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Research Article

Additional records and distribution (2011-2012) of *Hemigrapsus sanguineus* (De Haan, 1835) along the French coast of the English Channel

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Abstract

The invasion process can be described as a succession of stages initiated by the transport of organisms from their native range to a new area where they persist, proliferate and spread. It is important to monitor the demographic development of invaders for management purposes. This study focuses on the different stages of population development during the invasion process and underlines the importance of understanding and monitoring the 'persistence phase'. The distribution of *Hemigrapsus sanguineus* (Asian shore crab) in the English Channel, along the French coast, was first undertaken in 2008. In 2010, 35 sites were surveyed and it appeared that the abundance of this species had already established a 2–5 fold increase since 2008. The present study presents the geographical distribution of *H. sanguineus* in 2011 and 2012 which includes a further 39 sites (72 sampling stations in 2012). All populations observed during previous years persisted in 2011 and 2012. In 2012, *H. sanguineus* was detected at 61 sites; 36 intensely colonised (including 3 newly colonised sites compared to 2011); 22 had trace numbers and 3 sites had 'proven presence'. In addition to males with carapaces up to 39 mm width (CW), abundances increased by a factor of 2 since 2010, which testifies for the naturalized status of the species along the French coast of the English Channel. Since 2008, La Hougue proved to be the most abundantly colonised site along the French coast. By 2011 it had an average density of 101±19 ind.m^{-2}, with an abundance of 258±54 individuals (under 30 boulders). Populations were subsequently halved in 2012. Increasing densities and abundances recorded between 2008 and 2011 at la Hougue suggest that *H. sanguineus* had reached the 'expansion phase', but the dynamics of *H. sanguineus* populations at the most colonised sites (12 sampling sites with abundance >200 individuals under 30 boulders), suggest that maximum values had already peaked and that the 'persistence phase' was probably reached. The implementation of pluri-annual surveys seems of prime importance to correctly evaluate population dynamics of alien species.

Key words: *Hemigrapsus sanguineus*; Asian shore crab; invasive marine species; English Channel

Introduction

The collection of basic information on the occurrence and spatial distribution of alien species, their rate of spread and their biological and ecological traits is a stepping stone for the assessment of biological invasions (Katsanevakis et al. 2013). More specifically, it is necessary to assess the demographic strategies and ecological characteristics of alien species to estimate their impact on ecosystems. Invasive species can change the structure and the functioning of marine ecosystems (Grosholz 2002) at all biological levels (genome, individual, population, species, communities and ecosystem) via predation, parasitism, pathogen transfers and also physical and chemical modifications of habitats (Beisel and Lévêque 2010).

Hemigrapsus sanguineus (De Haan, 1835), one of today's most studied invaders in the USA is native to the north-western Pacific, and was observed for the first time in France in 1999 at Le Havre (Breton et al. 2002). A survey of the spread of this species along the French coast of the English Channel was not initiated until the spring of 2008 (Dauvin et al. 2009). The crab was detected at 35 sites in the upper and middle mediolittoral zones, under boulders. Regular harvesting of juveniles and ovigerous females and the extent of the breeding season the small size of the first spawning (carapace witdth <10 mm) are proof of the strong reproductive capacity of this naturalised species along the French coast (Dauvin 2009a, b; Dauvin and Dufossé 2011).

A density of 69 ind.m^{-2} was observed in 2010 on the Cotentin Peninsula (La Hougue: Dauvin and Dufossé 2011): this was one of the highest concentrations reported in 2010, in Europe. However, it remained low compared to densities observed on the east coast of USA for *H. sanguineus* and off the Island of Sylt in the Wadden Sea in northern Germany (2011) where densities exceeded 100 crabs per square metre (Brousseau et al. 2003; Jensen et al. 2002; Landschoff et al. 2013). Indeed, the highest densities recorded were 305 ind.m^{-2} in Long Island (Kraemer et al. 2007) and 320 ind.m^{-2} at Townsends and Hereford Inlets, New Jersey (Mc Dermott 1998). *H. sanguineus,* through its increasing densities and its successful colonisation ability (expanding some 12 km per year along the eastern coast of the United States, Leppäkoski and Olenin 2000), could considerably impact on the structure and functioning of marine ecosystems in the near future. Serious adverse impacts would include predation on mussels and/or juvenile oysters (Bourdeau and O'Connor 2003; Brousseau et al. 2001) which are cultivated along the French coast, and/or by interspecific competition (for space and/or resources) with indigenous species e.g. *Carcinus maenas*.

This study presents the demographic development and geographical distribution of *H. sanguineus* along the French coast of the English Channel.

Information on the demographic development of invaders is a prerequisite for the implementation of management procedures. Erroneous knowledge about the dynamics of an invader could lead to inaccurate assessments of the risks and thus overlook critical insight for protocol development (Crooks 2005).

Material and methods

Study area and sampling procedure

Surveys were conducted in four geographical areas during different seasons in 2011 and 2012. From west to east: (*i*) the Cotentin Peninsula was investigated from Saint-Jean-Le-Thomas to La Hougue each year during the summer period (19 sampling sites), (*ii*) the coast of the 'Calvados Department' (from Grandcamp-Maisy to Honfleur) was prospected each year in spring (18 sampling sites), (*iii*) the Albâtre and Picarde coasts were sampled in spring and summer 2012 (21 sampling sites) and (iv) the Opal Coast, from Authie estuary to the Belgium border was studied during spring 2012 (14 sampling sites). Sites sampled in 2011 and 2012 in areas (*i*) and (*iv*) are the same as those studied in 2010 by Dauvin and Dufossé (2011), while areas (*ii*) and (*iii*) represent 39 additional, new sites. Thus, in 2012, a total of 72 sites were studied along ca. a 700 km stretch of coastline (Appendices 1 to 4): 33 sites surveyed since 2008, a further 18 since 2011 and another 21 in 2012.

The sampling procedure was performed according to Dauvin and Dufossé (2011) at low tide in the mid-littoral zone on rocky substrates. Abundances were determined by collecting individuals underneath clusters of 30 boulders (boulders were selected at random and considered as representative for each site); a total of 90 boulders per site (3 clusters). Densities were estimated after specimens were collected from 1 m^2 quadrats which were randomly placed in the mid-littoral zone at each site (again 3 replicates). Within each quadrat, rocks and boulders were turned over from the centre to the side and all crabs collected by hand. The sand under the boulders was disturbed to collect buried individuals. To ensure that no crab escaped the sampling area, each sampling was performed by two people (one to turn the boulders over and one to collect the crabs). To standardise and ensure consistency, sampling was handled by a limited number of individuals. Crabs were placed in specifically marked plastic bags for both density and abundance. In the laboratory, crabs were counted, sexed and carapace width (CW) measured between the third antero-lateral teeth (Delaney et al. 2008). Crabs < 10mm (CW) were sexed under the microscope. Abundances were expressed as number of individuals under 30 boulders, and densities as number of individuals per square metre.

Data processing

Three stages of invasion were defined according to abundance data. A site was considered (i)'colonised' when more than 10 crabs were found, (*ii*) 'trace' when 1 to 10 crabs collected and (*iii*) 'not detected' when no crab was found. 'Proven presence' indicates sites where sampling procedures were inoperable but where *H. sanguineus* was

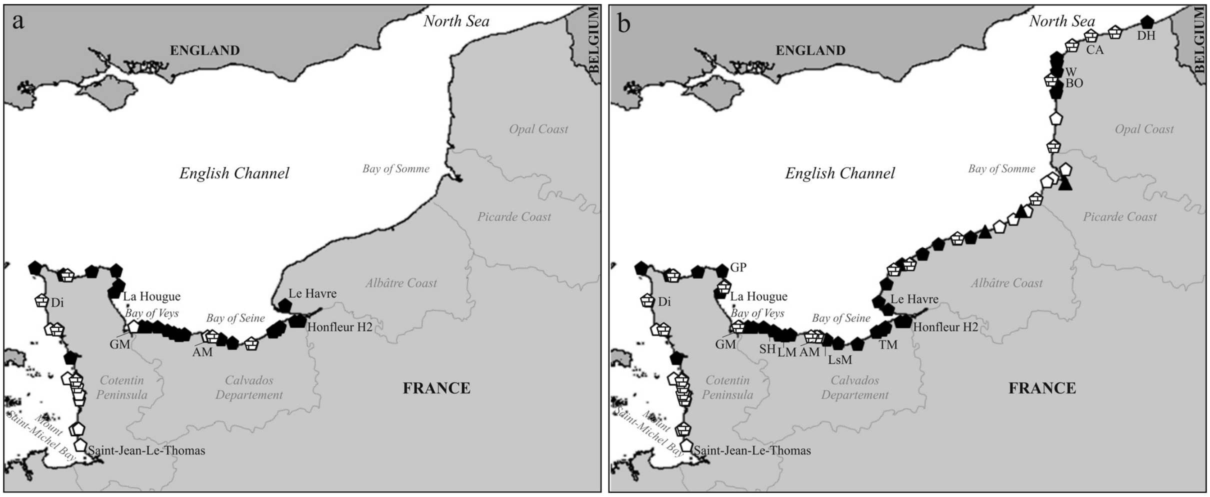

Figure 1. Distribution of *H. sanguineus* along the French coast of the English Channel in (a) 2011 and (b) 2012 In 2011, the Albâtre, Picarde and Opal Coast were not sampled. Stage of invasion: ⬠ not detected, trace (1-10 ind. under 30 boulders), ⬟ colonised (>10 ind. under 30 boulders), ▲ proven presence. (Di: Dielette; GP: Gatteville-Phare; GM: Grancamp-Maisy; SH: St Honorine des Pertes; LM: Longues sur Mer; AM: St Aubin sur Mer; LsM: Lion sur Mer; TM: Trouville sur Mer; BO: Boulogne-sur-Mer harbour; W: Wimereux; CA: Calais harbour; DH: Dunkirk harbour).

encountered. Frequency distributions (%) of carapace- width (1 mm classes) were also determined. A t-test was used to determine differences in abundance of *H. sanguineus* between 2010–2011 and 2011–2012 for each study area (*e.g.* Cotentin Peninsula). Data examined for 2010 is from Dauvin and Dufossé (2011). A Mann-Whitney Wilcoxon test was used to determine differences in abundance between 2010–2011 and 2011–2012 for the sampling sites (*e.g.* La Hougue). For all statistical tests, the risk level was set at 5%.

Results

<u>*Hemigrapsus sanguineus*</u> *distribution*

In 2012, *H. sanguineus* was detected at 61 sites out of a total 72 sampled (Figure 1b). Three new sites supported the Asian crab, namely Dielette in the Cotentin Peninsula, and Grancamp-Maisy and St Aubin sur Mer along the Calvados coast. The presence of the crab was considered as 'trace' at 22 sites, 'colonised' at 36 sites and 'proven presence' at the remaining 3 sites. The most colonised areas were the Northern and the Eastern parts of the Cotentin Peninsula, the Calvados coast, South of the Albâtre Coast and North of the Opal Coast (Boulogne-sur-Mer to Dunkirk harbour) (Table 1, Table 2 and Figure 1).

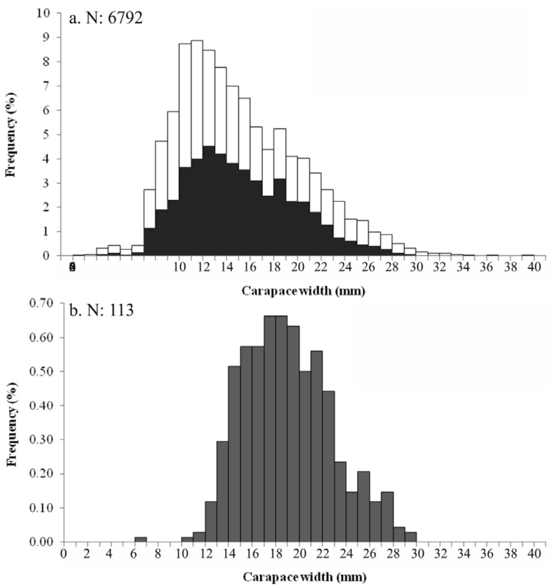

Figure 2. Size distribution (%) of carapace width classes (CW; mm) of *H. sanguineus* sampled along the French coast of the English Channel in 2012 (a. white: size distribution of both sexes, black: size distribution of females; b. grey: size distribution of ovigerous females).

Table 1. Abundance (individuals under 30 boulders, mean ± s.d.; rounded up to the nearest unit), density (ind.m^{-2}, mean ± s.d.; rounded up to the nearest unit), sex ratio (male/female) and % of ovigerous females (number of ovigerous females/total number of females) of *Hemigrapsus sanguineus* along the Opal Coast (sampled spring 2012) and the Albâtre and Picarde coast (sampled summer 2012). See Appendices 1 and 4 for sampling dates.

Location	Abundance Under 30 boulders	Density	Sex ratio M/F	% of Ovigerous Females
The Opal Coast				
Berck	1±0	-	-	-
Le Touquet	0	-	-	-
Le Portel	16±1	4±3	1.54	0
Boulogne harbour site 'roro'	16±12	1±1	-	0
Boulogne harbour	2±1	1±1	-	0
Wimereux 'Pointe de la Crèche'	97±25	16±6	1.11	3.01
Wimereux 'Fort de Croy'	209±106	-	0.92	0
Wimereux 'Pointe aux Oies'	42±12	5±3	1.40	0
Ambleteuse	32±14	0	0.78	3.70
Gris Nez Cap	38±26	5±4	0.68	0
Blanc Nez Cap	1±1	-	-	-
Calais harbour	2±1	0	1.00	0
Grand-Fort-Philippe (Aa)	1±1	3±4	-	-
Dunkirk harbour	77±12	6±3	1.07	0
The Albâtre and Picarde Coast				
Ault	2±3	-	0.50	0
St Martin en Campagne	0	-	-	-
Dieppe outside harbour	55±3	-	1.10	12.82
Saint-Aubin	20±4	9±1	2.23	59.09
Saint-Valéry	8±3	3±2	2.89	22.22
Veulettes	24±12	9±2	1.13	61.70
Grandes Dalles	18±3	5±1	1.65	38.46
Senneville	6±1	3±1	7.67	66.67
Benouville	23±4	8±3	1.27	48.78
Etretat	7±1	3±1	3.00	57.14
St Jouin de Bruneval	33±5	10±3	0.92	44.78
Ste Adresse	11±3	4±1	1.93	46.67
Le Havre	62±5	19±5	0.97	37.70

Size distribution and sex-ratio

A total of 6,792 individuals were collected in 2012 with sizes ranging from 1–39 mm (carapace width, CW) for males and from 3–29 mm for females (Figure 2). Three modal classes were observed: 4–5 mm CW for very young individuals, 11–12 mm for medium-sized individuals and 18–19 mm for large individuals. Medium and large individuals were observed during spring and summer, contrary to very young individuals which were generally observed in the spring. In 2012, 443 ovigerous females were observed throughout the sampling area (essentially during the summer); ranging from 6 to 29 mm; 53.1% were mature before reaching 19 mm (CW; Figure 2). The male/female sex ratio was examined during the reproductive period in summer 2012. Male/female sex ratio favoured males with a ratio of > 1 for all four geographical areas. An increased ratio of 1.79 was found along the Cotentin Peninsula, but an even greater ratio of 2.89 was found along the Albâtre and Picarde coast.

Abundances and densities

Population abundances remained unchanged in all areas between 2010–2011 and 2011–2012 (t-test, $p>0.05$). Heavily colonised sites in 2012 (i.e. >200 individuals under 90 boulders), were numerous and included Gatteville-Phare, La Hougue, St Honorine des Pertes, Longues sur Mer, Lion sur Mer, Trouville sur Mer, Honfleur 2, Wimereux 'Fort de Croy', Wimereux 'Pointe de la Crèche' and Dunkirk harbour (Figure 1b). In 2012, densities ranged from 1 ind.m^{-2} to 70±21 ind.m^{-2} (St Honorine des Pertes in the 'Calvados Department'; Table 1 and 2).

At Wimereux 'Pointe de la Crèche', Dunkirk harbour, St. Honorine des Pertes and Honfleur 2, abundances were higher than during previous years (Wilcoxon-Mann-Whitney test, $p<0.05$). In 2011 the most abundantly colonised site on the French coast (La Hougue) had up to 101±19 ind.m^{-2} and 258±54 individuals under 30 boulders. In contrast to sites previously cited in 2012, densities and abundances at La Hougue had significantly halved compared to 2011.

Table 2. Abundance (individuals under 30 boulders, mean ± s.d.; rounded up to the nearest unity), density (ind.m^{-2}, mean ± s.d.; rounded up to the nearest unity), sex ratio (male/female) and % of ovigerous females (number of ovigerous females/total number of females) of *Hemigrapsus sanguineus* along the Calvados Department (sampled spring 2011 and 2012) and the Cotentin Peninsula (sampled summer 2011 and 2012). See Appendices 2 and 3 for sampling dates.

	Abundance Under 30 boulders		Density		Sex ratio M/F		% of Ovigerous Females	
	2011	2012	2011	2012	2011	2012	2011	2012
The Calvados Department								
Grancamp-Maisy	0	1±1	-	10±7	-	-	-	-
Grancamp-Maisy 2	39±14	59±26	19±3	18±12	1.19	0.85	0.00	-
Pointe du Hoc	59±10	32±13	25±6	9±2	0.88	0.84	0.00	-
Vierville sur Mer	70±13	62±6	31±3	37±19	0.81	0.95	0.00	-
St Honorine des Pertes	31±17	176±18	40±13	70±21	0.91	0.71	0.00	-
Port en Bessin	14±5	26±3	-	12±2	1.38	0.63	0.00	-
Longues sur Mer	37±5	69±23	20±3	65±12	1.10	0.65	2.00	-
Arromanches	63±24	46±4	18±2	25±15	0.95	0.98	5.00	-
St Aubin sur Mer	0	5±7	-	1±1	0	0.75	0.00	-
Luc sur Mer	1±1	8±2	0	1±1	0.97	2.29	0.00	-
Lion sur Mer	163±8	115±28	38±2	16±3	1.00	1.19	0.00	-
Ouistreham	8±2	44±4	0	31±13	0.92	1.10	8.00	-
Cabourg	78±4	26±9	-	5±1	0.87	0.87	0.00	-
Trouville sur Mer	44±17	77±15	16±2	27±2	0.76	1.36	0.00	-
Villerville 2	13±4	27±5	-	9±5	0.97	1.22	0.00	-
Villerville 1	22±13	22±14	-	30±13	1.44	2.19	0.00	-
Honfleur 2	47±7	184±55	19±9	69±27	1.90	0.57	0.00	-
Honfleur 1	10±2	11±10	-	4±2	1.00	1.15	1.00	-
The Cotentin Peninsula								
Saint-Jean-Le-Thomas	0	0	-	-	-	-	-	-
Granville harbour	0	0	-	-	-	-	-	-
Granville outside harbour	0	1±1	-	-	-	-	-	-
Agon-Coutainville	0	2±1	-	-	-	0.40	-	20.00
Blainville sur Mer	0	1±1	-	-	-	-	-	-
Gonneville	1±2	1±0	-	-	2.00	2.00	100	100
Le Senéquet	0	-	-	-	-	-	-	-
Gouville-sur-Mer	4±5	6±0	-	-	0.83	2.00	66.67	100
Saint Germain sur Ay	33±18	34±8	-	8±2	0.78	0.56	83.92	66.00
Carteret harbour	1±1	10±3	-	-	3.00	1.11	-	79.00
Carteret outside harbour	0	0	-	-	-	-	-	-
Dielette	8±2	4±2	-	1±1	0.60	1.60	66.67	80.00
Goury	15±1	11±3	-	6±2	0.70	3.71	69.23	57.00
Querqueville	87±17	26±6	39±6	8±2	0.60	1.11	60.81	43.00
Salines	8±4	8±3	-	5±1	1.00	4.00	27.78	60.00
Fermanville harbour	28±7	5±4	-	3±2	0.91	2.00	61.36	100
Gatteville-Phare	135±25	98±26	57±26	38±4	0.74	1.81	72.44	50.00
Saint-Vaast	19±6	6±1	-	2±1	2.11	1.83	22.22	50.00
La Hougue	258±54	96±32	101±19	40±13	0.67	1.14	56.80	67.00

Discussion

All populations of *H. sanguineus* observed since 2008 (Cotentin Peninsula and Opal Coast) and in 2011 (the Calvados Department), (Figure 1a) were maintained in 2012. In the most colonised areas, primary and secondary vectors of introduction and spread, such as fishing and commercial harbours (Caen, Honfleur, Le Havre, Boulogne-sur-Mer, Calais and Dunkirk) were present. Bivalve farming areas (oysters and mussels) also exist in these areas.

Maximum sizes observed in 2011 (35 mm CW for females and 41 CW for males: Dauvin and Dufossé 2011) and in the present study (29 mm CW for females and 39 mm CW for males) are comparable to those recorded in Japan and the United-States where 42 mm CW was registered for males (Fukui 1988, and McDermott 1998, respectively).

Very young individuals (4–5 mm, CW), corresponding to recruits of the 0+ year, ovigerous females (respectively 9.1% and 6.5% of the global population sampled in 2012), as well as the small size of the first spawning (ca. 6 mm, Figure 2) are supplementary proof of the strong reproductive capacity of this species along the French coast.

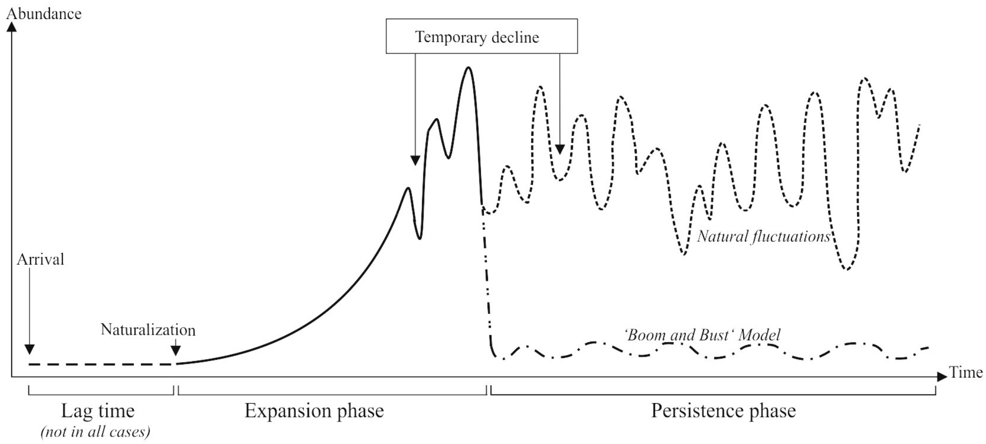

Figure 3. Theoretical evolution of the abundance of an introduced species (modified from Boudouresque et al. 2005).

No ovigerous females were reported in spring 2008 (Opal Coast; Dauvin et al. 2009) contrary to 2012 observations. Very young individuals are more difficult to see and catch by hand which may explain why they were poorly represented compared to other size classes.

Male/female sex ratio observed in 2012 was favourable to males irrespective of geographical sampling area. Prior French surveys had always shown differences between the Opal Coast, where males were more numerous than females (sex ratio = 1.31 in 2008 and 1.74 in 2010: Dauvin et al. 2009 and Dauvin and Dufossé 2011, respectively), and the Cotentin Peninsula, where the sex-ratio was favorable to females (0.81 in 2008, Dauvin 2009a; 0.81 in 2009, Dauvin 2009b; 0.66–0.81 in 2010; Dauvin and Dufossé 2011).

In general, the mating of *H. sanguineus* requires one female per male. Females do not mate with additional males after copulation. A single copulation provides viable sperm for at least two broods and females are again available for mating shortly after spawning (Epifanio 2013). Thus, females can have 5 to 6 broods per year (Fukui 1988) with more than 50,000 eggs per brood (McDermott 1991). A decrease of females could contribute to an important decrease of the reproductive success of this species.

Surveys conducted since 2008, indicate that *H. sanguineus* is 'naturalised' on the French coast and that there has been an increase in population abundance between 2008 and 2010 (Dauvin and Dufossé 2011), suggesting that *H. sanguineus* had reached the 'expansion phase' at this stage.

Based on theoretical schemes, a decline of individual numbers may be associated with the occurrence of the 'persistence phase' where the number of invaders decreases after having reached maximum abundance during the 'expansion phase' (Boudouresque et al. 2005, Figure 3). Depending on the species considered, different dynamics may be observed during the 'persistence phase'. The 'Boom and Bust' model (Williamson 1996) observe a natural and very important decline in numbers. Others suggest an oscillatory behavior with natural fluctuations (Parker et al. 1999).

In Rye, New York, USA, *H. sanguineus* densities increased up to ca. 120 $ind.m^{-2}$ from 1998 to 2001, before declining to 80 $ind.m^{-2}$ between 2002 and 2005 (Kraemer et al. 2007). In Scituate (Massachusetts USA), densities of *H. sanguineus* also increased, from ca. 45 $ind.m^{-2}$ to 175 $ind.m^{-2}$ between 1999 and 2010 and subsequently dropped to 100 $ind.m^{-2}$ in 2011 (O'Connor 2013). The invasion by *H. sanguineus* on US and European shores is relatively recent, and the demography of this species during the 'persistence phase' remains largely unknown.

Natural fluctuations can also be observed during the 'expansion phase' where maximum abundance is not reached (Figure 3), but variations are generally more moderate than during the persistence phase. During this research, the winter of 2012 was particularly severe; extreme winter conditions were recorded in Europe and Asia (World Meteorological Organization 2013). Between January 25 and February 16, 5–10 consecutive ice days (max air temperature < 0°C) were recorded from

Cotentin to the Opal Coast (World Meteorological Organization 2013). Thus, the decrease of abundances and densities observed in La Hougue could be as a consequence of this harsh winter. In the context of different plausible scenarios, it is possible that maximum abundances have not yet been reached and values may be much higher in a few years time. Thus, the implementation of pluri-annual surveys, on all target sites examined in 2012 is critical, to accurately evaluate population dynamics and help observe changes in impacted communities.

In Europe, the presence of *Hemigrapsus takanoi* has been observed in sympatry with *H. sanguineus* (Dauvin et al. 2009; Van Den Brink et al. 2012). At Dunkirk harbour in 2010, 111±42 *H. takanoi* were found under 30 boulders (Gothland et al. in press). Life history of *H. takanoi* is not well documented but it appears similar to *H. penicillatus*. The latter presents some features such as early sexual maturity (6.4 mm CW; Fukui 1988), a high dispersal ability (larval phase) and a high fecundity (5,000 to 10,000 eggs, 5 to 6 broods per year; Pillay and Ono 1978), which can create a strong competitor for *H. sanguineus.* Thus, current and future European surveys about the dynamics of *H. sanguineus* populations could bring complementary information to American works and surveys where no *H. takanoi* are found.

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References

Beisel JN, Lévêque C (2010) Introductions d'espèces dans les milieux aquatiques. Faut-il avoir peur des invasions biologiques? Editions Quae, éditions Cemagref, Cirad, Ifremer, Inra, Versailles, France, Collection synthèses, 232 pp

Boudouresque CF, Ruitton S, Verlaque M (2005) Large-scale disturbances, regime shift and recovery in littoral systems subject to biological invasions. In: Velikova V, Chipev N (eds) (2005) Unesco-Roste/ BAS Wokshop on regime shifts, June 14-16, 2005, Varna, Bulgaria, pp 85–101

Bourdeau PE, O' Connor NJ (2003) Predation by the nonindigenous Asian shore crab *Hemigrapsus sanguineus* on macroalgae and molluscs. *Northeastern Naturalist* 10: 319–334, http://dx.doi.org/10.1656/1092-6194(2003)010[0319:PBTNAS]2.0.CO;2

Breton G, Faasse M, Noël P, Vincent T (2002) A new alien crab in Europe: *Hemigrapsus sanguineus* (Decapoda: Brachyura: Grapsidae). *Journal of Crustacean Biology* 22 (1): 184–189, http://dx.doi.org/10.1651/0278-0372(2002)022[0184:ANACIE]2.0.CO;2

Brousseau DJ, Filipowicz A, Baglivo JA (2001) Laboratory investigations of the effects of predator sex and size on prey selection by the Asian crab, *Hemigrapsus sanguineus*. *Journal of Experimental Marine Biology and Ecology* 262: 199–210, http://dx.doi.org/10.1016/S0022-0981(01)00290-8

Brousseau DJ, Kriksciun K, Baglivo JA (2003) Fiddler crab burrow usage by the Asian crab, *Hemigrapsus sanguineus*, in a Long Island Sound salt marsh. *Northeastern Naturalist* 10: 415–420, http://dx.doi.org/10.1656/1092-6194(2003)010[0415:FCBUBT]2.0.CO;2

Crooks JA (2005) Lag times and exotic species: the ecology and management of biological invasions in slow-motion. *Ecoscience* 12: 316–329, http://dx.doi.org/10.1007/s10530-010-9799-3

Dauvin JC (2009a) Establishment of the invasive Asian shore crab *Hemigrapsus sanguineus* (De Haan, 1835) (Crustacea: Brachyura: Grapsoidea) from the Cotentin Peninsula, Normandy, France. *Aquatic Invasions* 4: 467–472, http://dx.doi.org/10.3391/ai.2009.4.4.6

Dauvin JC (2009b) Asian shore crabs *Hemigrapsus* spp. (Crustacea: Brachyura: Grapsoidea) continue their invasion around the Cotentin Peninsula, Normandy, France: Status of the *Hemigrapsus* population in 2009. *Aquatic Invasions* 4: 605–611, http://dx.doi.org/10.3391/ai.2011.6.3.09

Dauvin JC, Dufossé F (2011) *Hemigrapsus sanguineus* (De Haan, 1837) (Crustacea: Brachyura: Grapsoidea) a new species in European waters: the case of the French English Channel coast (2008–2010). *Aquatic Invasions* 6: 329–338, http://dx.doi.org/10.3391/ai.2009.4.3.3

Dauvin JC, Tous Rius A, Ruellet T (2009) Recent expansion of two invasive crabs species *Hemigrapsus sanguineus* (De Haan, 1853) and *H. takanoi* Asakura and Watanabe, 2005 along the Opal coast, France. *Aquatic Invasions* 4: 451–465, http://dx.doi.org/10.1007/s10530-007-9114-0

de Haan W (1835) Crustacea. In: von Siebold PF (ed), Fauna Japonica sive Descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batava imperium tenent, suscepto, annis 1823-1830 collegit, notis, observationibus et adumbrationibus illustravit P.F. de Siebold. Conjunctis studiis C.J. Temminck et H. Schlegel pro Vertebratis atque W. de Haan pro Invertebratis elaborata Regis aupicus edita. Leiden, Lugundi-Batavorum. Decas II, 25-64, pls 9-15, 17, C, D. (For dates see Sherborn and Jentink, 1895; Holthuis, 1953 and Holthuis and T. Sakai, 1970)

Delaney D, Sperling C, Adams C, Leung B (2008) Marine invasive species: validation of citizen science and implications for national monitoring networks. *Biological Invasions* 10: 117–128, http://dx.doi.org/10.1016/j.jembe.2013.01.010

Epifanio CE (2013) Invasion biology of the Asian shore crab *Hemigrapsus sanguineus*: a review. *Journal of Experimental Marine Biology and Ecology* 441: 33–49, http://dx.doi.org/10.1016/j.jembe.2013.01.010

Fukui Y (1988) Comparative studies on the life history of the grapsid crabs (Crustacea, Brachyura) inhabiting intertidal cobble and boulder shores. *Publications of the Seto Marine Biological Laboratory* 33: 121–162

Gothland M, Dauvin JC, Denis L, Dufossé F, Jobert S, Ovaert J, Pezy JP, Tous Rius A, Spilmont N (in press) Habitat preference and population characteristics explain the distribution and colonisation ability of the invasive shore crab *Hemigrapsus takanoi. Estuarine, Coastal and Shelf Science*

Grosholz E (2002) Ecological and evolutionary consequences of coastal invasions. *Trends in Ecology and Evolution* 17: 22–27, http://dx.doi.org/10.1016/S0169-5347(01)02358-8

Jensen GC, McDonald PS, Armstrong DA (2002) East meets west: competitive interactions between green crab *Carcinus maenas*, and native and introduced shore crab *Hemigrapsus* spp. *Marine Ecology Progress Series* 225: 251–262, http://dx.doi.org/10.3354/meps225251

Katsanevakis S, Gatto F, Zenetos A, Cardoso AC (2013) How many marine aliens in Europe? *Management of Biological Invasions* 4: 37–42, http://dx.doi.org/10.3391/mbi.2013.4.1.05

Kraemer GP, Sellberg M, Gordon A, Main J (2007) Eight year record of *Hemigrapsus sanguineus* (Asian shore crab) invasion in Western Long Island South Estuary. *Northeastern Naturalist* 14(2): 207–224, http://dx.doi.org/10.1656/1092-6194(2007)14[207:EROHSA]2.0.CO;2

Landschoff J, Lackschewitz D, Kesy K, Reise K (2013) Globalization pressure and habitat change: Pacific rocky shore crabs invade armored shorelines in the Atlantic Wadden Sea. *Aquatic Invasions* 8: 77–87, http://dx.doi.org/10.3391/ai.2013.8.1.09

Leppäkoski E, Olenin S (2000) Non-native species and rates of spread: lessons from the brackish Baltic Sea. *Biological Invasions* 2: 151–165, http://dx.doi.org/10.1023/A:1010052809567

McDermott JJ (1991) A breeding population of the western Pacific crab *Hemigrapsus sanguineus* (Crustacea: Decapoda: Grapsidae) established on the Atlantic coast of North America. *The Biological Bulletin* 181: 195–198, http://dx.doi.org/10.2307/1542503

McDermott JJ (1998) The Western Pacific brachyuran *Hemigrapsus sanguineus* (Grapsidae) in its new habitat along the Atlantic coast of the United States: feeding, cheliped morphology and growth. In: Schram FR, von Vaupel Klein JC (ed), Crustaceans and the Biodiversity Crisis. Brill. Leiden, The Netherlands, pp 425–444

O'Connor NJ (2013) Invasion dynamics on a temperate rocky shore: from early invasion to establishment of a marine invader. *Biological Invasions* (in press), http://dx.doi.org/10.1007/s10530-013-0504-1

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1: 3–19, http://dx.doi.org/10.1023/A:1010034312781

Pillay K, Ono Y (1978) The breeding cycles of two species of grapsid crabs (Crustacea: Decapoda) from the north coast of Kyushu, Japan. *Marine Biology* 45: 237–248, http://dx.doi.org/10.1007/BF00390606

Van den Brink A, Wijnhoven S, McLay C (2012) Competition and niche segregation following the arrival of *Hemigrapsus takanoi* in the formerly *Carcinus maenas* dominated Dutch delta. *Journal of Sea Research* 73: 126–136, http://dx.doi.org/10.1016/j.seares.2012.07.006

Williamson MH (1996) Biological Invasions. Chapman & Hall, London, 244 pp

World Meteorological Organization (2013) Assessment of the observed extreme conditions during late boreal winter 2011/2012. WCDMP-No.80, 16 pp

Supplementary material

The following supplementary material is available for this article:

Appendix 1. Location of *Hemigrapsus sanguineus* specimens along the Opal Coast. N: numbers of specimens collected underneath 90 boulders in 2012.

Appendix 2. Location of *Hemigrapsus sanguineus* specimens along the Cotentin. N: numbers of specimens collected underneath 90 boulders in 2011 and 2012.

Appendix 3. Location of *Hemigrapsus sanguineus* specimens along the Calvados Department. N: numbers of specimens collected underneath 90 boulders in 2011 and 2012.

Appendix 4. Location of *Hemigrapsus sanguineus* specimens along the Picarde and Albâtre coast. N: numbers of specimens collected underneath 90 boulders in 2012.

Appendix 1. Location of *Hemigrapsus sanguineus* specimens along the Opal Coast. N: numbers of specimens collected underneath 90 boulders in 2012.

Location	Coordinates		Date	N
	Latitude, N	Longitude, E		
Berck	50°23.601'	1°33.502'	25/04/2012	3
Le Touquet	50°32.211'	1°35.632'	25/04/2012	0
Le Portel	50°42.500'	1°33.771'	07/05/2012	48
Boulogne harbour site 'roro'	50°43.507'	1°33.943'	24/04/2012	48
Boulogne harbour	50°43.682'	1°35.334'	23/04/2012	6
Wimereux 'Pointe de la Crèche'	50°45.157'	1°35.679'	04/05/2012	291
Wimereux 'Fort de Croy'	50°45.766'	1°35.962'	04/04/2012	627
Wimereux 'Pointe aux Oies'	50°47.283'	1°36.200'	11/04/2012	126
Ambleteuse	50°48.181'	1°35.955'	03/05/2012	96
Gris Nez Cap	50°52.261'	1°35.379'	12/04/2012	114
Blanc Nez Cap	50°55.491'	1°42.388'	12/04/2012	3
Calais harbour	50°57.286'	1°51.503'	10/04/2012	6
Grand-Fort-Philippe (Aa)	51°00.453'	2°05.977'	10/04/2012	3
Dunkirk harbour	50°03.018'	2°22.106'	06/04/2012	231

Appendix 2. Location of *Hemigrapsus sanguineus* specimens along the Cotentin. N: numbers of specimens collected underneath 90 boulders in 2011 and 2012.

Location	Coordinates		Date	N
	Latitude, N	Longitude, E		
Saint-Jean-Le-Thomas	49°43.689'	1°31.908'	08/08/2011	0
Saint-Jean-Le-Thomas	49°43.689'	1°31.908'	27/07/2012	0
Granville Harbour	49°50.044'	1°36.442'	08/08/2011	0
Granville harbour	49°50.044'	1°36.442'	27/07/2012	0
Granville outside harbour	49°49.962'	1°36.563'	08/08/2011	0
Granville outside harbour	49°49.962'	1°36.563'	27/07/2012	2
Agon-Coutainville	49°00.933'	1°36.512'	11/08/2011	0
Agon-Coutainville	49°00.933'	1°36.512'	04/08/2012	7
Blainville sur Mer	49°03.775'	1°36.811'	30/07/2011	0
Blainville sur Mer	49°03.775'	1°36.811'	28/07/2012	3
Gonneville	49°04.890'	1°36.824'	16/07/2011	3
Gonneville	49°04.890'	1°36.824'	26/07/2012	3
Le Senéquet	49°05.500'	1°39.735'	20/08/2011	0
Le Senéquet	-	-	-	-
Gouville-sur-Mer	49°05.578'	1°36.793'	16/07/2011	11
Gouville-sur-Mer	49°05.578'	1°36.793'	26/07/2012	18
Saint Germain sur Ay	49°13.134'	1°38.636'	17/07/2011	100
Saint Germain sur Ay	49°13.134'	1°38.636'	26/07/2012	102
Carteret harbour	49°22.483'	1°47.354'	17/07/2011	4
Carteret harbour	49°22.483'	1°47.354'	27/07/2012	29
Carteret outside harbour	49°22.785'	1°48.640'	17/07/2011	0
Carteret outside harbour	49°22.785'	1°48.640'	27/07/2012	0
Dielette	49°33.400'	1°52.050'	12/08/2011	24
Dielette	49°33.400'	1°52.050'	27/07/2012	13
Goury	49°42.850'	1°56.750'	12/08/2011	44
Goury	49°42.850'	1°56.750'	07/07/2012	33
Querqueville	49°40.150'	1°40.810'	12/08/2011	262
Querqueville	49°40.150'	1°40.810'	07/07/2012	78
Salines	49°39.500'	1°38.750'	12/08/2011	26
Salines	49°39.500'	1°38.750'	07/07/2012	25
Fermanville harbour	49°41.203'	1°28.353'	17/08/2011	84
Fermanville harbour	49°41.203'	1°28.353'	07/07/2012	15
Gatteville-Phare	49°41.673'	1°16.038'	17/08/2011	406
Gatteville-Phare	49°41.673'	1°16.038'	07/07/2012	295
Saint-Vaast	49°35.400'	1°15.990'	17/08/2011	56
Saint-Vaast	49°35.400'	1°15.990'	07/07/2012	17
La Hougue	49°34.500'	1°16.380'	17/08/2011	773
La Hougue	49°34.500'	1°16.380'	07/07/2012	289

- not sampled

Appendix 3. Location of *Hemigrapsus sanguineus* specimens along the Calvados Department. N: numbers of specimens collected underneath 90 boulders in 2011 and 2012.

Location	Coordinates		Date	N
	Latitude, N	Longitude, E		
Grancamp-Maisy	49°23.4888'	1°03.4422'	30/03/2011	0
Grancamp-Maisy	49°23.4888'	1°03.4422'	04/04/2012	3
Grancamp-Maisy 2	49°23.7840'	1°00.5670'	19/04/2011	116
Grancamp-Maisy 2	49°23.7840'	1°00.5670'	04/04/2012	176
Pointe du Hoc	49°23.8284'	0°58.1286'	22/04/2011	178
Pointe du Hoc	49°23.8284'	0°58.1286'	04/04/2012	95
Vierville sur Mer	49°23.1690'	0°54.8244'	04/04/2011	209
Vierville sur Mer	49°23.1690'	0°54.8244'	05/04/2012	187
St Honorine des Pertes	49°21.3366'	0°48.3300'	01/04/2011	94
St Honorine des Pertes	49°21.3366'	0°48.3300'	05/04/2012	529
Port en Bessin	49°21.1800'	0°45.5118'	18/04/2011	42
Port en Bessin	49°21.1800'	0°45.5118'	10/04/2012	78
Longues sur Mer	49°20.8440'	0°41.2992'	06/04/2011	110
Longues sur Mer	49°20.8440'	0°41.2992'	11/04/2012	207
Arromanches	49°20.6742'	0°38.2398'	21/04/2011	188
Arromanches	49°20.6742'	0°38.2398'	11/04/2012	137
St Aubin sur Mer	49°20.1306'	0°23.7540'	31/03/2011	0
St Aubin sur Mer	49°20.1306'	0°23.7540'	18/04/2012	15
Luc sur Mer	49°19.3758'	0°21.2886'	28/03/2011	3
Luc sur Mer	49°19.3758'	0°21.2886'	03/05/2012	23
Lion sur Mer	49°18.9288'	0°20.3658'	29/03/2011	490
Lion sur Mer	49°18.9288'	0°20.3658'	18/04/2012	344
Ouistreham	49°16.8612'	0°14.8314'	25/04/2011	25
Ouistreham	49°16.8612'	0°14.8314'	18/04/2012	131
Cabourg	49°17.7876'	0°05.4444'	20/04/2011	23
Cabourg	49°17.7876'	0°05.4444'	12/04/2012	79
Trouville sur Mer	49°23.7870'	0°06.8316'	15/04/2011	132
Trouville sur Mer	49°23.7870'	0°06.8316'	24/04/2012	230
Villerville 2	49°23.7870'	0°06.8316'	15/04/2011	38
Villerville 2	49°23.7870'	0°06.8316'	24/04/2012	81
Villerville 1	49°24.1320'	0°07.4778'	14/04/2011	66
Villerville 1	49°24.1320'	0°07.4778'	17/04/2012	67
Honfleur 2	49°25.7016'	0°13.7880'	14/04/2011	142
Honfleur 2	49°25.7016'	0°13.7880'	17/04/2012	552
Honfleur 1	49°25.6908'	0°15.1326'	14/04/2011	30
Honfleur 1	49°25.6908'	0°15.1326'	17/04/2012	32

- not sampled

Appendix 4. Location of *Hemigrapsus sanguineus* specimens along the Picarde and Albâtre coast. N: numbers of specimens collected underneath 90 boulders in 2012.

Location	Coordinates		Date	N
	Latitude, N	Longitude, E		
Le Crotoy	50°12.8198'	1°37.5892'	08/05/2012	0
St Valery sur Somme	50°11.2114'	1°38.3548'	08/05/2012	Pp
Cayeux sur Mer	50°11.1588'	1°29.4861'	08/05/2012	0
Le Hourdel	50°13.0448'	1°33.8684'	08/05/2012	0
Ault	50°06.4932'	1°27.1764'	10/05/2012	6
Le Tréport harbour	50°03.6792'	1°22.5918'	10/05/2012	Pp
Le Tréport outside harbour	50°04.3458'	1°23.3076'	10/05/2012	0
St Martin en Campagne	49°58.3421'	1°12.2309'	11/05/2012	0
Dieppe harbour	49°55.3897'	1°04.9521'	21/06/2012	0
Dieppe outside harbour	49°56.0955'	1°05.6980'	21/06/2012	164
Varengeville sur Mer	49°55.0206'	1°00.4403'	21/06/2012	Pp
Saint-Aubin	49°53.7427'	0°52.6803'	05/07/2012	59
Saint-Valéry	49°52.2788'	0°42.7783'	05/07/2012	25
Veulettes	49°51.2077'	0°35.6078'	05/07/2012	72
Grandes Dalles	49°49.0002'	0°30.0008'	05/07/2012	53
Senneville	49°47.0981'	0°25.2373'	04/07/2012	17
Benouville	49°43.8170'	0°15.9792'	04/07/2012	68
Etretat	49°42.4265'	0°11.6973'	04/07/2012	20
St Jouin de Bruneval	49°38.4581'	0°08.9218'	04/07/2012	99
Ste Adresse	49°30.7010'	0°03.9157'	03/07/2012	33
Le Havre	49°29.0818'	0°06.0680'	03/07/2012	184

Pp : proven presence