Relationship between habitat and recruitment of the Asian shore crab *Hemigrapsus sanguineus* (De Haan, 1835) and the indigenous shore crab *Carcinus maenas* (Linnaeus, 1758) on Normandy seashores

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Abstract

On the French coast, *Hemigrapsus sanguineus* (*H.s*) was observed for the first time in 1999 in Le Havre. Since then, *H. sanguineus* adult population has been spreading along the French coast of the English Channel and have strong interaction with the indigenous crab *Carcinus maenas* (*C.m*). Juveniles populations of *H. sanguineus* and *C. maenas* are preferentially present in mussel beds (279 ± 108 ind·m^{-2} for *H.s* and 238 ± 77 ind·m^{-2} for *C.m*) and barnacles (63 ± 16 ind·m^{-2} for *H.s* and 28 ± 9 ind·m^{-2} for *C.m*). On the contrary, within macroalgae dominated habitats, only juveniles of *C. maenas* were observed (30 ± 11 ind·m^{-2}).

Keywords: competition; English Channel; intertidal; *Mytilus edulis*; non-indigenous species

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Relation habitat-recrutement du crabe sanguin *Hemigrapsus sanguineus* (De Haan, 1835) et du crabe vert *Carcinus maenas* (Linnaeus, 1758) le long des côtes Normandes

Résumé

En France, *Hemigrapsus sanguineus* (*H.s*) a été observé pour la première fois en 1999 au Havre. Depuis, la population de *H. sanguineus* adulte est abondante le long des côtes françaises de la Manche et a une interaction avec le crabe vert *Carcinus maenas* (*C.m*) au niveau de l'intertidal. Les populations de juvéniles de *H. sanguineus* et de *C. maenas* sont préférentiellement localisées au niveau des moulières intertidales (279 ± 108 ind·m^{-2} pour *H.s* et 238 ± 77 ind·m^{-2} pour *C.m*), des balanes (63 ± 16 ind·m^{-2} pour *H.s* et 28 ± 9 ind·m^{-2} pour *C.m*). Au niveau des algues, uniquement des juvéniles de *C. maenas* ont été observés (30 ± 11 ind·m^{-2}).

Mots-clés : compétition ; espèce non-indigène ; intertidal ; Manche ; *Mytilus edulis*

Introduction

Non-indigenous species may be transported across entire oceans while their introductions are facilitated by human activities (Boudouresque 2008; Galil, Clark & Carlton 2011; Ojaveer *et al.* 2018) which cause severe impacts on estuaries and coastal habitats in their introduced range (Ruiz, Carlton, *et al.* 1997; Ruiz, Fofonoff, *et al.* 1999; Williams & Grosholz 2008). Invasive species have the potential to impact marine communities either through direct predation or through competition with indigenous species for critical resources (Cohen & Carlton 1998). In the English Channel, in contrast to the subtidal zone that showed very little change in faunal assemblages over the last five decades (Capasso *et al.* 2010; Hinz *et al.* 2011; Gaudin 2017), rocky shore communities have been rapidly changing (Hawkins, Sugden, *et al.* 2009) as the intertidal zone is subject to greater temperature amplitudes, especially during severe winters or warm summers (Hawkins, Southward & Genner 2003; Hawkins, Sugden, *et al.* 2009).

Reproduction traits and niche allocation processes play an important role in non-indigenous species establishment and spread (Bremner 2008; Herborg *et al.* 2007). The Asian shore crab *H. sanguineus* (De Haan, 1853), indigenous to the Western Pacific, has been a remarkable marine invader in the Western and Eastern Atlantic. This species was first observed in the Western Atlantic in New Jersey in 1988 (Williams & McDermott 1990). Since then, it has shown a great ability to colonize rocky intertidal habitats along the East coast of North America (McDermott 1998; Brousseau, Goldberg & Garza 2014). In the Eastern part of Atlantic, the first observation was reported in Le Havre

and in the Dutch Delta system in 1999 (Breton *et al.* 2002; Wolff 2005). Since 2011, *H. sanguineus* populations have been monitored along the French coast of English Channel (from Mont-Saint-Michel Bay to Dunkirk) where the population presents a high colonisation dynamic. Finally, the species was recently recorded from the UK (Seeley, Sewell & Clark 2015). Development of Asian shore crabs includes five zoeal stages and a megalopal stage (Epifanio *et al.* 1998; Hwang, Lee & Kim 1993; Hwang & Kim 1995). Mean duration from hatching to metamorphosis is 25 days in optimum conditions (Epifanio *et al.* 1998).

The Green crab *Carcinus maenas* (Linnaeus, 1758) is an indigenous species along the Atlantic European coast which lives under boulders on rocky shores, as does *H. sanguineus*. However, *C. maenas* may also be found on sand and sand-mud shores (Cohen, Carlton & Fountain 1995; WDFW 2002) while *H. sanguineus* is absent from these habitats. In the Western Atlantic coast, this species was introduced in the early 1800s and has considerably expanded its range along the Atlantic coasts of the US and Canada (Audet *et al.* 2003). It invaded California in 1929 (Jensen, McDonald & Armstrong 2002) and expanded its range to the west coast of Vancouver Island (Jamieson *et al.* 2002). *C. maenas* is considered to be an effective predator where it spreads generating negative effects on biodiversity (Cohen, Carlton & Fountain 1995; McDonald, Jensen & Armstrong 2000; Lohrer & Whitlatch 2002). After hatching, the larva is wrapped in a fragile transparent membrane, it is the protozoan stage. Four larval stages (zoeal) and a transitional stage (megalopal) follow the protozoan stage. The four Zoea stage swim freely in the water column. Once the megalopal larva finds a suitable habitat, it settles there and moults (Williamson 1903; Crothers 1967; Yamada 2001). According to Berrill (1982), the megalopal form evolves very rapidly once it settles on the bottom. It then reaches the first benthic stage which resembles an adult form measuring from 1.3 mm to 1.7 mm in Carapace Width (CW) (Berrill 1982; Mohamedeen & Hartnoll 1989). Early benthic stages are not distributed randomly in the habitat. They occupy complex microhabitats with high densities of molluscs, eelgrass and filamentous algae (Moksnes 2002).

Small individuals (<10 mm) of *H. sanguineus* and *C. maenas* are not observed under boulders along the French coast of the English Channel. Pezy & Dauvin (2015) observed that mussel beds are a favourable recruitment habitat for juveniles of *H. sanguineus* and *C. maenas*. Thus, the aim of this paper is to investigate the potential habitat role of macro algae and barnacles for *H. sanguineus* and *C. maenas* along the Normandy coasts and to compare the densities observed in these two habitats with the densities found in mussel beds. In addition, this investigates temporal and spatial dynamics of the *H. sanguineus* and *C. maenas* populations after settlement in three different habitats: mussel beds, barnacles and algae.

Material and methods

Study area

Located along the English Channel, in Normandy, the wide intertidal zone from the Mont-Saint-Michel Bay to the Bay of Somme forms a linear 638 km coastline which is composed of a mixture of sandy and rocky areas. The study was made on the Calvados coast between Grandcamp-Maisy and the Seine estuary (Figure 1). Boulders are present on rocky shore along the coast. The study area stands open to the sea with rocky, limestone shoreline and a gentle slope. Along the Calvados coast, intertidally, there are deposits of sand that move onshore or offshore depending on the direction and strength of winter storms, with a megatidal range from 8 m during spring tides and 3 m during neap tides. The salinity varies from 32.3 in April to 32.4 in August–September which is quite stable along the year; and the seawater temperature increases from 7.1 °C–10.9 °C in April to 18.7 °C–19.1 °C in August–September (SOMLIT data from Luc-sur-mer marine station).

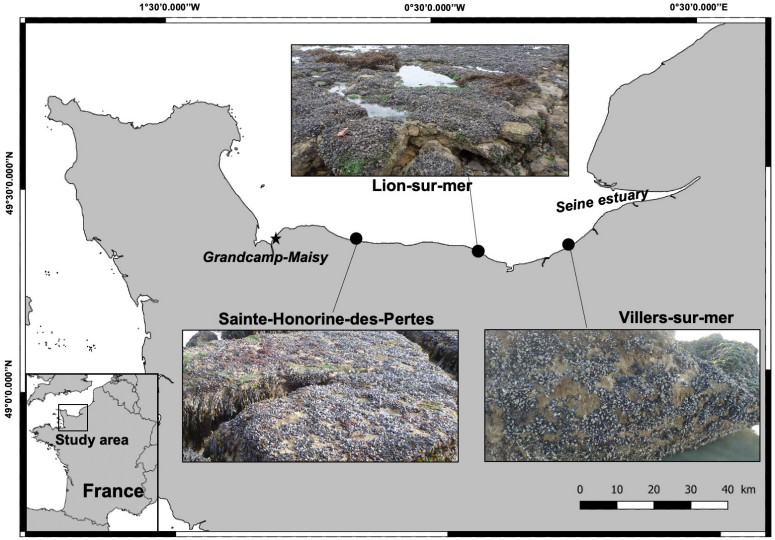

Figure 1: Location of the three sampled sites in Normandy with for each site a picture of the mussel bed habitat.

Juvenile populations

The juvenile *H. sanguineus* habitat corresponds to the mussel beds (*Mytilus edulis* (Linnaeus, 1758)) (composed of adult and juveniles individuals) sampled in 2013 by Pezy & Dauvin (2015) in three different locations (Sainte-Honorine-des-Pertes, Lion-sur-mer and Villers-sur-mer) (Figure 1). Two others habitats were also sampled in these

same locations: Barnacles (*Semibalanus balanoides* (Linnaeus, 1767)) and Algae (*Ulva lactuca* (Linnaeus, 1753), *Fucus spiralis* (Linnaeus, 1753)). Sampling was carried out on 27th September 2014 and on 26th September 2015. At each site, estimates of crab abundance were based on six replicates 1/16th m^2 quadrats (0.0625 m^2) which were placed randomly, and densities were reported as number of individuals per m^2. Mussel beds, barnacles and algae were sampled by rock scraping with a spatula, and the scraped surface was brushed to avoid missing organisms. Samples were stored in plastic bags and transferred to the laboratory. Living crabs were removed from the samples immediately after reaching the laboratory, and then fixed in absolute ethanol before being measured and identified.

Laboratory observations

Crabs collected in mussel beds, barnacles and algae were identified to the species level and counted. Carapace width was measured under a binocular microscope using an ocular micrometer. Size classes were based on 0.1 mm intervals for the smallest individuals (i.e. from scrap samples).

Statisical analyses

A one-way ANOVA was performed to assess the *Hemigrapsus sanguineus* and *Carcinus maenas* density differences between sites and years for each habitat independently. In addition, a two-way ANOVA with interaction was also performed to test the densities and size between the habitat and species. Prior to each ANOVA, a Shapiro-Wilk normality test and a Bartlett's test for homogeneity and variance were performed to check whether the asumptions of ANOVAs were met. Finally, if differences were observed, a Tukey Significant Difference test was applied.

Data analysis was performed by non-metric multidimensional scaling ordination (MDS), and Hierarchical Ascendant Classification (HAC) created using group average linking with the Bray-Curtis similarity measure. To identify within different groups which species primarily accounted for the observed assemblage difference, SIMPER (SIMilarity PERcentage) routines were performed using a decomposition of Bray-Curtis similarity on densities data (Clarke & Gorley 2006).

Results

Size structure by habitat

Over both sampling periods, a total of 2 068 crabs were collected at the different sites and habitats. A total of 905 *Hemigrapsus sanguineus* (*H.s*) and 770 *Carcinus maenas* (*C.m*) were collected on mussel beds (Figure 2). The Carapace Width (CW) ranged from 1,0 mm to 22,0 mm for *H.s* and from 1,0 mm to 20,0 mm for *C.m* (Figure 2;

Table 1). In mussel beds, the *H.s* juvenile population structure was mostly comprised of two size classes between 1.0 mm–1.6 mm and 1.7 mm–3.4 mm, whereas for *C.m*, the majority of individuals were distributed between 1.0 mm to 5.2 mm (Figure 2).

Table 1: Mean density with standard deviation (number of individuals per m^2), range size (minimum and maximum size, in mm) and mean size (mm) of *Hemigrapsus sanguineus* (*H.s*) and *Carcinus maenas* (*C.m*) carapace width at Sainte-Honorine-des-Pertes, Lion-sur-mer, Villers-sur-mer for the mussel beds, barnacles and algae habitats in 2014 and 2015.

			2014		2015	
			H.s	***C.m***	***H.s***	***C.m***
Sainte-Honorine-des-Pertes	**Mussel beds**	Mean density	644.4 ± 180.8	22.2 ± 24.3	248.1 ± 63.1	346.3 ± 57.3
		Range size	1.0–22.0	1.6–17.4	1.0–15.5	1.0–16.0
		Mean size	2.4	4.9	2.6	2.6
	Barnacles	Mean density	82.5 ± 22.9	20.4 ± 13.0	98.1 ± 23.7	33.3 ± 9.9
		Range size	1.0–2.4	1.2–2.6	1.0–2.4	1.4–2.8
		Mean size	1.5	1.8	1.5	2.2
	Algae	Mean density	-	13.0 ± 4.5	-	25.9 ± 5.7
		Range size	-	4.5–17.5	-	4.6–18.2
		Mean size	-	8.5	-	8.3
Lion-sur-mer	**Mussel beds**	Mean density	172.2 ± 99.1	127.8 ± 69.1	233.3 ± 153.3	263.0 ± 157.5
		Range size	1.6–14.9	1.1–20.0	1.0–11.1	1.0–10.2
		Mean size	3.3	3.9	2.3	2.0
	Barnacles	Mean density	55.5 ± 17.2	33.3 ± 9.9	77.8 ± 15.7	44.4 ± 9.9
		Range size	1.0–2.6	1.0–3.0	1.1–3.2	1.0–3.6
		Mean size	1.6	2.1	1.7	2.0
	Algae	Mean density	-	29.6 ± 16.7	-	46.3 ± 16.3
		Range size	-	1.2–10.2	-	1.1–8.0
		Mean size	-	3.2	-	2.4
Villers-sur-mer	**Mussel beds**	Mean density	266.7 ± 104.0	107.4 ± 38.3	111.1 ± 48.2	559.3 ± 113.9
		Range size	1.1–21.7	2.0–12.0	1.1–15.2	1.0–8.4
		Mean size	3.2	3.7	6.0	2.6
	Barnacles	Mean density	24.1 ± 10.9	13.0 ± 4.5	38.9 ± 6.1	22.2 ± 7.0
		Range size	1.6–3.4	2.0–5.8	1.1–2.6	2.0–4.8
		Mean size	2.3	3.8	1.9	3.0
	Algae	Mean density	-	25.9 ± 9.1	-	40.7 ± 13.5
		Range size	-	1.2–3.5	-	1.0–4.0
		Mean size	-	2.1	-	2.0

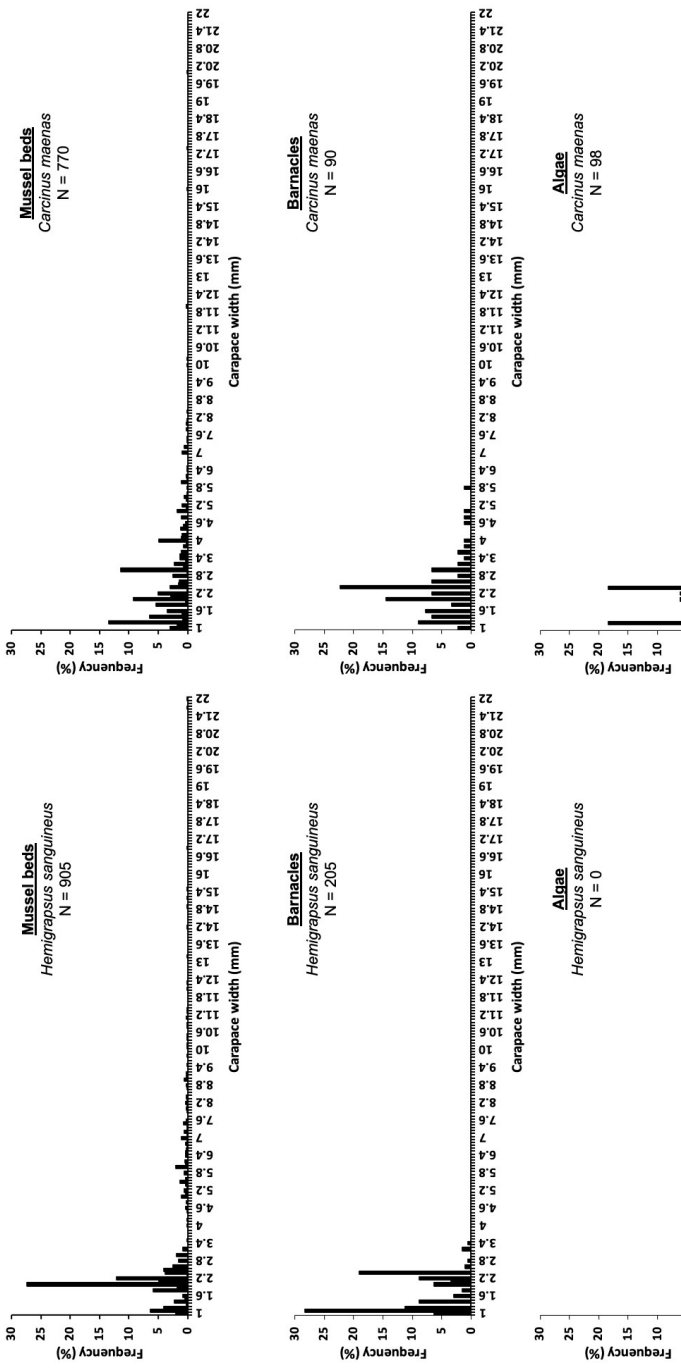

Figure 2: Size distribution (%) of the carapace width (mm) of *Hemigrapsus sanguineus* and *Carcinus maenas* sampled at the three sites in 2014 (27th September) and 2015 (26th September) in mussel beds, barnacles and algae.

A total of 205 *Hemigrapsus sanguineus* and 90 *Carcinus maenas* were collected on barnacles (Figure 2). The CW ranged from 1.0 mm to 3.22 mm for *H.s* and from 1.0 mm to 10.2 mm for *C.m* (Figure 2; Table 1). For the barnacle habitat, two size classes dominated for *H.s* (1.0 mm–1.6 mm and 1.7 mm–2.6 mm), whereas for *C.m* the size structure was comprised between 1.0 mm to 4.0 mm (Figure 2; Table 1).

A total of 98 *Carcinus maenas* were collected on algae, whereas no *H.s* were sampled in this habitat (Figure 2). The *C.m* CW range was ranged from 1.0 mm to 18.2 mm with two dominant size classes of 1.0 mm–1.6 mm and 2.0 mm–2.8 mm (Figure 2; Table 1).

There was no overall significant difference in the mean size between *C.m* and *H.s* on both habitats (Table 2). However, the mean size on the mussel beds (*H.s*: 2.9 ± 2.4 mm; *C.m*: 2.7 ± 1.8 mm), the barnacles (*H.s*: 1.6 ± 0.6 mm; *C.m*: 2.3 ± 0.9 mm) and the algae habitat (*C.m*: 3.7 ± 3.4 mm) were significantly different (Table 2).

Table 2: Results of two-way ANOVA tests with interaction on *Hemigrapsus sanguineus* and *Carcinus maenas* density and size for the three different habitats with Tukey test.

	Factors	df	F	*p*	Tukey test
Density	Habitat	2	91.37	< 0.001	Mussel beds ≠ Barnacles; Algae
	Species	1	0.95	0.33	
	Habitat:Species	2	2.06	0.13	
	Σ	210			
Size	Habitat	2	37.82	< 0.001	Mussel beds ≠ Barnacles ≠ Algae
	Species	1	1.37	0.24	
	Habitat:Species	2	8.72		
	Σ	2 036			

Density

The mean densities with standard deviation were detailed by habitat (mussel beds, barnacles and algae), species (*Hemigrapsus sanguineus*, *Carcinus maenas*) and years (2014, 2015) in the Table 1.

No significant temporal effect (2014–2015) between *H.s* and *C.m* in the three different habitats was observed (Tables 1, 3). In the mussel beds, *C.m* density did not differ between the three sites, whereas, the density of *H.s* was significantly higher at Sainte-Honorine-des-Pertes than in the other two sites (Tables 1, 3). In the barnacle habitat, *C.m* density was significantly higher at Lion-sur-mer than in the other sites and *H.s* density was significantly higher at Villers-sur-mer than in the other sites (Tables 1, 3). For the algae habitat, the *C.m* density was significantly lower at Saint-Honorine-des-Pertes than for the other two sites (Tables 1, 3).

The mean density of *H.s* (279.3 ± 108.1 ind·m^{-2}) and *C.m* (237.7 ± 76.7 ind·m^{-2}) were higher in the mussel beds than in the two other habitats (Figure 3; Tables 1, 3).

However, the density of *C.m* in the barnacle habitat (27.8 ± 9.1 ind·m^{-2}) was similar to *C.m* density in the algae (30.2 ± 11.0 ind·m^{-2}) (Figure 3; Tables 1, 3). Except for algae with the absence of *Hemigrapsus sanguineus*, there was no significant difference between the *H.s* and *C.m* densities (Figure 3; Tables 1, 3).

Table 3: Results of one-way ANOVA tests on the three different habitats (mussel beds; barnacles; algae) for *Carcinus maenas* (*C.m*) and *Hemigrapsus sanguineus* (*H.s*) for site (SHP; LM; VM) and year (2014; 2015) factors with Tukey test (SHP: Sainte-Honorine-des-Pertes; LM: Lion-sur-mer; VM: Villers-sur-mer).

		Factors	**df**	**F**	***p***	**Tukey test**
Mussel beds	*C.m*	Site	2	2.23	0.12	
		Year	1	50.64	< 0.001	
	H.s	Site	2	8.55	< 0.01	SHP ≠ LM; VM
		Year	1	6.64	< 0.05	
Barnacles	*C.m*	Site	2	11.86	< 0.001	LM ≠ SHP; VM
		Year	1	6.95	< 0.05	
	H.s	Site	2	31.22	< 0.001	VM ≠ SHP; LM
		Year	1	2.74	0.11	
Algae	*C.m*	Site	2	5.82	< 0.01	SHP ≠ LM; VM
		Year	1	10.22	< 0.01	
		Σ	30			

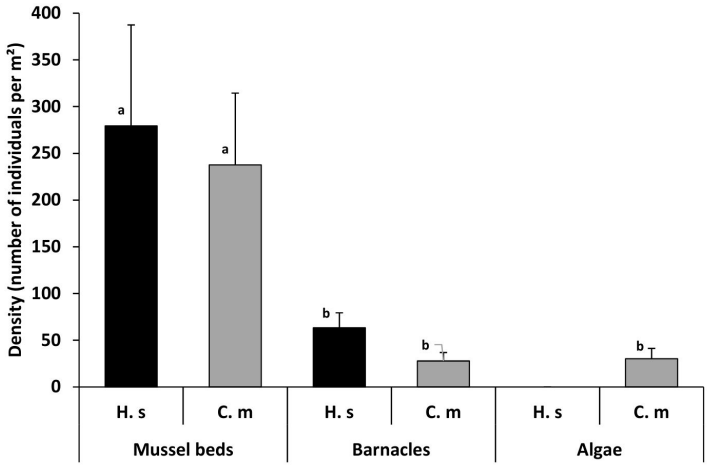

Figure 3: Annual mean density with standard deviation (number of individuals per m^2) for *Hemigrapsus sanguineus* (*H.s*) and *Carcinus maenas* (*C.m*) in the mussel beds, barnacles and algae across the three different sites in Normandy. Significant differences (Tukey-test, $p < 0.05$) are indicated by letters a and b.

At a similarity value of 40 %, the cluster dendrogram allows us to separate the stations into three main groups (Figure 4). The first group includes both site of mussel beds with an average similarity of 59.9 % with a contribution of *H. sanguineus* of 60.6 % and a contribution of *C. maenas* of 39.4 % (SIMPER analysis). The second group includes both site of barnacles with an average similarity of 71.2 %, for a contribution of *H. sanguineus* of 67.9 % and a *C. maenas* contribution of 32.1 % (SIMPER analysis). The third group includes both site of algae with an average similarity of 75.1 % for a 100 % contribution of *C. maenas* (SIMPER analysis).

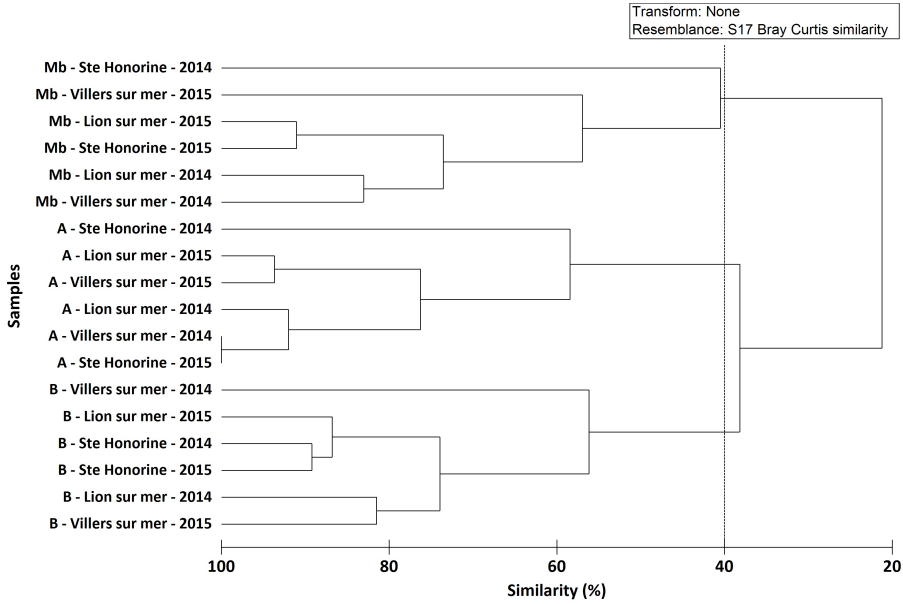

Figure 4: Cluster dendrogram showing distribution of the three habitat (Mb : mussel beds; B : Barnacles; A : Algae) at the three sites (Sainte-Honorine-des-Pertes; Lion-sur-mer; Villers-sur-mer) for the two years (2014 and 2015) according to the Bray-Curtis similarity of the densities.

Discussion

In Normandy, the *Hemigrapsus sanguineus* and *Carcinus maenas* adult populations have been studied since 2008 (Dauvin 2009) and since 2011 with the same protocol of three 1 m^2 quadrats and a sampling of all decapods under boulders at each site. However, this strategy was not adapted to the sampling of juvenile populations. The study on these two juvenile populations is necessary in order to understand the effect of a non-indigenous species (*Hemigrapsus sanguineus*) on an indigenous species (*Carcinus maenas*). Mussel beds appear to be a very favourable juvenile crab habitat especially for non-indigenous crabs, such as *H. sanguineus* and *Eriocheir sinensis* H. Milne Edwards,

1853 (Pezy, Dauvin & Vincent 2015). In fact, the high biodiversity of algae and macrozoobenthos present in mussel beds could be a source of food for the development of juvenile crabs and could also provides efficient protection against predators. In 2013, Pezy & Dauvin (2015) observed in mussel beds a juveniles *H. sanguineus* mean density of 373.3, 189.3 and 5.3 individuals per m^2 at Lion-sur-mer, Villers-sur-mer and Sainte-Honorine-des-Pertes respectively. The densities observed at Lion-sur-mer and Villers-sur-mer were similar to those observed in 2014 and 2015. However, on the Sainte-Honorine-des-Pertes site, the density observed in 2013 was lower than the densities observed in 2014 and 2015. This result could be explained by the fact that in 2013 the mussel beds were sampled in the lower intertidal part whereas, in 2014/2015, the samples were taken in the mid intertidal part, near the adult *H. sanguineus* population. The proximity of the adult population could favour larval recruitment in these three habitats. However, it is also possible that the juvenile population present in these habitats migrate under the nearby blocks after their development. There is therefore a need to pursue this monitoring. However, in 2016, a large mortality of mussels took place (personal observation) along the Calvados coastline, making it impossible to survey this habitat.

In the Wadden Sea (south of North Sea), Geburzi, Brandis & Buschbaum (2018) have detected a lagin recruitment between *C. maenas* and *H. sanguineus* with a peak in early July for *C.m* and a peak at the end of August to mid-September for *H.s*. This observation could explain the larger range of *C. maenas* in the three habitats. In fact, this offset in recruitment periods could be favourable for *C. maenas*, with juveniles already present in habitat that potentially limits the expansion of the non-indigenous species *H. sanguineus*. At the second benthic stage, juveniles of *C. maenas* appear to prefer mollusc habitat with less vegetation cover (Moksnes 2002), this behaviour can explain the important densities of *C. maenas* in mussel's beds in Normandy. At the adult stage, *C. maenas* occupies various habitat, as sheltered marine areas and estuaries. This species is found on rocky, sandy; muddy bottoms in eelgrass beds (*Zostera marina* Linnaeus, 1753) and marshes (Cohen, Carlton & Fountain 1995). This species, occupies the intertidal and subtidal zone where it is observed at depths of 5 m to 12 m (Crothers 1968; Williams, Floyd & Rossong 2006).

In Normandy, along the intertidal rocky littoral shore (supra and mediolittoral area), the adult *Hemigrapsus sanguineus* ecological niche overlaps with the adult *Carcinus maenas* ecological niche. Thus, this spatial competition between the non-indigenous species (*H. sanguineus*) and the indigenous species (*C.m*) could be limited by the fact that the ecological niche of *C.m* is broader (encompassing estuaries, sandy shores, …) than the *H.s* ecological niche. In fact, *H. sanguineus* is known to be a predominantly intertidal species in all stages after metamorphosis (Landschoff *et al.* 2013; van den Brink, Wijnhoven & McLay 2012; Lohrer, Fukui, *et al.* 2000), whereas *C. maenas* lives in subtidal and intertidal zones, and in estuaries with a large salinity gradient.

Another study has also pointed out that *H. sanguineus* spatially competes for habitat with *Carcinus maenas* (Lohrer & Whitlatch 2002). For instance, along the

East coast of the USA in Long Island Sound, Lohrer & Whitlatch (2002) conducted a suite of experiments to investigate predator/prey relationships between *H. sanguineus* and *C. maenas*. A four-year survey showed a precipitous decline in green crab density which coincided with a sharp rise in the number of Asian shore crabs. The study also highlighted that yearling *H. sanguineus* consume newly settled *C. maenas* and likely reduce other species recruitment in areas where the two species are present. However, it is worth noting that the presence of juvenile green crabs does not affect the survival of juvenile *H. sanguineus*. Along the Normandy coasts, the presence of *C. maenas* juveniles in algae reveals that *C. maenas* have always colonized a range of habitats, including algae, and in the latter habitat, there is no competition with *H. sanguineus*.

Since the mass mortality episode in 2016, mussels have re-established themselves along the Calvados coasts. It would be interesting to test the assumption that the presence of *C. maenas* and *H. sanguineus* larvae in the three juvenile habitats is linked to the adult populations found in the vicinity of these sites. Thus, it would be also interesting to test a distance gradient of juvenile habitats from adults to understand the links between them.

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