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Biological traits explain the distribution and colonisation ability of the invasive shore crab *Hemigrapsus takanoi*

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ABSTRACT

Comprehending marine invasions requires a better knowledge of the biological traits of invasive species, and the future spread of invasive species may be predicted through comprehensive overviews of their distribution. This study thus presents the current distribution of a non-indigenous species, the Asian shore crab *Hemigrapsus takanoi*, as well as the species population characteristics (size distribution and cohorts), based on a five-year survey (2008–2012) along the French coast of the English Channel. Two large populations were found near harbours: one on the Opal Coast (where density reached 61 ± 22 ind.m^{-2}, mean ± s.d., in Dunkirk harbour) and one on the Calvados coast (density up to 26 ± 6 ind.m^{-2}, mean ± s.d, in Honfleur harbour). *H. takanoi* exhibited a short life cycle, a rapid growth, an early sexual maturity and a high adult mortality. These features, combined with previously described high fecundity and high dispersal ability, endow this species with an 'r-selected strategy'. This strategy, which usually characterises species with a high colonisation ability, would explain the success of *H. takanoi* for colonising the French coast of the Channel. However, the species was found only in harbours and their vicinity; *H. takanoi* thus exhibited a discontinuous distribution along the 700 km of coastline. These results are discussed regarding sediment preference and potential introduction vectors. *Hemigrapsus takanoi* is now considered as established on the French coast and further studies are needed to evaluate the consequences of its introduction on the structure and functioning of the impacted shores.

1. Introduction

The introduction of invasive species, mainly due to the rise of maritime trade, is one of the most important human-induced perturbations disrupting coastal ecosystems, together with fishing, pollution, destruction of habitats and climate change (Jackson et al., 2001). The success of invasive species is driven by their biological characteristics, by the introduction vector and the recipient area (Brockerhoff and McLay, 2011). Invasive species can change the structure and functioning of marine ecosystems (Grosholz, 2002), at all biological levels (genome, individual, population, species, communities and ecosystem; Reise et al., 2006), *via* predation, parasitism, disease introduction, and physicochemical modifications of habitats (Beisel and Lévêque, 2010). Among the alien species identified in France, two Asian shore crabs, *Hemigrapsus takanoi* Asakura and Watanabe, 2005 and *Hemigrapsus sanguineus* (de Haan, 1835), have been reported on the French Atlantic coast. Brachyuran crabs are among the most common invaders around the world with 73 crab species described as alien, mostly in areas of intense maritime traffic (Brockerhoff and McLay, 2011). *H. takanoi* and *H. sanguineus*, both native from the north-western Pacific, were observed in France for the first time in 1994 at La Rochelle (Noël et al., 1997) and in 1999 at Le Havre (Breton et al., 2002), respectively. They were also found in the southern part of the North Sea in Germany, The Netherlands and Belgium (Gollasch, 1999; Nijland

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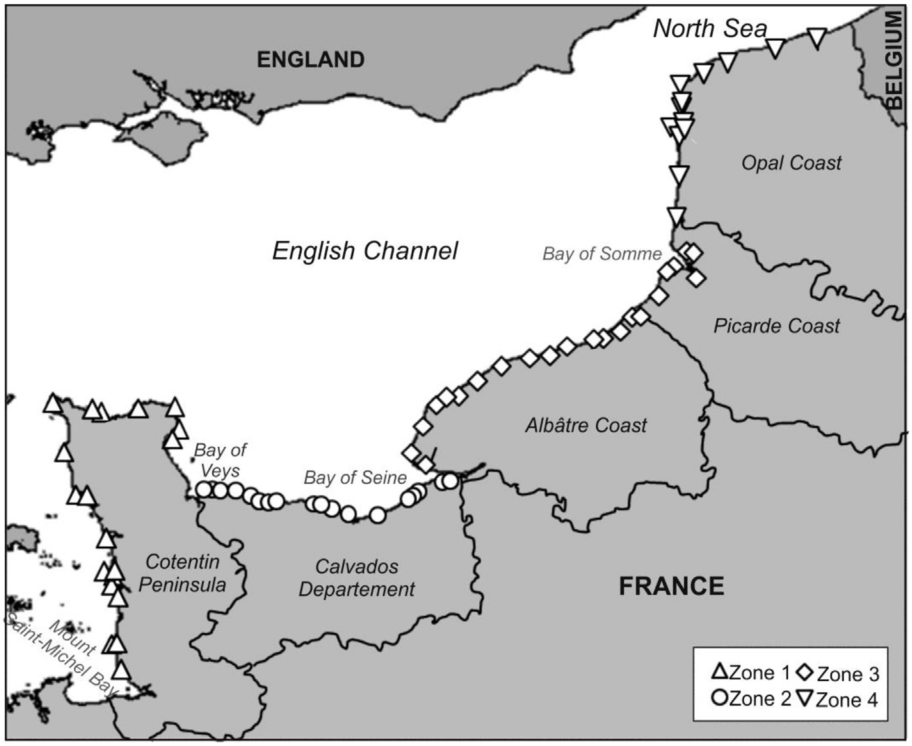

Fig. 1. Location of the sites studied along the French coast of the English Channel. Sampling was performed as follow: Zone 1, in summer from 2008 to 2012; Zone 2, in spring 2011 and 2012; Zone 3, in spring 2012 and summer 2012; Zone 4: spring 2008, 2010 and 2012.

and Beekman, 2000; Breton et al., 2002; Nuyttens et al., 2006; d'Udekem d'Acoz, 2006; Kerckhof et al., 2007; Obert et al., 2007; Van den Brink et al., 2012; Landschoff et al., 2013). Both species were probably introduced along the European coasts via ballast waters (Breton et al., 2002) and/or by the importation of the Pacific oyster *Crassostrea gigas* (Noël et al., 1997). In the Channel-North Sea area (the second busiest sea route in the world, "the North Europe Range"), aquaculture and ballast water represent respectively 29% and 13% of the major vectors of introduction and spread of invasive species (e.g. over 10 million tons of water were discharged around the coasts of the English Channel in 2009; Quemmerais-Amice et al., 2012). The larval stages of these varunid crabs may tolerate large variations in salinity (e.g. 15–35 for *H. takanoi*; Mingkid et al., 2006) and temperature (e.g. 15–30 °C for *H. sanguineus*; Epifanio et al., 1998), which contribute to the success of their colonisation. Along the French coast of the English Channel, they have been detected under boulders in the upper and mediolittoral, from Mount-Saint-Michel Bay to the Belgium border (Dauvin, 2009b; Dauvin and Delhay, 2010; Dauvin and Dufossé, 2011). Habitat preferences were suggested, with *H. takanoi* mainly colonising silted harbours, and *H. sanguineus* usually living on exposed shores (Schubart, 2003).

The comprehension of marine invasions requires a better knowledge of biological traits (Brockerhoff and McLay, 2011); furthermore, the future spread of invasive species may be predicted through comprehensive overviews of their distribution (Dauvin and Dufossé, 2011). The aims of this study were thus (1) to present the current geographical distribution of *Hemigrapsus takanoi* in comparison with earlier surveys (Dauvin et al., 2009; Dauvin, 2009a,b) and in relation with sediment characteristics (grain size) and, (2) to evaluate the dynamics of the French populations (through an analysis of densities, size distribution and the presence of ovigerous females) and their colonisation ability.

2. Material and methods

2.1. Study area

Surveys were conducted in 4 geographical areas with various periodicities from 2008 to 2012 (Fig. 1). These areas were, from west to east: (1) the Cotentin Peninsula was investigated each year during summer (zone 1: 19 sampling sites from Saint-Jean-Le-Thomas to Saint-Vaast-la-Hougue; for 2008 and 2009 data see Dauvin, 2009a, b), (2) the coast of the 'Calvados Departement' (from Grandcamp-Maisy to Honfleur) was prospected in spring 2011 and 2012 (zone 2: 18 sampling sites), (3) the Albâtre and Picarde coasts were sampled in spring and summer 2012 (zone 3: 21 sampling sites) and (4) the Opal Coast, from the Authie estuary to the Belgium border was studied during spring 2008, 2010 and 2012 (zone 4: 16 sampling sites; for 2008 data see Dauvin et al., 2009). In 2012, a total of 74 sites were prospected along approx. 700 km of coastline (Appendices 1–4).

2.2. Sampling procedure

At each sampling site, all crabs found under three series of 30 boulders were collected. Boulders were randomly selected in the mediolittoral and were considered as representative for each site. This sampling design was adopted for the estimation of the average abundances of shore crabs (Dauvin et al., 2009). On sites where boulder cover was sufficient (14 sites), three 1 m^2 quadrats were used to estimate crab density; in each quadrat, rocks and boulders were turned over and all individuals were collected. To standardise and ensure consistency, sampling was limited to two to three people per geographical area. In the laboratory, crabs were counted, sexed and identified, according to Asakura and Watanabe (2005), and measured (carapace width, CW) between the third antero-lateral teeth (Delaney et al., 2008). Furthermore, from 2008 to

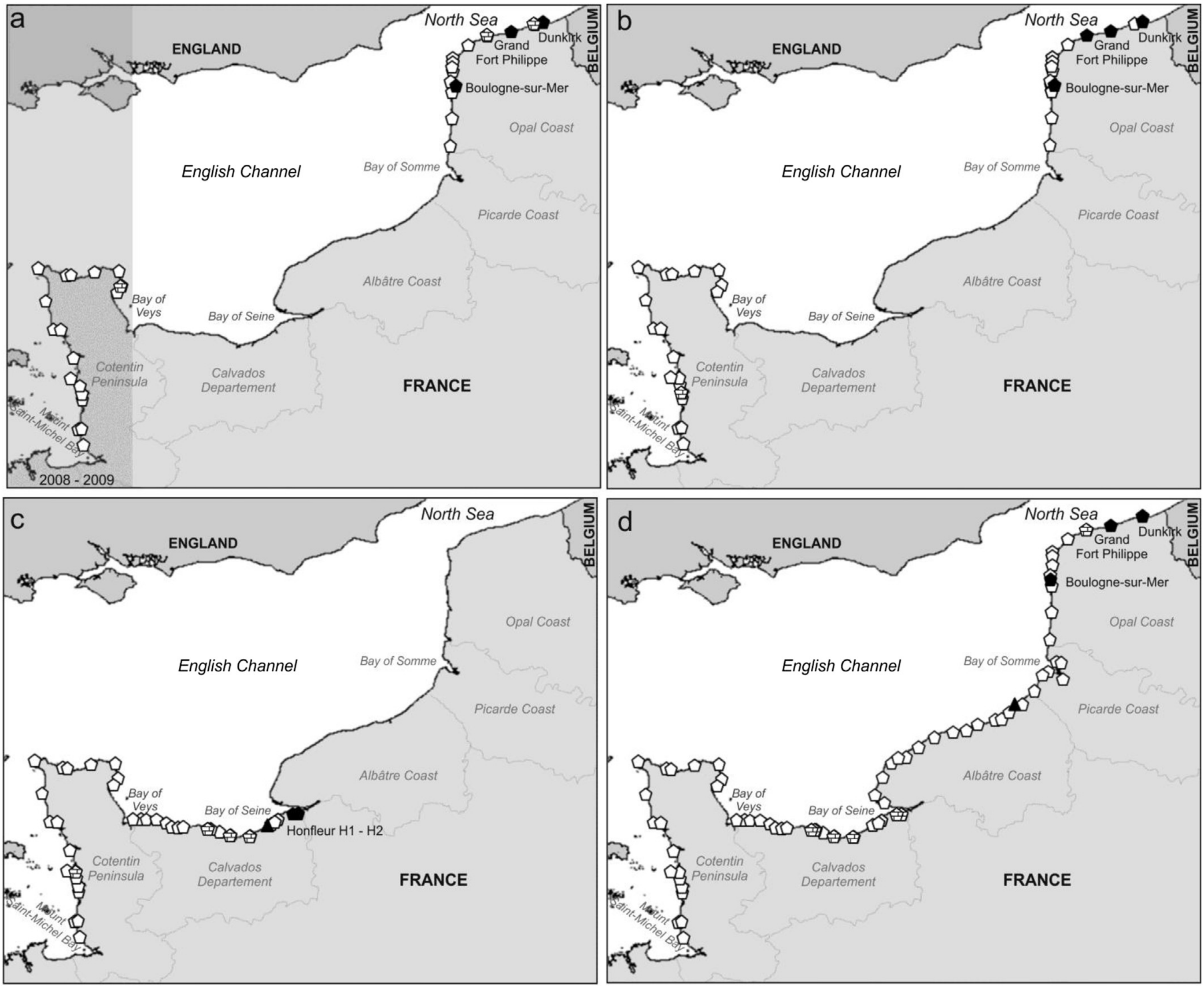

Fig. 2. Distribution of *H. takanoi* along the French coast of the English Channel in (a) 2008–2009, (b) 2010, (c) 2011 and (d) 2012. Stage of invasion: ⬠ not detected, ⬠ trace (1–10 ind. under 30 boulders), ⬟ colonised (>10 ind. under 30 boulders), ▲ proven presence.

2012, at total of 73 sediment samples (ca. 300 g) were manually collected for grain size analysis.

2.3. Sample and data analysis

The results from the 2010–2012 survey, as well as previously published data (Dauvin et al., 2009; Dauvin, 2009a,b; Dauvin and Delhay, 2010) were compiled. Three stages of invasion were defined according to abundance data (calculated as mean abundances under 30 boulders): (1) a site was considered as 'colonised' when more than 10 crabs were found under 30 boulders, (2) the presence of the species was considered as 'trace' when 1 to 10 crabs were found under 30 boulders and (3) the species was considered as 'not detected' when no crab was found under 30 boulders. The 'proven presence' was indicated for sites where *Hemigrapsus takanoi* was observed but, due to insufficient cover boulders, none of the two sampling strategies could be applied. Frequency distributions (%) of carapace-width classes (1 mm class) of *Hemigrapsus takanoi* were also determined. Cohort recognition and estimation of mean size for each modal group were performed following the method of Bhattacharya (1967) incorporated in FISAT II software (FAO-ICLARM Stock Assessment Tools II, version 1.2.2; Gayanilo et al., 2005). Cohorts were assumed to be single with a separation index greater than 2.

The grain-size distribution was determined using a classical dry sieving procedure (Bale and Kenny, 2005). Granulometric fractions were pooled in categories according to Larsonneur (1977). The relationship between sediment grain-size and the presence of *Hemigrapsus takanoi* was studied through multivariate analysis performed with the PRIMER software (version 5.2.9; Clarke and Warwick, 1994). The data matrices (% of grain size per categories) were used to create triangular similarity matrices, based on the Bray–Curtis similarity coefficient (no transformation was applied to the data). Separate one-way ANOSIMs (5000 permutations) were used to assess sediment differences between groups (presence or absence of *H. takanoi*). When differences were detected, the similarity of percentages (SIMPER) test was used to determine which categories contributed the most to the dissimilarity between sites. A Mann–Whitney Wilcoxon test was used to determine differences between groups (MINITAB software, version 15). For all tests the probability level was set to 0.05.

3. Results

3.1. Species distribution and status of the invasion

In 2012, *Hemigrapsus takanoi* individuals were detected in ten sampling sites along the French coast of the English Channel, always in sympatry with *Carcinus maenas* and *Hemigrapsus sanguineus* (Fig. 2 and Table 1). Three sites, all located along the Opal Coast were considered as colonised. The presence of *H. takanoi* was considered as trace at seven sites and, for the first time, at Luc sur Mer. It is of note that at Grand Fort Philippe, near Dunkirk harbour, crabs were found in burrows on each sampling occasion; this behaviour was observed only at this site.

Every population observed along the Opal Coast since 2008 was maintained, in contrast to the Cotentin Peninsula where *Hemigrapsus takanoi* was present only as trace. Indeed, 1 to 3 individuals were collected at Saint-Vaast in 2008 and 2009 (Dauvin, 2009a, b) and along the west Cotentin coast, 1 individual at Blainville-sur-Mer (Dauvin and Delhay 2010) and Gonneville respectively in 2010 and 2011. Along the Opal Coast, the sites in the Northern part of Boulogne-sur-Mer were the most abundantly colonised, especially Dunkirk harbour where 111 ± 42 individuals (mean ± s.d.) under 30 boulders were observed in 2010. Along the Calvados Coast the highest abundance was recorded at Honfleur in 2011, with 49 ± 15 individuals (mean ± s.d.) under 30 boulders, whereas only two individuals were observed in 2012 at the same location. The Albâtre and Picarde coast were weakly impacted; *H. takanoi* was observed only at le Tréport harbour (only some individuals were observed under the few boulders present in this location).

3.2. Densities

The overall densities of *Hemigrapsus takanoi* (Table 1) ranged from 1 ind.m^{-2} (on the Calvados coast in 2009 and 2010) to 61 ind.m^{-2} (Dunkirk harbour, 2008). In 2012, the highest densities were observed along the Opal Coast at Boulogne harbour (24 ± 30 ind.m^{-2}; mean ± s.d.), Grand Fort Philippe (23 ± 18 ind.m^{-2}) and Dunkirk harbour (21 ± 5 ind.m^{-2}). In 2012, densities of *Carcinus maenas* and *Hemigrapsus sanguineus* observed at these sites did not exceed those of *H. takanoi*; their densities ranged from 2 to 19 ind.m^{-2} and 1 to 6 ind.m^{-2} respectively (Table 2).

Table 2
Densities (ind.m^{-2}, mean ± s.d.; rounded up to the nearest unity) of *Carcinus maenas* and *Hemigrapsus sanguineus* (Gothland et al., 2013) in sites where *H. takanoi* were observed in 2012.

Sites	*C. maenas*	*H. sanguineus*
The 'Calvados Departement' Coast		
St Aubin sur mer	5 ± 5	1 ± 1
Luc sur mer	5 ± 1	1 ± 1
Ouistreham (*harbour*)	10 ± 6	31 ± 13
Cabourg (*harbour*)	7 ± 2	5 ± 1
Trouville sur mer	2 ± 2	27 ± 2
Honfleur H2 (*outside harbour*)	1 ± 2	69 ± 27
Honfleur H1 (*outside harbour*)	1 ± 1	4 ± 2
Means of the Calvados coast	*4 ± 5*	*25 ± 23*
Maximum observed along the coast	*14*	*70*
The Opal Coast		
Boulogne (*harbour*)	9 ± 1	1 ± 1
Calais (*harbour*)	19 ± 16	0*
Grand Fort Philippe (*muddy sand zone*)	6 ± 3	3 ± 4
Dunkirk (*harbour*)	2 ± 1	6 ± 3
Means of the Opal Coast	*11 ± 10*	*5 ± 5*
Maximum observed along the coast	*31*	*16*

* Observed under 90 boulders.

3.3. Size distribution and cohorts

During the 5-year period, 2824 *Hemigrapsus takanoi* individuals were measured. On the Opal Coast and the Calvados coast, the individual size ranged from 2 to 28 mm for males and from 3 to 27 mm for females (Fig. 3). The most abundant classes were 14–15 mm in the Calvados and 11–12 mm to 13–14 mm on the Opal Coast. The size-frequency distribution of *H. takanoi* showed three to four distinct cohorts (Fig. 4). Newly recruited individuals appeared in 2012 on the Opal and the Calvados coasts (4.9 ± 1.2 mm and 3.0 ± 0.7 mm), but only on the Opal coast (4.3 ± 0.7 mm) in 2008. Two cohorts were detected simultaneously during each sampling year: C1, the most abundant one (constituted of 70–83% of individuals collected; mean size: 11.3–13.7 mm and 13.7–14.4 mm in the Opal and Calvados coast respectively) and C2 (mean size: 16.9–19.3 mm and 18.3–19.0 mm in the Opal and Calvados coast respectively). A last cohort (C3), composed of the largest individuals (weakly represented; mean size: 20.5–25.0 mm), was observed only in 2011 in the Calvados coast and each sampling year in the Opal Coast. Seven (7) ovigerous females, ranging from 13.2 to

Table 1
Abundances (individuals under 30 boulders, mean ± s.d.; rounded up to the nearest unity) and densities (ind.m^{-2}, mean ± s.d.; rounded up to the nearest unity) of *Hemigrapsus takanoi* along the French coast of the English Channel from 2008 to 2012 (From [1a]Dauvin, 2009a, [1b]Dauvin, 2009b and [1c]Dauvin and Delhay, 2010, [2a]Dauvin et al., 2009).

	Under 30 boulders					Density			
	2008[a]	2009[b]	2010[c]	2011	2012	2008[a]	2010	2011	2012
The Cotentin Peninsula (1)									
Saint-Vaast (*harbour and oyster farming*)	3	1 ± 1	0	0	0	–	–	–	–
Blainville sur mer (*oyster farming*)	0	0	1 ± 1	0	0	–	–	–	–
The 'Calvados Departement' Coast									
St Aubin sur mer	–	–	–	1 ± 1	1 ± 1	–	–	0	1 ± 1
Luc sur mer	–	–	–	0	1 ± 1	–	–	0	0
Ouistreham (*harbour*)	–	–	–	7 ± 3	6 ± 3	–	–	0	1 ± 1
Cabourg (*harbour*)	–	–	–	7 ± 6	7 ± 7	–	–	–	3 ± 3
Trouville sur mer (*harbour*)	–	–	–	6 ± 1	0	–	–	3 ± 2	0
Honfleur H2 (*outside harbour*)	–	–	–	49 ± 15	2 ± 2	–	–	26 ± 6	3 ± 1
Honfleur H1 (*outside harbour*)	–	–	–	16 ± 5	2 ± 2	–	–	–	1 ± 1
The Opal Coast (2)									
Boulogne (*harbour*)	30 ± 20	–	35 ± 9	–	23 ± 5	13 ± 6	9 ± 3	–	24 ± 30
Calais (*harbour*)	2	–	25 ± 26	–	6 ± 7	–	4 ± 2	–	2 ± 3
Grand Fort Philippe (*estuarine muddy sand zone*)	13 ± 9	–	67 ± 31	–	31 ± 9	15 ± 6	23 ± 11	–	23 ± 18
Dunkirk (*harbour*)	73 ± 22	–	111 ± 42	–	51 ± 22	61 ± 22	44 ± 22	–	21 ± 5
Dunkirk (*outside harbour*)	2 ± 3	–	0	–	*	0	0	–	*

* Not sampled.

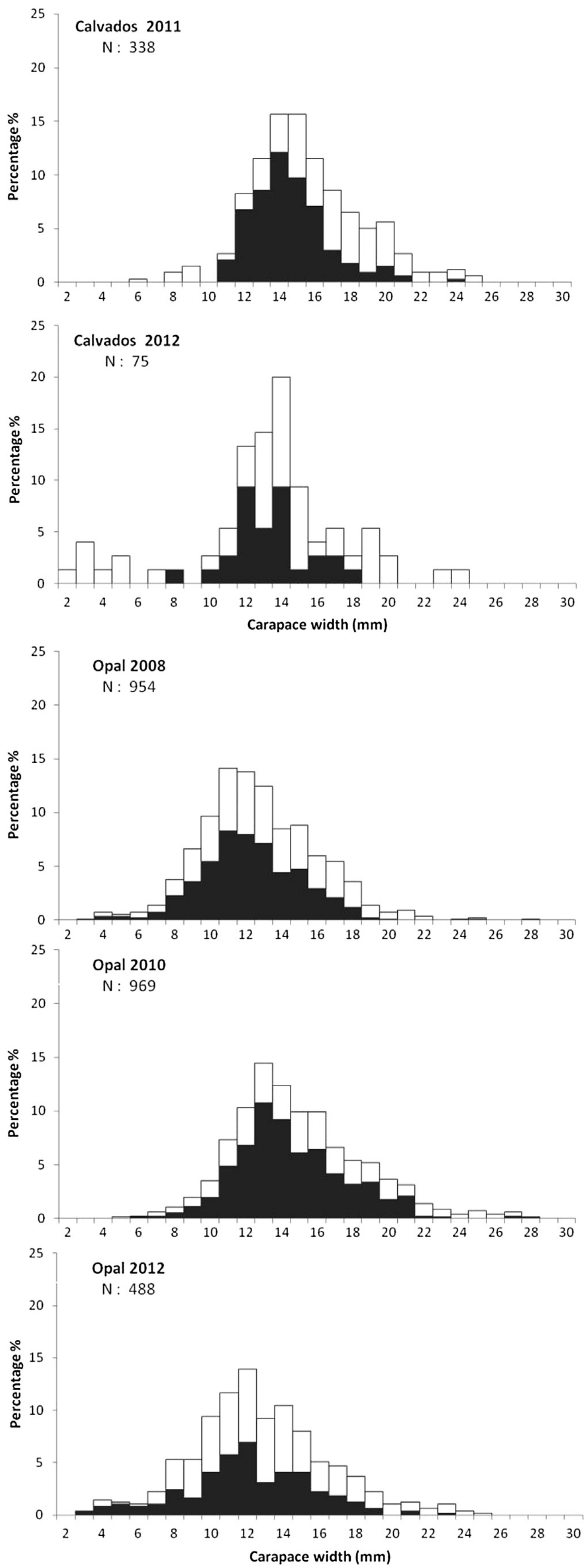

Fig. 3. Size distribution (%) of carapace width classes (CW; mm) of *H. takanoi* sampled along the Calvados coast in 2011 and 2012 and in the Opal Coast in 2008, 2010 and 2012 (white: size distribution of both sexes; black: size distribution of females).

20.3 mm in carapace width, were observed during the sampling period in March–April 2010 along the Opal Coast. Considering cohorts and size frequencies by sex, C2 and C3 individuals (ca. size >17 mm) were mainly males. In 2012, the number of males was higher than the number of females; the male/female sex-ratio was 1.3 on the Opal Coast and 1.7 on the Calvados coast. This sex-ratio contrasted with previous years, being respectively of 0.92 and 0.58 along the Opal Coast in 2008 and 2010 and of 0.84 in 2011 along the Calvados coast.

3.4. Sedimentology

Eighteen (18) and 55 sediment samples were collected at sites where *Hemigrapsus takanoi* were detected or not, respectively (Table 3 and Appendix 1–4). A significant difference was found in the grain-size distribution between sites, according to the presence or absence of *H. takanoi* (ANOSIM; R 0.252, p 0.01). An average dissimilarity (AD) of 44% was observed between groups (SIMPER analysis). This was due to the higher contributions of silt (10.8%), fine sand (17.3%) and medium sand (25.4%) and lower contributions of coarse sand (15.5%), fine gravel (10%) and coarse gravel (20.8%) in sites where *H. takanoi* were found. Sites with *H. takanoi* were characterised by significantly higher proportions of silt and sand (fine and medium) and lower proportions of coarse gravel ($p < 0.05$, Wilcoxon Mann Whitney test).

4. Discussion

4.1. Discontinuous distribution of H. takanoi: the potential role of sedimentology and introduction vectors

The continued occurrence of juveniles, the presence of ovigerous females (in 2010 on the Opal Coast) and the presence of populations since 2008 indicate that *Hemigrapsus takanoi* is now established on the French coast. In 2012, *H. takanoi* were observed on 10 sites: 3 of them being considered as "colonised" and 7 where *H. takanoi* was observed as "trace". At the highest, more than 111 individuals under 30 boulders were found (Dunkirk harbour in 2010) and the maximal densities observed (Dunkirk harbour, 61 ± 22 ind.m^{-2}; Dauvin et al., 2009) corresponded to one of the highest observed in Europe; 80 ind.m^{-2} were observed in 2010 at Veerse Meer in the Dutch delta (Van den Brink et al., 2012). Compared to *Hemigrapsus sanguineus* (Dauvin and Dufossé, 2011; Gothland et al., 2013), few populations of *H. takanoi* were observed along the French coast. Since 2008, populations of *H. takanoi* have occurred in two specific geographical areas: the Opal and Calvados coasts. Several authors (Schubart, 2003; Dauvin et al., 2009) suggest a segregation of the habitats colonised by this non-indigenous species. This was corroborated by our results since *H. takanoi* individuals specifically occurred along the Opal and Calvados coasts in areas with boulders scattered on muddy sediments, where silt and sand were dominant. The same pattern was observed in the Wadden Sea (Landschoff et al., 2013), where individuals were found under boulders on hard substrata composed of stones and shells but also on soft substratum (Asakura and Watanabe, 2005; Van den Brink et al., 2012). At Grand Fort Philippe, where *H. takanoi* were found in burrows, the proportion of silt was higher than on the other sites (21.33% ± 3.25%). This burrowing behaviour illustrated their adaptive capacity to find shelter, and the relative proportion of fine particle appears as a determining factor

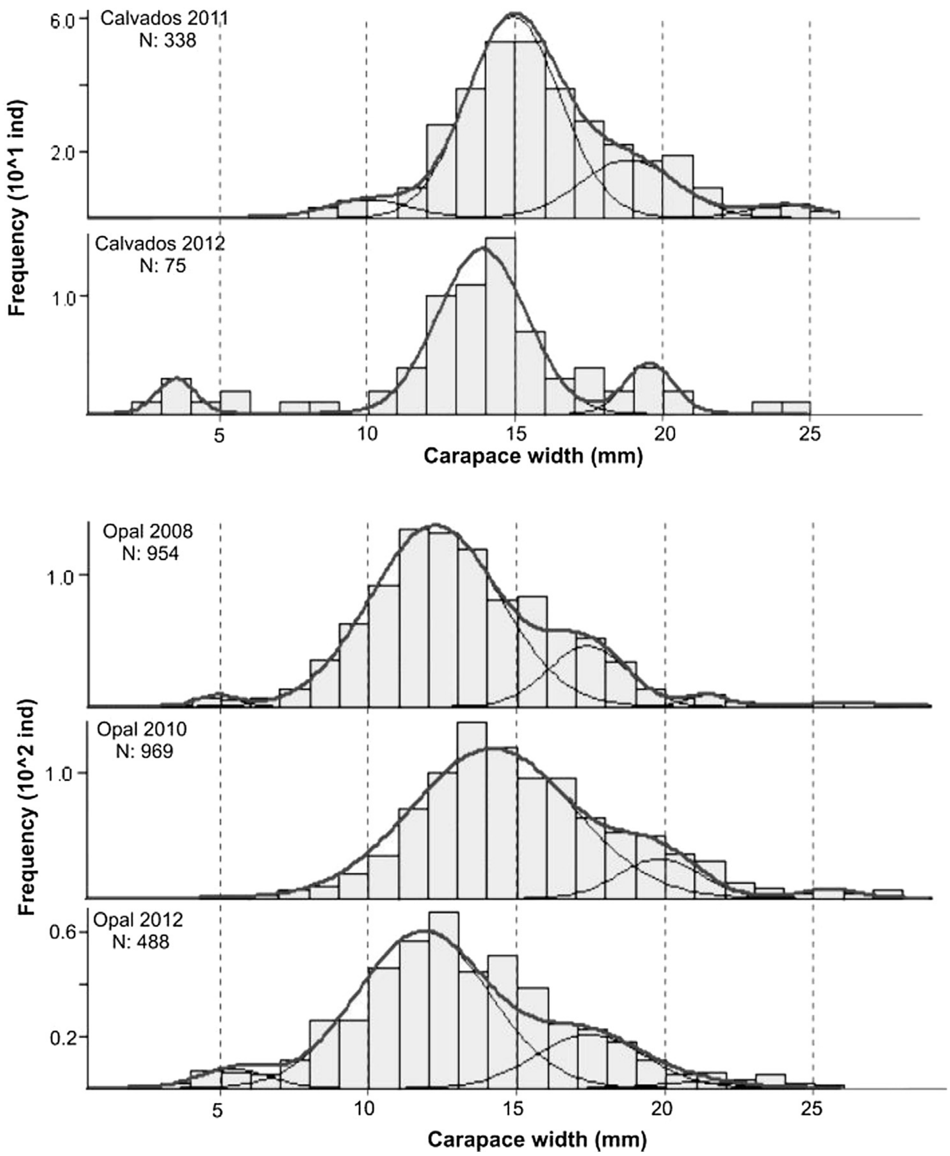

Fig. 4. Decomposition of the size frequency distribution of *H. takanoi* by the Bhattacharya method for the Calvados coast population (2011 and 2012) and the Opal Coast population (2008, 2010 and 2012).

in the typology of habitats for *H. takanoi*, which explains its discontinuous distribution along the coast. A similar behaviour was observed for *Hemigrapsus oregonensis* (Dana, 1851) along the Pacific coast of North America where it was found burrowing in the mud beneath rocks (Steinberg and Epifanio, 2011). Consequently, habitats with *H. takanoi* are mainly harbours or are located near harbours which are environments characterised by a low hydrodynamism and, therefore, fine sediments. Harbour environments are also generally characterised by specific abiotic characteristics such as pollution and physical disturbance (Crooks et al., 2011). Polluted marine habitats have been shown to favour invaders by the negative impact on the natives and by the fact that exotic

Table 3
Grain-size composition of sediments with and without the presence of *H. takanoi* and summary of SIMPER and Mann Whitney Wilcoxon test for each group.

Categories of sediment	Sites		% Contribution to the dissimilarity between groups (SIMPER, AD: 44.0)	Wilcoxon Mann Whitney test (p)
	With *H. takanoi* (N: 18; %; AS: 64.5)	Without *H. takanoi* (N: 55; %; AS: 63.8)		
Silt	10.8 ± 12.1	1.3 ± 2.0	11.3	$P < 0.001^*$
Fine sand	17.3 ± 12.6	5.9 ± 6.0	15.3	$P < 0.001^*$
Medium sand	25.4 ± 12.7	17.7 ± 15.9	19.9	0.0133*
Coarse sand	15.5 ± 8.5	19.9 ± 15.4	14.1	0.3469
Fine gravel	10.0 ± 5.7	12.4 ± 8.2	8.9	0.5181
Coarse gravel	20.8 ± 11.7	42.8 ± 21.3	30.5	$P < 0.001^*$

$^*P < 0.05$; AS: average similarity; AD: average dissimilarity.

species were 'pre-adapted' to the invaded ecosystem ('selection regime modification' hypothesis; Byers, 2002) due to unfavourable environmental conditions during the transport (Crooks et al., 2011). This underlines the potential importance of the tolerance capacities of these species and suggests faculties of adaptation to abiotic conditions, thus ensuring its expansion.

Sites with *Hemigrapsus takanoi* are also areas where many vessels transit (Fig. 5), which constitute an important vector of introduction and/or spread for potentially invasive species. For example, Honfleur (next to Le Havre harbour), Boulogne-sur-Mer, Calais and Dunkirk are important commercial or fishing harbours (Carpentier et al., 2009). Many crustaceans (such as *H. takanoi*) have planktonic larvae that can be among the most common organisms in ballast water (Weis, 2010); furthermore, adult individuals may also be transported on ship hulls (Gollasch, 1999). Although several introduction vectors exist (aquaculture, ship ballast (water, sediment, rock, sand), burrow into wood, intentional release, aquarium trade and freshwater canals), shipping remains the most important source of introduction in Europe (Galil et al., 2009). Since 1870, many decapods such as *Callinectes sapidus* (Rathbun, 1896), *Chionoecetes opilio* (O. Fabricius, 1788), *Dyspanopeus sayi* (Smith, 1869), *Eriocheir sinensis* (H. Milne-Edwards, 1853), *Palaemon macrodactylus* (Rathbun, 1902), *Rhithropanopeus harrisii* (Gould, 1841) and *Hemigrapsus sanguineus* were introduced *via* ship ballast water from the Atlantic or the Pacific to Europe (Noël, 2011). Catford et al. (2009) suggest that invasion is essentially a function of propagule pressure, abiotic characteristics of the invaded ecosystem and biotic characteristics of the recipient community and invading species. The propagule pressure is critical for the introduction of invaders but also for the continued success (Colautti and MacIsaac, 2004). A high propagule pressure, in conjonction with multiple introduction events, also increases the chance that an invader will be introduced into a favourable environment (Catford et al., 2009). This is particularly relevant for *H. takanoi* populations which, as shown by their discontinuous distribution and specific location, are probably sustained and propagated due to the propagule pressure combined with the presence of propagation vectors. The Channel-North Sea Route is the second busiest sea route in the world, thus connecting harbours, where aquaculture and ballast water represent 42% of the major vectors of introduction and spread of invasive species (Quemmerais-Amice et al., 2012). It is thus probable that, through larval dispersal, the French *H. takanoi* populations contributed (1) as a source population for the European propagation *via* ballast water discharge or oyster transports (Noël et al., 1997), populations of the southern part of the North Sea (in Germany, The Netherlands and Belgium) probably resulting from a secondary colonisation from larvae of established French populations since the 1990's and (2) to maintain *H. takanoi* along the French coast by a self recruitment of larvae from perennial populations. These hypotheses may, however, only be checked using molecular genetic tools. The literature does not indicate the reproductive capacities for *H. takanoi* females, but for *H. penicillatus* (long confused with *H. takanoi*),

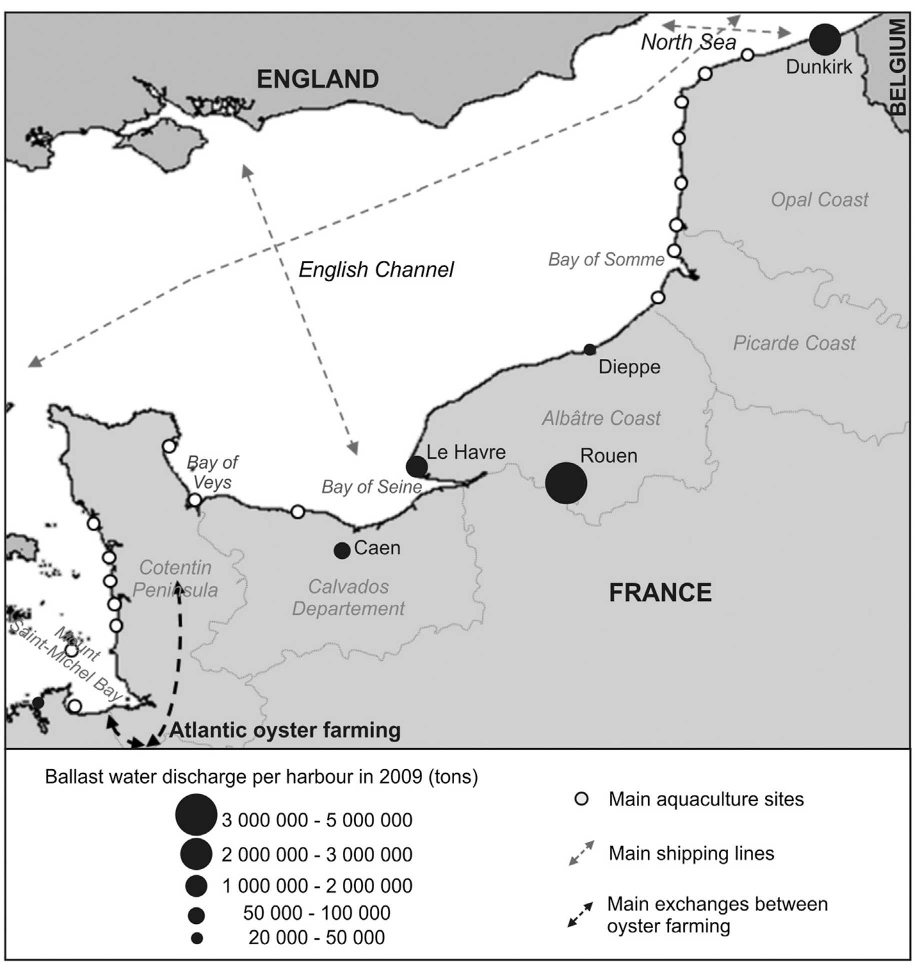

Fig. 5. Main shipping lines and aquaculture sites, vectors of introduction and spread for potentially invasive species on the French coast of the English Channel. Modified from Quemmerais-Amice et al., 2012.

females may exhibit a high fecundity, with 5–6 breeding periods per year (Pillay and Ono, 1978) and 5000 to 10,000 eggs per brood (Fukui, 1988). Lefebvre et al. (2003) simulated the larval dispersal of different populations of the Ophiurid *Ophiothrix fragilis* in the English Channel using a 2D hydrodynamical Lagrangian model. It appeared that larval exchanges between populations in the western and eastern Bay of Seine and of the Pays de Caux (Albâtre and Picarde coast) were the most important, whereas populations of Dover Strait and Normano-Breton Gulf were mainly self-sustained. Simulated dispersal of ophioplutei was based on a planktonic life of 26 days. Considering that the larval duration of *H. takanoi* is similar to *H. sanguineus*, the planktonic life of *H. takanoi* would range from 16 days at 25 °C to 55 days at 15 °C (Epifanio et al., 1998). Thus, extrapolating the results of Lefebvre et al. (2003), it can be hypothesised that, in the presence of a North-East wind, *H. takanoi* individuals found in the Western Cotentin coast may result from a larval supply originating from populations of the Bay of Seine. The presence along the coast of the Cotentin Peninsula of mussel and oyster farms, other potential vectors of introduction, can also explain the sparse presence of *H. takanoi* along this coast.

4.2. Biological traits contributing to the invasiveness

The "propagule pressure" and the important adaptive capacities to abiotic conditions are contributing factors of the invasiveness of *Hemigrapsus takanoi*. However, this species also exhibits biological traits that may equally contribute to its success, such as its high fecundity, the ability to store sperm for multiple broods, high dispersal and a long larval life which facilitates dispersal and favour rapid expansion (Weis, 2010). For other species in the genus *Hemigrapsus*, multiple broods are common; e.g. respectively, 2 and more than 5 broods per year were observed for *Hemigrapsus oregonensis* (May–July and September; Steinberg and Epifanio, 2011) and *Hemigrapsus sanguineus* in natives or invasive ranges (McDermott, 1991). *H. takanoi* is also characterized by an early sexual maturity, a rapid growth and a short life cycle. The occurrence of homologous cohorts detected each year, whatever the geographical area, allows inferences about the recruitment and longevity of *H. takanoi*. The presence of newly recruited cohort was indicative of a recruitment period starting in spring. In 1994, Noël et al. (1997) observed along the French Atlantic coast 51 ovigerous females ranging from 8 to 23 mm in carapace width. No information concerning the sampling period was provided, but they specified that the spawning period began in May. Landschoff et al. (2013) estimated that the current breeding period of *H. takanoi* in the Oosterschelde was likely to be about from May to September. As for *H. sanguineus*, the duration of the reproductive period for *H. takanoi* is long (6 months, from April–May to September–October) compared to *H. sexdentatus* (H. Milne Edwards, 1837), *H. nudus* (Dana, 1851) and *H. oregonensis* which are reproductively active for a ca. 6 days (within a 3-week mating period from March to April, Brockerhoff and McLay, 2005; Anderson and Epifanio, 2010), 2 months (early May to mid June) and 3 months (first brood from May until July and a second brood in late September; Jensen, 1995; Steinberg and Epifanio, 2011), respectively. Sampling at the beginning of spring thus allowed harvesting early ovigerous females but also allowed to observe the first recruits. Populations of *H. takanoi* were essentially composed by C1 individuals (mean size: 11.3–14.4 mm; carapace width), the size maturity of *H. penicillatus* females (not indicated for *H. takanoi*) being of ca. 6.4–10.3 mm and about 11 months old (Fukui, 1988), which is approximately the size of C1 individuals in this study. It was likely that C1 and C2 (mean size: 16.9–19.3 mm) represented year classes 1^+ and 2^+. Considering that few C3 individuals and the outliers (size>20 mm) represented the 3^+ year class, the longevity of *H. takanoi* was estimated between 2 and 3 years. The size range of the French populations of *H. takanoi* (from 2 to 28 mm) corresponded to those observed in Japan for *H. penicillatus* (1.6–30.6 mm; Fukui, 1988) and in France in 1994 (5–28 mm; Noël et al., 1997). Thus, *H. takanoi* seems to mainly devote its energy to growth and multiplication, which corresponds to a population with an 'r-selected strategy' (McArthur and Wilson, 1967; Pillay and Ono, 1978). The demographic 'r-selected strategy' characterises species that are capable of fast colonisation of space and/or resource thanks to their efficient multiplication. One of the main characteristics of r-strategy species is fluctuating densities with a high mortality (Frontier et al., 2008). In 2012, the number of crabs sampled was half that collected in 2010–2011 and males constituted the major part of all populations. These variations are unpredictable and may reflect changes in the availability of resources and/or space resulting from more rigorous weather conditions, but also competition between species. In 2012, the winter was particularly severe: in January and early February extreme winter conditions were recorded, with 5–10 consecutive ice days (maximum air temperature below 0 °C) recorded from the Cotentin to the Opal Coast (World Meteorological Organization, 2013) and the decrease in the number of individuals could be the consequence of this hard winter. The *H. takanoi* strategy as an invasive species might represent a competitive advantage, especially compared to the green crab *Carcinus maenas* which is characterised by slow growth, slow reproduction cycle and late breeding. Maturity of the green crab usually occurs at an age of 2–3 years, with a minimum size of about 30 mm (carapace width; Berrill, 1982; Van den Brink et al., 2012). High densities in *H. sanguineus* are usually observed on sites where densities of *H. takanoi* were up to 50 ind.m^{-2} (Table 2; Dauvin and Dufossé, 2011; Gothland et al., 2013). As with *H. takanoi*, *H. sanguineus* may also exhibit a high fecundity, multiples broods (5–6) per year, with more than 50,000 eggs per brood (McDermott, 1991). *H. sanguineus* is also characterised by an early sexual maturity, the size maturity of females being of approx. 14–19 mm (carapace width) and about 22 months old. In contrast with *H. takanoi*, the longevity of *H. sanguineus* may exceed three years (Fukui, 1988). All these features make *Hemigrapsus* spp. good competitors for space and resources compared to *C. maenas* along the French coast of the English Channel and thus justify the importance of surveys to assess the dynamics of these populations. In 2012, populations of *H. takanoi* had decreased compared to previous years, but given the 'r-selected strategy', abundances and densities may increase rapidly. The combined presence of these two species may heavily impact the biodiversity and the functioning of coastal ecosystems especially in biotic communities of harbours, which are typically characterised by a low biodiversity.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2014.03.012.

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