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Research Article

Are mussel beds a favourable habitat for settlement of *Hemigrapsus sanguineus* (De Haan, 1835)?

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Abstract

Along the French coast of the English Channel, *Hemigrapsus sanguineus* (De Haan, 1835) is abundant under boulders on exposed shores that have high-energy hydrodynamic conditions in the intertidal zone. However, small individuals (< 6 mm) are rare in the muddy gravel sediments under boulders and the settlement habitat for post-larvae is largely unknown. This study explored whether mussel beds could represent a settlement zone for *H. sanguineus*. At the end of the summer of 2013, there were many post-larvae and small crabs in some mussel beds, with up to 528 individuals/m². However, at one location, no juveniles of *H. sanguineus* were found in mussel bed habitat despite the presence of adults on the same shore. We conclude that mussel beds are an important habitat for the settlement of juvenile crabs.

Key words: Asian shore crabs, invasive marine species, English Channel

Introduction

The introduction of alien shore crabs into coastal environments is mainly the result of human activities that are becoming more frequent with the ever-increasing maritime traffic levels (Williams 1984; Ng et al. 2008). Nevertheless, the introduction of invasive species is a complex phenomenon, and there is a pressing need to assess the risks linked to biological invasions. In some cases, the introduced species can have a strong negative, or even a positive, effect on native species and/or communities (Carlton 1989; Ruiz et al. 1997; Cohen and Carlton 1998; Occhipinti-Ambrogi 2007). The Asian shore crab *Hemigrapsus sanguineus* (De Haan, 1835) is an introduced non-native crab originating from the Asian Pacific Ocean. It is mainly present in the intertidal zone, and was first observed on the Atlantic coast of Europe at Le Havre in 1999 (Breton et al. 2002). This species is currently found from the western part of the English Channel along the Cotentin coast to the southern part of the North Sea (Breton et al. 2002; Dauvin 2009a,b; Dauvin et al. 2009; Dauvin and Dufossé 2011; Gothland 2013; Gothland et al. 2013).

Since 2011, *Hemigrapsus* populations have been surveyed in the middle shore zone along the Calvados coast, from Grandcamp-Maisy in the west to Honfleur in the east (Pezy 2011; Jobert 2012; Gothland et al. 2013; Rocroy 2013). In spite of the presence of ovigerous females during the period from May to November (Gothland 2013), *H. sanguineus* individuals with a carapace-width less than 6 mm are very rare in under-boulder samples collected from April to August, and are not sufficiently abundant to explain the renewal of adult populations found under the boulders. This observation necessarily means that larval settlement must occur in other intertidal habitats; consequently, we investigated whether mussel beds were used as a settlement habitat by *H. sanguineus*. To the best of our knowledge, mussel beds had never been investigated as a potential settlement habitat for (Epifanio 2013; Gothland 2013; Gothland et al. 2013).

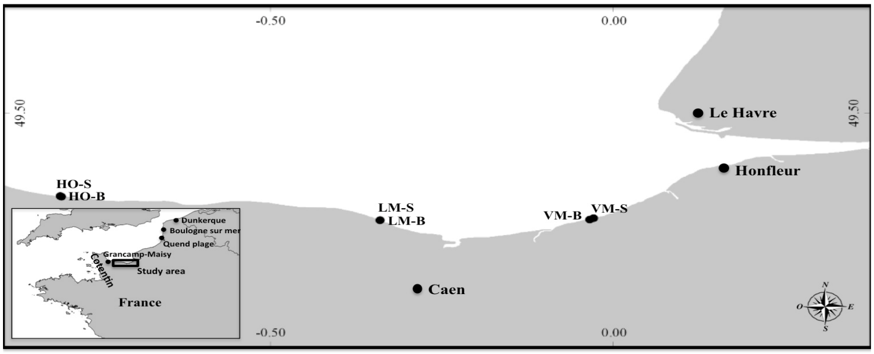

Figure 1. Location of the three sites sampled along the Calvados coast in April 2013 and August-September 2013 (HO: Sainte-Honorine-des-Pertes; LM: Lion-sur-Mer; VM: Villers-sur-Mer) (B: boulder; S: mussel beds).

Materials and methods

Three locations with abundant adult populations in boulder were identified and then boulder habitat and mussel bed habitat were sampled during April 2013, as well as at the end of the summer of 2013. The study area consisted of an open-to-the-sea, rocky, limestone shoreline with a gentle slope. Intertidally, there were deposits of sand that moved onshore or offshore depending on direction and strength of winter storms (J.-P. Pezy, personal observation). The salinity varied from 32.3 in April 2013 to 32.4 in August-September; and the seawater temperature increased 7.5–10.2°C in April 2013 to 19.4–17.8°C in August-September 2013 (http://somlit-db.epoc.u-bordeaux1.fr/bdd.php). The tidal range in this area was from 8 m during spring tide and 3 m during neap tide (http://www.shom.fr/).

The *Hemigrapsus* population was sampled along the Calvados coast at three sites (Sainte-Honorine-des-Pertes, Lion-sur-Mer and Villers-sur-Mer) (Figure 1) where large numbers of the crabs were known to be present since 2011 (Gothland et al. 2013; Jobert 2012; Pezy 2011; Rocroy 2013). Surveys were conducted at two different seasons in 2013: in April for individuals under boulders; and in August-September for individuals in mussel beds.

Sampling under boulders

The composition of the substrate under the boulders was 54–75 % gravels, 23–44 % sands and 1–5 % silt-clays (J.-P. Pezy, unpublished data). Collection of crabs was performed at low tide in middle of the intertidal zone on limestone substrates. The size distributions of *H. sanguineus* under boulders in rocky intertidal communities were determined by collecting individuals from underneath three clusters of 30 boulders for a total of 90 boulders per site. Boulders were selected at random and considered as representative for each site, with an approximate size of 30 × 30 cm (Dauvin et al. 2009; Dauvin, 2009a,b; Dauvin and Dufossé 2011). The boulders were lifted, brushed to collect the small individuals and the surface of the sediment was also sampled to collect the small individuals; so this strategy permitted to collect all small and large crabs. The entire sample was placed in a plastic pot and taken to the laboratory. Because all sizes of crabs were present in the collection pots, there may have been some cannibalism, which would reduce the numbers of small individuals; nevertheless, as the transport time was less than 30 minutes, this phenomenon was probably limited. The boulder habitat was sampled on 10 April 2013 at Villers-sur-Mer and on 12 April 2013 at Sainte-Honorine-des-Pertes and Lion-sur-Mer.

Abundance estimates were based on specimens collected from 1 m^2 quadrats randomly placed in the intertidal zone at each site (again 3 replicates) on the same dates. Within each quadrat, rocks and boulders were turned over from the centre to the edges and all crabs collected by hand. The sand under the boulders was disturbed to collect buried individuals. To minimize the numbers of crabs avoiding capture, sampling was performed by two persons: one to turn the boulders over and one to collect the crabs.

Sampling in mussel beds

During August-September 2013, we sampled crabs from mussel beds that occurred on rocky shores or on large boulders. Mussel beds were sampled

Figure 2. Photo showing mussel beds before and after scraping a 1/16 m^2 quadrat at Sainte-Honorine-des-Pertes.

on 9 August in Sainte-Honorine-des-Pertes, on 26 August in Villers-sur-Mer, and on 2 September in Lion-sur-Mer (2 September). At each site, estimates of crab abundance were based on six replicate 1/16 m^2 quadrats [0.0625 m²] placed haphazardly, and densities reported as number of individuals per m^2. Mussel beds were sampled by scraping all the mussels off of the rocks with a spatula, and the scraped surface was brushed to avoid missing organisms (Figure 2). The samples were stored in plastic bags and transferred to the Marine Station of Luc-sur-Mer. Live crabs were removed from the samples immediately after arriving in the laboratory, and then fixed in alcohol before being measured.

Laboratory observations

All the crabs collected under boulders were identified counted and sex determined by the shape of the abdomen. All the crabs collected in mussel beds were just identified to species and counted; they were too small for sex determination. The carapace width (CW) for large individuals was measured with an electronic calliper, to a precision to 0.01 mm, as the distance between the third anterolateral teeth according to Delaney et al. (2008). In the case of small individuals from the mussel-bed scrape samples; carapace width was measured under a binocular microscope using an ocular micrometer. Size classes were based on 1-mm intervals for crabs collected from under-boulder samples and into 0.1-mm intervals for crabs from scrape samples.

Statistical analyses

Possible between-sex differences in the carapace-width distributions were tested with a Kolmogorov-Smirnov test. Analysis of variance was used to analyse whether the mean densities of *H. sanguineus* differed between the three sites. Separate tests were used for the under-boulder and mussel-bed habitats. Prior to each ANOVA, the Shapiro-Wilk normality test and Bartlett's test for homogeneity of variance were performed to confirm the assumptions of ANOVA were met, and it was unnecessary to transform the data. Tukey Honestly Significant Difference test was used to determine which means differed.

Results

Carapace width distributions by habitat

We measured 1,814 crabs collected from under boulders (for the three sites combined). The carapace width range was from 6 to 35 mm (Figure 3). The size distribution of males was not different from that of females (Kolmogorov-Smirnov test; $P = 0.108$).

For the mussel beds, 192 small individuals were collected from the three sites combined with a CW range of 1.0 to 8.0 mm (Figure 3). Two peaks were observed: 1.0–1.2 mm CW for post-larvae and 1.8–2.2 mm CW for newly settled juveniles.

Abundance and average size

For the individuals collected under boulders, densities within replicates ranged from 10 to 118 individuals per m^2 (Table 1). Between-replicate ranges did not overlap; hence, mean abundance differed significantly (ANOVA, $F_{2,6} = 24.82$; $P = 0.00125$) between locations. The average CW within replicates ranged from 9.9 to 19.6 mm (Table 1) and overall mean size was different between sites (ANOVA; $F_{2,6}$=7.105; $P = 0.0262$). The mean CW of *H. sanguineus* differed significantly between Sainte-Honorine-des-Pertes and

Table 1. Density (number of individuals per m^2) and average size in three quadrats of *H. sanguineus* under boulders, estimated at three sites during April 2013. R1: Replicate 1. Means sharing the same superscript did not differ significantly (Tukey's HSD test; P > 0.05).

Location	Density				Average size (mm)			
Site	R1	R2	R3	Average	R1	R2	R3	Average
Villers-sur-Mer	10	19	14	14.3 ^{a}	12.1	13.1	18.7	14.6 ^{a,b,c}
Sainte-Honorine-des-Pertes	118	86	84	96.0 ^{b}	19.6	19.4	17.0	18.7 ^{b}
Lion-sur-Mer	37	45	66	49.3 ^{c}	12.0	12.5	9.9	11.5 ^{c}

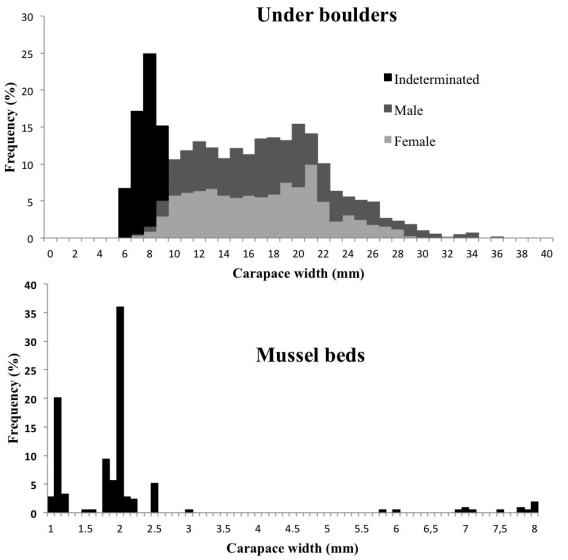

Figure 3. Size distribution (%), as carapace width (CW; mm) of *Hemigrapsus sanguineus* sampled along the Calvados coast of the English Channel in 2013 in two different habitats (under boulders and from mussel beds).

Lion-sur-Mer but the mean CW for Villers-sur-Mer was not significantly different the two other sites (Table 1).

In mussel beds, densities within replicates ranged from 0 at Saint-Honorine-des-Pertes to 560 individuals per m^2 at Lion-sur-Mer (Table 2) and the between location effect was highly significant (ANOVA; $F_{2,15} = 23.36$; $P < 0.0001$). Mean abundance differed significantly between all three sites (Table 2). The average CW of juvenile crabs ranged from 1.6 to 7.5 mm within replicates but did not differ significantly between locations (ANOVA; $F_{2,15} = 0.139$; $P = 0.871$).

Discussion

During our spring and summer surveys along the French coast of the Channel, large *Hemigrapsus sanguineus* was recorded only in the intertidal zone, mainly at the level of the middle shore zone and only under boulders (Dauvin 2009a,b; Dauvin et al. 2009; Dauvin and Dufossé 2011; Gothland et al. 2013). Newly-settled crabs and small individuals were not collected under boulders but were, for first time, detected in mussel beds. Mussel beds appear to provide protection for newly settled crabs (1.1–6.0 mm CW) from predation by fish, other crustaceans, and larger conspecifics.

Epifanio et al. (1998) had shown that newly metamorphosed juveniles of *Hemigrapsus sanguineus* had a mean CW of 1.6 mm, which corresponded to our data for individuals just after the megalopa stage (1.1 mm in the samples studied here). For *H. sanguineus*, the growth in carapace-width was linear (rate= 0.06 $mm.d^{-1}$), and females could reach sexual maturity at a size of 15 mm CW in approximately 7.5 months (Epifanio 2013). Larval duration depended on salinity and temperature, while the interval from hatching to the megalopa stage was about 16 days under optimum conditions (Epifanio et al. 1998). The post-larvae of *H. sanguineus* had a specific growth rate ranging from 0.19 d^{-1} to 0.23 d^{-1} at high salinities and temperatures (Epifanio et al. 1998; Epifanio 2013).

In terms of estimated density per m², the mean (± SD) density of megalopae and newly metamorphosed *H. sanguineus* juveniles was 373±153 individuals m^{-2} at Lion-sur-Mer and 189±51 $ind.m^{-2}$ at Villers-sur-Mer, with a maximum of 560 $ind.m^{-2}$ for one replicate at Lion-sur-Mer (about five times higher than the maximum density of individuals > 6 mm). It is surprising that no *H. sanguineus* megalops larvae or newly metamorphosed juveniles were observed in the intertidal mussel beds at Saint-Honorine-des-Pertes at a station with a number of adults, i.e., 96 individuals/m^2 at this station in spring 2013 against 49 individuals/m^2 at Lion-sur-Mer and 14 individuals/m^2 at Villers-sur-Mer.

The comparison of mean size of crabs in mussel beds is, however, a bit misleading because four of the replicates at Saint-Honorine-des-Pertes contained no crabs, and the mean CW of the 32

Table 2. Density (number of individuals per m^2) and average size in six quadrats of *H. sanguineus* in mussel beds, estimated at three sites during August-Sept. 2013. R1: Replicate 1. Means sharing the same superscript did not differ significantly (Tukey's HSD test; P > 0.05).

Location	Density							Average size (mm)						
	R1	R2	R3	R4	R5	R6	Average	R1	R2	R3	R4	R5	R6	Average
Villers-sur-Mer	192	144	272	144	160	224	189.3 ^{a}	1.8	4.0	3.0	3.0	2.0	3.5	2.9
Sainte-Honorine-des-Pertes	0	0	16	0	16	0	5.3 ^{b}	0.0	0.0	7.0	0.0	8.0	0.0	7.5
Lion-sur-Mer	272	528	176	416	288	560	373.3 ^{c}	2.0	1.6	3.2	2.1	1.8	2.5	2.2

individuals collected in the two replicates where crabs were present was 7.5 mm, which clearly was larger than the mean CW of the other two locations, i.e., they were not newly metamorphosed juveniles (Table 2). Indeed, the density of Asian shore crabs under boulders at Saint-Honorine-des-Pertes during summer 2013 reached 124 individuals/m^2 (J.-P. Pezy, unpublished data), which was the highest density currently reported for the English Channel rocky shores (Gothland et al. 2013). We suggested that, at this location, settlement occurred in the lower part of the intertidal zone where mussel beds were more extensive and the few animals that we collected (mean CW = 7.5 mm) represented the larger individuals migrating up to the boulder habitat. Unfortunately, we did not sample these deeper mussel beds and further study of the full depth range of mussel habitat as a settlement zone for *H. sanguineus* is warranted.

Among other intertidal habitats that might be candidates for settlement of *H. sanguineus* are: crevices in the hard substratum; barnacle concentrations; *Crassostrea gigas* oyster reefs; hard surfaces under brown algae (mainly *Fucus* spp.); gravelly soft-bottom sediments; and mussel beds. Since these latter habitats are very common along the Calvados Coast, it may prudent to focus first on the mussel-bed habitat given the results of the present study. Moreover, along the eastern Channel coast, at 'Quend Plage' in the Picardy region, some adult individuals of *H. sanguineus* have been observed in the mussel cultivation structures (Ruellet, personal communication, in the framework of the CANOPI project, Réseau d'Observation du Littoral Normand Picard). Lastly, it is established that mussels and oysters are preferred prey of *Hemigrapsus* (Brousseau et al. 2001); hence, their colonization of wild and cultured bivalve beds is to be expected.

The present study supported our hypothesis that the size gap between juveniles sampled under boulders and post-larvae just after metamorphosis could be resolved if we took into account the dense mussel beds of the intertidal zone at the colonized sites. Therefore, we concluded that mussel beds are an important habitat for settlement of juvenile crabs, but other intertidal habitats could also be considered. After their settlement, *H. sanguineus* migrated under the boulders where they were better protected from predators. In a highly colonized zone at Saint-Vaast-la-Hougue, where population densities were comparable to those reported by Dauvin (2009a,b) at Sainte-Honorine-des-Pertes, Gothland (2013) had shown that *H. sanguineus* occupied the intertidal zone differently throughout the year. The species migrated from the upper part of the intertidal zone in spring and summer to the lower part of the intertidal zone during unfavourable seasons in terms of temperature, i.e. autumn and winter.

In terms of possible effects on native species, Loher and Whitlach (2002), in a study where both species are non-native and invasive, showed that the yearling *H. sanguineus* consumed newly settled European green crab *Carcinus maenas* (Linnaeus, 1758), thus reducing recruitment of the latter species. In the mussel beds of our study area, the density of megalopae and newly metamorphosed *C. maenas* was 323±188 ind.m^{-2} (mean ± standard deviation) at Lion-sur-Mer, 176±201 ind.m^{-2} at Villers-sur-Mer, with a maximum of 704 ind.m^{-2} for one replicate at Lion-sur-Mer (J.-P. Pezy, unpublished data). It is unknown whether *H. sanguineus* represents a significant source of mortality for the *C. maenus* population but this question should be evaluated because green crab supports a small fishery.

One caveat in interpreting the results of this study is the different timing of sample collections in boulder and mussel-bed habitats. A study over a whole year at the same sites might give better resolution of reproductive and settlement periods in both habitats. However, in 2013 the first ovigerous female was observed in mid-May (Rocroy 2013) and we can reasonably assume that no newly settled juveniles were present in mussel-bed habitat during April.

In conclusion, this study indicated mussels beds represent a previously unknown settlement habitat for larval *H. sanguineus.* Additional studies in the English Channel appear warranted to: 1) to test the hypothesis of competition and predation between megalopae and newly metamorphosed juveniles of *H. sanguineus* and *C. maenas* in mussel beds, 2) to identify other potential intertidal settlement habitats for *H. sanguineus*, such as *Crassostrea gigas* oyster beds and algae communities in crevices, and 3) to explore the presence and abundance of *H. sanguineus* adults in mussel and oyster cultivation zones, as well as in the shallow subtidal zone (i.e., between 0–10 m beneath low water mark).

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