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Dynamics (from 2010–2011 to 2014) of *Sabellaria alveolata* reefs on the western coast of Cotentin (English Channel, France)

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HIGHLIGHTS

- *Sabellaria alveolata* reefs surface of the west coast of the Cotentin estimated in 2010–2011 and 2014.
- Very slight decrease of colonized surface between both periods.
- But considerable degradation of the bio-constructions between both periods.
- *Sabellaria* size structures on four target sites reflecting the absence of recent settlement.
- Haphazard transport of pelagic larvae from Bay of Mont Saint-Michel permanent reefs ensuring temporary reefs northwards.

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ABSTRACT

The polychaeta *Sabellaria alveolata* (Linnaeus, 1767), commonly known as the honeycomb worm, is a gregarious polychaete present on the European coasts from Scotland to Portugal. It is an important reef-building species which enhances topographic complexity in colonized areas. In Europe, the most extensive reef formation is found in France in the Bay of Mont Saint-Michel. Nevertheless, since 2006, *Sabellaria* bio-constructions (platforms and reefs) have developed on hard substrates along the west coast of Cotentin and in the north of the Bay of Mont-Saint-Michel. The aim of this study is to compare the area covered by bio-constructions in 2010–2011 and in 2014 along 60 km of the west coast of Cotentin, focusing on the temporal changes at four target sites: Champeaux, Lingreville, Blainville-sur-Mer, and Saint-Germain-sur-Ay. The results show a very slight decrease of colonized surface-area between these two periods at the scale of the whole study area, but a significant decrease at two target sites, with considerable degradation of the bio-constructions which appear to be temporary on the west Cotentin coast. Our study also reveals the presence of flourishing permanent bio-constructions at Champeaux, which exhibit the highest densities (>40, 000 ind.m^{-2}). The winter size structure of *S. alveolata* populations on the target sites and during a winter–summer survey at Blainville-sur-Mer reflects the absence of settlement in 2013 and 2014, and the absence of older individuals able to survive over several years. Our results suggest a haphazard transport of pelagic larvae from the *S. alveolata* permanent reefs in the Bay of Mont Saint-Michel, which leads to the spread of temporary reefs northwards. The evolution of these constructions can be very rapid (<10 years); it is suggested that cold winters and high-energy hydrodynamic conditions generated by strong storms have contributed to a rapid degradation of the reefs at the beginning of the 2010s.

1. Introduction

Some polychaete annelids belonging to the Sabellariidae family are reef builders: i.e. species of the genus *Idanthyrsus*, *Gunnarea*, *Phragmatopoma* and *Sabellaria* (Gruet, 1982). These annelids are

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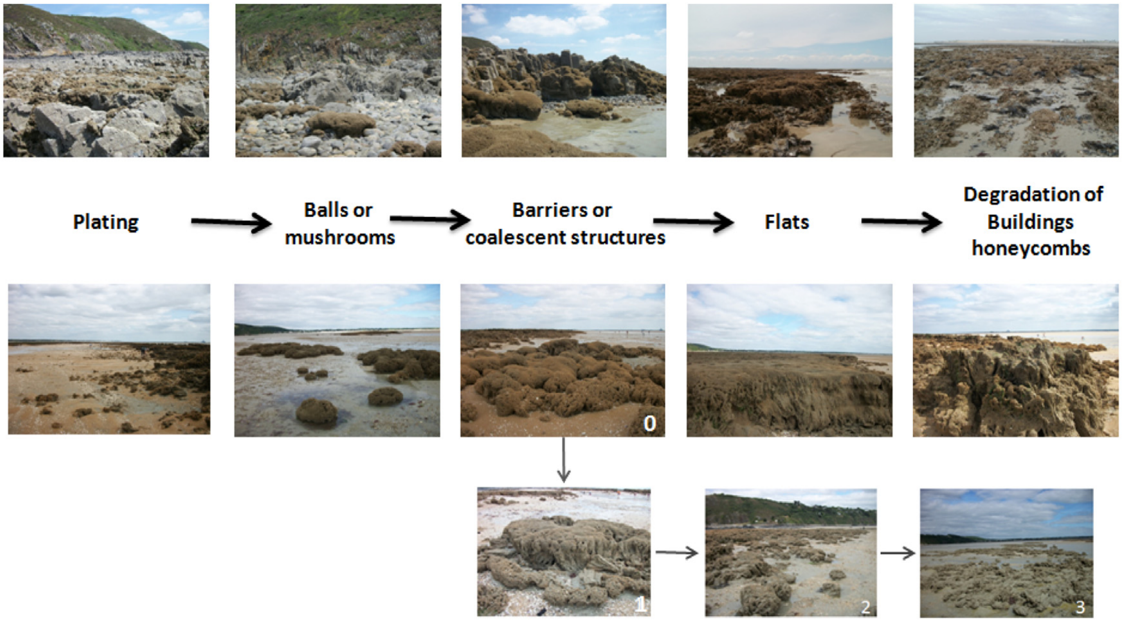

Fig. 1. Different stages of reef dynamics on hard and soft substrates, with degree of degradation (After Gruet, 1971, 1982; Gruet and Bodeur, 1997). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

engineer species responsible for the formation of significant bioconstructions worldwide (Ayral, 2000). In Europe, two species of the genus *Sabellaria* are recorded: *Sabellaria alveolata* (Linnaeus, 1767), and *Sabellaria spinulosa* (Leuckart, 1849). *S. alveolata*, commonly known as the honeycomb worm, is the species that builds the most extensive reef formations in the intertidal zone and shallow waters of the Mediterranean Sea (Gruet, 1971, 1982; Anadon, 1981; Porras et al., 1996; La Porta and Nicoletti, 2009). Its geographic range is from the coasts of Scotland and England in the north to Morocco in the south; it is also present in the Mediterranean Sea (Gruet, 1971; Wilson, 1974; Porras et al., 1996). In France, *S. alveolata* is found from the North Sea to the Atlantic seaboard north of the Gironde estuary, and is also present along the coast of the Mediterranean (Gruet, 1971). The largest reef in Europe – the Saint-Anne reef – is located on the south side of the Bay of Mont-Saint-Michel (BMSM). Other sites in France have extensive *Sabellaria* reefs, such as Champeaux located in the eastern part of the BMSM, the Bay of Bourgneuf and on the coasts of the islands of Yeu and Ré on the Atlantic seaboard (Gruet, 1971, 1982).

S. alveolata constructs a variety of platform and reef structures, with platforms being built on rocks (Gruet, 1971). Platform formations do not generally exceed 30 cm in height and are located in the upper part of the mid-littoral zone, representing early stages which rarely develop into larger structures (Gruet, 1972a,b). The reefs are much larger in size (>30 cm) and can be located on a soft substrate, as observed at Champeaux, or on a hard substrate as at Saint-Germain-Sur-Ay on the northern part of the west coast of Cotentin (Basuyaux, 2011). On hard substrates, platform constructions can evolve into reefs located between the low water spring tide level and the low water neap tide level.

Several types of reefs have been observed: construction balls or mushrooms, barriers or coalescent structures and flats (Gruet, 1970, 1971, 1972a,b, 1977, 1981, 1982, 1986; Gruet and Bodeur, 1997). The ball structures can reach a height of 1 m. They can subsequently aggregate together to form coalescent structures. These biogenic structures are able to form flats up to 2 m in height, which correspond to the final developmental phase of the reefs. After reaching this stage, reefs can show a degradation (Fig. 1) mainly due to hydrodynamic disturbance during cold winters and severe storms, but which may also be related to sediment cover or human activities (Gruet and Bodeur, 1997; Ayral, 2000; Dubois et al., 2002, 2006; Desroy et al., 2011) including trampling (Plicanti et al., 2016).

These honeycomb worm reefs are of ecological interest when they are established on a soft-bottom as in the BMSM, where they show a high level of Taxonomic Richness (TR) in contrast with the surrounding intertidal soft-bottom *Macoma balthica* community characterized by very low TR (Dubois et al., 2002, 2006). However, these structures are subject to various human impacts (fishing on foot, trampling, shellfish farming, etc.), concentrated on spots where target species are harvested by recreational fishers during the spring tide, which lead to degradation of these formations (Desroy et al., 2011). In Europe, 'reefs' are recognized as a marine habitat to be protected and are listed under Annex I of the EU Habitats Council Directive 92/43/EEC. This species is currently under review for the European Habitats Red List, in which this habitat is considered as Near Threatened. The habitat '*Sabellaria alveolata* Reefs' also benefits from a Biodiversity Action Plan in the UK (http://www.jncc.gov.uk/page-5155).

Since the 1960s, the presence of honeycomb worm reefs on the west coast of Cotentin has been reported in several studies (Hommeril, 1962; Hommeril and Larsonneur, 1963; Guillaumont et al., 1987). These formations appear scattered along the coast and non-permanent. Between 2006 and 2007 (Dauvin, personal observations; Delhay, 2010, 2012), a new phase of colonization was observed on this part of the Channel coast, and the presence of *Sabellaria* reefs in 2010–2011 extended from Saint-Germain-sur-Ay in the north to Champeaux in the BMSM farther south (Basuyaux, 2011) (Fig. 2).

In the 1970s, the oyster *Crassostrea gigas* (Thunberg, 1793) was introduced to the Atlantic coast of France in order to restore oyster farming affected by a disease of *C. angulata* (Lamark, 1819); there has been a rapid increase in the number of oyster farms in France, particularly in Normandy which is nowadays the most important centre of oyster production in France. As in the Bay of Mont-Saint-Michel, there are many commercial oyster and mussel farms along the west coast of Cotentin. The consequences of aquaculture on ecosystems are known to be multiple, including changes in benthic composition and food competition with shellfish culture (Crawford et al., 2003; Desroy et al., 2011). According to shellfish farmers,

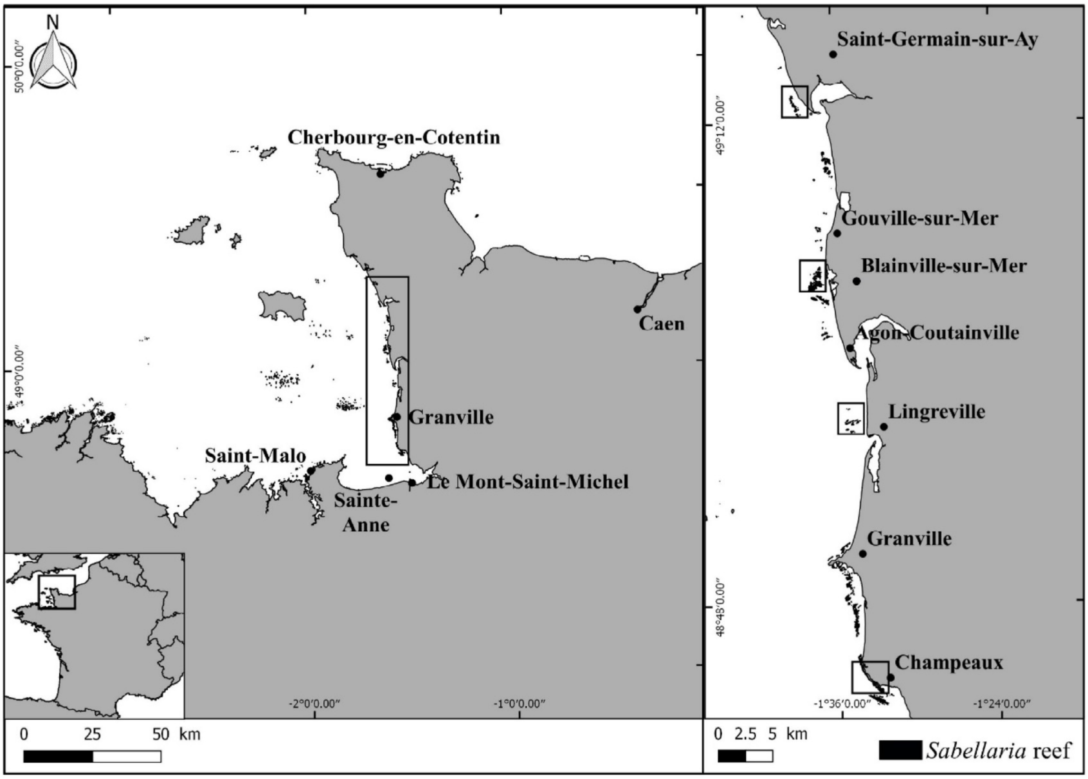

Fig. 2. A. General geographical context of the study sites. B. Location of study sites. C. 'Côte des Havres' on the west Cotentin coast, with presence of platforms and reefs in 2014.

honeycomb worms were almost absent before 2009 in shellfish sectors on the western coast of Cotentin, except at Lingreville. Between 2009 and 2010, a significant colonization of *S. alveolata* occurred, leading to difficulties of exploitation, primarily for oyster farming. In the late years 2000, the SMEL ('*Synergie Mer Et Littoral*' scientific structure) received a request from professional fishers of the western coast of Cotentin to estimate the interactions between *Sabellaria* reef formations and shellfish farming, mainly in terms of surface-area covered. In partnership with the M2C laboratory, this led to a new cartographic monitoring of the species *S. alveolata*, which was carried out in 2014 on the entire west coast of the Cotentin, from Saint-Germain sur-Ay to Champeaux (∼60 km). Mapping studies were conducted previously in this sector in 2010–2011 by the SMEL, and a total of 535 spots were reported covering a total area of 228 ha (Basuyaux, 2011).

Based on these monitoring surveys of the honeycomb worm, the aims of this paper are (1) to compare the distribution of the platforms and reefs between April 2010 to April 2011 (denoted hereafter as 2010–2011) and 2014; (2) to estimate the population structures of the honeycomb worm *S. alveolata* in different selected sectors of the study area as well as on the two types of structure (platforms and reef); and (3) to determine the general spatio-temporal dynamic pattern of *S. alveolata* distribution along the western coast of the Cotentin over the last decade within the context of environment changes over this period.

2. Materials and methods

2.1. Study sites

The study area covers ∼60 km of coastline. Four sites were selected on the coast to compare the presence of honeycomb worms between 2010–2011 and 2014: Saint-Germain-sur-Ay (SGSA), Blainville-sur-Mer (BLSM), Lingreville (LING) and Champeaux (CHAM) (Fig. 2).

The sites of SGSA, BLSM and LING consist of wide extents of rocky flats in front of a coastal dune barrier. These three sites are characterized by the presence of small estuaries (Lessay, Blainville and La Vanlée; Dauvin et al., 2014). Considerable sediment movements occur on these three sites (Levoy et al., 1997, 2001), which contribute to transport of the clam *Ruditapes* spp. (Beck et al., 2015). Shellfish farming activity is well developed on these sites and many oyster culture tables are set on the rocky flats (Basuyaux, 2011). According to Basuyaux (2011), honeycomb worms are found only on hard substrates, located in or near the shellfish farms.

The CHAMP site is located in the eastern part of the Bay of Mont-Saint-Michel, where *Sabellaria* reefs are developed on rocky and also soft-bottom substrates, as in the case of the study site, in an environment characterized by muddy sand. Shellfish farming on these areas is much less developed than north of Granville. By contrast, recreational fishers are very active. The Champeaux reef is a long-established biogenic structure (Gruet, 1971, 1981, 1982), covering a large area (29 ha in 2001 (Dubois, 2003). All developmental stages are found on this reef.

2.2. Field protocol and data analysis for mapping Sabellaria bio-constructions

In 2010–2011, Basuyaux (2011) identified all the reefs present along the coast from Saint Germain-sur-Ay in the north to Champeaux in the south. Each of the observed bio-constructions (see Fig. 2) was transcribed onto GIS software. In 2014, the same identification method was performed to assess the evolution of honeycomb worm reefs. Mapping of the different areas was carried out from April to July 2014, requiring 25 working days in the field to cover the entire coast. Observations were made *in situ* supported by aerial photography shot in 2013 (Orthophotographie Basse-Normandie, 2013).

The fieldwork was carried out during spring tides at low water, involving identification of bio-constructions and delimitation

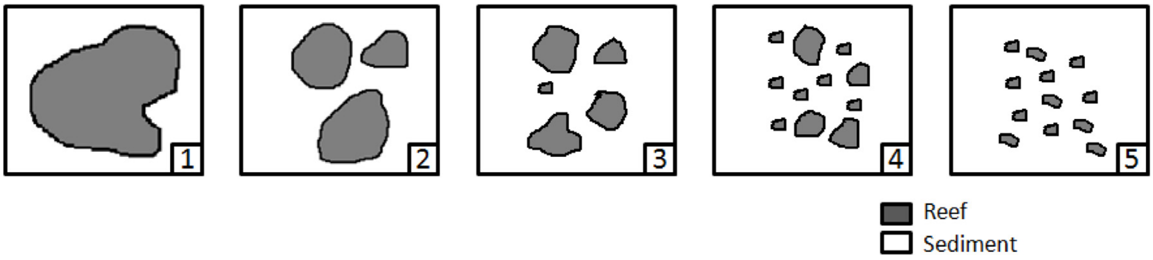

Fig. 3. Degree of fragmentation.
Source: From Dubois et al. (2006).

of their extent. The observations were made on foot or from a quad depending on the area covered by the construction. A preliminary field analysis for 2010–2011 was performed using printed maps. The outlines of the reefs or platforms were drawn onto these maps. In 2014, these outlines were transcribed onto a tablet (GETAC 410) using the Cartolander software. For each bio-construction delimited in this way, several parameters were noted to describe the specific reef structure (height, presence of epibionts, degradation of the structure, fragmentation, etc.). A photo was taken of each structure.

Data acquired in the field were transcribed onto MapInfo. This software allowed us to create maps for each sector. Two maps for each sector were drawn up: one representing the height of the bio-constructions in 2010–2011 and the other for 2014.

Data entered on MapInfo were transferred to an Excel spreadsheet. The constructions were compared between the two periods to assess the changes (development/degradation) taking place in the honeycomb worm reefs. When the distribution of heights and surface-areas was not normal, we performed ANOVA and Kruskal–Wallis (KW) statistical tests to compare the honeycomb worm constructions between 2010–2011 and 2014. ANOVA or Wilcoxon–Mann–Whitney (WMW) tests were used to test the differences of the population size structure.

In 2010–2011, no observations were made concerning fragmentation or degradation. For 2014, we make use of the reef fragmentation scale proposed by Dubois et al. (2006) to characterize the structure development in terms of five classes or degrees (1–5) from least to most fragmented (Table 1). Class 1 represents the flats while class 5 represents platforms or reefs in very small blocks (Fig. 3).

According to the field observations, many constructions appeared degraded in 2014. Therefore, we established a scale of degradation. The constructions are divided into 4 classes of degradation (0–3) from the least degraded to the most degraded: Class 0, constructions in very good condition, all the tubes seem to be inhabited; Class 1, some tubes are covered with sand, they are not inhabited (20% of tubes are degraded); Class 2, more than 50% of tubes are degraded, and Class 3, the construction is dead, all tubes are destroyed and green algae (*Ulva* spp.) covers the bio-construction (Fig. 1).

2.3. Population size structure

Winter samples were taken in 2014 on February 18 at BLSM, March 3 at CHAM, March 18 at SGSA and March 31 at LING. Samples were collected during spring tides at low water. Moreover, the BLSM was sampled on three other dates (16 April, 18 June and 18 August) to assess temporal variations of the population size structure. Honeycomb worms were removed from the reef using a round metal corer (diameter 312.5 cm^2, which corresponds to 1/32 m^2) to a depth of 15 cm. On each platform (height of construction <30 cm) and reef (height of construction >30 cm), eight cores were taken to obtain a sampling area of 0.25 m^2, corresponding to the minimum area recommended by the REBENT (www.rebent.org) for the hard substratum of the intertidal zone. The cored sample was placed in a 6 L container and brought back to the laboratory for further processing.

Table 1
Areas of bio-construction honeycombs (ha) in 2010 and 2014 and degrees of degradation (in %) in 2014.

Area (ha)	Year		Degrees of degradation in 2014			
	2010	2014	1	2	3	4
SGSA	11.2	12.2	0	65	34	1
BLSM	80.0	61.0	0	0	31.5	68
LING	17.5	10.2	0	22	52	26
CHAM	31.4	36.5	56	14	19	10

In the laboratory, samples were stained with Rose Bengal and fixed in 10% formaldehyde solution. After 24 h, samples were sorted and washed on a 0.5-mm sieve mesh. After sorting all the worms, they were preserved in alcohol (70% ethanol) and counted separately for each core. It is well-known that gregarious species like *S. alveolata* exhibit high patchiness in recruitment, and the number of individual measured only provides a vague picture of the population structure. Besides, pooling individuals from several cores prevents us from estimating some of the variability in size structure. Therefore, about 300 individuals from each site and each structure (platforms and reefs) were randomly picked from the eight replicates taken at each station and at each sampling period at BLSM. Then, the opercular crowns of a total of 3760 individuals were measured under a binocular microscope with an ocular micrometer following the method described in Dubois et al. (2006). From these measurements, we established size structure histograms with a 0.15-mm size class to show the distribution of the population size structure of *S. alveolata* on the four sites.

2.4. Environmental data

As cold winters (Hommeril and Larsonneur, 1963; Crisp, 1964; Firth et al., 2015) and strong storms (Gruet, 1982) are known to be main environmental factors explaining reef degradation, we selected meteorological data from the Gouville-sur-Mer and Granville weather stations, representative of the local geography (Fig. 2). These data comprise air temperature, number of winter frost days and wind speed (>12 m s^{-1}) in the South-West and North-west sectors [220°; 320°], conditions which predominate in controlling environmental effects along the western coast of Cotentin (North–South exposure). The sea temperature data was recorded on an intertidal site at Blainville-sur-Mer for the 2005–2015 period, which corresponds to the establishment and degradation of honeycomb worm reef on the western coast of Cotentin. The risk of storms between 2005 and 2015 is also analysed using the classification of Hess and Brezowsky (James, 2007), and these data are coupled with data measured in the field.

To improve knowledge of the wind climate in the study area, we also present wind roses for the Bay of Mont-St-Michel and

Table 2
Frequency (in %) of the wave height (in metres) during two autumnal and winter periods, i.e. from 1 November 2013 until 31 March 2014 and from 1 November 2014 until 31 March 2015, measured on an intertidal site at Agon-Coutainville (data from the National Observatory Network DYNALIT with the authorization of Prof Franck Levoy). Total number of observations in 2013–2014: 5693; no value available for 2014–2015.

Sector	Wave height (01/11/2013–31/03/2014)					Wave height (01/11/2014–31/03/2015)				
	0.1–0.2	0.2–0.5	0.5–1.0	1.0–2.2	Total	0.1–0.2	0.2–0.5	0.5–1.0	1.0–2.2	Total
N	0.0	0.1	0.0	–	**0.1**	0.0	0.1	0.0	–	**0.1**
NNW	–	0.1	0.0	–	**0.1**	0.1	0.5	–	–	**0.6**
NW	0.0	1.4	0.2	0.0	**1.6**	0.2	1.0	0.5	0.0	**1.8**
WNW	0.5	2.9	2.4	1.4	**7.2**	1.3	4.3	3.0	0.9	**9.6**
W	6.9	27.7	24.4	8.9	**67.9**	7.7	33.0	23.7	7.8	**72.2**
WSW	0.6	3.6	4.6	1.8	**10.6**	0.8	3.5	2.6	0.7	**7.6**
SW	0.0	2.1	3.3	2.5	**7.9**	0.1	1.8	2.5	1.0	**5.4**
SSW	0.0	0.4	1.6	2.2	**4.2**	0.1	0.4	1.6	0.4	**2.5**
S	–	0.1	0.1	0.1	**0.3**	–	–	0.1	0.1	**0.2**
	8.0	**38.4**	**36.6**	**16.8**	100	**10.3**	**44.7**	**34.1**	**10.9**	100

off the coast of Gouville-sur-Mer, using data from the Aladin meteorological model of Météo-France.

Furthermore, the mean wave height has been measured in an intertidal zone at Agon-Coutainville since the beginning of 2013. In Table 2, the swell heights are presented for two autumnal and winter periods, i.e. from 1 November 2013 to 31 March 2014 and from 1 November 2014 to 31 March 2015.

3. Results

3.1. Time-evolution of the bio-constructions

Fig. 4 shows maps giving a general view of the presence and location of honeycomb worm constructions at the four selected sites. First of all, the location of the bio-constructions appears stable at the scale of the two observation periods in 2010–2011 and 2014. The highest bio-constructions are present on the two southern sites, especially at CHAM where the bio-constructions exceed 90 cm. At SGSA in the North, there is very little change between the two sampling periods, whereas at BLSM, the 0–30-cm class become dominant in 2014. At LING, the least colonized site, there is also a decrease in the surface-area of the highest bio-constructions. Similarly, at CHAM, the highest constructions show a decline between the observation periods.

3.2. Comparison of heights and surface-areas of bio-constructions

Table 1 reports the areas in ha covered by bio-constructions in 2010–2011 and 2014 compared over the whole study zone. In 2010–2011, the total area was 227.6 ha, while in 2014, the total area was 248.5 ha. There is no significant difference between the total areas measured in 2010–2011 and in 2014 ($KW = 0.18$, $p = 0.67$). In 2014, many of the bio-constructions were degraded, especially at BLSM and LING, while at CHAM they remained in good condition (Table 1).

3.3. Size of bio-constructions

The areas of honeycomb worm bio-constructions along the studied coastline and at the four selected sites are sorted into five height classes for both years of observation (Fig. 5). ANOVA tests show no significant difference of height classes between 2010–2011 and 2014 throughout the study zone ($F_{1,8} = 0.016$, $p = 0.90$) and for the four selected zones ($F_{1,8} = 0.064$, $p = 0.81$).

3.4. Fragmentation and degradation of honeycomb worm reefs in 2014

Over the whole study area, the dominant degree of fragmentation corresponds to class 5 (Fig. 6). Highly fragmented honeycomb worm reefs cover 140 ha of the observed surfaces. Class 5 is predominant at Lingreville, while class 2 dominates at Champeaux, but associated with a high percentage of classes 3 and 4 (Fig. 6).

The areas of honeycomb worm constructions across the study zone are classified into four degrees of degradation (Fig. 6). Degrees 2 and 3 dominate in the study area taken as a whole, showing that, in 2014, most of the surface covered by bio-constructions was in an advanced phase of degradation, reaching a very large proportion at LING (Fig. 6), while CHAM displays a dominantly low degree of degradation (Table 1).

3.5. Size population structure

The densities of *S. alveolata* observed at CHAM are significantly higher (WMW: platform, $p = 0.003$ and reef, $p = 0.0003$) than those observed at BLSM and SGSA, where the densities are closely similar. At CHAM, densities reach 40,000 ind m^2, while at BLSM and SGSA, densities do not exceed 5000 and 10,000 ind m^2, respectively. The densities of *S. alveolata* at LING are very low and the size structure cannot be determined due to the very low numbers of collected individuals.

When the distinction between platform and reef is taken into account, we obtain higher densities on the platforms that on the reefs at CHAM (WMW test, $p = 0.015$) and BLSM (but there is no significant difference between platform and reef on this latter site). Conversely, SGSA shows higher densities of *S. alveolata* on the reef (WMW test, $p < 0.001$) than on the platforms.

During the winter (February–March; 2042 measured individuals), the opercular crown size ranges from 0.45 mm for the smallest individuals up to 3.30 mm for the largest individuals (Fig. 7). Following the suggestion of Dubois et al. (2006), who assumed that the juveniles have an opercular crown <1.35 mm, the population structure on SGSA shows a majority of adult individuals (68% of the population on the platform and 84% on the reef). By contrast, juveniles predominate on BLSM and CHAM, with 70% and 82% on the platform and 78% and 62% on the reef, respectively. There is a significant difference between platform and reef for each site: on CHAM and SGSA, the individuals on the reef are significantly older than on the platform (WMW, $p \leq 0.001$). Conversely, on the BLSM site, the population of the platform is significantly older than the population of the reef (WMW, $p = 0.005$).

3.6. Time-evolution of the size population structure at BLSM

The temporal survey of the BLSM population from February to August shows two main phases (Fig. 8(A)): firstly, an increase in densities between February and April, then a strong decline between April and June, with a slight recovery in August on the platform. Hence, there is a significant difference between dates (ANOVA; $p \leq 0.001$); a *post-hoc* Tukey test shows that significant

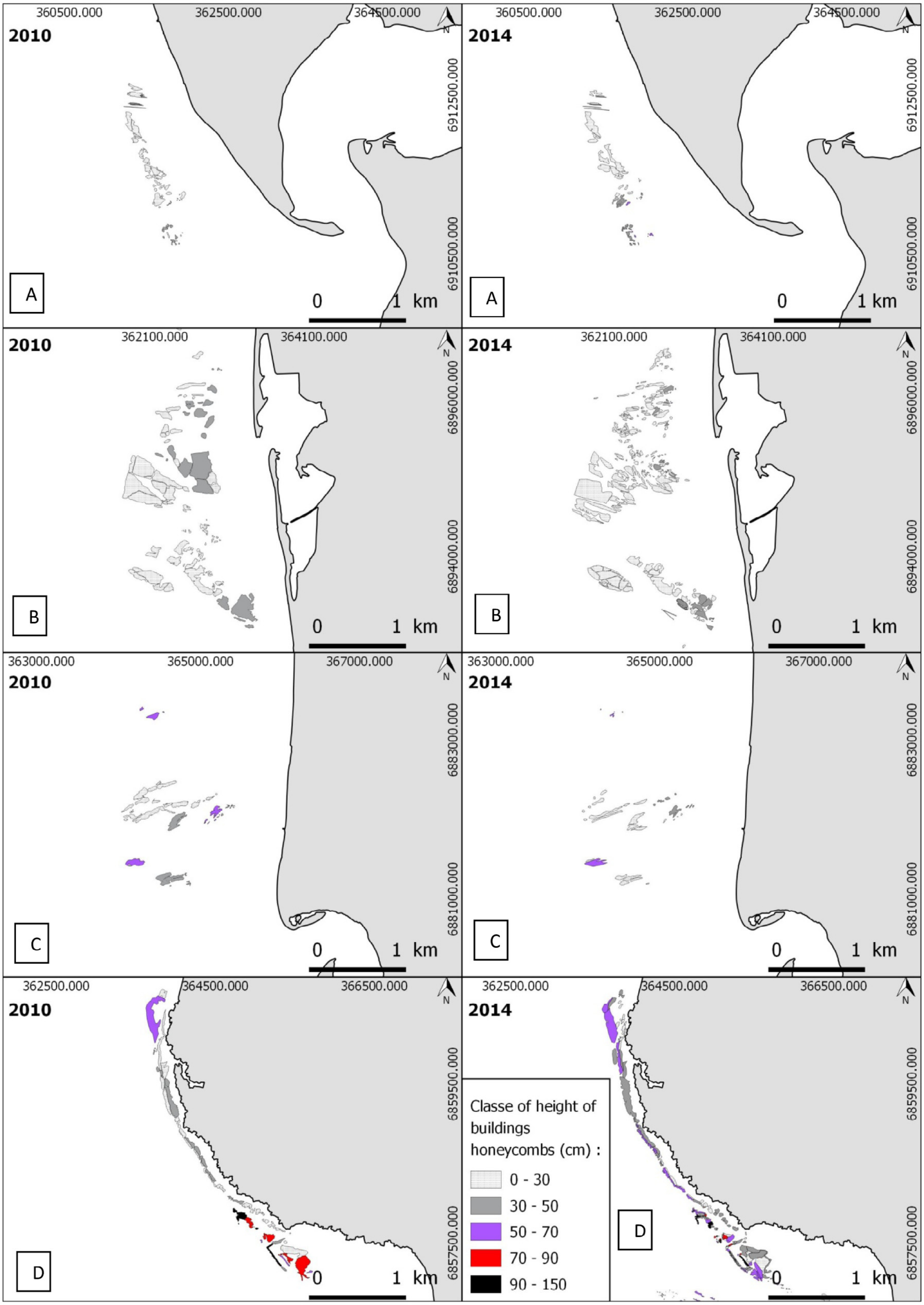

Fig. 4. Presence of honeycomb worm reefs on four sites between 2010–2011 and 2014. From upper part to lower part of diagram (A) SGSA, (B) BLSM, (C) LING and (D) CHAM.

differences in density are only developed on platforms between April and June ($p < 0.01$), on reefs between February and April ($p < 0.0001$), between April and June ($p < 0.001$) and between April and August ($p < 0.001$). Nevertheless, there are no significant differences in densities between platforms and reefs throughout the survey.

The size population structures show significant differences between platforms and reefs in February (Fig. 7) (WMW; $p = 0.005$)

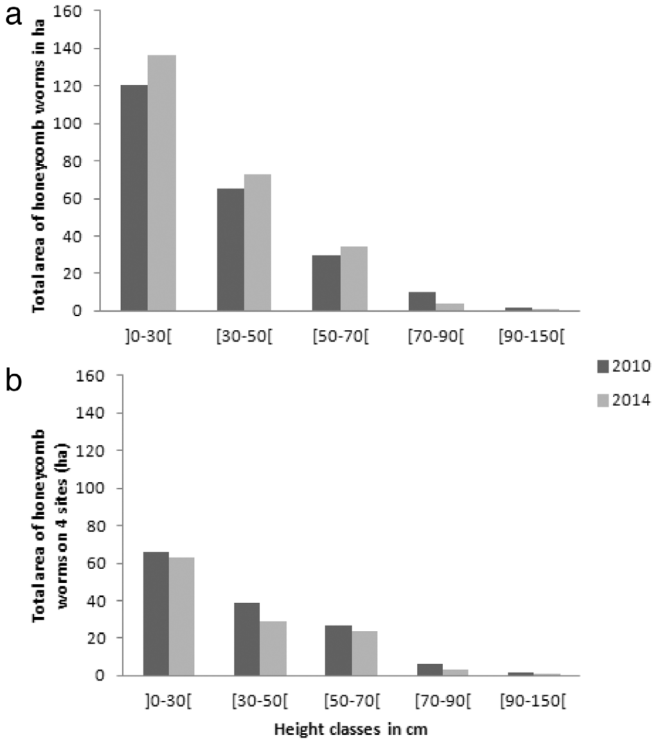

Fig. 5. a. Total area covered by honeycomb worm bio-constructions (ha) over the whole study zone per height class (cm) in 2010–2011 and 2014. b. Total area of honeycomb worm bio-constructions (ha) on the four sites per height class (cm) in 2010–2011 and 2014.

and at BLSM only in August (WMW; $p < 0.001$) (Fig. 8(B)–(G)). A slight growth of the honeycomb worm population, identified by a decreased proportion of juveniles, is observed between February (70% of the population on the platform and 78% on the reef) and April (35% of platform and 40% on the reef). In June, the population appears to be slightly younger than in April, with an increase in the percentage of juveniles (75% on the platform and 69% on the reef). In August, only the percentage of juveniles on the platform decreases (47%), whereas it remains stable on the reef (68%). Overall, the population on the platform appears slightly older than that on the reef, and no recruitment of juveniles is observed between February and August on BLSM.

3.7. Spatial diversity and temporal changes of environmental conditions (2005–2015)

3.7.1. Spatial diversity of the environmental conditions

In the Bay of Mont-St-Michel, the sheltered nature of the site decreases the frequency of strong westerly winds and protects against cold north-easterly airflow (Fig. 9). Over three years of common measurements (2004–2006), the number of frost days is one third lower at Granville than at Gouville-sur-Mer (10.0 days versus 16.7 days, respectively). The intensity of frosts is also lower at Granville: the extreme minimum temperature is about −3.4 °C in the South as against −6.1 °C in the North (Fig. 9). At a smaller scale, the southern sector appears to be sheltered by the cliffs of Champeaux, where there are flourishing honeycomb worm reefs, which effectively block the flow of cold air from the continent.

3.7.2. Temporal changes of environmental conditions (2005–2015)

The meteorological forcing on the development of *Sabellaria* reefs exhibits a strong inter-annual variability (Figs. 10 and 11). The winters show two main patterns: (i) winters with a high frequency of weather systems coming from the Atlantic: strong westerly winds but mild temperatures, such as in 2007, 2008 and especially in 2014, and (ii) winters marked by several northerly advection events: colder temperature but weaker winds, such as in 2006, 2010 and 2013. Table 2 reports the frequency (in %) of wave height during two autumnal and winter periods, i.e. from 1 November 2013 until 31 March 2014 and from 1 November 2014 until 31 March 2015, measured in an intertidal site at Agon-Coutainville. These data show a clear pattern with about 70% of waves in the west sector and a higher % of high wave heights in 2013–2014 (16.8%) than in 2014–2015 (10.9%). The low temperatures in 2010 and 2013 followed by numerous westerly storms in the winter of 2014 contributed to the degradation of the *Sabellaria* reefs on the three sites north of Granville.

4. Discussion

4.1. Sabellaria alveolata bio-construction along the Cotentin coast

At the scale of our local observations, from Champeaux in the south to Saint-Germain-sur-Ay in the north, two main kinds of honeycomb worm bio-constructions can be identified. (1) In the south, the Champeaux reef is considered as a permanent flourishing reef of considerable height (Gruet, 1971, 1981, 1982). It reaches a maximum height of 1.5 m in 2010–2011 and in 2014 (Fig. 4); and 2) bio-constructions occur regularly along the coast from Carolles south of Granville to Saint-Germain-sur-Ay in the north, but since they did not reach 0.9 m in 2010–2011 or in 2014, these reefs should be considered as temporary bio-constructions. Since the beginning of the nineteenth century, several documentary sources have indicated the presence of honeycomb worm reefs along the western coast of Cotentin that appear and disappear over the course of time (Lucas and Lefevre, 1955; Hommeril, 1962; Hommeril and Larsonneur, 1963; Guillaumont et al., 1987).

The irregular presence of platform and reef bio-constructions in the north of the Bay of Mont-Saint-Michel can be explained by the haphazard transport of larvae coming from the Bay of Mont-Saint-Michel, leading to the spread of these *S. alveolata* formations. According to Ayata et al. (2009), the hydrodynamic characteristics of the Bay of Mont-Saint-Michel could play a role in larval retention within the bay due to the presence of gyres (Salomon and Breton, 1993), thus facilitating larval exchanges between the permanent reefs of the bay, i.e. St. Anne and Champeaux, and the self-recruitment of larvae trapped within the bay between these two reefs (Dubois, 2003; Dubois et al., 2007).

In addition, through modelling of larval dispersal over 6 weeks (long planktonic larval duration for *S. alveolata*), Ayata et al. (2009) have shown that there is a possible extension of the larval plume due to south-westerly winds which cause a transport of larvae northwards along the Cotentin coast. Due to the tidal currents and presence of gyres around the Channel Islands (Salomon and Breton, 1993), it is unlikely that the *S. alveolata* populations to the north of Granville participate in the self-recruitment of juveniles along the Cotentin coast. The supply of larvae in this area depends on the southern populations in the Bay of Mont-Saint-Michel. The modelling of currents (Salomon and Breton, 1993) indicates a westward movement of water masses in the sector north of Saint Germain. This model is corroborated by the recent monitoring of buoys (Pien et al., 2014). Moreover, the northward transport of larvae from the BMSM would be insufficient to allow the settlement of bio-constructions observed north of Saint-Germain-sur-Ay. The oyster *Crassostrea gigas* (Thunberg, 1793), with a long planktonic cycle of 25 days similar to *Sabellaria alveolata*, meets the same larval supply requirements with a massive and regular recruitment on rocks located south of Granville from oyster farms in the Bay of Mont-Saint Michel. By contrast, this recruitment is

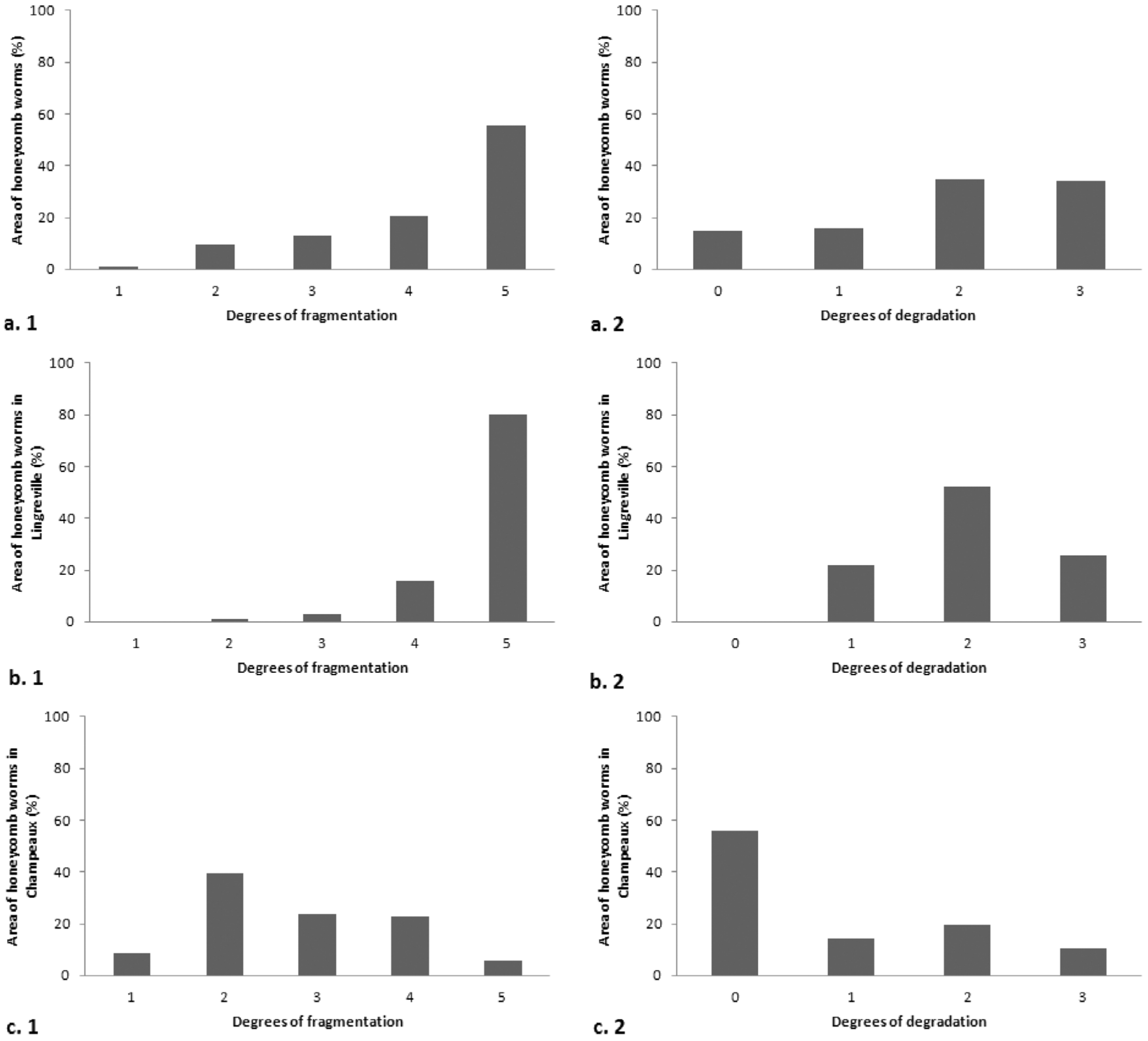

Fig. 6. a. States of fragmentation and degradation of honeycomb worm bio-constructions over the whole study zone b. States of fragmentation and degradation of honeycomb worm bio-constructions at LING. c. States of fragmentation and degradation of honeycomb worm bio-constructions at CHAM. (1: Fragmentation, 2: Degradation).

much more sporadic on rocks situated farther north (Pien et al., 2014).

Since *S. alveolata* has a long life cycle of 4–5 years (Gruet, 1982; Dubois et al., 2007), we suggest that, after a year with massive recruitment, bio-constructions would exhibit a rapid phase of increase (3–4 years, such as between 2006 and 2010) (Delhay, 2010; Basuyaux, 2011), followed by a phase of degradation such as between 2010–2011 and 2014 (Figs. 4 and 6). For 2014, fragmentation indices indicate that bio-constructions were also more fragmented to the north along the Cotentin coast. These differences may be explained by the continuous arrival of new larvae at Champeaux in the south, which ensured the sustainability of the bio-constructions, in contrast to the north where there was a haphazard transport of larvae. Thus, in the absence of any new arrival of larvae, the bio-constructions will disappear at the end of a natural cycle of reef development. In addition, severe winters (Hommeril and Larsonneur, 1963) and strong storms, such as those occurring in 2014, could also contribute to the fragmentation and degradation of the bio-constructions in an area subject to high-energy hydrodynamic conditions (Levoy et al., 1997, 2001), which also favour the displacement of sand and clams (Beck et al., 2015). As shown in our study, environmental conditions are contrasted between the North and the South of the area. The environmental impact appears to be greater in the northern part of the area than in the southern part near Granville. In this way, the higher mortality in the northern part of the study area could be due to the lower air temperatures and a weakening of the reef due to increased wave energy.

Along the Cotentin coast, *S. alveolata* is only observed south of Saint-Germain-sur-Ay, and is totally absent farther north (Basuyaux, 2011). Several hypotheses may be proposed to explain this observation. First of all, the composition of the bedrock changes from south to north along the west coast of the Cotentin. Several rock types are present in the sector south of Saint-Germain-sur-Ay, including calc-alkaline granites but also metaquartzites, sandstones and schists. However, farther north, sandstones are the dominant lithology (Graindor, 1976). Our observations show that honeycomb worms do not colonize sandstone and granite. Hence, the predominant occurrence of sandstone and granite north of Saint-Germain-sur-Ay could explain the absence of *S. alveolata*. In addition, honeycomb worms require large amounts of sand of a particular grain size to create bio-constructions, and such clastic materials can be insufficiently abundant in this sector. Lucas and Lefevre (1955) have described the conditions favourable for honeycomb worm settlement on the west coast of Cotentin. The water should be agitated, containing sand as suspended sediment load.

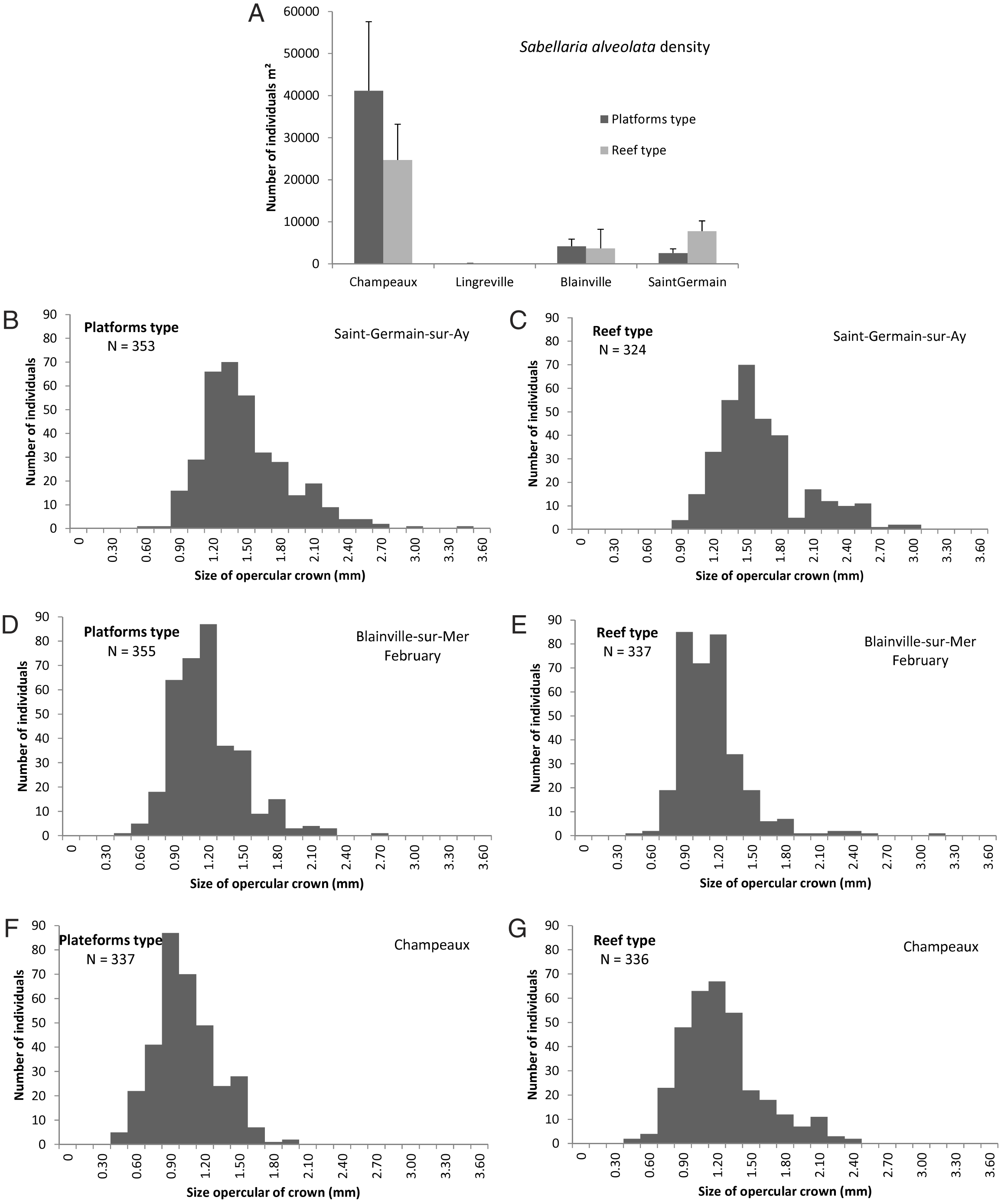

Fig. 7. A. *Sabellaria alveolata* density (mean ± S.E.) by structure and site. B-G. *Sabellaria alveolata* size-class histograms based on measurement of the opercular crown according to each structure at CHAM, SGSA and BLSM. N, number of individuals measured.

Honeycomb worms have a preference for calcareous sand composed of 25% siliceous particles.

Our field observations were made during spring tides at low water, allowing us to delimit the surface-areas covered by *S. alveolata* bio-constructions, and were carried out in a similar manner in 2010–2011 and in 2014. *In situ* observations and measurements are combined with the use of georeferenced aerial photographs of good quality. By applying a similar metrology, we are able to reduce the uncertainties which are thus comparable between the two periods. In 2014, bio-constructions along the Cotentin coast (Fig. 4) occupied areas of similar magnitude as observed in 2010–2011 (228 ha in 2010–2011 as against 248 ha in 2014). At the scale of the four studied sites, there is a slight decrease from 140 ha in 2010–2011 to 120 in 2014, which is mainly due to a reduction in surface-area at two sites (BLSM and LING), while there is a slight increase at SGSA and CHAM (Table 1). A degradation has been observed at the BLSM site since 2011, and continues up to the present day (Delhay, 2012; Dauvin personal observation). From 2010 to 2012, *Sabellaria* reefs were monitored by field sampling during springtime from a small local colonized zone north of Blainville-sur-Mer to observe changes in surface-area over three successive years (Delhay, 2012). In 2010 (sampling from 30 April to 2 May), the estimated surface-area was 70.63 ha, whereas it was 49.14 ha in 2011 (sampling from 18–21 February) and 40.62 ha in

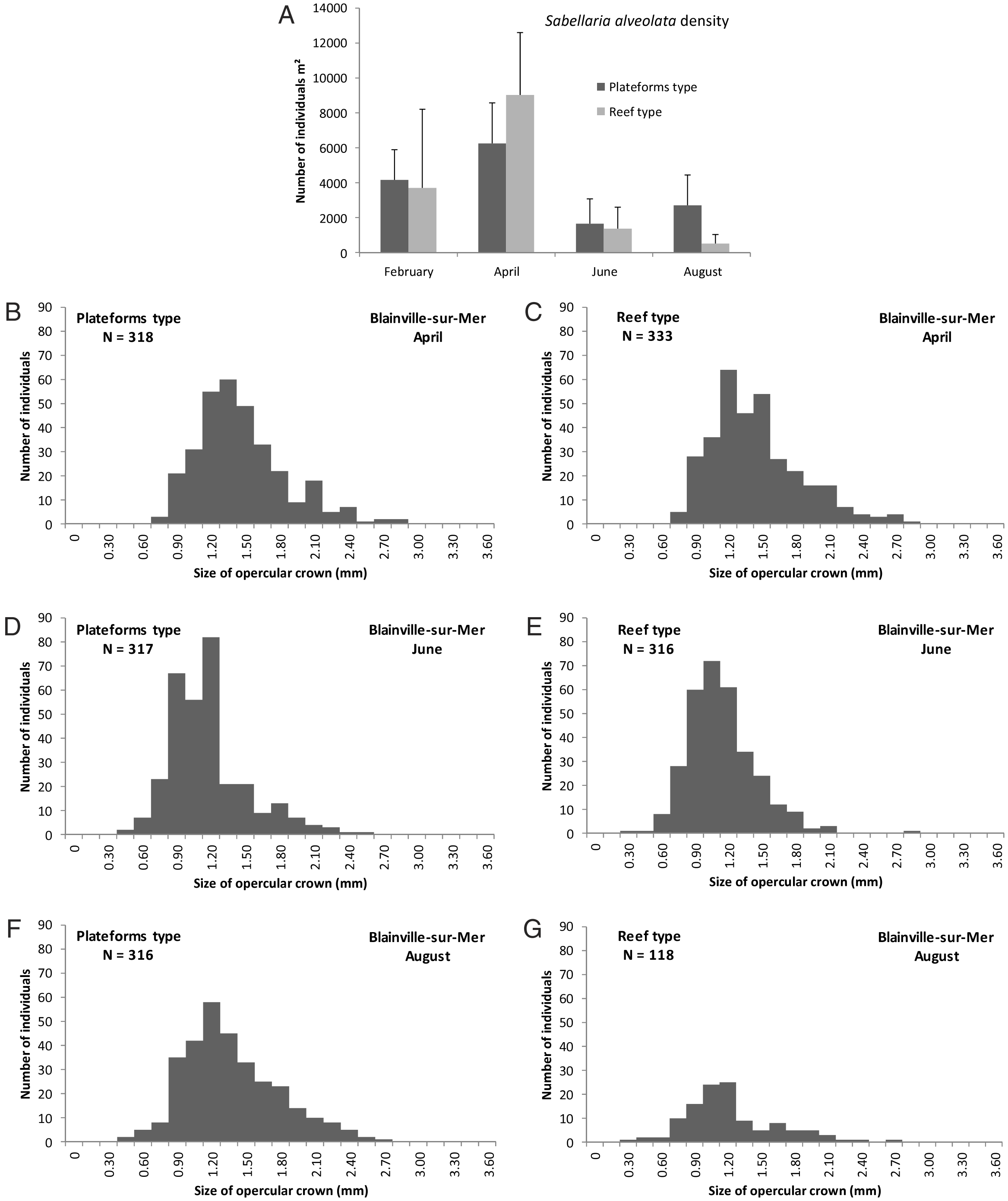

Fig. 8. A. *Sabellaria alveolata* density (mean ± S.E.) by structure and date. B-G. *Sabellaria alveolata* size-class histograms based on measurement of the opercular crown according to each structure at BLSM for the four sampling dates. *N*, number of individuals measured.

2012 (sampling 2–3 March). The estimated surface-area of reefs between 2010 and 2011 is about 43.10 ha and about 40.50 ha between 2011 and 2012. In 2011, 17 ha that had been colonized by *S. alveolata* in 2010 were no longer colonized, while 6 ha became colonized between 2010 and 2011. Between 2011 and 2012, about 8.5 ha of reef was lost while newly colonized areas accounted for only 0.12 ha. Hence, there was a rapid reduction in surface-area between 2010 and 2011 (40%), which slowed down to a loss of only 6% between 2011 and 2012. Similarly, a short-term decrease was observed in 2014 during the survey of BLSM, reflecting a rapid local change between the middle of the winter and the summer, during a destruction phase followed by colonization of the reef by algae (Fig. 6; Schlund et al., submitted for publication).

Apart from field operations, other mapping methods have been used to estimate the surface-areas and volumes of *S. alveolata* reefs. LIDAR surveys have been implemented to map *S. alveolata* reefs at Sainte-Anne in the Bay of Mont-Saint-Michel (Noernberg et al., 2010). Similarly, a combination of field observations and aerial photographs was used to estimate the evolution of the main worm reef complexes at BLSM on the west coast of Cotentin between 2010–2011 and 2012 (Delhay, 2012). These results demonstrate that LIDAR data and photographic techniques can provide additional accurate information to improve our

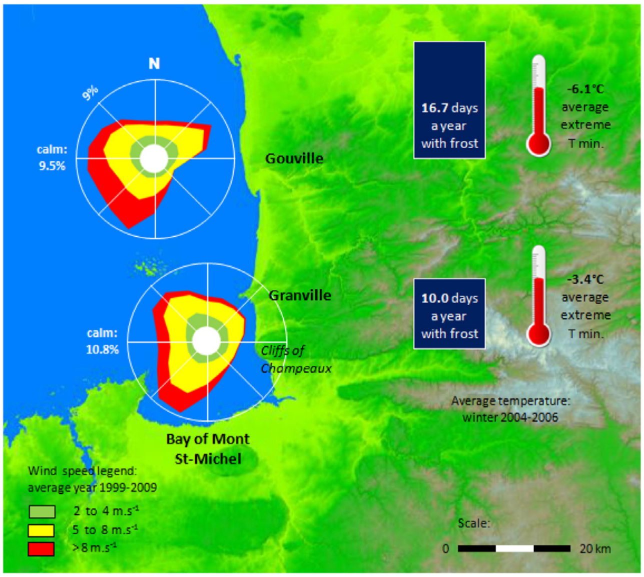

Fig. 9. Climatic difference between the northern and southern parts of the studied sector on the western coast of Cotentin. Wind rose over the period 1999–2009, according to hourly modelled data (Aladin, Météo-France). Extreme temperature and frosts over the period 2004–2006 at Gouville-sur-Mer and Granville (Météo-France data) (base map IGN).

knowledge of the main honeycomb worm reef-building species in heterogeneous environments on the Cotentin coast.

4.2. Population size structure in 2014

In 2014, the highest *Sabellaria alveolata* densities were recorded at Champeaux (40,000 ind m^2), while there remained only a few individuals per m^2 at Lingreville, clearly showing the almost complete disappearance of honeycomb worms between 2010–2011 and 2014 at this site. The maximum values were of the same order of magnitude as those reported by Gruet (1981, 1982) for Champeaux or other reefs on the Atlantic coast of France (Gruet, 1982). It is noteworthy that densities appear to be higher on platforms than on reefs such as at Saint-Germain-sur-Ay and Champeaux. This could be explained by the developmental stage of the bio-construction from which the samples were taken. Indeed, platforms represent a growing stage, while the reefs can be considered as the ultimate stage of evolution of the bio-construction and the beginning of a phase of population decline. At the Blainville-sur-Mer site, the observations show the opposite, but the estimated densities are not significantly different between platforms and reefs.

The analysis of population size structure indicates a greater abundance of adults than juveniles on the Saint-Germain-sur-Ay site. By contrast, there are more juveniles at Blainville-sur-Mer and Champeaux. This probably reflects a difference in the renewal of populations at the scale of the north Cotentin coast. Dubois (2003) and Dubois et al. (2007) recognized that, in the Bay of Mont-Saint-Michel, *S. alveolata* has an extended reproductive period with semi-continuous spawning from April to October associated with a long pelagic phase of about 6 weeks (Ayata et al., 2009). According to our observations in 2014, there were very few individuals with an opercular crown < 0.75 mm (indicative of juvenile settlement) in winter on three sites located in the southern and the northern parts of the colonized zones (very little or no settlement in 2013) (Fig. 7). No small individuals (opercular crown < 0.75 mm) were collected during the winter–summer survey at BLSM, suggesting the absence of spring recruitment at this site in 2014. The collected individuals were adults older than 2 years, and probably 3–4 years in the case of the larger individuals with an opercular crown $>$ 3 mm, especially at the SGSA site to the north. Therefore, the size

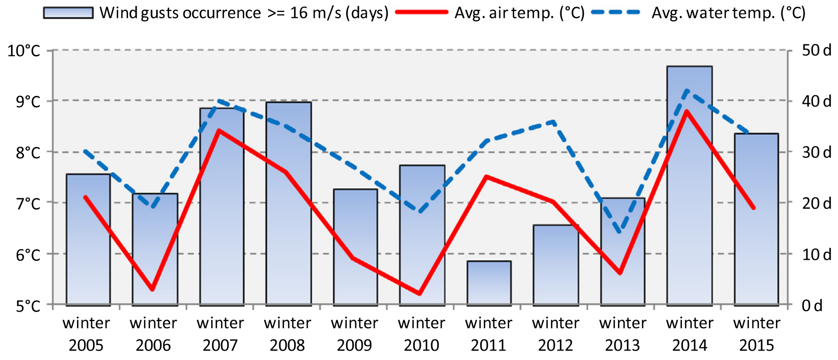

Fig. 10. Wind gust occurrences (days) and average air temperature at Gouville-sur-Mer and average water temperature (°C) at Blainville-sur-Mer, in winter between 2005 and 2015 (data Météo-France).

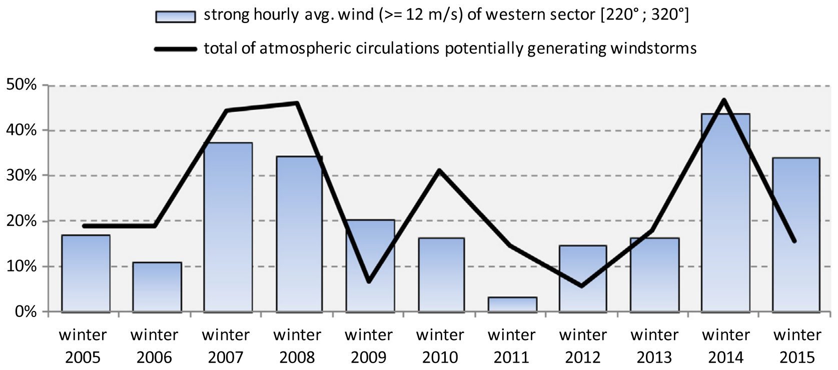

Fig. 11. Frequency of strong west winds (data Météo-France) and atmospheric circulation patterns potentially generating windstorms in winter over Northern France, between 2005 and 2015 (classification after James, 2007).

population structures illustrate the discontinuous renewal of the population along the western coast of Cotentin.

4.3. Interactions of Sabellaria reefs with human activities

During the same period (winter–summer 2014), studies were carried out on the macrofaunal TR associated with *Sabellaria alveolata* bio-constructions at the four target sites (Schlund et al., submitted for publication). The results show a higher TR on the platforms than on the reefs, and a higher epifaunal TR outside the areas with bio-constructions. Thus, it appears that *S. alveolata* does not favour epifaunal TR on hard substrates; moreover, high abundances of the honeycomb worm have a negative impact on TR similarly to the previous observations of Gruet (1982).

Moreover, intensive recreational fishing activity is concentrated on the low mid-littoral and infralittoral fringe on the west coast of Cotentin, whereas the *Sabellaria* bio-constructions are located in the middle and upper mid-littoral zones. Anthropogenic reef degradation seems very limited in this area and does not represent the same challenge for preservation of the natural heritage as in the case of the Sainte-Anne reef in the Bay of Mont Saint-Michel (Desroy et al., 2011).

Moreover, in spite of expected difficulties of exploitation, primarily for oyster farming during the expansion phase of *Sabellaria* reefs on the western coast of Cotentin, the interactions with oyster cultivation appears to be limited in space and time in this sector (Basuyaux, 2011; Lecornu, 2014). This is probably because the total surface-area covered by the bio-constructions remains very small (<2.5 km^2 in 2014). Thus, for a total coastline length of $\sim$60 km and a 2-km-wide intertidal zone (corresponding to an area of $\sim$120 km^2), the *Sabellaria* bioconstructions occupies $\sim$2% of the zone. In comparison, oyster farming occupies an area of 4.76 km^2, with a total length of mussel bed lines of 239 km on the same intertidal zone.

4.4. Concluding remarks

Our study concerns the dynamics of *Sabellaria* bio-constructions (platforms and reefs) on the western coast of Cotentin (English Channel, France). We compare the changes in surface-area covered by *Sabellaria* bio-constructions between 2010–2011 and 2014, focusing on four sites located along $\sim$60 km of this coastline. Our approach is supplemented by analyses of the population dynamics on these four sites. Environmental data are used to account for the results.

The study was initiated at the end of the years 2000 after a massive settlement of larvae and the development of reefs near oyster culture tables. Depending on the spring–summer wind conditions, settlement along the coast of the Cotentin is ensured by larval transport from the permanent populations of the Bay of Mont-Saint-Michel.

Three main periods are identified over a time span of about a decade: (1) a colonization phase from 2007 to 2009, with an increase of the surface covered by bio-constructions and the formation of spectacular reefs (>1 m height) at some locations such as BLSM and LING; (2) a phase of maximum expansion, with flourishing reefs in 2010–2011; and (3) a phase of degradation beginning in 2011 (but observed annually at BLSM from 2010 to 2012, Delhay, 2012) and continuing until 2014 with a marked degradation of the reef at LING (the site where this was first observed at the end of the years 2000) and the almost complete disappearance of living *Sabellaria* in 2014 at this location.

We correlate the degradation of the reefs with natural factors: i.e. low air and seawater temperatures during the winters of 2009–2011, with stronger winds from the SW to NW sectors in 2013–2014 generating higher energy hydrodynamic conditions and sediment transport in an area with strong tidal currents. These environmental conditions are known to be unfavourable for the development of *Sabellaria* reefs, while the absence of recent recruitment in 2013–2014 (see Figs. 7 and 8) leads to a slow decay.

Since there is an increase of interest in the description of the past and present distribution of *Sabellaria* across its entire European range (see Cunningham et al., 1984; Frost et al., 2004; Firth et al., 2015) and the human impact of such biogenic habitats (see Plicanti et al., 2016), our local investigation will contribute to an understanding of *Sabellaria* population dynamics in a broad latitudinal approach.

Furthermore, as suggested in Schlund et al. (submitted for publication), it is difficult to propose a permanent protection of the temporary bio-constructions such as those observed in the Saint-Anne and Champeaux reefs (Desroy et al., 2011). Nevertheless, these temporary reefs merit special attention due to the impact of professional and recreational fishing activities, especially when considering that these bio-constructions are present and flourishing on the western coast of Cotentin.

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