |
| *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 |
|                       | Barrière: « La Berche, Ile 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 | 19/10/2005 | 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 |
|                       | Canoël: « Vilaine estuary » (Morbihan and Finistere coast, France)      | 47°30′08″N 2°23′43″W | 24/10/2005 | Noël and Gruet 2008 |
|                       | Pénif: « 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 |
|                       | Locmiquiloc: « 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-Hougue (Cotentin, France)                                | 49°35′34″N 1°15′48″W | 11/08/2008 | Daunis 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, Albertstrad (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 | Nuytens 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 | Gollasch 1999 |
|                       | The tidal zone near Norddeich (Germany)                                 | 54°13′10″N 8°49′50″E | 02/12/2007 | Obert et al. 2007 |