Evolution et interactions des *Sabellaria* en secteurs conchylicoles

Les hermelles étaient pratiquement absentes des secteurs conchylicoles de la côte ouest de la Manche durant les dernières décennies. Une forte colonisation a eu lieu entre 2009 et 2011, créant des difficultés d'exploitation essentiellement pour l'ostréiculture. Depuis ces années, la présence de cette espèce a semble-t-il régressé en secteur conchylicole.

Les hermelles peuvent constituer des récifs, dont l'importance peut conduire à un rôle écologique majeur, notamment par les fonctions écosystémiques qu'ils apportent. Aussi des mesures de gestion et/ou de protection de ces habitats peuvent être prises en fonction des sites. Cette étude vise à mieux qualifier les interactions entre la conchyliculture et les hermelles, afin d'établir d'éventuels effets positifs, négatifs ou neutres entre cette activité et cette espèce.

Basuyaux Olivier [1],

Erika Schlund [2],

Billie Lecornue [1],

Jean Claude Dauvin [2], 2015

SMEL [1] –M2C/CNRS [2]

CONVENTION N° 2014 PCM 24

Avec la participation technique de :

Stéphane Rogue & Arnaud Lehallais (Conseil départemental de la Manche) : Mise en œuvre du logiciel Cartolander

Guillaume Fauveau (Agence des aires Marines Protégées) : Réalisation de la mise en page des cartographies

Jean Paul Robin (Université de Caen Basse-Normandie) : Assistance à la réalisation des statistiques

Aurélie Foveau (CNRS) : Détermination des espèces benthiques

.

Table des matières

Objectif de l'étude 5

Introduction 6

Synthèse des résultats 14

A. Cartographie de la présence de *Sabellaria alveolata* sur l'ouest Cotentin 14

B. Rôle fonctionnel des hermelles en secteur conchylicole, au travers d'un inventaire des espèces présentes en comparaison avec les récifs historiques de la Baie du Mont Saint-Michel 24

C. Identification d'un indicateur de suivi des populations d'hermelles permettant d'évaluer l'évolution des récifs de façon annuelle à moindre coût. 28

D. Evaluation de l'incidence économique du développement des hermelles dans le cadre d'une approche écosystémique du fait des modifications que peuvent engendrer les récifs d'hermelles sur les pratiques culturales conchylicoles. 29

Conclusion 32

Bibliographie 33

Annexes 36

Objectif de l'étude

Dans le cadre de l'appui zootechnique à la production conchylicole, la présence des Hermelles sur les concessions ostréicoles a été évaluée. L'objectif est d'étudier les interactions entre la conchyliculture et une espèce (*Sabellaria alveolota*) pouvant présenter un rôle fonctionnel important et ceci dans un cadre global d'évolution de la présence de cette espèce sur la côte Ouest de la Manche. Dans un premier temps une cartographie permettant d'apprécier l'évolution des récifs d'Hermelles de l'Ouest Cotentin a été réalisée, des indicateurs de suivis simples ont été mis en œuvre. Le rôle écologique de ces récifs sur substrat dur sera comparé à celui des récifs de Champeaux et de Saint Anne (substrat meuble) dont l'intérêt dans la biodiversité a été mis en évidence. L'objectif est d'évaluer les différences de ces deux types de structures. La cartographie 2014 est comparée avec celle réalisée par le SMEL en 2010-2011.

Les enjeux principaux de ce projet sont d'apporter des connaissances sur les aspects du développement des hermelles ainsi que leur rôle fonctionnel dans l'écosystème conchylicole. Ainsi, quatre grandes actions sont développées :

- Cartographie de la présence de *S. alveolata* sur l'ensemble de la façade ouest du Cotentin pour évaluer l'évolution des peuplements depuis la dernière cartographie réalisée en 2011.

- Rôle fonctionnel des hermelles en secteur conchylicole, au travers d'un inventaire des espèces présentes en comparaison avec les récifs historiques de la Baie du Mont Saint-Michel.

- Identification d'un indicateur de suivi des populations d'hermelles permettant d'évaluer l'évolution des récifs de façon annuelle à moindre coût.

- Evaluation de l'incidence économique du développement des hermelles dans le cadre d'une approche écosystémique du fait des modifications que peuvent engendrer les récifs d'hermelles sur les pratiques culturales conchylicoles.

Introduction

Sabellaria alveolata (Linné, 1767) communément appelée hermelle, est une annélide polychète sédentaire de la famille des Sabellaridae trouvée sur les estrans européens et notamment connue pour sa capacité à construire des récifs biogéniques. Holt *et al*. (1998) définissent ces récifs comme étant « des structures solides et massives créées par l'accumulation d'organismes, générant un changement dans la topographie du paysage et formant un habitat avec des limites bien définies contrastant avec les unités sédimentaires avoisinantes ». Plusieurs espèces de la famille des Sabellaridae ont cette capacité de bioconstruction, telles que certains polychètes grégaires des genres *Gunnarea*, *Idanthyrsus* et *Phragmatopoma*, construisant également des structures récifales. Cependant, à l'échelle européenne, les hermelles élaborent les plus importantes structures biogéniques, attirant un grand nombre d'espèces intertidales. Les autres polychètes grégaires se développent essentiellement sur les côtes sud-africaines, équatoriales et californiennes (Dubois, 2003).

En France, *S. alveolata* est particulièrement fréquente au niveau de la Baie du Mont Saint-Michel et la Baie de Bourgneuf, où l'on trouve les récifs les plus imposants d'Europe (Gruet et Bodeur, 1997 ; Dubois *et al*., 2002 ; Desroy *et al*., 2011). Dubois *et al.* (2002) ont, de plus, montré que la richesse spécifique de la faune associée aux récifs d'hermelles y est plus grande que dans les sédiments alentours. Ces formations récifales vont également jouer un rôle de nurserie pour des espèces d'intérêts commerciaux telles que les poissons plats, ou un rôle d'alimentation pour les oiseaux ou les poissons.

Ces structures sont soumises à de nombreux impacts anthropiques directs (pêche à pied, piétinement) et indirects (aménagements côtiers, conchyliculture) à l'origine de la dégradation de ces formations (Dubois, 2003). A ce titre, les récifs sont des sites remarquables, inscrits dans l'annexe I de la Directive Habitat 92/43/CEE (code 1170 – 4) comme étant des habitats naturels d'un grand intérêt pour le patrimoine naturel et la biodiversité.

Répartition géographique de S. alveolata

Les populations d'hermelles ont une aire de répartition s'étendant de l'ouest de l'Ecosse (Solway Firth) au nord des côtes mauritaniennes (Gruet, 1972 ; Ayata *et al.*, 2009) (Fig. 1). Bien que celles-ci soient étendues, les formations récifales bien développées telles que celles de Bourgneuf ou celles de la Baie du Mont Saint-Michel sont rares.

Contrairement à *S. spinulosa*, seconde espèce du genre Sabellaria également trouvée sur nos côtes mais en zone subtidale (Dubois, 2003), *S. alveolata* se développe essentiellement en zone intertidale, dans des conditions environnementales très diverses, telles qu'en milieu exposé et battu (Cornouaille anglaise) ou en milieu abrité (Baie de Bourgneuf) (Dubois *et al.*, 2004). Elle supporte également la dessalure puisqu'elle est rencontrée dans les zones abritées de l'estuaire de la Loire (Dubois, 2003).

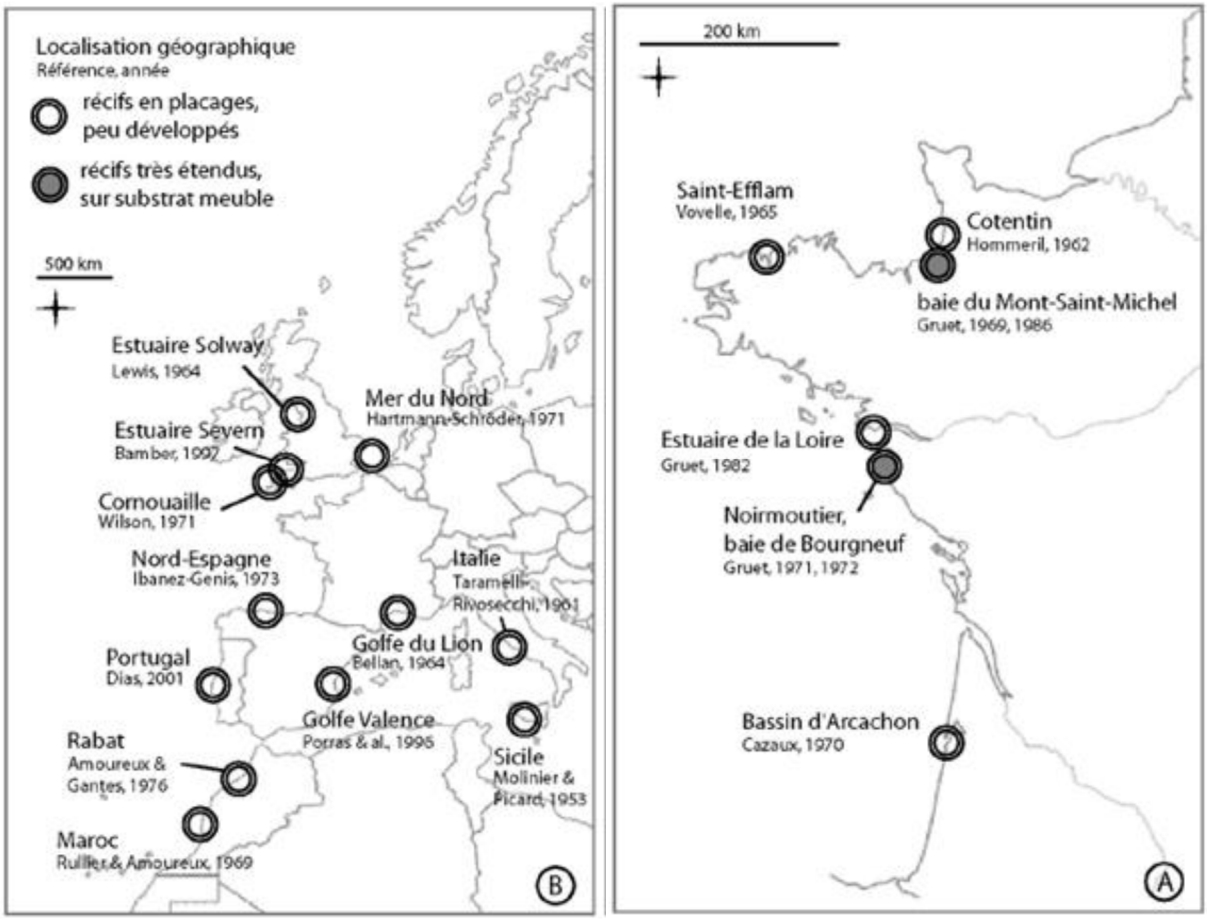


Figure 1 : Cartographie des principales régions d'Europe et de France où ont été signalés et décrits des récifs à Sabellaria alveolata. Modifiée et complétée d'après Gruet (1982)

Hommeril (1962) a été le premier à évoquer les deux modes d'implantation sur fond rocheux (substrat dur) et sur fond graveleux (substrat sableux) sur la côte ouest du Cotentin.

La côte ouest du Cotentin

Hommeril (1962) recense la présence d'hermelles sur la côte ouest du Cotentin, sur le secteur de Gouville-sur-Mer. Actuellement, sur cette côte, les hermelles sont présentes de Saint-Germain-sur-Ay (au Nord) jusqu'à Champeaux (au Sud), zone qui se caractérise par un certain nombre de havres formant des éventails deltaïques (Basuyaux, 2011) (**Fig. 2**).

En 2011, 535 aires d'hermelles ont été recensées sur la côte ouest du Cotentin, représentant une surface totale d'occupation de 98 ha dont 45 ha de récifs (Basuyaux, 2011). Pour les études, la zone a été subdivisée en huit secteurs : Saint-Germain-sur-Ay, Pirou, Gouville/Blainville-sur-Mer, Lingreville, Donville, Granville, Jullouville et Champeaux (**Annexe I**). Des abondances particulièrement fortes sont relevées sur le secteur de Blainville, Lingreville et Granville (partie sud).

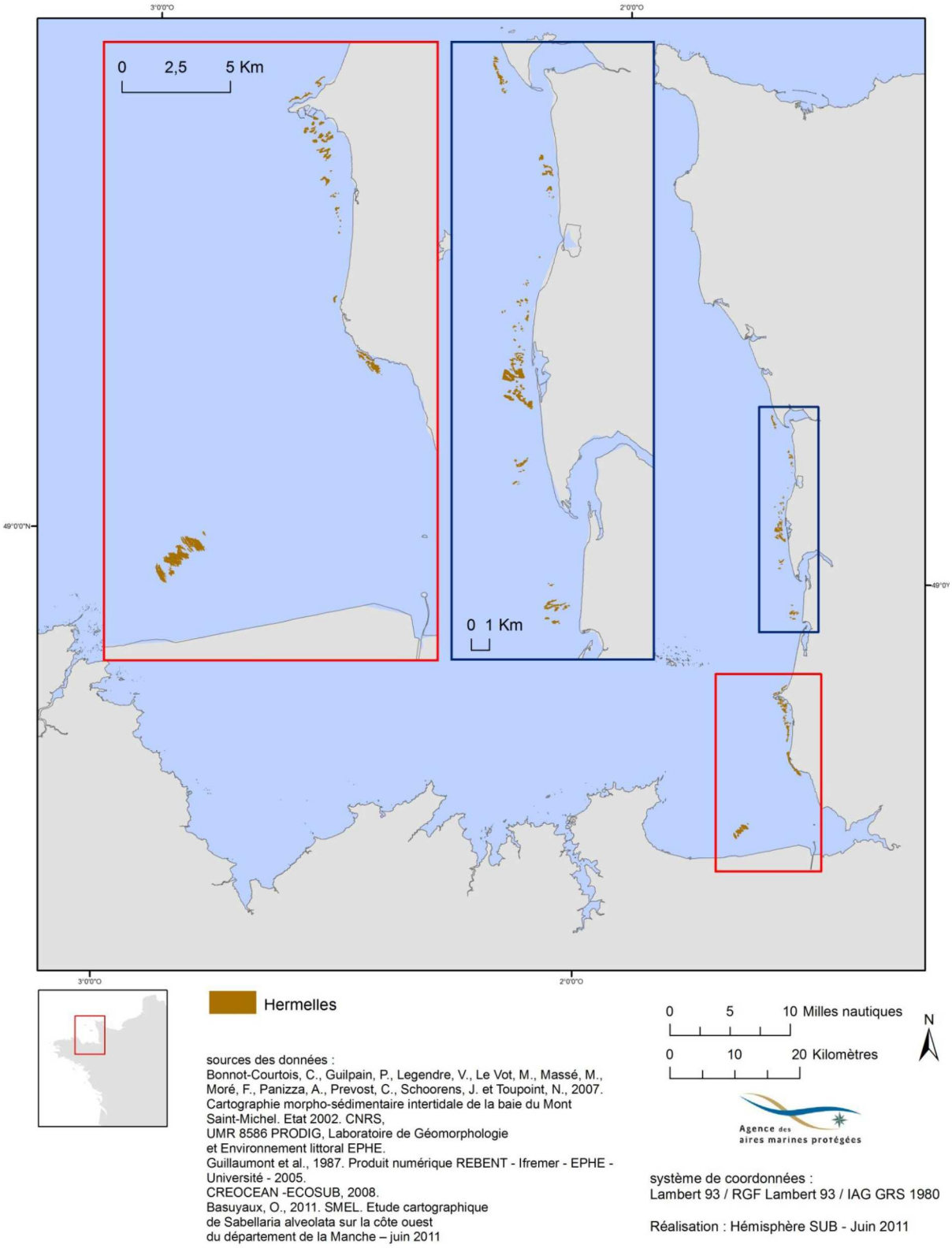


Figure 2 : Cartographie de la répartition des hermelles (représentées par les taches brunes) sur la côte ouest du Cotentin (Hemisphère Sub, 2011).

Biologie de l'espèce

S. alveolata est une annélide tubicole de la famille des Sabellaridae pouvant mesurer de 2 à 5 cm de long (Dubois *et al.*, 2005, 2006). Sa longévité est relativement grande, de 3 à 4 ans, avec quelques cas rares vivant jusqu'à 10 ans (Dubois *et al.*, 2005 ; Ayata *et al.*, 2009). Morphologiquement, cette espèce présente quatre parties distinctes ainsi qu'une spécialisation des métamères (**Fig. 3, Annexe II**):

- la partie céphalique porte des soies modifiées en palées correspondant à la couronne operculaire ;

- la région thoracique et parathoracique porte des soies transformées en « pagaies » permettant les déplacements de l'animal dans son tube. La partie ventrale parathoracique contient les glandes accessoires sécrétant le ciment solidifiant le tube ;

- la région abdominale comportant les produits génitaux. Les métamères constituant cette partie portent chacun une paire de branchies. Le nombre de métamères augmente avec l'âge de l'individu ;

- la région caudale se terminant par la partie rectale par laquelle sont éliminés les fèces (Dubois *et al.*, 2004).

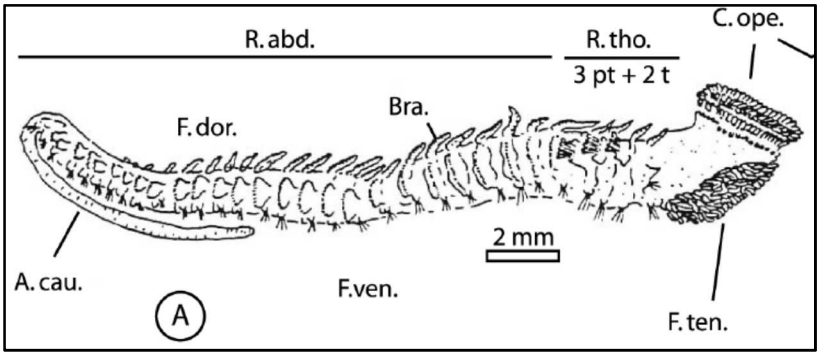


Figure 3 : Description morpho-anatomique d'une hermelle. R.abd.: région abdominale, R.tho.: région thoracique (3 segments parathoraciques + 2 segments thoraciques), C.ope. : couronne operculaire, F.dor : face dorsale, Bra : branchies, A.cau. : appendice caudal, F.ven. : face ventrale, F.ten. : filaments tentaculaires (d'après Gruet, 1982).

Cette espèce, microphage filtreur, filtre de manière active les particules fines en suspension. Les taux de filtration ont ainsi été estimés à 0.75 $ml.h^{-1}.ind^{-1}$, ceux-ci diminuant

exponentiellement lorsque la concentration de matières en suspension augmente, mais n'empêchant pas l'hermelle de s'alimenter (Dubois *et al.*, 2003). Le seston supérieur à 4 µm est alors capturé par les filaments tentaculaires grâce au battement des cils présents sur ces filaments et transporté jusqu'à la bouche par un transport mucocilliaire.

Chez cette espèce gonochorique et polytélique, les gonades ne sont pas distinctes. Cependant, les sexes sont clairement identifiables par la couleur de l'abdomen, celui-ci étant blanc-laiteux chez le mâle et rose-violacé chez la femelle. Les individus de cette espèce ont la capacité de se reproduire dès la première année, avec une reproduction possible toute l'année, bien qu'il y ait deux pics majeurs en mars-avril et en juin-juillet (Dubois *et al.*, 2004). Leur capacité de reproduction est élevée puisqu'une femelle mature peut libérer entre 300 000 et 600 000 oeufs (Gruet et Bodeur, 1997). La durée de vie larvaire est estimée entre 6 semaines et 11 mois, l'hydrodynamisme ayant une influence majeure sur la rétention des larves, de même que les conditions météorologiques (Ayata *et al.*, 2009). Le recrutement des juvéniles est important dans la dynamique récifale assurant la résilience du récif (Ayata *et al.*, 2009 ; Desroy *et al.*, 2011). De plus, de précédentes études indiquent une attraction d'ordre biochimique des larves prêtes à la métamorphose par les adultes. La substance attractive se trouverait à l'intérieur du tube, ce qui explique en partie le grégarisme de l'espèce (Gruet et Bodeur, 1997).

Formation des tubes

L'hermelle vit dans un tube composé de grains de sable qu'elle va capter à l'aide des filaments tentaculaires situés sur la partie ventrale du prostomium lorsque les particules sont en suspension. Ceux-ci sont ensuite menées à la bouche par des gouttières intertentaculaires. Les grains sont ensuite englués dans un ciment organique au niveau de l'organe constructeur, situé sous la cavité buccale (Dubois *et al.*, 2004). Le Cam *et al.* (2011) ont d'ailleurs mis en évidence le comportement viscoélastique du matériau, ce qui permet aux tubes de dissiper l'énergie mécanique des vagues ainsi que le stress mécanique transmis dans les tubes jusqu'aux individus. Le tube est constitué de sables moyens bioclastiques (200 – 500 µm) que les individus sélectionnent en fonction de leur forme et de leur nature minéralogique, les sables mixtes constitués de grains arrondis de quartz semblant être le matériau de prédilection de l'espèce (Dubois *et al.*, 2004). Le tube est constitué de deux gaines concentriques, l'une interne, très mince, de nature organique riche en soufre et l'autre, externe, arénacée (Dubois *et al.*, 2004)

(**Fig. 4A**). Le diamètre interne du tube, de l'ordre de 5 mm, croit avec la croissance de l'individu de même que les grains de sable utilisés (Dubois *et al.*, 2004). L'ouverture (**Fig. 4B**) peut être de taille et de forme variables, en fonction de l'hydrodynamisme et de la densité des individus (Dubois, 2003). Le tube est en perpétuelle extension durant la vie de l'individu, tant qu'il y a un apport de matériau possible, pouvant ainsi atteindre 50 cm de hauteur (Dubois *et al.*, 2003). Cependant, les précédentes études indiquent que les hermelles ne vivent que dans les 15 premiers centimètres du tube, la partie proximale se comblant rapidement de vase et de fèces (Dubois *et al.*, 2004). Les tubes sont indispensables à la survie des hermelles qui ne peuvent vivre en dehors ou sans la partie utilisée comme matrice pour sa reconstruction (Dubois, 2003).

Figure 4 : A : Distinction des deux gaines d'un tube de S. alveolata ; B : Ouverture des tubes d'une bioconstruction de S. alveolata. Crédit photos

Dynamique récifale

Les hermelles peuvent construire deux types de bioconstructions, les récifs et les placages, pouvant se développer sur substrat meuble ou sur substrat dur (**Fig. 5**). Ces deux types de bioconstructions sont essentiellement définis par la hauteur de ces dernières. En effet, une bioconstruction en placage ne dépasse pas la dizaine de centimètres (Desroy *et al.*, 2011).

Figure 5 : Bioconstruction d'hermelles sur substrat meuble (à gauche) et sur substrat dur (à droite). Crédit photo : ES

Les structures évoluent en plusieurs étapes. La structure initiale se développe en forme de « boule ». Lorsque la densité de « boules » augmente, celles-ci fusionnent formant des barrières puis des platiers. Ces derniers correspondent au stade ultime de développement de la bioconstruction, pouvant parfois atteindre deux mètres de hauteur (Dubois, 2003) (**Annexe III**). Les récifs biogéniques jouent des rôles fonctionnels clés dans les écosystèmes et contribuent aux processus biologiques et physiques, par la stabilisation du substrat en retenant les sédiments, ainsi que par la diversité de micro-habitats qu'ils peuvent fournir en augmentant les espaces accessibles pour la colonisation de nouvelles espèces. L'accumulation de fèces et de pseudo-fèces, de même que d'autres dépôts organiques, sont des sources importantes de nourriture pour d'autres organismes (Desroy *et al.*, 2011).

Synthèse des résultats

Les résultats complets obtenus dans le cadre de ce travail feront l'objet deux 2 publications scientifiques dont l'intégralité des textes sont disponible en annexe, seule une synthèse sera présentée.

Dynamics (2010-2014) of the Sabellaria alveolata reefs on the west coast of Cotentin (France)

Billie Lecornu, Erika Schlund, Olivier Basuyaux, Jean-Claude Dauvin

Soumis fin décembre 2015 auprès de « Estuarine, Coastal and Shelf Science »

Macrofaunal biodiversity associated with Sabellaria alveolata reefs on the west coast of Cotentin (France)

Erika Schlund, Olivier Basuyaux, Billie Lecornu, Jean-Claude Dauvin

Soumis le 16 novembre 2015 auprès de « Springer Plus »

A. Cartographie de la présence de *Sabellaria alveolata* sur l'ouest Cotentin

La cartographie des différents secteurs a été effectuée du mois d'avril à juillet 2014. Les observations sont faites *in situ* à partir des prises de vues aériennes de 2013 (orthophotos 2013).

L'évaluation a été réalisée à partir de vérité terrain systématique sur l'ensemble de la zone étudiée. Cette évaluation a été assistée à l'aide d'une tablette/GPS incluant le logiciel cartolander.

Les différents critères notés étaient :

La hauteur en centimètre:]0-10] ;]10-30] ;]30-50] ;]50-70] ;]70-90] ;]90-150]

Le taux de recouvrement en pourcentage:]0-20] ;]20-40] ;]40-60] ;]60-80] ;]80-100]

La fragmentation du récif : (5) récif composé de très petits blocs, (4) récif composé de blocs petits et moyens, (3) récif composé de blocs de tailles variées, (2) récif composé de plusieurs gros blocs, (1) récif composé d'un seul gros bloc

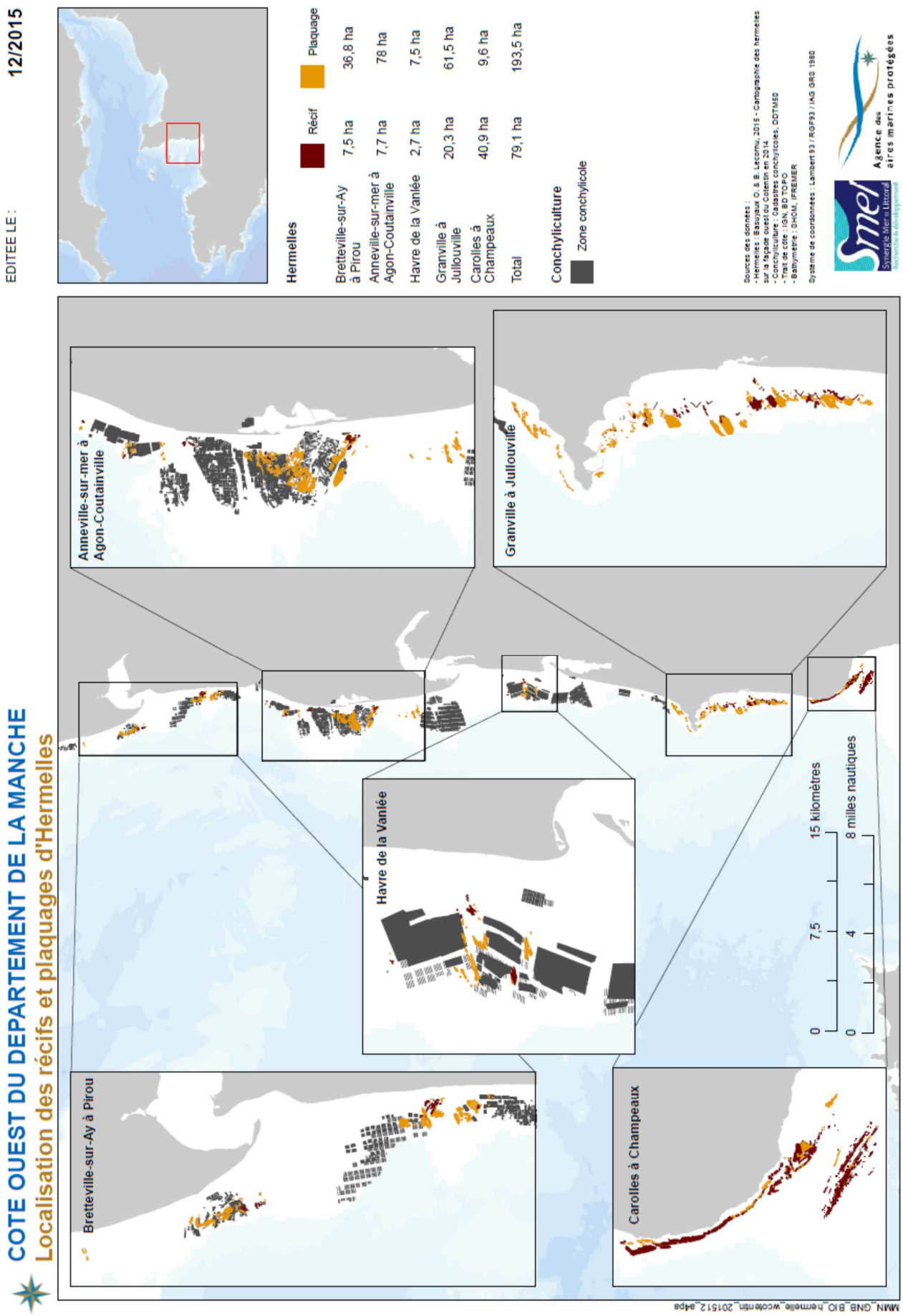
L'état de dégradation : (0) non dégradé, (1) début de dégradation, (2) dégradé, (3) très dégradé

La présence d'épibiose : (oui) incluant le taux de recouvrement, (non)

Une cartographie a été établie sur la façade ouest du Cotentin, elle est disponible au format d'une couche SIG sur le site du SMEL (www.smel.fr).

La cartographie de l'ensemble de la côte a permis de mettre en évidence les secteurs où sont présents les habitats d'hermelles. Des sites comme celui de Champeaux sont connus pour contenir des récifs. De nombreuses études et des suivis de l'état du récif sont régulièrement effectués (IFREMER, MNHN). La présence de l'espèce *Sabellaria alveolata* sur le littoral normand ne se limite pas qu'à Champeaux. Des constructions sont régulièrement observées sur le littoral allant de Carolles à Sain-Germain-sur-Ay. Elles mesurent rarement plus d'1 m de hauteur mais leurs superficies peuvent être importantes. Le récif de Champeaux est considéré comme un récif florissant car chaque année sa superficie est relativement constante et ses hauteurs restent de taille considérable. Les autres constructions, présentes au nord, sont des constructions temporaires. Depuis le début du XIXème, beaucoup d'écrits relatent la présence de ces bancs d'hermelles qui apparaissent et disparaissent certaines années (Lucas et Lefevre, 1955). La présence discontinue de ces constructions sur le littoral est probablement expliquée par le transport de larves provenant de la Baie du mont Saint-Michel. D'après Ayata *et al*. (2009), les spécificités hydrodynamiques de la baie pourraient permettre la rétention des larves à l'échelle de la baie et faciliter les échanges larvaires entre le récif de Sainte-Anne et celui de Champeaux. Un auto-recrutement des larves a lieu dans la baie entre les deux récifs (Dubois, 2003). De plus, grâce à la modélisation de la dispersion larvaire, Dubois (2003) a montré la possibilité d'une extension du panache larvaire le long de la côte de la Manche. Une autre étude a permis de montrer que les larves présentes dans la baie du Mont-Saint-Michel peuvent remonter vers le nord grâce au courant le long de la côte ouest du Cotentin (Pien, 2014). Mais ces transferts sont très dépendants de l'intensité et la direction des vents (Salomon et Breton, 1993).

Le cycle de vie des hermelles de 4 à 5 ans (Dubois, 2007) peut aussi expliquer les implantations irrégulières des hermelles sur cette côte. A la fin du cycle si aucun nouvel apport de larves n'a lieu, les constructions peuvent être amenées à se détériorer et donc à disparaître.


COTE OUEST DU DEPARTEMENT DE LA MANCHE
Localisation des récifs et plaquages d'Hermelles
EDITEE LE :
12/2015
Hermelles
Récif
Plaquage
Bretteville-sur-Ay à Pirou 7,5 ha 36,8 ha
Anneville-sur-mer à Agon-Coutainville 7,7 ha 78 ha
Havre de la Vanlée 2,7 ha 7,5 ha
Granville à Jullouville 20,3 ha 61,5 ha
Carolles à Champeaux 40,9 ha 9,6 ha
Total 79,1 ha 193,5 ha
Conchyliculture
Zone conchylicole
Sources des données :
- Hermelles : Basuyaux O. & B. Lecornu, 2015 - Cartographie des hermelles sur la façade ouest du Cotentin en 2014
- Conchyliculture : Cadastres conchylicoles, DDTM50
- Trait de côte : IGN, BD TOPO
- Bathymétrie : SHOM, IFREMER
Système de coordonnées : Lambert 93 / RGF93 / IAG GRS 1980
Smel
Synergie Mer et Littoral
Recherche & développement
Agence des aires marines protégées
Anneville-sur-mer à Agon-Coutainville
Granville à Jullouville
Havre de la Vanlée
Bretteville-sur-Ay à Pirou
Carolles à Champeaux
0
7,5
15 kilomètres
0
4
8 milles nautiques
MMN_GNB_BIO_hermelle_wcotentin_201512_a4pa

Sabellaria alveolata est présente jusqu'au sud de Saint-Germain-sur-Ay, après cette limite elle est totalement absente. Plusieurs hypothèses peuvent expliquer ce phénomène. Tout d'abord, la composition de la roche change entre le sud et le nord de Saint-Germain-sur-Ay. Au sud, plusieurs types de roches sont présents, comme le microgranite calco-alcalin mais aussi des métaquartzites, alors que plus au nord le grès est très présent (Graindor, 1976). Les hermelles ne se fixent pas sur le grès et le granit (Dauvin, communication personnelle). La présence importante de grès au nord de Saint-germain-sur-Ay pourrait expliquer l'absence des hermelles. De plus, les hermelles ont besoin de quantités importantes de sable pour créer des bioconstructions. A partir de cette zone le sédiment sableux laisse place à un grand platier rocheux qui s'étend du nord de Saint-germain-sur-Ay à Portbail, limitant ainsi l'accès au sédiment sableux.

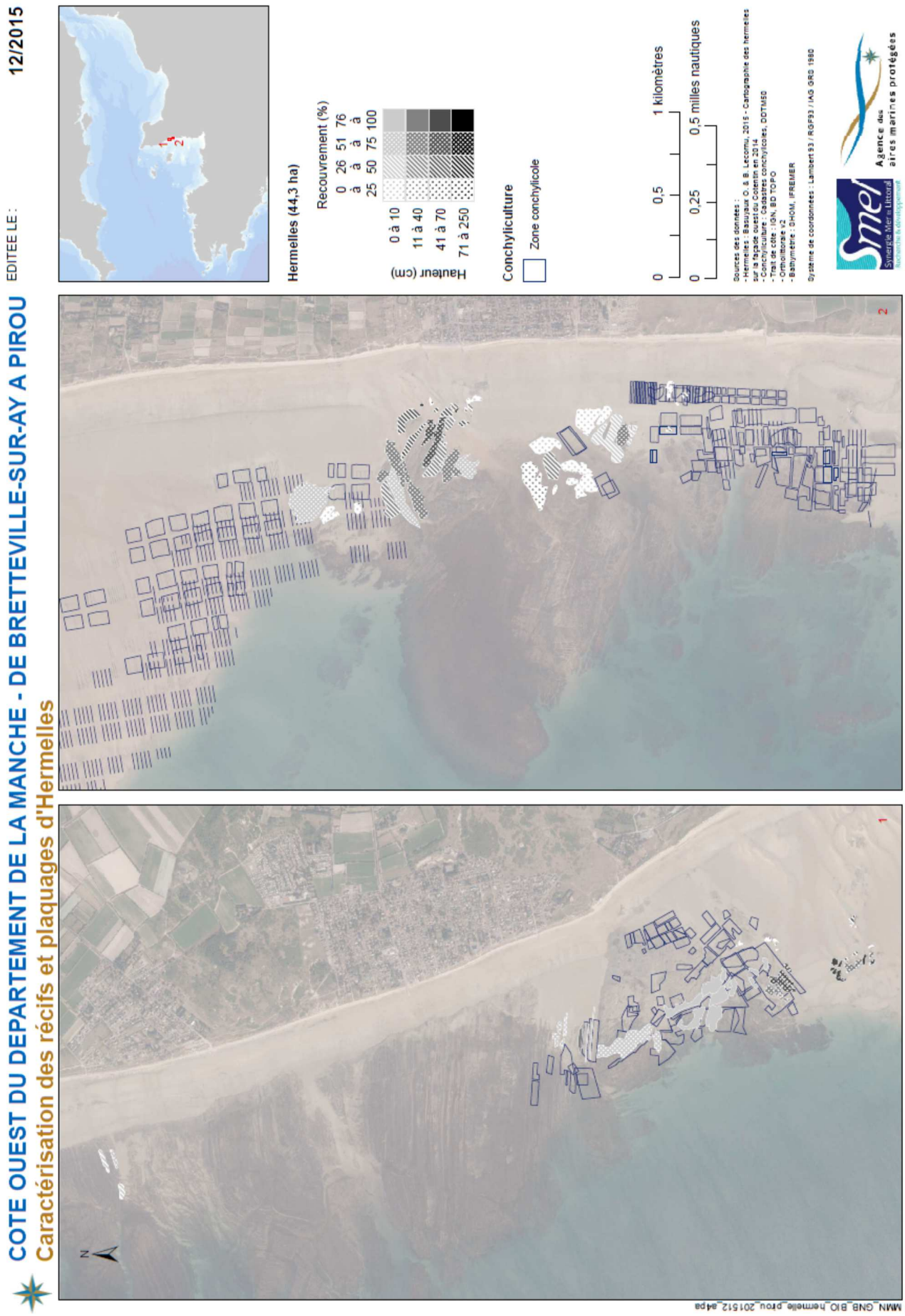
Dans l'archipel de Chausey et l'archipel des Ecréhou, les hermelles sont absentes. Ceci est peut être dû aux courants, les courants présents à Chausey n'ont pas ou peu de connectivités avec les courants présents dans la Baie du Mont-Saint-Michel (Salomon et Breton, 1993).
Les conditions favorables pour que des hermelles s'installent sur le littoral ont été décrites par Lucas et Lefevre (1955). L'eau doit être agitée et chargée en sable. *Sabellaria alveolata* a une préférence pour le sable calcaire composé d'un quart de sédiment siliceux. De plus, pour qu'elle s'installe, il faut des hivers doux et sans tempête.

D'après cette étude, une différence est observée entre les bioconstructions présentes au nord et au sud de Granville. Les tailles des structures sont moins importantes au nord, elles ne dépassent que rarement 90 cm de hauteur. De plus, la majorité des constructions est sous forme de placage. Au sud, leurs hauteurs sont plus importantes, elles peuvent atteindre 150 cm. Les récifs sont plus présents. Les indices de fragmentations indiquent que les structures sont plus fragmentées au nord. Ces différences observées entre le nord et le sud peuvent être expliquées par l'apport discontinu de larves limitant ainsi l'ampleur des constructions. La différence de nature du sédiment (Guillaumont, 1987) peut également avoir une influence sur l'ampleur des constructions.

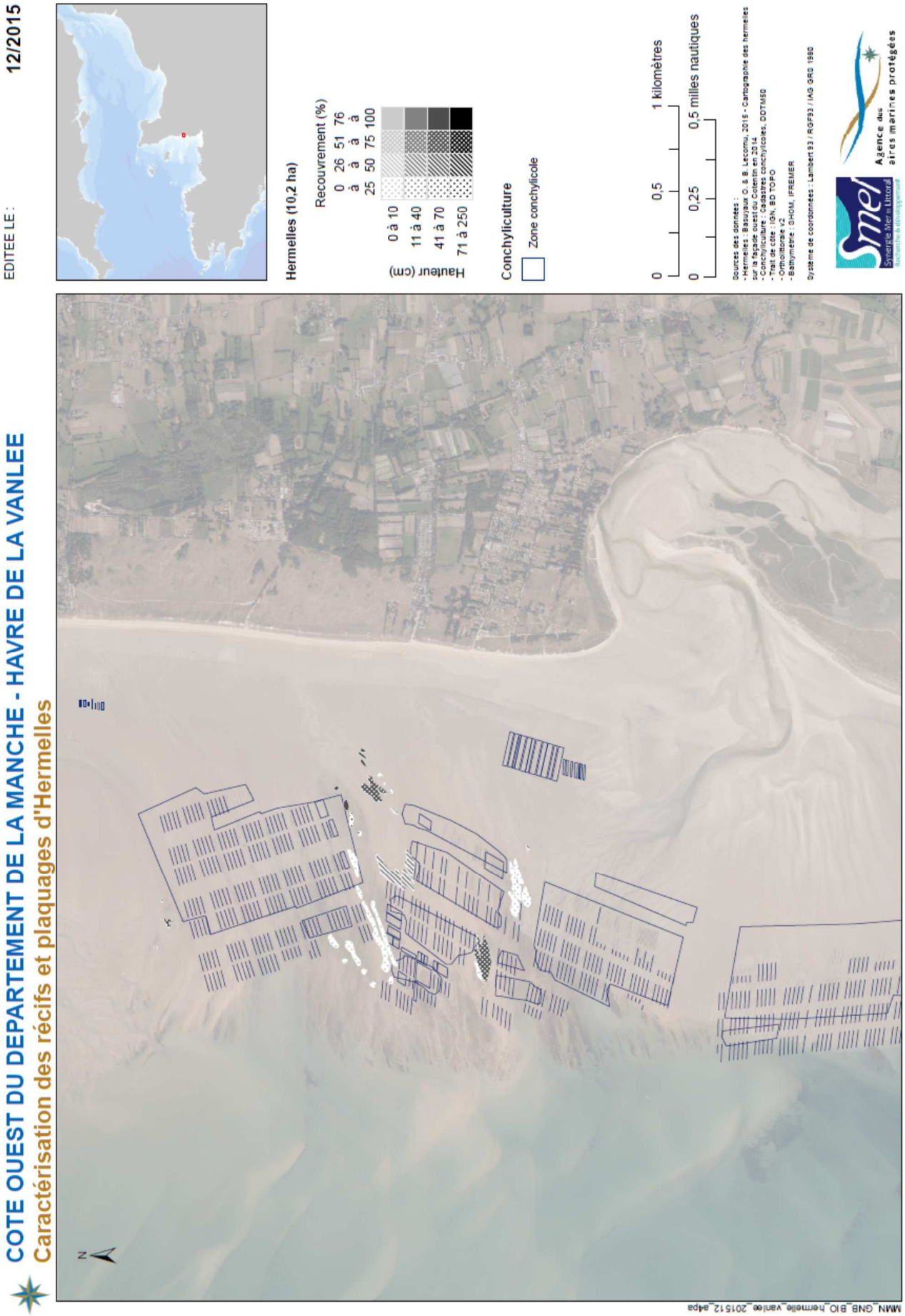
Les constructions les plus dégradées sont présentes de Saint-Germain-sur-Ay à Granville. La dégradation des habitats d'hermelles est due à plusieurs facteurs : l'hydrodynamisme, le vent et l'ensablement (Gruet, 1972). Les hivers froids, la perte de sable dû à l'aménagement du littoral et le recrutement variable des larves sont aussi des facteurs provoquant la dégradation des récifs (JNCC, 2008). Desroy (2011) indique que la présence de suspensivores cultivés tels que comme l'huître *Crassostrea gigas* et la moule *Mytilus edulis*

peuvent entraîner une augmentation de la compétition trophique avec les larves de *Sabellaria alveolata* et ainsi empêcher le recrutement larvaire. De plus, la présence de conchylicultures augmente la charge en particules dans le milieu, ce qui constitue une gêne pour l'activité de filtration des individus de *Sabellaria alveolata* (Dubois, 2003).

La pêche à pied récréative effectuée de manière intensive dans certains secteurs, augmente le piétinement et donc l'affalement des récifs.


COTE OUEST DU DEPARTEMENT DE LA MANCHE - DE BRETTEVILLE-SUR-AY A PIROU
Caractérisation des récifs et plaquages d'Hermelles
EDITEE LE :
12/2015
Hermelles (44,3 ha)
Recouvrement (%)
0 à 25
26 à 50
51 à 75
76 à 100
Hauteur (cm)
0 à 10
11 à 40
41 à 70
71 à 250
Conchyliculture
Zone conchylicole
0
0,5
1 kilomètres
0
0,25
0,5 milles nautiques
Sources des données :
- Hermelles : Basuyaux O. & B. Lecornu, 2015 - Cartographie des hermelles sur la façade ouest du Cotentin en 2014
- Conchyliculture : Cadastres conchylicoles, DDTM50
- Trait de côte : IGN, BD TOPO
- Ortho-photo : v2
- Bathymétrie : SHOM, IFREMER
Système de coordonnées : Lambert 93 / RGF93 / IAG GRS 1980
Smel
Synergie Mer et Littoral
Agence des aires marines protégées
MMN_GNB_BIO_hermelle_prou_201512_a4pa

COTE OUEST DU DEPARTEMENT DE LA MANCHE - D'ANNEVILLE-SUR-MER A AGON-COUTAINVILLE
Caractérisation des récifs et plaquages d'Hermelles
12/2015
N
1
2
Hermelles (85,7 ha)
Recouvrement (%)
0 à 25
26 à 50
51 à 75
76 à 100
Hauteur (cm)
0 à 10
11 à 40
41 à 70
71 à 250
Conchyliculture
Zone conchylicole
0
1
2 kilomètres
0
0,5
1 milles nautiques
Sources des données :
- Hermelles : Basuyaux O. & B. Lecornu, 2015 - Cartographie des hermelles sur la façade ouest du Cotentin en 2014
- Conchyliculture : Cadastres conchylicoles, DDTM50
- Trait de côte : IGN, BD TOPO
- Orthoittorale v2
- Bathymétrie : SHOM, IFREMER
Système de coordonnées : Lambert 93 / RGF93 / IAG GRS 1980
Syndicat Mixte du Littoral Normand
Agence des aires marines protégées
MMN_GNB_BIO_hermelle_anneville_201512_a4pa


COTE OUEST DU DEPARTEMENT DE LA MANCHE - HAVRE DE LA VANLEE
Caractérisation des récifs et plaquages d'Hermelles
EDITEE LE :
12/2015
Hermelles (10,2 ha)
Recouvrement (%)
0 à 25
26 à 50
51 à 75
76 à 100
Hauteur (cm)
0 à 10
11 à 40
41 à 70
71 à 250
Conchyliculture
Zone conchylicole
0
0,5
1 kilomètres
0
0,25
0,5 milles nautiques
Sources des données :
- Hermelles : Basuyaux O. & B. Lecornu, 2015 - Cartographie des hermelles sur la façade ouest du Cotentin en 2014
- Conchyliculture : Cadastres conchylicoles, DDTM50
- Trait de côte : IGN, BD TOPO
- Orthophotos v2
- Bathymétrie : SHOM, IFREMER
Système de coordonnées : Lambert 93 / RGF93 / IAG GRS 1980
Smel
Synergie Mer et Littoral
Agence des aires marines protégées
MMN_GNB_B10_hermelle_vanlee_201512_a4pa

COTE OUEST DU DEPARTEMENT DE LA MANCHE - GRANVILLE A JULLOUVILLE
Caractérisation des récifs et plaquages d'Hermelles
EDITEE LE :
12/2015
Hermelles (81,8 ha)
Recouvrement (%)
0 à 25
26 à 50
51 à 75
76 à 100
Hauteur (cm)
0 à 10
11 à 40
41 à 70
71 à 250
0
1
2 kilomètres
0
0,5
1 milles nautiques
Sources des données :
- Hermelles : Basuyaux O. & B. Lecornu, 2015 - Cartographie des hermelles sur la façade ouest du Cotentin en 2014
- Conchyliculture : Cadastres conchylicoles, DDTM50
- Trait de côte : IGN, BD TOPO
- Orthoitoralie v2
- Bathymétrie : SHOM, IFREMER
Système de coordonnées : Lambert 93 / RGF93 / IAG GRS 1980
Syndicat Mixte du Littoral Normand
Agence des aires marines protégées
MMN_GNB_BIO_hermelle_granville_201512_a4pa

COTE OUEST DU DEPARTEMENT DE LA MANCHE - CAROLLES A CHAMPEAUX
Caractérisation des récifs et plaquages d'Hermelles
EDITEE LE :
12/2015
Hermelles (50, 6 ha)
Recouvrement (%)
0 à 25
26 à 50
51 à 75
76 à 100
Hauteur (cm)
0 à 10
11 à 40
41 à 70
71 à 250
0
0,5
1 kilomètres
0
0,25
0,5 milles nautiques
Sources des données :
- Hermelles : Basuyaux O. & B. Lecornu, 2015 - Cartographie des hermelles sur la façade ouest du Cotentin en 2014
- Conchyliculture : Cadastres conchylicoles, DDTM50
- Trait de côte : IGN, BD TOPO
- Orthoiltorale v2
- Bathymétrie : SHOM, IFREMER
Système de coordonnées : Lambert 93 / RGF93 / IAG GRS 1980
Agence des aires marines protégées
MMN_GNB_BIO_hermelle_champeaux_201512_a4pa

B. Rôle fonctionnel des hermelles en secteur conchylicole, au travers d'un inventaire des espèces présentes en comparaison avec les récifs historiques de la Baie du Mont Saint-Michel

Afin de comparer la biodiversité présente dans ce récif par rapport aux zones conchylicoles, l'étude a été réalisée sur trois secteurs conchylicoles : Saint-Germain-sur-Ay, Blainville-sur-Mer et Lingreville en comparaison avec le récif de Champeaux. La méthode d'échantillonnage s'est appuyée sur la méthode utilisée dans le cadre du réseau REBENT (Réseau Benthique coordonné par l'IFREMER). Une étude a été réalisée afin de comparer la biodiversité sur les sites où les hermelles sont présentes par rapport à des sites situés à proximité mais non colonisés.

1. Densité de populations d'hermelles

Dubois *et al.* (2002) ont relevé des densités importantes sur le récif de Champeaux, atteignant 60 000 ind.m-², ce qui rejoint les résultats de cette étude. Contrairement aux trois autres sites de l'étude, le site de Champeaux présente des densités nettement plus élevées. Les densités observées à Lingreville sont très faibles et suggèrent que le site de Lingreville a subi une forte dégradation depuis les observations faites en 2011. Gruet et Bodeur (1997) expliquent, en effet, que les « ennemis naturels » des populations d'hermelles sont l'hydrodynamisme et le froid. Or, entre 2010 et 2013, les hivers ont été particulièrement rudes. De plus, de nombreuses tempêtes ont affecté les côtes entre janvier et février 2014, modifiant ainsi l'hydrodynamisme de la zone. Ces conditions n'étant pas favorables aux hermelles, leurs populations ont pu en être affectées.

L'étude de densité de population a également permis de mettre en évidence des différences significatives entre les deux surfaces, placage et récif. Les sites de Saint-Germain-sur-Ay et Champeaux présentent des densités significativement plus grandes sur le placage que sur le récif. Ceci pourrait être expliqué par l'état de développement de la bioconstruction sur laquelle ont été effectués les prélèvements. En effet, le placage est une bioconstruction en pleine croissance, tandis que le récif peut être considéré comme le stade ultime d'évolution de la bioconstruction et être initiateur d'une phase de déclin de la population sur cette structure.

Ainsi, **hormis les bioconstructions de Champeaux, les structures récifales de la côte ouest du Cotentin pourraient être des structures temporaires.**

2. Structure de population

Dubois *et al.* (2006) ont montré que les juvéniles passent à leur taille adulte lorsque leur couronne operculaire mesure entre 1,35 et 1,50 mm. Dans cette étude, l'analyse des structures de populations indique une plus grande abondance d'adultes sur le site de Saint-Germain-sur-Ay. En revanche, plus de juvéniles ont été identifiés sur les sites de Blainville-sur-Mer et Champeaux. Cette plus grande abondance de juvéniles, à l'échelle de la zone d'étude suggère qu'il y a eu un recrutement de juvéniles en 2013 sur les sites de l'étude, avec des conditions peut-être moins propices dans le nord de la zone, vers le site de Saint-Germain-sur-Ay. De plus, pas ou peu d'individus dont la couronne operculaire mesure moins de 0,75 mm ont été recensés dans cette étude en raison de l'échantillonnage hivernal avant les pics de reproduction qui ont lieu en mars-avril et juin-juillet dans la baie du Mont Saint-Michel (Dubois et al., 2004). La complexité de la surface tend à multiplier les habitats favorables aux juvéniles, mais joue également un rôle parfois déterminant dans la structure des populations en offrant des refuges ou des supports préférentiels pour différentes classes de taille et d'âge d'individus (Dubois, 2003). Le suivi de structure de population d'hermelles réalisé sur les bancs de Blainville-sur-Mer indique une croissance des individus de 0,3 mm en deux mois.

3. Biodiversité associée aux bioconstructions des hermelles

L'étude de la macrofaune associée aux bioconstructions à *S. alveolata* a révélé une richesse taxonomique de 75 taxa sur l'ensemble de la zone d'étude. De plus, cette richesse taxonomique diffère entre les sites et les structures, elle est plus grande sur le placage que sur le récif (sauf à Saint-Germain-sur-Ay), avec une répartition des taxa selon un gradient Nord/Sud. Dans leur étude, Dubois *et al.* (2006) avaient identifiés 65 taxa sur le site de Champeaux, or ici, seuls 38 taxa ont été identifiés sur ce même site. Ceci peut s'expliquer en partie par un effort d'échantillonnage probablement plus important dans le cas des travaux de Dubois *et al.* (2006), comme le confirment les courbes de raréfaction. Les conditions hivernales des années passées sont également à considérer. En effet, les conditions météorologiques ont une influence sur les hermelles mais pourraient également en avoir sur le recrutement d'autres

espèces. De plus, Desroy *et al.* (2011) ont avancé que la richesse spécifique au niveau des récifs dégradés étaient beaucoup plus importante que sur les autres niveaux d'évolution des structures récifales. Ceci suggère donc que certaines stations échantillonnées dans cette étude seraient plus dégradées que d'autres. Ainsi, le récif de Saint-Germain-sur-Ay, présentant un indice de diversité Fisher α élevé serait la station la plus favorable au développement de la biodiversité, et le récif de Champeaux le moins propice. Cette variabilité en termes de biodiversité peut également s'expliquer par la fragmentation des bioconstructions. En effet, Godet *et al*. (2011) ont montré que la biodiversité est accrue lorsque les récifs ne sont pas fragmentés (tels que sur le récif de Sainte-Anne). Or, sur les quatre sites de l'étude, les bioconstructions sont morcelées de façon relativement importante (en comparaison avec les bancs de Sainte-Anne dans la Baie du Mont Saint-Michel). D'autre part, comme l'ont mis en évidence Dubois *et al*. (2006), les bioconstructions à *S. alveolata* présentent une grande biodiversité du fait que les assemblages de taxa soient composés par des mélanges de taxa typiquement retrouvés sur différents substrats durs et meubles. Ainsi sont trouvés des taxa typiques : de substrat dur (*Perinereis cultrifera*), de cuvettes en milieu rocheux (*Littorina littorea*), de sédiment sableux (*Goniadella bobrezkii*), de sédiment vaseux (*Eteone longa*), de zone subtidale (*Sthenelais boa*), de sédiment hétérogène infralittoral (*Amphipholis squamata*), de roches et blocs circalittoraux (*Spirobranchus triqueter*) ou encore d'habitat terrestre (*Axelsonia littoralis*). La présence de ces différents taxa s'explique par la présence d'une multitude de micro-habitats formés par les anfractuosités des structures récifales. Enfin, la richesse taxonomique et la biodiversité ne sont pas corrélées aux abondances d'hermelles.

4. Origine sédimentaire des grains des tubes

Cette étude a permis de confirmer la grande hétérogénéité sédimentaire de la côte ouest du Cotentin, avec des particules sédimentaires dont la taille varie majoritairement de 0,125 mm à 1,6 mm selon les sites. De plus, les analyses granulométriques indiquent l'existence d'une différence de disponibilité entre les sédiments à proximité du placage et à proximité du récif avec des particules plus grossières proches du récif. Cependant, de par leur morpho-anatomie, mais également en fonction de leur âge et donc de leur taille, les hermelles doivent sélectionner les grains qu'elles utilisent pour fabriquer leurs tubes (Gruet et Bodeur, 1997). En effet, Dubois *et al.* (2004) indiquent que les hermelles fabriquent leurs tubes avec des particules dont la taille

varie entre 200 et 500 µm. Cette observation se confirme également pour les hermelles de la côte ouest du Cotentin.

5. Comparaison de la biodiversité présente sur les récifs de *Sabellaria alveolata* et sur les secteurs bathymétriques similaires où l'espèce est absente

Cette partie consiste à comparer la biodiversité présente sur un récif d'hermelles et celle présente à proximité afin de voir si ces récifs sont un îlot de biodiversité. Cette étude montre tout d'abord qu'il y a bien une différence dans la composition spécifique d'un récif et celle hors récif. D'après les échantillonnages, dans la majorité des récifs, ce sont les annélides qui dominent alors qu'en dehors de ces récifs ce sont les mollusques. Une différence est aussi observée au niveau de la diversité végétale. Les algues les plus présentes sur les récifs sont les ulves alors que sur substrat dur, ce sont les fucales qui dominent.
Les indices de biodiversité calculés pour la faune indiquent que l'espèce *Sabellaria alveolata* domine les autres espèces sur les récifs. Alors que hors récif, les espèces sont co-dominantes. De plus, les résultats indiquent que la richesse spécifique est plus importante hors récif.

Les échantillonnages effectués en juillet (à Blainville-sur-mer et Lingreville) présentent des différences par rapport à ceux effectués plus tôt dans l'année. Ils indiquent que, quel que soit le substrat, il n'y a pas de dominance d'une espèce. De plus, la biodiversité est aussi élevée sur récif que sur substrat dur. L'analyse de la composition spécifique de ces deux sites indique que l'espèce *Sabellaria alveolata* est absente sur le récif. D'après les photos prises des quadrats, les récifs de Lingreville et de Blainville-sur-mer sont très dégradés. Sur ces récifs, les ulves sont très présentes. Les ulves pourraient attirer les organismes brouteurs et donc augmenter la biodiversité sur les récifs mais, d'après Dubois (2003), elles n'ont pas d'impact sur la composition spécifique de la faune associée et leur présence est éphémère. C'est surtout la dégradation des récifs qui favoriserait l'installation de nouvelles espèces. Comme dit précédemment, la biodiversité est plus importante sur un récif dégradé que sur un récif en bon état (Desroy, 2011).

Cette étude indique que la richesse spécifique la plus faible est observée sur le récif de Champeaux et que la biodiversité serait plus importante sur le substrat meuble. Ce résultat est étonnant car d'après les précédentes études le récif est un réservoir de biodiversité contrairement au substrat meuble alentour qui est très pauvre (Dubois, 2003). Toutefois, ces résultats sont à prendre avec discernement car la nature du substrat a conduit à utiliser deux

méthodes différentes (quadrats et carottage). Sur substrat dur, la méthode reconnue pour étudier la biodiversité est la méthode Rebent qui utilise des quadrats alors que c'est la méthode par carottage qui est préconisée sur substrat meuble. Cette méthode pose problème sur récifs car ils sont constitués de nombreuses cavités qui abritent une épifaune et une endofaune (Dubois, 2003). Les quadrats ne sont pas suffisant pour échantillonner cette faune. La comparaison est donc à prendre avec précaution.

C. Identification d'un indicateur de suivi des populations d'hermelles permettant d'évaluer l'évolution des récifs de façon annuelle à moindre coût.

Comme il a été dit précédemment, la conchyliculture est très présente dans les secteurs situés au nord de Granville. Elle pourrait expliquer la dégradation plus importante des habitats d'hermelles présents au nord de Granville. Mais d'après les résultats obtenus de la comparaison faite entre l'état des structures présentes en zone ostréicole et celles présentes hors de cette zone à Blainville-sur-mer, **l'ostréiculture ne serait pas le principal facteur provoquant la dégradation**. En effet, à Blainville-sur-mer, la majorité des bioconstructions sont dégradées, qu'elles soient situées sous les tables à huîtres ou à l'écart de ces zones. En revanche, **les tables pourraient avoir un léger impact sur la croissance horizontale et verticale des constructions**. Les constructions dans les zones ostréicoles ont des surfaces et des hauteurs moins importantes que hors de ces zones.

La pêche à pied récréative est très présente sur la côte normande. Lors de gros coefficients de marée, les pêcheurs sont en masse sur la côte et certains, ne connaissant pas les propriétés des hermelles, auraient tendance à les piétiner.

Depuis quelques années, le littoral normand a connu des hivers rudes. Les tempêtes et la présence de neige en forte quantité n'ont pas favorisé la croissance des hermelles.

Cette étude a permis de montrer que **la régression des constructions, observée dans certains secteurs, n'est pas causée par un seul facteur mais surement par une accumulation de facteurs comme l'apport irrégulier de larves, la pêche à pied, le nombre croissant de tempêtes**…

Afin de refaire régulièrement une observation de l'évolution des bioconstructions d'hermelles sur la côte, il est nécessaire d'alléger la méthode. En allégeant cette méthode, le suivi pourra être effectué en une courte durée (3 à 4 sorties). Tous les secteurs ne nécessitent pas d'être suivis régulièrement. Certains semblent avoir plus d'intérêt que d'autres. Par exemple, le secteur de Champeaux ne nécessite pas d'être contrôlé car régulièrement des études sont faites par d'autres organismes (IFREMER, MNHN…). En revanche, **le secteur de Granville peut être intéressant car c'est un milieu très anthropisé** du fait de la proximité avec le port de plaisance et le milieu urbain. Il serait intéressant de voir comment évolue l'espèce *Sabellaria alveolata* dans un tel milieu. **Le secteur de Lingreville pourrait aussi être suivi** car il a longtemps été constitué de beaux récifs qui sont aujourd'hui très dégradés. Il serait intéressant de voir comment évoluent ces récifs dans les prochaines années, s'ils tendent à disparaître ou au contraire à se développer de nouveau. Ensuite, **le secteur de Blainville-sur-mer est intéressant car l'ostréiculture est très présente**. Il serait judicieux de surveiller l'évolution des hermelles dans un secteur ostréicole pour observer le niveau de compétition trophique entre les deux espèces.

Sur chaque secteur, il sera nécessaire d'observer la hauteur et le taux de recouvrement des constructions, ainsi que l'état des constructions à différents niveaux bathymétriques. Pour cela, grâce aux cartes de référence, trois **zones d'étude de 20 m²** situées à des niveaux bathymétriques différents sur chaque secteur où les hermelles sont présentes seront sélectionnés. Sur chacune de ces zones le **taux de recouvrement des constructions, l'état de fragmentation et de dégradation, la hauteur maximale des constructions et présence d'épibioses** (huîtres, moules, algues…) seront estimés selon les méthodes décrites précédemment. De plus une photo de chaque zone peut être nécessaire afin de constituer une série historique.

D. Evaluation de l'incidence économique du développement des hermelles dans le cadre d'une approche écosystémique du fait des modifications que peuvent engendrer les récifs d'hermelles sur les pratiques culturales conchylicoles.

Comme il l'a été démontré précédemment, les hermelles se développent en récif ou en placage. Le secteur peut être aisément distingué 2 zones : le sud de Granville qui présente des

récifs et placage bien établis et qui reçoit régulièrement des apports de larves issues des grands récifs de la baie du Mont Saint Michel. Et d'autre part, le nord de Granville où peuvent être observées régulièrement des constructions parfois récifales mais non pérennes. La dégradation de ces constructions est très souvent l'œuvre des conditions météorologiques conduisant à des destructions directes (houles, tempêtes, froid…) ou indirectes en limitant les apports de larves en fonction de l'orientation des vents. D'autres facteurs peuvent localement avoir une incidence sur le développement des hermelles, tels que la pêche à pied ou les cultures marines. Ceci conduit à traiter ces deux secteurs de façon différente.

Il n'y a pas de cultures marines au sud de Granville ; ainsi l'incidence économique au regard de la conchyliculture est neutre. Il peut être noté toutefois la présence d'huîtres sauvages dans ce secteur, entrainant la fréquentation de pêcheurs plaisanciers, certains pouvant entraîner des dégradations au niveau des constructions d'hermelles.

Au nord de Granville, les cultures marines sont représentées par la mytiliculture d'une part, et l'ostréiculture d'autre part.

La mytiliculture s'est développée dans les secteurs sableux où la cartographie établie montre l'absence de développement d'hermelles. Il n'y a donc que peu de compétition spatiale entre les deux espèces. Toutefois, **une compétition trophique (diatomées) est possible** mais extrêmement difficile à chiffrer.

En revanche, **l'ostréiculture** occupe souvent des secteurs où les hermelles peuvent s'établir et **entre donc en compétition spatiale et trophique directe. Une interaction positive entre les deux espèces peut être observée**; les tables à huîtres offrent une protection physique contre la houle permettant ainsi aux hermelles de s'établir et, réciproquement, les récifs permettent d'amortir les vagues. Ainsi, au regard de cette étude et de l'évolution spatiale et temporelle des hermelles, le déplacement de parcs ostréicoles au regard de cette problématique ne se justifie pas au nord de Granville. Toutefois, le regard des ostréiculteurs à l'égard du développement des hermelles peut être très contrasté d'un professionnel à un autre en fonction des connaissances sur cette espèce. Le développement très rapide des hermelles sur des concessions ostréicoles a pu entraîner des inquiétudes de la part de quelques professionnels. La communication de cette étude pourrait leur permettre une meilleure appréhension du sujet.

Huîtres	Facteurs	Hermelles
Compétition	Trophique	Compétition
Compétition	Spatiale	Compétition
Nul	Déplacement tracteur	Négatif
Positif	Protection / Abris	Positif
Nul	Pêche à pied	Plutôt positif (pêche à pied des huîtres interdites dans les concessions)

Tableau 1 : Niveau d'interactions entre les huîtres et les hermelles selon quelques facteurs

Des interactions entre l'ostréiculture et le développement des hermelles existent mais les coûts engendrés par ce développement restent marginaux.

Conclusion

Cette étude a permis de réaliser une nouvelle cartographie des constructions d'hermelles sur la façade ouest du Cotentin. Elle est comparée à celle réalisée en 2010. Cette mise en perspective permet de conclure à une zonation, entre le sud de Granville où les constructions sont relativement stables, et le nord de Granville où elles sont soumises à des apports de larves discontinus entraînant parfois la disparition des constructions dans certains secteurs (Lingreville, Blainville sur mer).

Elle met en évidence que le développement rapide des hermelles dans les secteurs rocheux entraîne une perte locale de biodiversité. Cette diversité s'accroît ensuite avec la fragmentation du récif et sa dégradation.

Cette étude montre que l'ostréiculture ne serait pas la principale cause de dégradation des hermelles au nord de Granville. Le facteur d'évolution principal de ces constructions est plutôt d'ordre météorologique (vent, froid…) pouvant également générer une absence de larves au niveau de ces secteurs.

Le suivi de ces constructions pourrait être allégé en réalisant régulièrement une estimation de l'état des constructions sur 3 sites (Granville, Lingreville, Blainville sur mer) et sur 3 niveaux bathymétriques, permettant d'obtenir quelques éléments clefs.

Des interactions entre l'ostréiculture et le développement des hermelles existent mais la nature de ces interactions peut être positive dans certains cas (protection/abris), négative dans d'autres (occupation spatiale, ou compétition trophique) ce qui rend des coûts engendrés assez marginaux.

Bibliographie

AYATA, S. D., ELLIEN, C., DUMAS, F. *et al.* (2009). Modelling larval dispersal and settlement of the reef-building polychaete *Sabellaria alveolata:* role of hydroclimatic processes on the sustainability of biogenic reefs. Continental Shelf Research 29: 1605-1623

AYRAL, A., (2000). Le Banc des hermelles : Etat de santé et mesures de gestion. Rapport du Muséum National d'Histoire Naturelle, Station Marine de Dinard, 57p.

BASUYAUX, O., (2011). Etude et cartographie de *Sabellaria alveolata* sur la côte ouest du département de la Manche – Focus sur les abords de Granville. Rapport SMEL/CE-env/2011-01, 38p.

DESROY, N., DUBOIS, S. F., FOURNIER J., (2011). The conservation status of *Sabellaria alveolata* (L.) (Polychaeta : *Sabellaridae*) reefs in the Bay of Mont-Saint-Michel. Aquatic Conservation : Marine and Freshwater Ecosystems, 21 (5) : 462-471

DUBOIS S., RETIÈRE C.,OLIVIER F., 2002, Biodiversity associated with *Sabellaria alveolata* (Polychaeta : *Sabellaridae*) reefs : effects of human disturbances, Journal of the Marine Biological Association of the United Kingdom, 82 : 817 – 826.

DUBOIS, S., (2003). Ecologie des formations récifales à *Sabellaria alveolata* (L.) : valeur fonctionnelle et patrimoniale. Thèse de Doctorat du Muséum National d'Histoire Naturelle de Paris, Paris, 203 p.

DUBOIS S., BARILLE L., BARILLE A.L., GRUET Y., 2004, Conditions de préservation des formations récifales à *Sabellaria alveolata* (L.) en baie de Bourgneuf, Rapport pour la Direction Régionale de l'Environnement des Pays de la Loire, 48 p.

DUBOIS S., BARILLÉ L., COGNIE B., BENINGER P.G., 2005, Particle capture and processing mechanisms in *Sabellaria alveolata* (Polycheata : *Sabellariidae*), Marine Ecology Progress Series, 301: 159 – 171.

DUBOIS, S., COMMITO, J. A., OLIVIER, F. *et al.* (2006). Effects of epibionts on *Sabellaria alveolata* (L.) biogenic reefs and their associated fauna in the Bay of Mont-Saint-Michel. Estuarine, Coastal and Shelf Science, 68: 635 – 646

DUBOIS, S., COMTET, T., RETIERE, C. et al. (2007). Distribution and retention of *Sabellaria alveolata* larvae (Polychaeta: *Sabellariidae*) in the Bay of Mont-Saint-Michel, France. Marine ecology progress series, 346: 243-254

GODET L., FOURNIER J., JAFFRE M, DESROY N., 2011, Influence of stability and fragmentation of a worm-reef on benthic macrofauna, Estuarine, Coastal and Shelf Science, 92 : 472-479.

GRAINDOR, M. J., (1976). Carte des sédiments superficiels de la Manche, échelle 1:500 000. Ministère de l'insdustrie et de la recherche, service géologique national, Paris.

GRUET, Y., (1972). Aspects morphologiques et dynamiques de constructions de l'annélide polychète *Sabellaria alveolata* (Linné). Revue des travaux de l'Institut des Pêches Maritimes, 36 (2) : 131 -161

GRUET, Y., (1982). Recherches sur l'écologie des « récifs » d'hermelles édifiés par l'annélide polychète *Sabellaria alveolata* (Linné). Thèse de l'université des Sciences et Techniques de Nantes, Nantes, 238p.

GRUET Y., BODEUR Y., 1997, Les récifs d'hermelles, in Les biocénoses marines et littorales françaises des côtes atlantique, Manche et Mer du Nord, Synthèse, menaces et perspectives, DAUVIN J.-C. (Ed), Muséum National d'Histoire Naturelle, Paris, p. 168-175.

GUILLAUMONT, B., HAMON, D., LAFOND, L. R. *et al.*, (1987). Etude régionale intégrée du golfe normano-breton : Carte biomorphosédimentaire de la zone intertidale au 1/25 000 Côte Ouest du Cotentin et Baie du Mont Saint-Michel. St-Brieuc : Les Presses Bretonnes, 50p.

HEMISPHERE SUB, (2011), Espèces remarquables et d'intérêt particulier dans le golfe normand-breton, Rapport pour l'Agence des Aires Marines Protégées, 342 p.

HOLT, T. J., REES, E. I., HAWKINS, S. J. *et al.*, (1998). Biogenic reefs: An overview of dynamic and sensitivity characteristics for conservation management of marine SACs. Rapport de l'université de Liveerpool. Port Erin Marine Laboratory, 169 p.

HOMMERIL P., (1962), Etude locale (Gouville-sur-Mer, Manche) de la retenue des sédiments par deux polychètes sédentaires : *Sabellaria alveoata* (hermelle) et Lanice conchilega, Cahiers. Océanographiques4 : 245-257.

JNCC, (2008). *Sabellaria alveolata* Reefs. UK Biodiversity Action Plan Priority Habitat Descriptions. JNCC, [en ligne] http://www.jncc.gov.uk/page-5155

LECORNU B., (2014). Suivi de l'évolution des habitats de l'espèce *Sabellaria alveolata* (Linnée) sur la côte ouest de la Manche et étude de la biodiversité associée aux récifs. Mémoire de MII Aquacaen 2013-2014, Université de Caen. 91 pp.

JONES, C. G., LAWTON, J. H., SHACHAK, M., (1997). Positive and negative effects of organisms as physical ecosystem engineers. Ecological Society of America, 78 (7): 1946-1957

LE CAM, J. B., FOURNIER, J., ETIENNE, S. *et al.* (2011). The strength of biogenic sand reefs: Visco-elastic behaviour of cement secreted by the tube building polychaete *Sabellaria alveolata*, Linnaeus, 1767. Estuarine, Coastal and Shelf Science, 91 : 333-339

LUCAS, G., LEFEVRE, P., (1955). Contribution à l'étude de quelques sédiments marins et de récifs d'hermelles du Mont Saint-Michel. Archimer, [en ligne] http://archimer.ifremer.fr/

PIEN, S., MAHAEUX F., LE GENDRE R., DEDIEU K., SIMONS B., GAUQUELIN T., BASUYAUX O., FLEURY E. (2014). Colonisation des roches intertidales par les naissains de *Crassostrea Gigas* sur la côte ouest de la presqu'île du Cotentin. Pegaseas 2nd cross channel forum 2-3 Juillet 2014, CAEN.

SALOMON, J. C., BRETON, M., (1993). An atlas of long-term currents in the Channel. Oceanologica Acta, 16, (5-6): 439-448

SCHLUND, E., (2014). Structure de population d'hermelles *Sabellaria alveolata* et biodiversité associée à la bioconstruction des récifs sur substrat dur sur la côte Ouest du Cotentin. Mémoire de MII écologie 2013-2014, Université de Lille 1 Science et technologie, Lille. 37 pp.

Annexes

ARTICLE IN PRESS

Regional Studies in Marine Science ▮ (▮▮▮▮) ▮▮▮–▮▮▮

Contents lists available at ScienceDirect

Regional Studies in Marine Science

journal homepage: www.elsevier.com/locate/rsma

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

Billie Lecornu [a], Erika Schlund [b,c], Olivier Basuyaux [a], Olivier Cantat [d], Jean-Claude Dauvin [b,c,*]

[a] SMEL, Centre expérimental, ZAC Blainville-sur-Mer, F-50560 Blainville-sur-mer, France

[b] Normandie Univ., UNICAEN, UNIROUEN, CNRS, Laboratoire Morphodynamique Continentale et Côtière, UMR M2C, 24 rue des Tilleuls, F-14000 Caen, France

[c] CREC, Station Marine, Université de Caen Normandie, 54 rue du Docteur Charcot, BP 49, F-14530 Luc-sur-Mer, France

[d] Normandie Univ., UNICAEN, LETG-Caen Géophen, UMR 6554 CNRS, Esplanade de la Paix, F-14000, France

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.

ARTICLE INFO

Article history:
Received 6 June 2016
Received in revised form
19 July 2016
Accepted 19 July 2016
Available online xxxx

Keywords:
Sabellaria alveolata reefs
English Channel
Population size structure
Map of reefs
Meteorological environmental conditions

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.

© 2016 Elsevier B.V. All rights reserved.

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

* Corresponding author at: Normandie Univ., UNICAEN, UNIROUEN, CNRS, Laboratoire Morphodynamique Continentale et Côtière, UMR M2C, 24 rue des Tilleuls, F-14000 Caen, France.

E-mail address: jean-claude.dauvin@unicaen.fr (J.-C. Dauvin).

http://dx.doi.org/10.1016/j.rsma.2016.07.004
2352-4855/© 2016 Elsevier B.V. All rights reserved.

Please cite this article in press as: Lecornu, B., et al., Dynamics (from 2010–2011 to 2014) of *Sabellaria alveolata* reefs on the western coast of Cotentin (English Channel, France). Regional Studies in Marine Science (2016), http://dx.doi.org/10.1016/j.rsma.2016.07.004

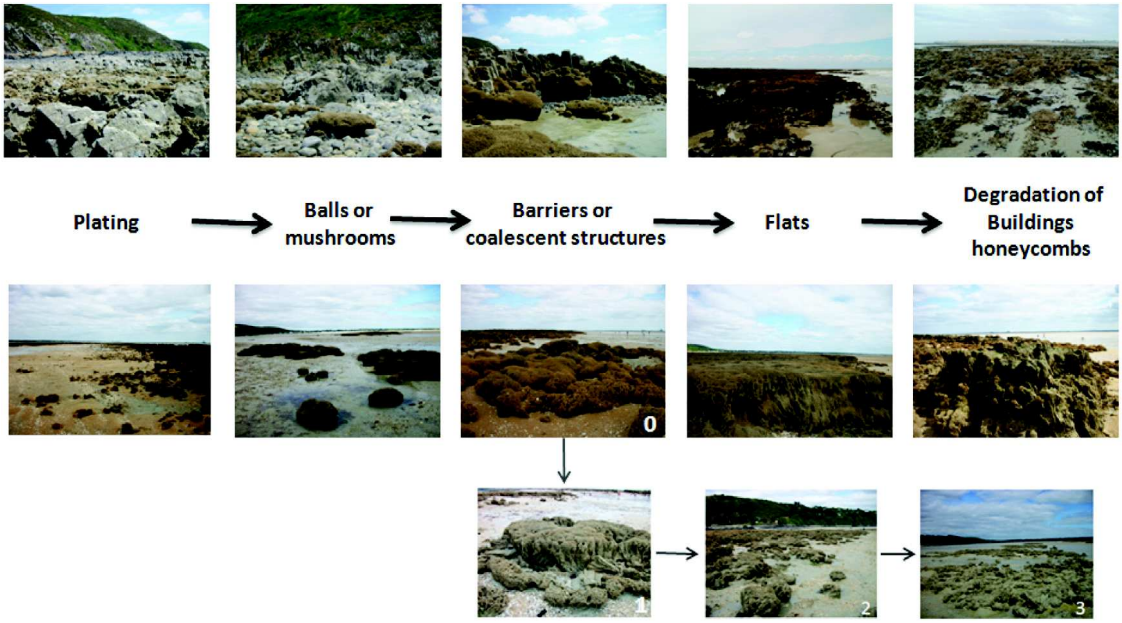


Fig. 1. Different stages of reef dynamics on hard and soft substrates, with degree of degradation (After Gruet, 1971, 1982; Gruet and Bodeur, 1997). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

engineer species responsible for the formation of significant bio-constructions 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,

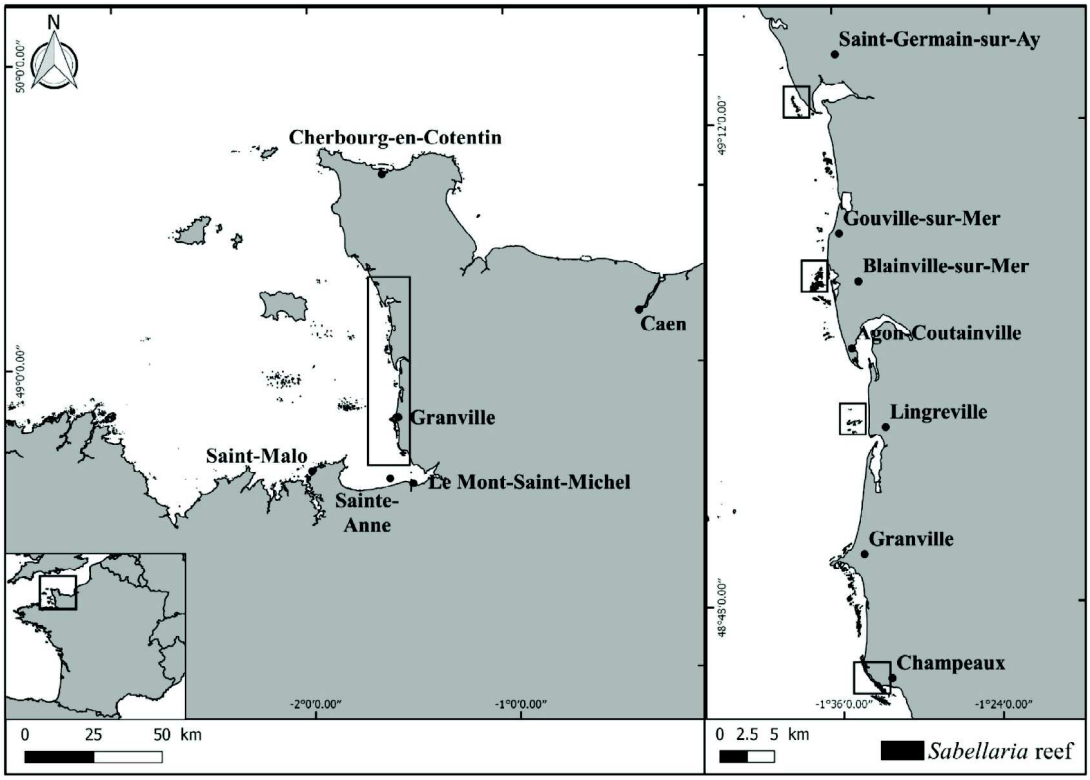


Fig. 2. A. General geographical context of the study sites. B. Location of study sites. C. 'Côte des Havres' on the west Cotentin coast, with presence of platforms and reefs in 2014.

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

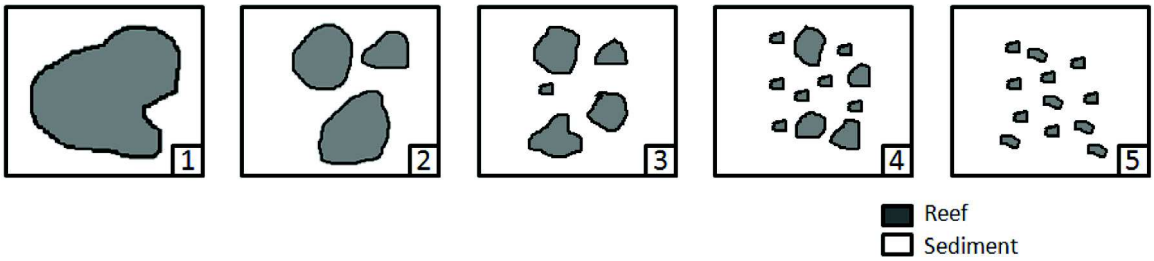


Fig. 3. Degree of fragmentation.
Source: From Dubois et al. (2006).

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

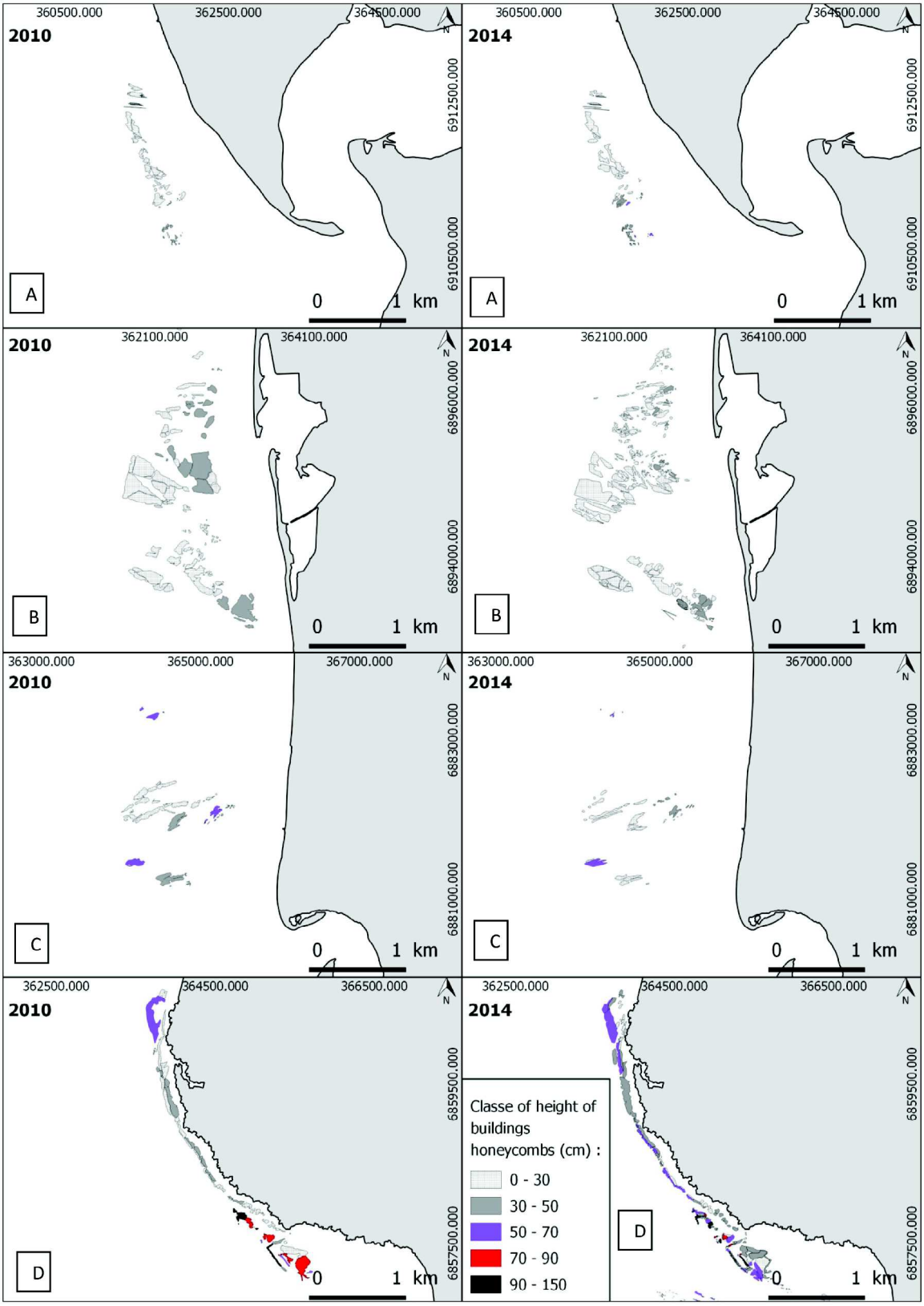


Fig. 4. Presence of honeycomb worm reefs on four sites between 2010–2011 and 2014. From upper part to lower part of diagram (A) SGSA, (B) BLSM, (C) LING and (D) CHAM.

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; $p = 0.005$)

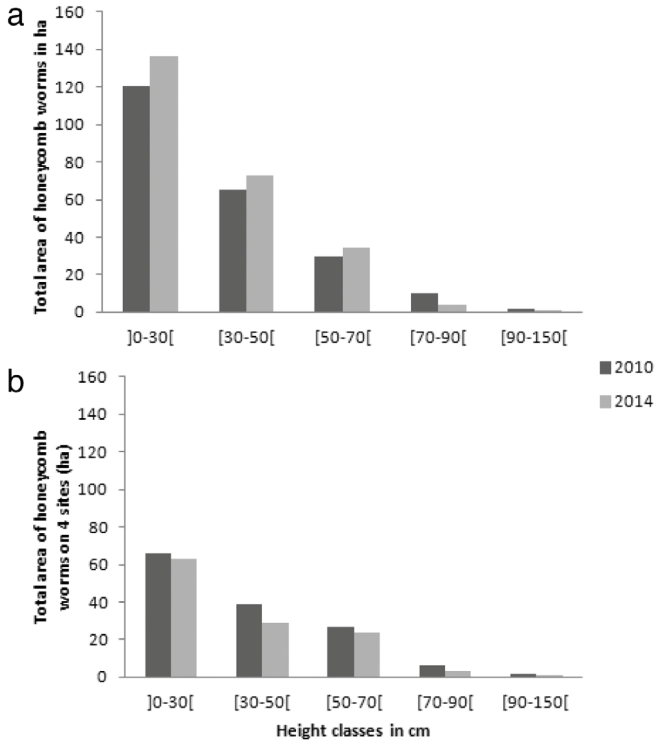


Fig. 5. a. Total area covered by honeycomb worm bio-constructions (ha) over the whole study zone per height class (cm) in 2010–2011 and 2014. b. Total area of honeycomb worm bio-constructions (ha) on the four sites per height class (cm) in 2010–2011 and 2014.

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

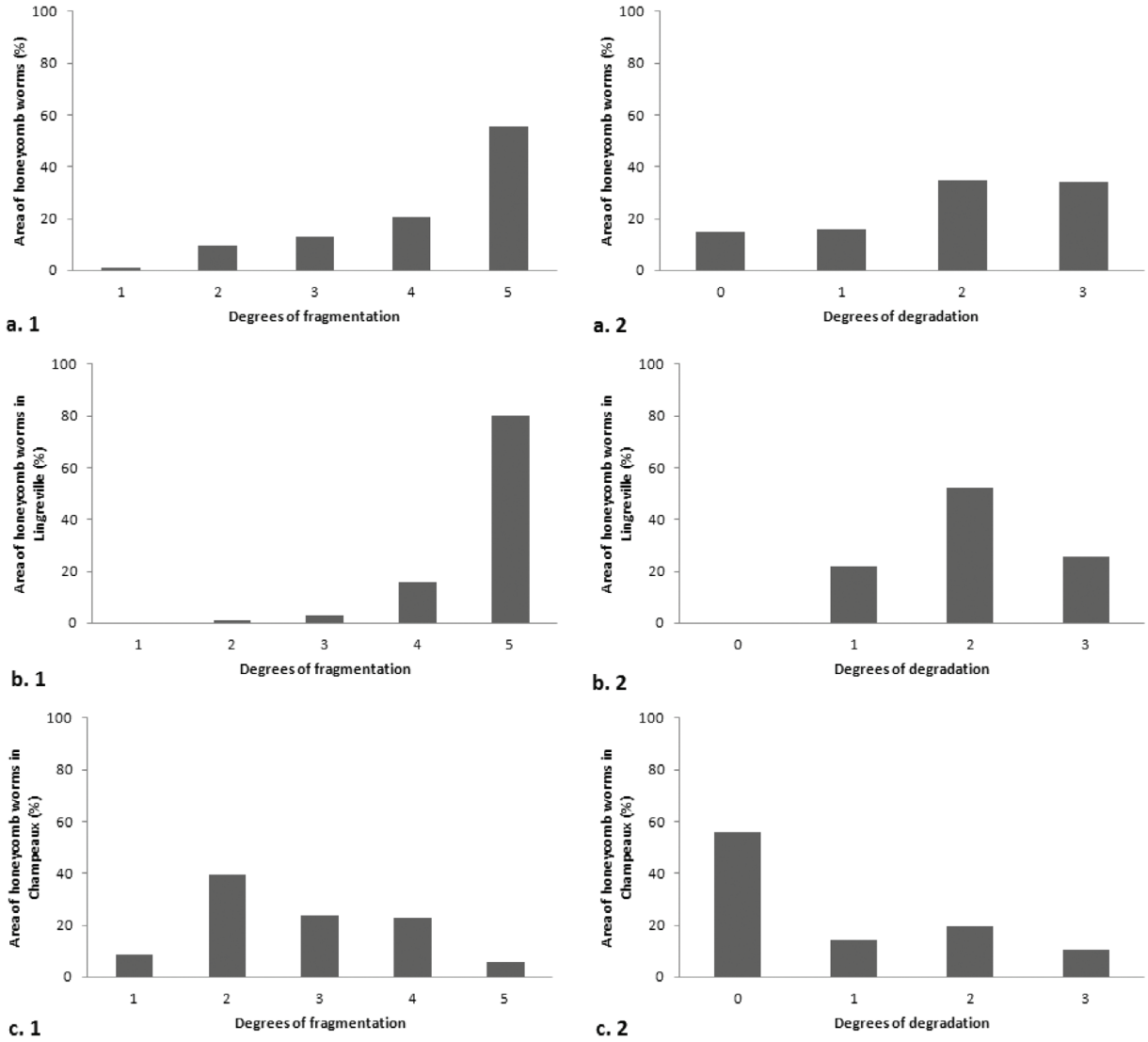


Fig. 6. a. States of fragmentation and degradation of honeycomb worm bio-constructions over the whole study zone b. States of fragmentation and degradation of honeycomb worm bio-constructions at LING. c. States of fragmentation and degradation of honeycomb worm bio-constructions at CHAM. (1: Fragmentation,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

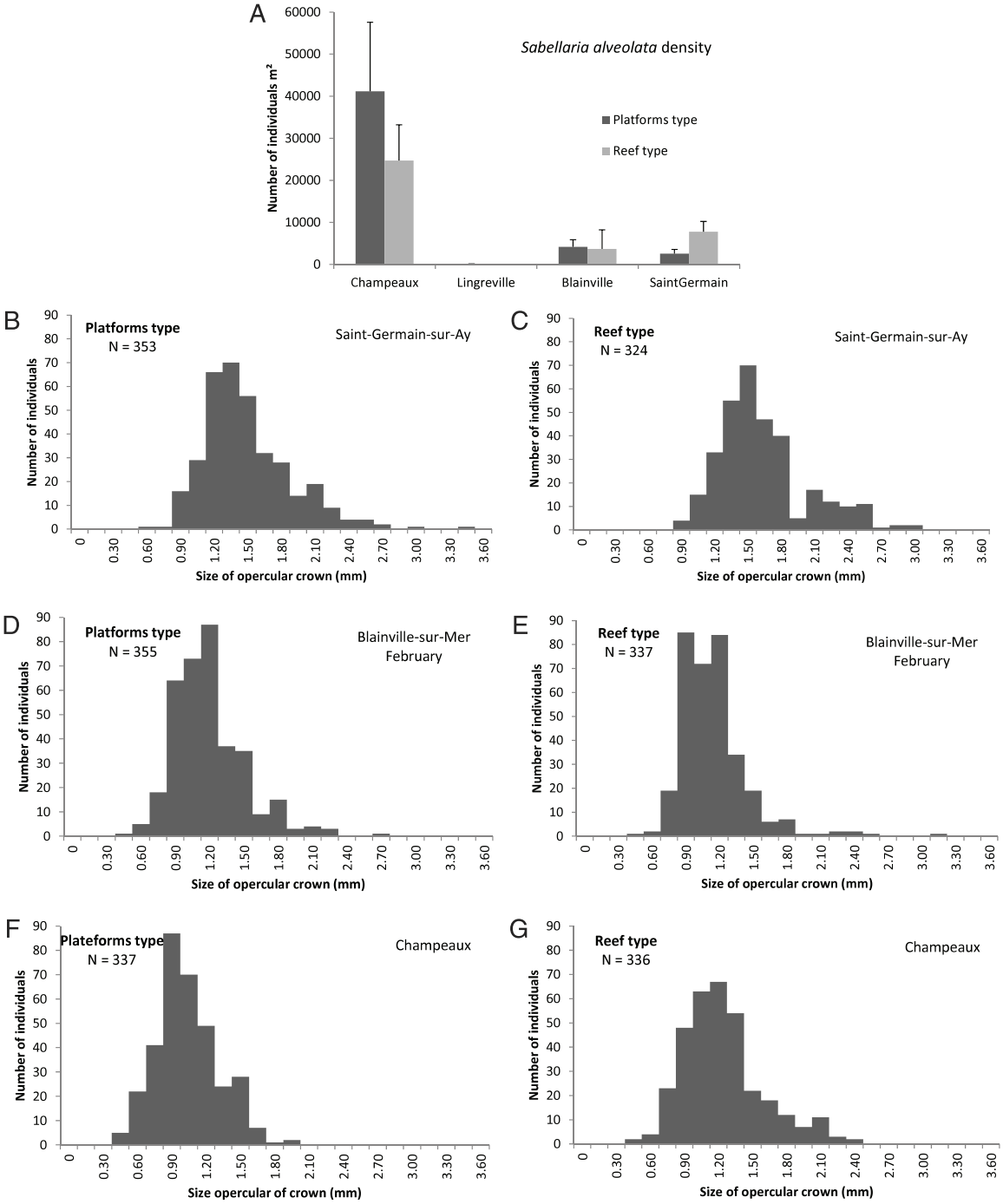


Fig. 7. A. *Sabellaria alveolata* density (mean ± S.E.) by structure and site. B-G. *Sabellaria alveolata* size-class histograms based on measurement of the opercular crown according to each structure at CHAM, SGSA and BLSM. N, number of individuals measured.

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

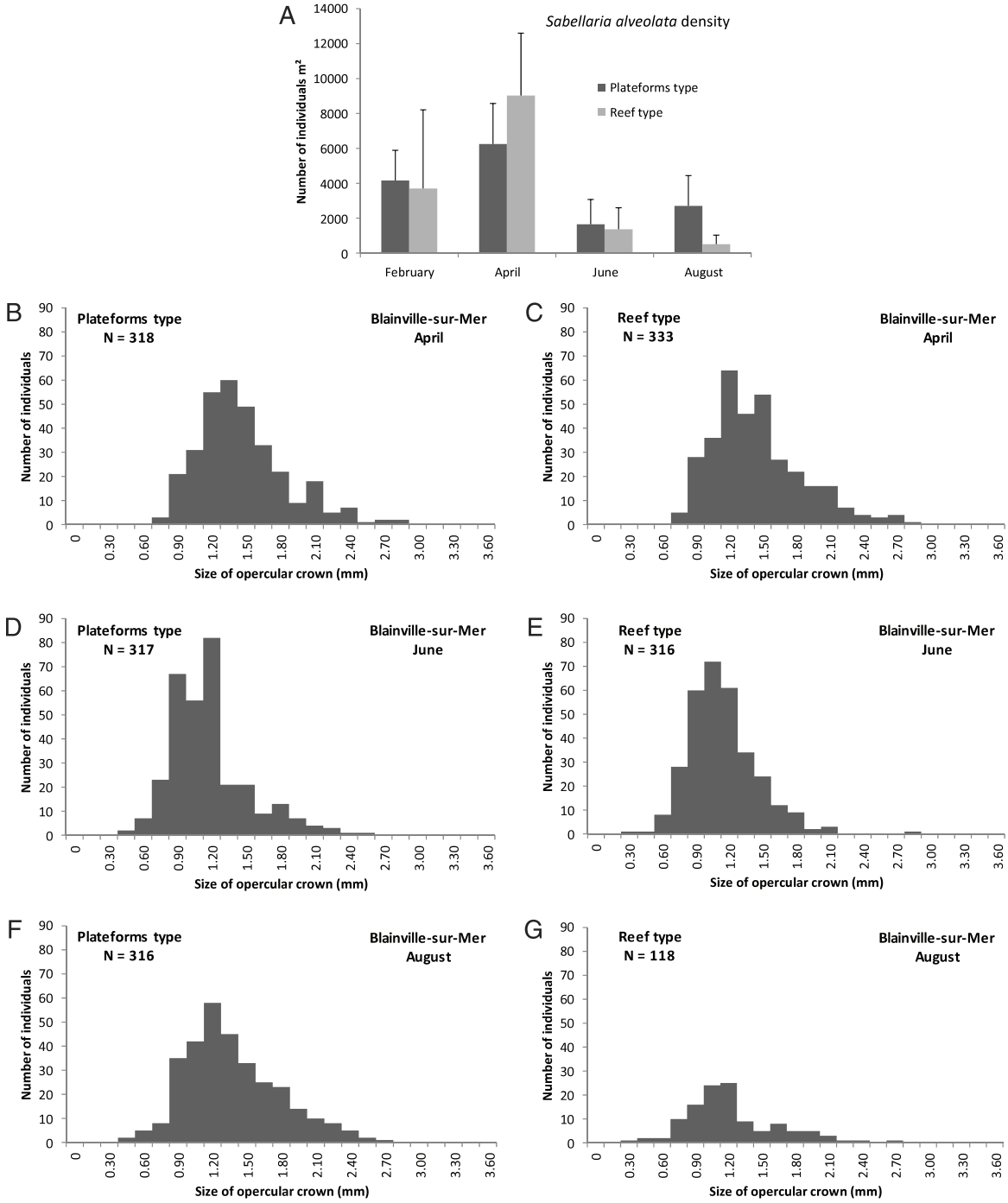


Fig. 8. A. *Sabellaria alveolata* density (mean ± S.E.) by structure and date. B-G. *Sabellaria alveolata* size-class histograms based on measurement of the opercular crown according to each structure at BLSM for the four sampling dates. *N*, number of individuals measured.

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

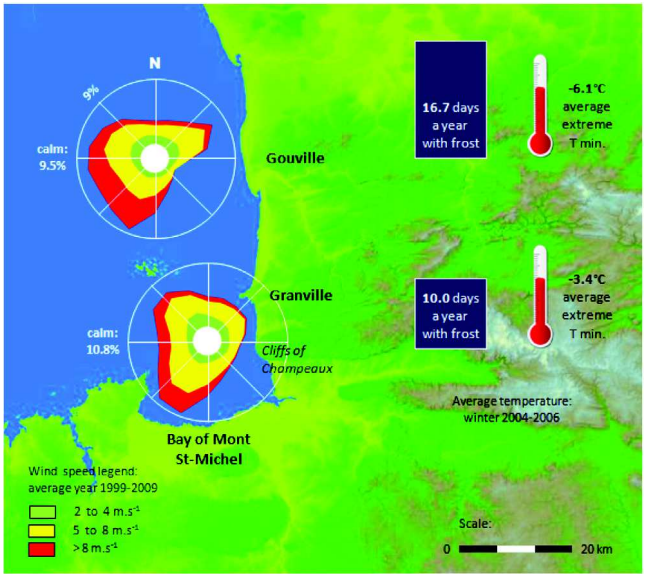


Fig. 9. Climatic difference between the northern and southern parts of the studied sector on the western coast of Cotentin. Wind rose over the period 1999–2009, according to hourly modelled data (Aladin, Météo-France). Extreme temperature and frosts over the period 2004–2006 at Gouville-sur-Mer and Granville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

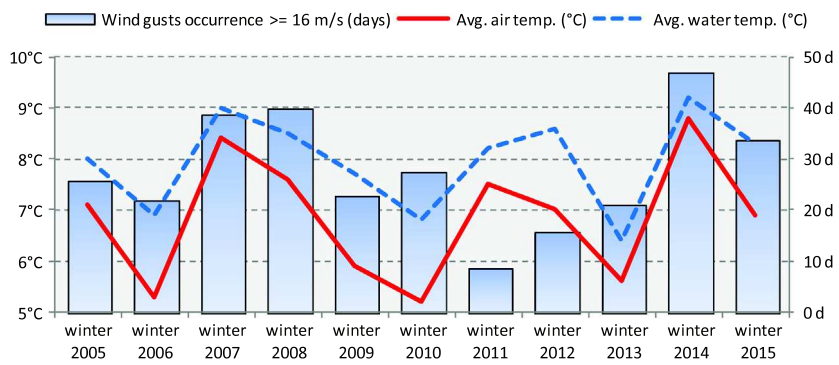


Fig. 10. Wind gust occurrences (days) and average air temperature at Gouville-sur-Mer and average water temperature (°C) at Blainville-sur-Mer, in winter between 2005 and 2015 (data Météo-France).

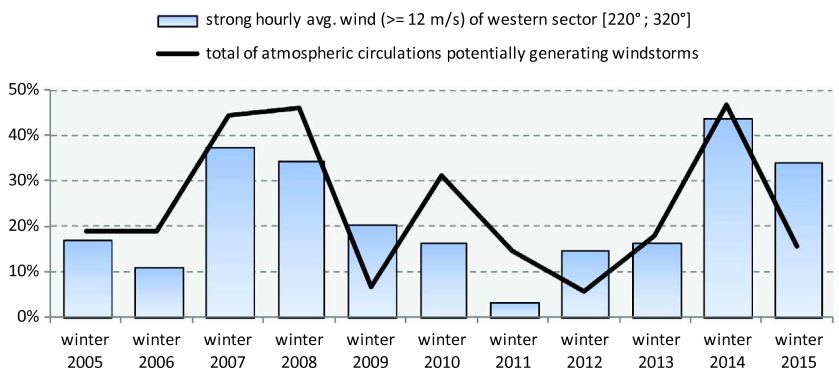


Fig. 11. Frequency of strong west winds (data Météo-France) and atmospheric circulation patterns potentially generating windstorms in winter over Northern France, between 2005 and 2015 (classification after James, 2007).

Please cite this article in press as: Lecornu, B., et al., Dynamics (from 2010–2011 to 2014) of *Sabellaria alveolata* reefs on the western coast of Cotentin (English Channel, France). Regional Studies in Marine Science (2016), http://dx.doi.org/10.1016/j.rsma.2016.07.004

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.

Acknowledgements

The authors thank all their colleagues who helped during the field work. We are especially grateful to A. Foveau for her helpful advice, especially in statistical analysis, and A. Baffreau for her invaluable advice on drafting the figures. This study was funded by the GEDANOR '*Programme of the Conseil Régional de Basse-Normandie*' entitled '*Evolution et interactions des* Sabellaria *en secteur conchylicole*' with the financial support of the '*Conseil Départemental*'. The honeycomb bio-constructions in the Blainville-sur-Mer area were observed from 2010 to 2012 in the framework of the project SURCOTE LITEAU funded by the French Environment Ministry (2014PCM24). The wave height data are from the National Observatory Network DYNALIT, with the authorization of Prof. Franck Levoy. The meteorological data from Gouville-sur-Mer and Granville, as well as the modelled wind data, were provided by Météo-France. The sea water temperature is derived from the REMONOR-SMEL monitoring programme. We also thank Michael Carpenter for the English revision.

References

Anadon, N., 1981. Contribucion al connocimiento de la fauna bentonico de la ria de Vigo. III. Estudio de los arrecifes de *Sabellaria alveolata* (L.) (Polychaeta, Sedentaria). Invest. Pesq. 45, 105–122.

Ayata, S.D., Ellien, C., Dumas, F., Dubois, S., Thiébaut, E., 2009. Modelling larval dispersal and settlement of the reef-building polychaete *Sabellaria alveolata*: Role of hydroclimatic processes on the sustainability of biogenic reefs. Cont. Shelf Res. 29, 1605–1623.

Ayral, A., 2000. Le Banc des hermelles: état de santé et mesures de gestion. Rapport du Muséum National d'Histoire Naturelle, Station Marine de Dinard, France, p. 57.

Basse-Normandie, Orthophotographie, 2013. Producted by the 'Région Basse-Normandie, Département du Calvados, Département de la Manche, Département de l'Orne, Etablissement Public Foncier de Normandie, Syndicat mixte Caen-Métropole' and European Union.

Basuyaux, O., 2011. Etude et cartographie de *Sabellaria alveolata* sur la côte ouest du département de la Manche – Focus sur les abords de Granville. Rapport SMEL/CE-env/2011-01. p. 38.

Beck, F., Pezy, J.P., Baffreau, A., Dauvin, J.C., 2015. Effects of clam rake harvesting on the intertidal *Ruditapes* habitat of the English Channel. ICES J. Mar. Sci. 72, 2663–2673.

Crawford, C.M., Macleod, C.K.A., Mitchell, I., 2003. Effects of shellfish farming on the benthic environment. Aquaculture 224, 117–140.

Crisp, D.J., 1964. The effects of the severe winter of 1962–63 on marine life in Britain. J. Anim. Ecol. 33, 165–210.

Cunningham, P.N., Hawkins, S.J., Jones, H.D., Burrows, M.T., 1984. The geographical distribution of *Sabellaria alveolata* (L.) in England, Wales and Scotland, with investigations into the community structure of, and the effects of trampling on *Sabellaria alveolata* colonies. Nat. Cons. Council, Peterborough, U.K., Contract No. HF3/11/22.

Dauvin, J.C., Delhay, J.B., Hacquebart, P., De Saint-Leger, E., Izabel, G., Tomas, L., Levoy, F., 2014. The evolution of surfaces and carrying capacity for Western Cotentin Estuaries. Cah. Biol. Mar. 55, 77–89.

Delhay, J.B., 2010. Communautés macrobenthiques intertidales du havre et de l'estran de Blainville-sur-Mer (côte ouest du Cotentin): exemple de l'endofaune des sédiments meubles du havre et des récifs d'hermelles. Rapport de Master 1. Université de Lille 1, France, p. 46.
Delhay, J.B., 2012. Outils cartographiques des espaces intertidaux de la côte ouest du Cotentin. Diplôme Supérieur de Recherches, Université de Lille 1, France.
Desroy, N., Dubois, S.F., Fournier, J., Ricquiers, L., Le Mao, P., Guerin, L., Gerla, D., Rougerie, M., Legendre, A., 2011. The conservation status of *Sabellaria alveolata* (L.) (Polychaeta: Sabellaridae) reefs in the Bay of Mont-Saint-Michel. Aquat. Conserv. Mar. Freshw. Ecosyst. 21, 462–471.
Dubois, S., 2003. Ecologie des formations re' cifales a' Sabellaria alveolata (L.): valeur fonctionnelle et patrimoniale (Ph.D. thesis), Museum National d'Histoire Naturelle de Paris, Dinard, p. 199.
Dubois, S., Commito, J.A., Olivier, F., Retière, C., 2006. Effects of epibionts on *Sabellaria alveolata* (L.) biogenic reefs and their associated fauna in the Bay of Mont-Saint-Michel. Estuar. Coast. Shelf Sci. 68, 635–646.
Dubois, S., Comtet, T., Retière, C., Thiébaut, E., 2007. Distribution and retention of *Sabellaria alveolata* larvae (Polychaeta: Sabellariidae) in the Bay of Mont-Saint-Michel, France. Mar. Ecol. Prog. Ser. 346, 243–254.
Dubois, S., Retière, C., Olivier, F., 2002. Biodiversity associated with *Sabellaria alveolata* (Polychaeta: Sabellaridae) reefs: effects of human disturbances. J. Mar. Biol. Assoc. U.K. 82, 817–826.
Firth, L.B., Mieszkowska, N., Grant, L.S., Bush, L.E., Davies, A.J., Frost, M.T., Moschella, P.S., Burrows, M.T., Cunningham, P.N., Dye, S.R., Hawkins, S.J., 2015. Historical comparisons reveal multiple drivers of decadal change of an ecosystem engineer at the range edge. Ecol. Evol. 5, 3210–3222.
Frost, M.T., Leaper, R., Mieszkowska, N., Moschella, P., Murua, J., Smyth, C., Hawkins, S.J., 2004. Recovery of a Biodiversity Action Plan Species in Northwest England: possible role of climate change, artificial habitat and water quality amelioration. Report to English nature by the Marine Biological Association of the United Kingdom, Peterborough, U.K.
Graindor, M.J., 1976. Carte des sédiments superficiels de la Manche, échelle 1:500 000. Paris: Ministère de l'industrie et de la recherche, service géologique national, France.
Gruet, Y., 1970. Faune associée des récifs édifiés par l'annélide *Sabellaria alveolata* (Linné) en baie du Mont-Saint-Michel: banc des Hermelles. Mém. Soc. Sc. Cherbourg 54, 1–21.
Gruet, Y., 1971. Morphologie, croissance et faune associée des récifs de *Sabellaria alveolata* (Linné) de la Bernerie-en-Retz (Loire Atlantique). Tethys 3, 321–380.
Gruet, Y., 1972a. Aspects morphologiques et dynamiques de constructions de l'annélide polychète *Sabellaria alveolata* (Linné). Rev. Trav. Inst. Pêch. Marit. 36, 131–161.
Gruet, Y., 1972b. Faune associée de 'récifs' d'Hermelles Polychète Sabellaridé: *Sabellaria alveolata*(Linné): cas de récifs morts à Crève-cœur (La Bernerie, Loire Atlantique). Bull. Soc. Sc. Bretagne 47, 69–80.
Gruet, Y., 1977. Peuplements de la côte rôcheuse de Sion-sur-l'Océan (Vendée) et faune associée aux "récifs" d'hermelles [*Sabellaria alveolata*(Linné), Annélide Polychète]. Bull. Ecol. 8, 37–55.
Gruet, Y., 1981. Peuplements de l'estran rocheux sur la côte normande de la baie du Mont Saint-Michel à Champeaux: situation et conditions générales. Bull. Soc. Linn. Normandie 109, 21–32.
Gruet, Y., 1982. Recherches sur l'écologie des récifs d'Hermelles édifiés par l'Annélide Polychète *Sabelllaria alveolata* (Linné) (Ph.D. thesis), Université des Sciences et Techniques, Nantes, France, p. 340.
Gruet, Y., 1986. Spatio-temporal changes of Sabellarian reefs built by the sedentary polychaete *Sabellaria alveolata* (Linné). PS.Z.N.I.: Mar. Ecol. 7, 303–319.
Gruet, Y., Bodeur, Y., 1997. Les récifs d'Hermelles. Patrimoine naturel, Paris/France 28, pp. 168–176.
Guillaumont, B., Hamon, D., Lafond, L.R., Le Rhun, J., Levasseur, J., Piriou, J.Y., 1987. Etude régionale intégrée du Golfe Normano-Breton. Carte biomorphosédimentaire de la zone intertidale au 1/25 000 Côte Ouest du Cotentin et Baie du Mont-Saint-Michel. Notice Explicative. Rapport Ifremer, Direction Environnement et Recherches Océaniques Département Environnement Littoral. Les Presses Bretonnes - St-Brieuc, France, 50 pp. + 7 cartes dépliantes couleur.
Hommeril, O., 1962. Etude locale (Gouville-sur-mer, Manche) de la retenue des sédiments par deux polychètes sédentaires: *Sabellaria alveolata* (Hermelle) et *Lanice conchilega*. Cah. Océanogr. 4, 245–257.
Hommeril, P., Larsonneur, C., 1963. Quelques effets morphologiques du gel intense de l'hiver 1963 sur le littoral bas-normand. Cah. Océanogr. 9, 638–649.
James, P.M., 2007. An objective classification for Hess and Brezowsky Grosswetterlagen over Europe. Theor. Appl. Climatol. 88, 17–42.
La Porta, B., Nicoletti, L., 2009. *Sabellaria alveolata* (Linnaeus) reefs in the central Tyrrhenian Sea (Italy) and associated polychaete fauna. Zoosymposia 2, 527–536.
Lecornu, B., 2014. Suivi de l'évolution des habitats de l'espèce *Sabellaria alveolata* (Linné) sur la côte ouest de la Manche et étude de la biodiversité associée aux récifs. Mémoire de Master 2 AQUACAEN Science des environnements continentaux et côtiers, Université de Caen, France, p. 95.
Levoy, F., Monfort, O., Larsonneur, C., 1997. Transports solides sur les plages macrotidales: traçage fluorescent et application à la côte ouest du Cotentin (France). Oceanol. Acta 20, 811–822.
Levoy, F., Monfort, O., Larsonneur, C., 2001. Hydrodynamic variability on megatidal beaches, Normandy, France. Cont. Shelf Res. 21, 563–586.
Lucas, G., Lefevre, P., 1955. Contribution à l'étude de quelques sédiments marins et de récifs d'hermelles du Mont-Saint-Michel. Rev. Trav. Inst. Scient. Techn. Pêches marit. 20, 85–112.
Noernberg, M.A., Fournier, J., Dubois, S., Populus, J., 2010. Using airbone laser altimetry to estimate *Sabellaria alveolata* (Polychaeta: Sabellariidae) reefs volume in tidal flat environments. Estuar. Coast. Shelf Sci. 90, 93–102.
Pien, S., Maheux, F., Le Gendre, R., Dedieu, K., Simon, B., Gauquelin, T., Basuyaux, O., Fleury, E., 2014. Colonisation of intertidal rocks by Crassostrea Gigas spat on the west coast of the Cotentin peninsula. PEGASEAS 2nd cross channel forum. In: Evariste, E., Dauvin, J.C., Claquin, P., Auber, A., Winder, A., Thenail, B., Fletcher, S., Robin, J.P. (Eds.), Trans-Channel forum proceedings 'Science and governance of the Channel marine ecosystem'. INTERREG IV A Programme. Université de Caen Basse-Normandie, Caen, France, p. 160.
Plicanti, A., Dominguez, R., Dubois, S.F., Bertocci, I., 2016. Human impacts on biogenic habitats: effects of experimental trampling on Sabellaria alveolata (Linnaeus, 1767) reefs. J. Exp. Mar. Biol. Ecol. 478, 34–44.
Porras, R., Bataller, J.V., Murgui, E., Torregrosa, T., 1996. Trophic structure and community composition of Polychaetes inhabiting some *Sabellaria alveolata* (L.) reefs along the Valencia gulf coast, Western Mediterranean. PS.Z.N.I.: Mar. Ecol. 17, 583–602.
Salomon, J.C., Breton, M., 1993. An atlas of long-term currents in the Channel. Oceanol. Acta 16, 439–448.
Schlund, E., Basuyaux, O., Lecornu, B., Dauvin, J.C., 2016. Macrofauna Associated with Temporary *Sabellaria alveolata* Reefs on the West Coast of Cotentin (France). SpringerPlus (in press).
Wilson, D.P., 1974. *Sabellaria* colonies at Duckpool, North Cornwall, 1971–1972. J. Mar. Biol. Assoc. U. K. 54, 393–436.

Please cite this article in press as: Lecornu, B., et al., Dynamics (from 2010–2011 to 2014) of *Sabellaria alveolata* reefs on the western coast of Cotentin (English Channel, France). Regional Studies in Marine Science (2016), http://dx.doi.org/10.1016/j.rsma.2016.07.004

Schlund *et al. SpringerPlus (2016) 5:1260*
DOI 10.1186/s40064-016-2885-y

SpringerPlus

RESEARCH

Open Access

Macrofauna associated with temporary *Sabellaria alveolata* reefs on the west coast of Cotentin (France)

Erika Schlund[1,2], Olivier Basuyaux[3], Billie Lecornu[3], Jean-Philippe Pezy[1,2], Alexandrine Baffreau[1,2] and Jean-Claude Dauvin[1,2*]

Abstract

The polychaete *Sabellaria alveolata* (Linnaeus, 1767) is an important ecosystem engineer building reef structures which add to the topographic complexity in colonized areas. In Europe, the most extensive reef formation is located in the Bay of Mont-Saint-Michel (France). Since 2006, *Sabellaria* bio-constructions have developed on hard substrates along the west coast of the Cotentin Peninsula between Champeaux and Saint-Germain-sur-Ay on the northern part of the Bay of Mont-Saint-Michel. In this sector, two distinct types of bio-construction can be distinguished: platforms and reefs. The aim of this study is to analyse the patterns of the associated macrofauna on these platforms and reefs, as well as outside, and test for a correlation between the presence of *Sabellaria* bio-constructions and the richness of the benthic macrofauna. Univariate analyses are used to compare the macrofauna on four sites (Champeaux, Lingreville, Blainville-sur-Mer and Saint-Germain-sur-Ay). The results show a higher taxonomic richness on the platform-type than on the reef-type structures, and also a higher taxonomic richness outside the bio-construction areas. This suggests that, on the examined sites, the presence of *S. alveolata* bio-constructions does not contribute to higher levels of benthic macrofaunal richness on hard substrates. Temporary bio-constructions along this coast exhibit reefs of interest at some sites as well as in very small zones which merit special attention.

Keywords: *Sabellaria* reefs, Macrofauna taxonomic richness, Bay of Mont-Saint-Michel, Cotentin coast, Temporary reefs

Background

Biogenic structures built by ecosystem engineers such as corals, molluscs and polychaetes provide favourable habitats for other benthic invertebrates and vertebrates; moreover, these structures can play an important role as nurseries for certain species of commercial interest and also represent an essential source of food for birds and fishes (Commito and Rusignuolo 2000). In Europe, 'reefs' are recognized as marine habitats to be protected and are listed under Annex I of the EU Habitats Council Directive 92/43/EEC under the Habitat Code 1170 (Reefs). The habitat '*Sabellaria alveolata* Reefs' also benefits from a Biodiversity Action Plan in the UK (http://www.jncc.gov.uk/page-5155).

The honeycomb worm *S. alveolata*, which belongs to the family Sabellaridae, is present in temperate regions of the world (India, North and South America), and is also known in Europe, where it ranges from the Bristol Channel (Wilson 1974) to the coast of Portugal (Dias and Paula 2001). The bio-constructions correspond to polychaete colonies which build up sediment agglomerates composed of tubes. The initial tubes bind to the rock in the mid-intertidal zone, thus forming structures called platforms. These platforms develop throughout the life of the individuals, eventually creating more massive structures—referred to as reefs—in up to 3–5 years (Gruet 1982). In France (Fig. 1), the major bio-constructions in the Bay of Bourgneuf (Vendée, on the Atlantic coast) and in the Bay of Mont-Saint-Michel (bordering the western

*Correspondence: jean-claude.dauvin@unicaen.fr
[1] UNICAEN, UNIROUEN, UMR M2C, CNRS 6143, Normandie Univ, 24 Rue des Tilleuls, 14000 Caen, France
Full list of author information is available at the end of the article

Springer Open

© 2016 The Author(s). This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

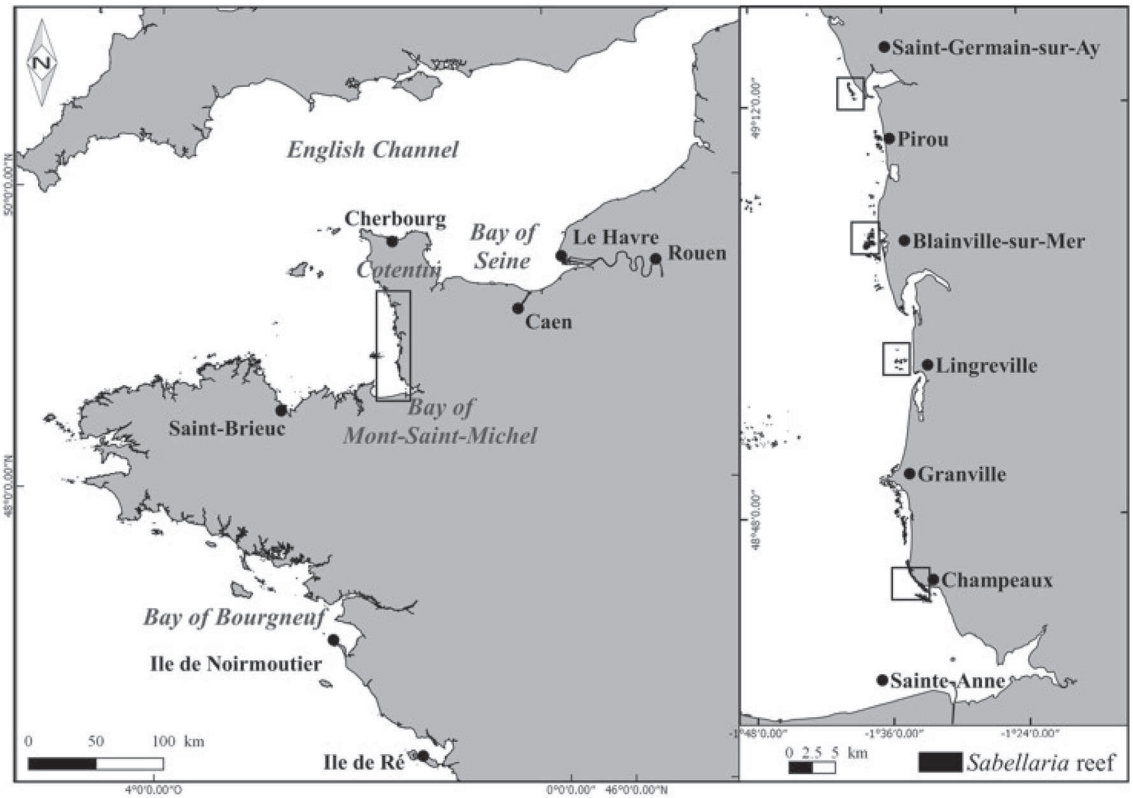


Fig. 1 Location of study sites on the west coast of Cotentin, France, western part of the English Channel and location of the Bay of Bourgneuf along the Atlantic coast

basin of the English Channel) represent the two largest structures of this type in Europe (Gruet and Bodeur 1997). *Sabellaria* reefs are also developed on sand flats in the lower intertidal zone of the Bay of Mont-Saint-Michel, where they form the Saint-Anne reef (Dubois et al. 2002, 2006).

The examination of numerous formations by Gruet (1972a, 1982) has provided a basis for distinguishing different phases of reef evolution. The natural evolution of a reef begins with the settlement of young recruits building up ball-shaped structures which then coalesce as they grow to form barriers; this is followed by destruction of the barriers, due to sedimentation, colonization by epibionts (mainly mussels or oysters) or extreme hydrodynamic conditions during storms (Gruet and Bodeur 1997; Dubois et al. 2006).

Environmental conditions (stable temperature, humid atmosphere, reduced light, etc.) favourable for marine macrofauna living in crevices are created during the phases of construction and destruction of a reef, i.e. growth, degradation, death and colonization (Gruet 1970, 1971, 1972a, b, 1977, 1981, 1982). Gruet (1971, 1982) and Gruet and Bodeur (1997) stressed that the Taxonomic Richness (TR) of the associated benthic macrofauna decreases in areas with high densities of the honeycomb worm (15,000–60,000 ind m^{-2}), and observed that TR is higher in degraded reef zones. The *S. alveolata* bio-constructions of the Sainte-Anne reef in the southern Bay of Mont-Saint-Michel have a high TR compared with the very low TR observed in the surrounding intertidal soft-bottom *Macoma balthica* community (Dubois et al. 2002, 2006). In the Mediterranean Sea, both in the shallow waters of the Valencia Gulf (Spain; Porras et al. 1996) and in deeper waters of the Tyrrhenian Sea (Italy; La Porta and Nicoletti 2009), high polychaete richness is reported to be associated with *S. alveolata* reefs, especially during the reef destruction phase. Anadon (1981) described the associated fauna in two reefs of the Ria de Vigo (Galicia, Spain), which show a similar pattern to that observed in Gruet's studies: i.e. a lower TR in areas with a high population density of the honeycomb worm. Dias and Paula (2001) described the associated fauna in two intertidal *S. alveolata* reefs from the central coast of Portugal, with two main patterns, i.e. crustaceans are dominant at the Magoita site and polychaetes at the Avencas site.

The modelling of larval dispersal (Ayata et al. 2009) shows that *S. alveolata* living on the western coast of Cotentin are unlikely to participate in renewal of the populations. Therefore, along the west coast of Cotentin north of Champeaux, the temporary *Sabellaria* structures (established for probably less than 10 years) are associated with a southerly source of larvae coming from populations at Saint-Anne and Champeaux in the Bay of Mont-Saint-Michel. In certain years, *Sabellaria* larvae can reach the studied sites owing to south-westerly winds plus the lower velocity of nearshore tidal currents (Ayata et al. 2009).

A considerable development of *Sabellaria* was observed on the west coast of Cotentin in the late years 2000. This development was particularly marked on the mid-littoral bedrock zone colonized by the macroalgae *Fucus serratus,* which can produce changes in habitat and functional modifications due to the establishment of high densities of the honeycomb worm *S. alveolata*.

The aim of this study is to assess the macrofauna richness associated with three types of habitat (*S. alveolata* platform, reef and outside reef) of the mid-intertidal zone at four sites (Champeaux, Lingreville, Blainville-sur-Mer and Saint-Germain-sur-Ay) located on the west coast of Cotentin, taking into account the northward expansion of the reefs in the years 2000.

Methods

Study area

The study area is located on the west coast of Cotentin, between Champeaux (in the south) and Saint-Germain-sur-Ay (in the north), in a sector where the first recent *Sabellaria alveolata* bio-constructions were observed in 2006 (Delhay 2010; Basuyaux 2011) (Fig. 1). In the intertidal zone of this highly dynamic coastline, bio-constructions show a discontinuous development since the hard substrate is interspersed with soft-bottom areas mainly composed of sand and gravel. Using the observations carried out in 2010–2011 (Basuyaux 2011), four sampling sites were selected in 2014 within the study area on the West Cotentin coast [i.e. from south to north: Champeaux (CHAM), Lingreville (LING), Blainville-sur-Mer (BLSM) and Saint-Germain-sur-Ay (SGSA)] to study the TR associated with the *Sabellaria* bio-constructions. In addition, except for CHAM, the selected sites are all located near deltaic estuaries with high-energy hydrodynamic conditions which induce sediment displacement on this wave-dominated shore (Beck et al. 2015).

Sabellaria reef formations were observed in the early 1960 s at a location north of Blainville-sur-Mer (Fig. 1) by Hommeril (1967). These reefs were affected by destruction just after the severe winter of 1962–1963 due the high sensitivity of *S. alveolata* to low temperatures (Hommeril and Larsonneur 1963). Later, mapping of the intertidal benthic communities carried out in 1982–1984 along the western coast of Cotentin (Guillaumont et al. 1987) identified a single small reef at Pirou to the south of Saint-Germain-sur-Ay as well as some fragmented reefs south of Granville extending as far as Champeaux. Since 2006, fragmented *Sabellaria* reef structures have been observed along the west coast of Cotentin in the north of the Bay of Mont-Saint-Michel, between Champeaux and Saint-Germain-sur-Ay (Fig. 1). In 2010–2011, these bio-constructions occupied an area of 2.28 km^2, divided into 535 more or less extensive patches between Champeaux and Saint-Germain-sur-Ay along ~60 km of coastline (Basuyaux 2011).

The bio-constructions are fragmented into a large number of units, but their generalorientation is parallel to the coast (Basuyaux personal observations), which is also mainly parallel to the prevailing tidal current (i.e. NW–SW sector) as in the Bay of Mont-Saint-Michel (Dubois et al. 2002). The distinctive feature of bio-constructions at the studied sites is that they are developed on hard substrates, except at CHAM where they develop on soft substrate (O. Basuyaux and J. C. Dauvin, personal observations). In the present study, bio-constructions are classified into two main groups: platforms and reefs; i.e. the platform type comprises bio-constructions which do not exceed 30 cm in height, while the reef type includes bio-constructions higher than 30 cm.

Field and laboratory procedures

Sampling was carried out on the four sites between February and April 2014 (on 18 February for BLSM, 3 March for CHAM, 18 March for SGSA and 31 March for LING (Table 1), using a circular corer of diameter of 0.20 m (about 1/32 m^2). Cores were burrowed into the reefs or the platforms as deeply as possible (mainly between 0.10 and 0.30 m depending on the height of the bio-construction). For each site, sixteen cores were sampled; eight from a platform zone and eight from a reef zone, making up a total of 64 cores. The collected sediment was preserved in 10 % formalin.

To study the temporal changes in TR at BLSM during the winter–summer period, two other samplings were carried out on both platforms and reefs on 18 June and 18 August 2014, making a total of 32 additional cores (Table 1).

In the laboratory, the *S. alveolata* tubes were disaggregated in seawater, and the macrofauna retained on a 500 μm mesh size was sorted, counted and identified to be lowest taxonomic level. Nematodes and other meiofauna were excluded from the analyses because the sorting method—i.e. mesh size—was unsuitable (Dubois et al. 2002).

Table 1 Sampling strategy in 2014

Site	WGS 84 coordinates	Sampling dates	Sample strategy
CHAM	48°43′52″N-1°33′25″W	3 March	Cores (Spatial comparison)
		28 April	Quadrats
LING	48°57′074″N-1°34′429″W	31 March	Cores (Spatial comparison)
BLSM	49°4′7″N-1°37′25″W	18 February	Cores (Spatial comparison)
		18 June and 18 August	Cores (Temporal comparison)
		16 April	Quadrats
SGSA	49°12′645″N-1°38′693″W	18 March	Cores (Spatial comparison)
		17 April	Quadrats

CHAM Champeaux, *LING* Lingreville, *BLSM* Blainville-Sur Mer, *SGSA* Saint-Germain-Sur-Ay

A second sampling strategy was performed to compare the TR of areas with *S. alveolata* reefs with areas of hard substrate without any bio-constructions located at the same elevation in the intertidal zone but about 100 m away from the reefs. This strategy was applied to the permanent reef at CHAM, as well as to BLSM and SGSA where the reefs remained well developed in 2014. The samples were collected on 16 April (BLSM) and 17 April (SGSA), and 28 April (CHAM), by scraping to 0.05 m depth over a quadrat surface-area of 0.1 m^2. For the three sites, ten quadrats representing a total area of 1 m^2 were sampled from a reef zone and from outside the reef structure on hard substrate. Thus, a total of 60 quadrats were collected from the three sampling sites, the samples being preserved, sieved on 0.5-mm mesh and identified in the same way as for the core samples.

Data analysis

Macrofauna data are analysed by combining species richness [after updating the species name and synonymy using WORMS (World Register of Marine Species): http://www.marinespecies.org; accessed on 15 December 2015] and Hill's diversity numbers (Hill 1973) as recommended by Heip et al. (1988): N1 = exp (H') with H' is the Shannon-Wiener diversity (Shannon 1948); and N2 = 1/SI, with SI is the Simpson's dominance index (Simpson 1949).

A Shapiro–Wilk normality test and a Bartlett's test for homogeneity of variance are performed prior to each ANOVA with the R software to validate the assumptions of ANOVA. Then, ANOVAs are performed to assess:

- the spatial and temporal abundance patterns of *S. alveolata* on reef and platform structures (core sampling);
- the spatial and temporal patterns of associated macrofauna (TR and total abundances) on reef and platform structures (core sampling);
- the TR inside and outside reef structures (quadrat sampling; TR and total abundances).

A Tukey Honestly Significant Difference test is used to determine differences between the sites, types of structure (reef or platform) and sampling dates.

To compare the faunal TR in the three communities, i.e. from the platform, from the reef or outside the reef area, *k*-dominance curves are plotted for each substratum type and site and the associated species, excluding *S. alveolata*, are ranked in order of their dominance in terms of abundance.

Results

Spatial pattern of Sabellaria alveolata *abundance (core sampling)*

Sabellaria alveolata is the most abundant species regardless of the site location or substrate type, apart from LING, where it does not appear among the dominant species and shows lower abundance on the degraded reef (Tables 2, 3). Comparison between the two different structures (platform and reef) do not reveal significant differences (ANOVA $F_{1.56} = 2.96$; $p = 0.09$), but there is a significant difference in the densities of *S. alveolata* between different sites (ANOVA $F_{3.56} = 7.55$; $p < 0.01$). The highest densities of *S. alveolata* are observed in the CHAM population (Tukey test) (Fig. 2).

Temporal pattern of Sabellaria alveolata *abundance at BLSM (core sampling)*

As observed with the spatial pattern, *Sabellaria alveolata* at BLSM exhibits higher densities than the other species over time (Table 4; see also "Appendix 2"). However, from February to August, the density of *S. alveolata* shows a clear decrease on both platform and reef stations (Fig. 3); a significant difference of *S. alveolata* abundance appears between winter (February), when the maximum occurs, and summer (August) (ANOVA $F_{2,42} = 21.96$; $p < 0.001$) (Tukey test).

Table 2 Relative percentage of *Sabellaria alveolata* density against total density at each site for sampling dates in 2014 (core sampling)

	February–March		June		August	
	Platform	Reef	Platform	Reef	Platform	Reef
CHAM	98	85	–	–	–	–
LING	1	0	–	–	–	–
BLSM	94	89	85	81	78	31
SGSA	55	77	–	–	–	–

CHAM Champeaux, *LING* Lingreville, *BLSM* Blainville-Sur-Mer and, *SGSA* Saint-Germain-Sur-Ay

Table 3 Top-ranked species densities (core sampling, mean per 1/32 m^2 ± SD) of macrofauna in *Sabellaria alveolata* bio-constructions

Site	Rank	Platform type		Reef type	
		Taxa	Mean density ± SD	Taxa	Mean density ± SD
Saint-Germain-sur-Ay	1	*Sabellaria alveolata*	80.00 ± 31.21	*Sabellaria alveolata*	242.75 ± 77.12
	2	*Golfingia (Golfingia) vulgaris*	16.13 ± 6.77	*Porcellana platycheles*	32.50 ± 30.16
	3	*Porcellana platycheles*	11.88 ± 14.79	*Golfingia (Golfingia) vulgaris*	14.13 ± 11.57
	4	*Notomastus latericeus*	6.63 ± 6.30	*Cirratulus cirratus*	2.63 ± 7.42
	5	*Gibbula umbilicalis*	5.75 ± 3.41	Nemertea	1.88 ± 1.73
Blainville-sur-Mer	1	*Sabellaria alveolata*	130 ± 53.86	*Sabellaria alveolata*	115.75 ± 140.50
	2	*Golfingia (Golfingia) vulgaris*	12.25 ± 8.41	*Gibbula umbilicalis*	7.13 ± 7.85
	3	*Acanthochitona crinita*	1.25 ± 1.39	*Porcellana platycheles*	2.13 ± 2.23
	4	*Perinereis cultrifera*	1.13 ± 1.81	*Golfingia (Golfingia) vulgaris*	1.25 ± 1.49
	5	*Spirobranchus triqueter*	1.00 ± 1.07	*Perinereis cultrifera*	1.00 ± 1.41
Lingreville	1	*Porcellana platycheles*	17.25 ± 26.72	*Sphaeroma serratum/monodi*	24.38 ± 10.32
	2	Nemertea	4.75 ± 3.54	*Porcellana platycheles*	7.88 ± 13.25
	3	*Mytilus edulis*	3.13 ± 2.47	Nemertea	5.88 ± 13.04
	4	*Gibbula umbilicalis*	2.25 ± 2.82	*Gibbula umbilicalis*	3.00 ± 1.85
	5	*Malacoceros fuliginosus*	1.75 ± 2.19	*Golfingia (Golfingia) vulgaris*	1.75 ± 2.38
Champeaux	1	*Sabellaria alveolata*	1182.88 ± 676.30	*Sabellaria alveolata*	771.88 ± 265.52
	2	*Eulalia ornata*	5.63 ± 4.27	*Sphaeroma serratum/monodi*	100.13 ± 66.25
	3	*Perinereis cultrifera*	3.75 ± 4.03	*Porcellana platycheles*	15.75 ± 37.17
	4	*Malacoceros fuliginosus*	2.75 ± 4.30	*Golfingia (Golfingia) vulgaris*	5.38 ± 9.53
	5	*Sphaeroma serratum/monodi*	2.63 ± 5.07	Actiniaria	3.50 ± 5.40

See "Appendix 1" for taxonomic details and complete species list

As observed with the spatial pattern, the temporal pattern of *Sabellaria alveolata* does not differ significantly between platform and reef structures (ANOVA $F_{1.42} = 0.004$; $p = 0.94$) (Fig. 3).

Spatial pattern of associated macrofauna on platform and reef structures (core sampling)

From the 64 cores, a total of 6731 individuals are identified (67 to species level) belonging to 80 taxa. The richest group is the polychaetes with 36 taxa. Although other species show much lower abundances than *S. alveolata*, it is noteworthy that their abundances are higher on the reefs than on the platforms.

The taxonomic richness is significantly different between the reefs and platforms and also between different sites (Table 5). Moreover, the interactions between the two different structures and their locations are not significantly different (Table 5). The Tukey test reveals that the CHAM and LING sites show the greatest differences in TR between reefs and platforms (Table 5; Fig. 4).

Site location is a significant factor influencing abundance, and the interactions between the two different structures and location are significantly different (Table 5). The SGAA and BLSM sites have lower macrofauna abundances compared with CHAM or LING (Tukey test).

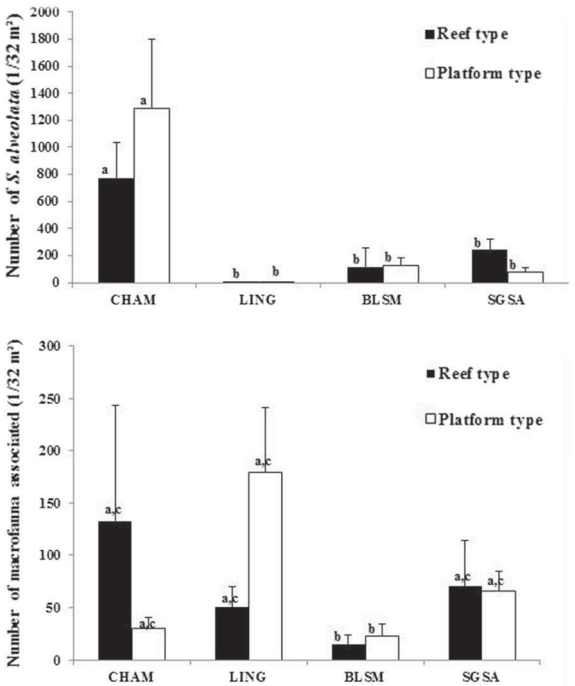


Fig. 2 Density of *Sabellaria alveolata* and other species (number of individuals on 1/32 m^2 and Standard Deviation). *CHAM* Champeaux, *LING* Lingreville, *BLSM* Blainville-Sur-Mer, *SGSA* Saint-Germain-Sur-Ay (core sampling). Means with the same superscript do not differ significantly (Tukey's HSD test; $p > 0.05$)

The faunal composition for the CHAM site differs from that observed for BLSM and SGSA. If we exclude *S. alveolata*, two groups dominate at these three sites (CHAM, BLSM and SGSA). Arthropods are represented by 18 taxa, including two dominant species: the decapod *Porcellana platycheles* and the isopods *Sphaeroma* spp. Mollusca are represented by 18 taxa, with the gastropod *Gibbula umbilicalis* as dominant species (Table 3; see also "Appendix 1"). The sipunculid *Golfingia vulgaris* is also present among the five top-ranking species on all four sites (Table 3).

The SGSA site shows the highest TR, both on the platforms and on the reefs (Fig. 4). Conversely, BLSM has the lowest TR. Mean values of SR, N1 and N2 on the four sites are higher on platforms than on reefs, except at SGSA (Fig. 4a). Figure 5a presents *k*-dominance curves for species abundance on each site, allowing us to identify additional differences in community structure: the CHAM reef community is dominated by *S. alveolata* (75 % of total abundance) (Table 3). The LING platform community is clearly dominated by *Porcellana platycheles* (78 % of total abundance). The composition of the macrofauna on the platform structures appears more erratic between sites. Moreover, the dominance of species on platforms at SGSA and CHAM is more equally distributed than at the two other sites, with dominant species showing lower abundances.

Table 4 Top-ranked species densities (core sampling, mean per 1/32 m^2 ± SD) of macrofauna in *Sabellaria alveolata* bioconstructions on different dates at Blainville-Sur-Mer

Date	Rank	Platform type		Reef type	
		Species	Mean density ± SD	Species	Mean density ± SD
February	1	*Sabellaria alveolata*	130.00 ± 53.86	*Sabellaria alveolata*	115.75 ± 140.50
	2	*Acanthochitona crinita*	1.25 ± 1.39	*Gibbula umbilicalis*	7.13 ± 7.85
	3	*Perinereis cultrifera*	1.13 ± 1.81	*Porcellana platycheles*	2.13 ± 2.23
	4	*Spirobranchus triqueter*	1.00 ± 1.07	*Perinereis cultrifera*	1.00 ± 1.41
	5	*Platynereis dumerilii*	0.88 ± 0.99	*Venerupis corrugata*	0.63 ± 0.52
June	1	*Sabellaria alveolata*	51.63 ± 44.42	*Sabellaria alveolata*	42.63 ± 38.63
	2	*Porcellana platycheles*	2.88 ± 5.36	*Gibbula umbilicalis*	6.50 ± 3.66
	3	*Gibbula umbilicalis*	2.00 ± 1.60	*Venerupis corrugata*	0.75 ± 1.03
	4	*Dynamene bidentata*	1.50 ± 1.60	*Porcellana platycheles*	0.63 ± 1.06
	5	*Eumida sanguinea*	0.50 ± 1.07	*Eumida sanguinea*	0.50 ± 0.53
August	1	*Sabellaria alveolata*	84.38 ± 54.22	*Sabellaria alveolata*	16.00 ± 16.09
	2	*Gibbula umbilicalis*	4.88 ± 4.36	*Gibbula umbilicalis*	12.38 ± 12.83
	3	*Platynereis dumerilii*	3.25 ± 4.89	*Cyathura carinata*	8.38 ± 6.16
	4	*Carcinus maenas*	2.50 ± 2.51	*Porcellana platycheles*	4.38 ± 3.25
	5	*Notomastus latericeus*	2.38 ± 1.69	*Perinereis cultrifera*	2.75 ± 1.49

See "Appendix 2" for taxonomic details and complete species list

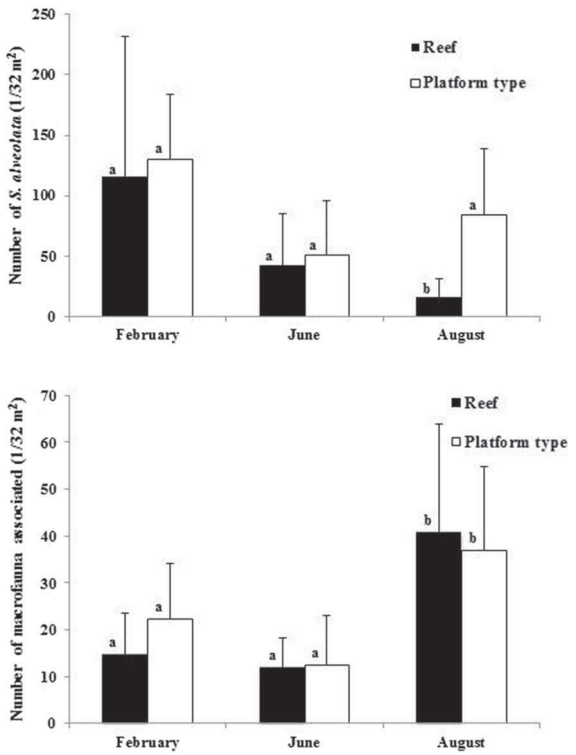


Fig. 3 Temporal changes in density of *Sabellaria alveolata* and other species (number of individuals on 1/32 m^2 and Standard Deviation) according to the different sampling dates at Blainville-sur-Mer (core sampling). Means with the same superscript do not differ significantly (Tukey's HSD test; $p > 0.05$)

Temporal pattern of associated macrofauna on platform and reef structures at BLSM (core sampling)

Sampling period and structure type are significant independent factors influencing the taxonomic richness (Table 6), with a higher TR on platform structures and during August (Tukey test). As regards the total abundance, only the sampling period appears as a significant factor (Table 6), with higher abundances during August (Tukey test).

In addition, we observe a change in the community structure from winter to summer (Table 4; Fig. 6). Indeed, when comparing the two substrates at the three sampling periods, the four most dominant species, excluding *S. alveolata*, are never the same. *K*-dominance curves reveal additional differences in species abundance between platform and reef (Fig. 5b). These curves show a more balanced distribution of numbers of individuals according to species for the platform than for the reef. The curve for the reef structure indicates that one or two species are dominant in February and June, while there is a more balanced distribution in August.

Taxonomic richness and macrofauna abundance inside and outside reef structures (quadrat sampling)

When comparing the macrofauna inside and outside reef structures, we find that both factors (with interaction) have a significant effect on the TR and total abundance (Table 7). Because of the absence of *Sabellaria alveolata* at LING, only the SGAA and CHAM sites are included in the analyses. The mean values of SR, N1 and N2 indicate a higher TR outside than inside the reef constructions (Fig. 7a), with a total of 47 taxa (23 taxa recorded on the reef type as against 35 taxa outside). A comparison of the spatial pattern between the three sites shows that diversity indices are higher at SGSA (Fig. 7b, c), while CHAM yields the lowest values. The fauna of CHAM on substrates outside the reef is different from that recorded at the other stations, with species characteristic of soft substrates such as the bivalves *Spisula solida*, *Macoma balthica* and *Venerupis philippinarum* (Table 8; see also "Appendix 3"). The most abundant species at the other stations are represented essentially by epifauna.

K-dominance curves for species abundance inside and outside reefs at each site provide additional information on the structure of the communities (Fig. 5c). Curves for the outside- reef substrate show a more balanced distribution of numbers of individuals according to species than on the reef structure. The reef community is heavily dominated by a single species, which alone accounts for 95 % of the total abundance of species at the CHAM site. The spatial distinction (reef and outside-reef) indicates

Table 5 Results of Two-way ANOVA on taxonomic richness and total abundance values for the spatial pattern of associated macrofauna on platform and reef structures (core sampling)

	Taxonomic richness			Total abundance		
	Df	F	*p*	Df	F	*p*
Reef/platform (A)	1	6.46	<0.05	1	0.36	0.55
Site (B)	3	10.89	<0.01	3	10.69	<0.01
A × B	3	0.09	0.97	3	15.10	<0.01
∑	8			8		

F: value of the Fisher law; *p* : probability of the factor or interaction; A = stations sampled in two structures; B = samples made at four sites; (A × B) = interaction between factor A and B

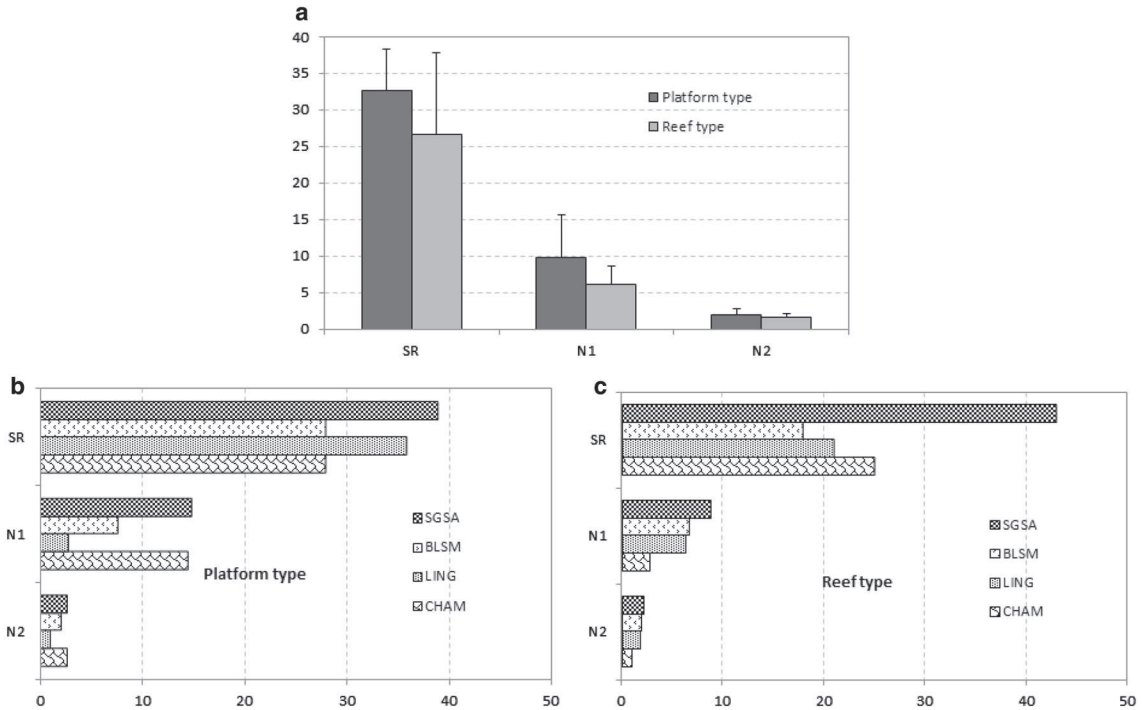


Fig. 4 **a** Values of species richness (SR) and Hill's numbers (N1, N2) for platform and reef-type structures (core sampling); **b, c** values of SR, N1 and N2 for platform and reef-type structures (values excluding *S. alveolata). CHAM* Champeaux, *LING* Lingreville, *BLSM* Blainville-Sur-Mer, *SGSA* Saint-Germain-Sur-Ay

that the SGSA site has a more uniform distribution of species, unlike CHAM.

Discussion

In this study, the taxonomic richness of the macrofauna is estimated at 93 taxa (77 identified to species level) based on samples collected from four sites ("Appendix 4"). Among the recorded taxa, 13 were sampled only outside the *Sabellaria alveolata* platforms and reefs.

Accounting for 36 taxa, polychaetes dominate the taxonomic richness on *Sabellaria* platforms and reefs along the west coast of Cotentin. The total number of taxa (80) found on these *Sabellaria* bio-constructions is of the same order of magnitude as that observed by Anadon (1981) on the *Sabellaria* reefs of the Ria de Vigo in Galicia, Spain. On the Cotentin coast, 26 polychaetes are recorded, with a dominance of the Phyllodocidae (*Eumida* spp.), Nereidae (*Perenereis* spp.) and Serpulidae (*Spirobranchus triqueter).* On the Portuguese coast, the total number of taxa is 137, which appears higher than on the Cotentin coast. Polychaetes are the most abundant group on the Cotentin reefs, while the crustaceans dominate in the case of Ria de Vigo. Porras et al. (1996) determined a total of 27 polychaete taxa with a numerical dominance of Cirratulidae, Syllinae, Serpulidae, Nereidae and Phyllodocidae in the *Sabellaria* reefs of the Gulf of Valencia (Spain). On the other hand, La Porta and Nicoletti (2009) recorded a total of 39 polychaetes from the *Sabellaria alveolata* reefs of the central Tyrrhenian Sea (Italy), where the most abundant associated families are the Nereidae, the Phyllodocidae and the Serpulidae. Apart from the polychaetes, the most diversified zoological groups identified in the *Sabellaria* reefs of the western coast of Cotentin are the molluscs, including bivalves and gastropods, and the arthropods, including crustaceans ("Appendix 4"). Among the molluscs, three main categories of taxa are identified: (1) sessile epibiont species, such as the mussel *Mytilus edulis* and the oyster *Crassostrea gigas,* (2) vagile epifauna such as the gastropod *Gibbula* spp. and (3) infauna species such as *Venerupis corrugata*, the cockle *Cerastoderma edule* and the Baltic tellin *Macoma balthica* (but only at the Champeaux site). The arthropods are dominated by the decapods *Porcellana platycheles* and the isopods *Sphaeroma* spp. and *Gnathia dentata*. The sipunculid *Golfingia vulgaris* is present in abundance at the four sampled sites. The fauna collected on the *Sabellaria* bio-constructions is in common with that of the surrounding hard-bottom and soft bottom substrates, especially the muddy sand and gravel sediments which favour the presence of infauna.

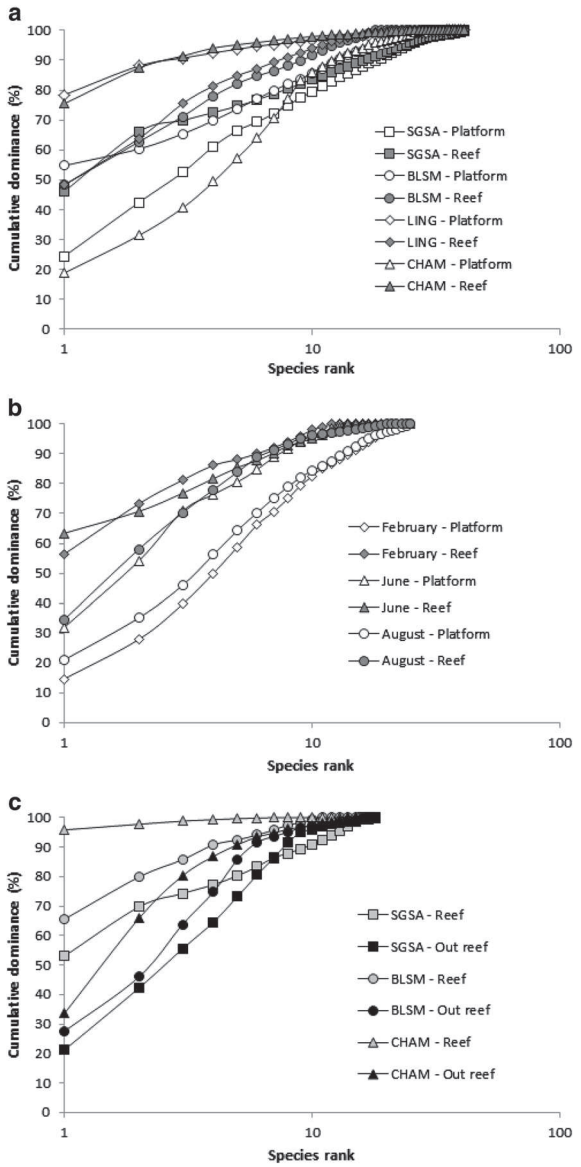


Fig. 5 *k*-dominance curves excluding *S. alveolata*. **a** Spatial comparison (core sampling), **b** Temporal comparison for BLSM (core sampling), **c** inside and outside reefs (quadrat sampling). *CHAM* Champeaux, *LING* Lingreville, *BLSM* Blainville-sur-Mer, *SGSA* Saint-Germain-Sur-Ay

Some taxonomic particularities have been highlighted by Gruet (1970, 1981, 1982), who studied the associated fauna in two areas colonized by *Sabellaria* on the coast of France (in the Bay of Bourgneuf on the Atlantic coast, and in the Bay of Mont-Saint-Michel bordering the western basin of the English Channel).

Gruet (1971) explored the fauna associated with different phases in the construction and destruction of reefs in the Bay of Bourgneuf (growth, flourishing, degradation, death and colonization) in comparison with the surrounding intertidal soft and hard substrates. In the case of dead reefs, Gruet (1971, 1972b) observed that the fauna was characteristic of the surrounding intertidal fauna, with the exception of very high densities of the amphipod *Corophium volutator*, which is a typical species of intertidal estuarine mudflats. Finally, this author (*op. cit.*) stressed that TR was higher during the colonization and destruction phases than during the flourishing reef phase. Subsequently, Gruet (1977) noted some particular features of the associated fauna of the *Sabellaria* reefs in relation to local topography and hydrodynamics.

Gruet (1970) was the first to describe in detail the associated fauna of the famous Saint-Anne reef of the Bay of Mont-Saint-Michel. He recorded a total of 60 taxa, and highlighted the abundance of crevice and cavity species such as the polychaete *Eulalia viridis*, the isopod *Spaeroma monodi* and the sipunculid *Golfingia vulgaris*. These three taxa are among the most dominant in our samples (Tables 3, 4, 8).

Dubois et al. (2002) described the macrofauna associated with the Saint-Anne reef, showing that polychaetes dominate the fauna (41 taxa), and that the associated fauna is more diverse than in the soft-bottom surrounding habitats; the total number of taxa counted in March 2000 from 24 samples was 63, which is lower than in our study (80). However, Dubois et al. (2002) collected a larger number of samples (124) using replicate quadrats ranging in area from 0.032 to 0.1 m^2. TR was found to change within the three stages of reef evolution, i.e. Ball-shaped structures, Platform and Degraded reef. These findings are similar to the results obtained in the present study, which reveal differences in fauna between the platform, reef and degraded reef at Lingreville. Hence, TR appears to be a function of the heterogeneity of the substrate and the successive stages. Moreover, our quadrat samples show that TR is higher outside the reef structure than inside: (1) the fauna recorded on the reef is in common with the surrounding hard and soft-bottom substrates; (2) the TR decreases with increasing abundance of the engineer species *Sabellaria alveolata*, which shows very dense populations >20,000–60,000 ind m^{-2}.

More recently, Dubois et al. (2006) studied the effect of the presence of epibionts (e.g. green algae (*Ulva* spp.) and the oyster *Crassostrea gigas*) on the TR of the Saint-Anne reef. These authors showed that the presence of the oyster had a significant positive effect on TR compared with areas lacking *C. gigas* and with algal-reef type structures.

Moreover, Gruet (1981) has provided some information on the fauna associated with living and dead *Sabellaria* platforms at Champeaux. This author (op.cit.) stressed that the fauna was poor in terms of TR (26 taxa identified) and abundance, probably in relation to its location on the

Table 6 Results of two-way ANOVA on taxonomic richness and total abundance values for the temporal pattern of associated macrofauna on platform and reef structures at BLSM (core sampling)

	Taxonomic richness			Total abundance		
	Df	**F**	***p***	**Df**	**F**	***p***
Date (A)	2	17.21	<0.01	2	15.44	<0.01
Reef/platform (B)	1	5.85	<0.05	1	0.12	0.73
A × B	2	0.72	0.49	2	0.67	0.52
∑	6			6		

F: value of the Fisher law; *p*: probability of the factor or interaction; A = samples made at three dates; B = stations sampled in two structures; (A × B) = interaction between factor A and B

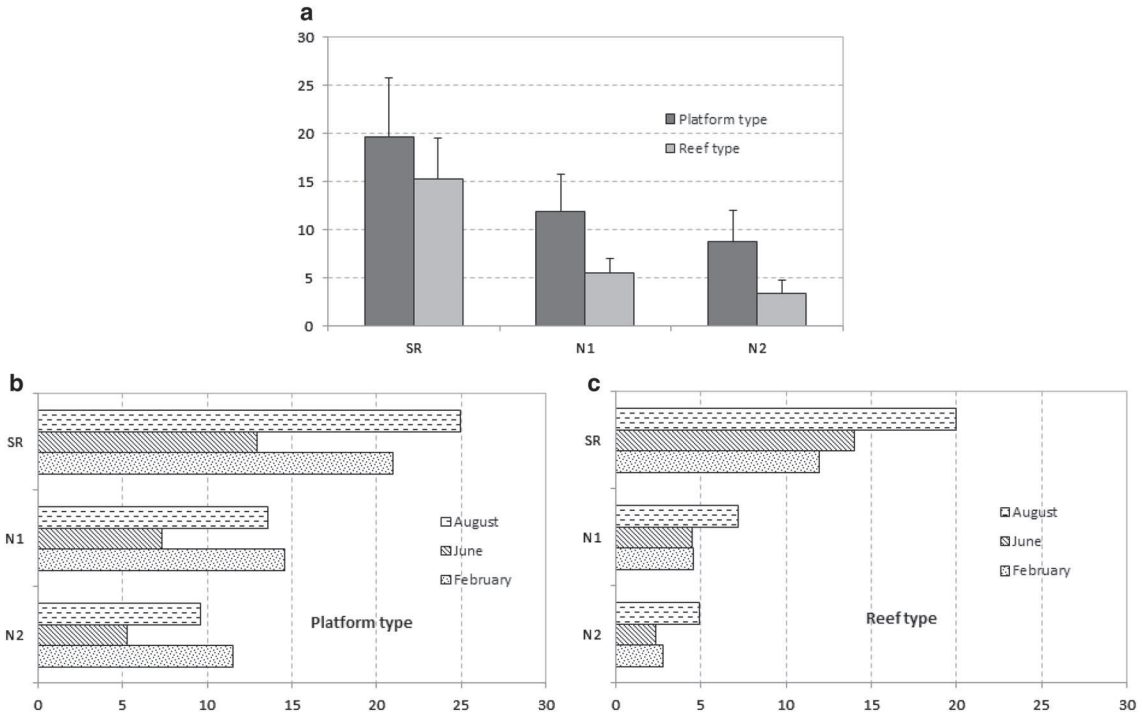


Fig. 6 **a** Values of species richness (SR) and Hill's numbers (N1, N2) for platform and reef-type structures (core sampling); **b, c** values of SR, N1 and N2 for platform and reef-type structures (values excluding *S. alveolata*, for different sampling dates at Blainville-sur-Mer)

Table 7 Results of Two-way ANOVA on taxonomic richness and total abundance values inside and outside reef structures (quadrat sampling)

	Taxonomic richness			Total abundance		
	Df	**F**	***p***	**Df**	**F**	***p***
Inside/outside (A)	1	28.45	<0.01	1	15.05	<0.01
Site (B)	2	7.02	<0.05	2	6.41	<0.05
A × B	2	3.96	<0.05	2	16.77	<0.01
∑	6			6		

F: value of the Fisher law; *p*: probability of the factor or interaction; A = stations sampled inside or outside the reef; B = samples made in three sites; (A × B) = interaction between factor A and B

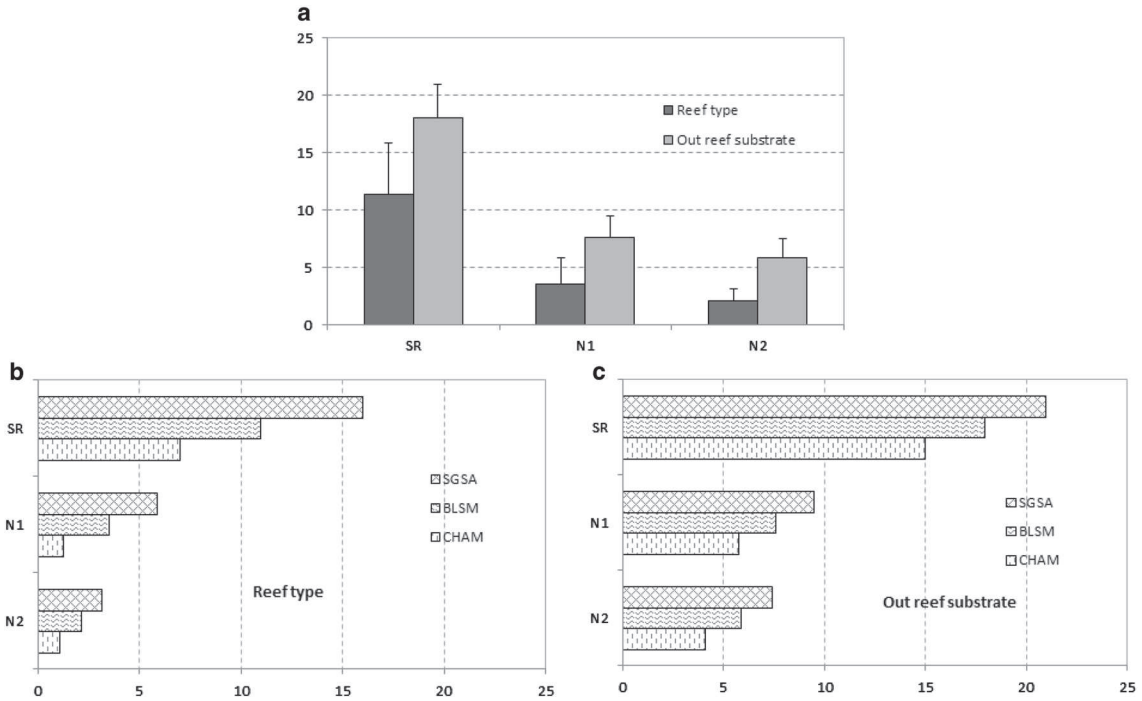


Fig. 7 **a** Values of species richness (SR) and Hill's numbers (N1, N2) inside and outside reefs (quadrat sampling); **b, c** values of SR, N1 and N2 inside and outside reefs (values without *S. alveolata*). *CHAM* Champeaux, *BLSM* Blainville-sur-Mer, *SGSA* Saint-Germain-Sur-Ay

Table 8 Top-ranked species densities (quadrat sampling, mean per 0.1 m^2 ± SD) of macrofauna inside and outside *Sabellaria alveolata* reefs at three sites from the west coast of Cotentin

Site	Rank	Inside Reef		Outside Reef	
		Species	Mean density ± SD		Mean density ± SD
Saint-Germain-sur-Ay		16[a]–3.9[b]		21[a]–7.9[b]	
	1	*Sabellaria alveolata*	22.90 ± 15.62	*Gibbula umbilicalis*	11.00 ± 11.87
	2	*Gibbula umbilicalis*	3.50 ± 3.31	*Boccardia polybranchia*	10.90 ± 27.62
	3	*Gibbula pennanti*	1.10 ± 1.66	*Gibbula cineraria*	6.90 ± 6.21
	4	*Gibbula cineraria*	0.30 ± 0.67	*Patella ulyssiponensis*	4.70 ± 3.33
	5	*Mytilus edulis*	0.20 ± 0.63	*Patella vulgata*	4.50 ± 5.04
Blainville-sur-Mer		11[a]–3.7[b]		18[a]–5.3[b]	
	1	*Sabellaria alveolata*	43.40 ± 24.36	*Gibbula pennanti*	8.50 ± 11.31
	2	*Gibbula umbilicalis*	7.80 ± 7.39	*Gibbula umbilicalis*	5.70 ± 7.04
	3	*Gibbula pennanti*	1.70 ± 3.68	*Gibbula cineraria*	5.50 ± 12.34
	4	*Gibbula cineraria*	0.70 ± 2.21	*Patella ulyssiponensis*	3.40 ± 3.37
	5	*Nassarius reticulatus*	0.60 ± 0.84	*Patella vulgata*	3.40 ± 3.50
Champeaux		7[a]–3.3[b]		15[a]–4.4[b]	
	1	*Sabellaria alveolata*	99.00 ± 58.93	*Spisula solida*	6.38 ± 2.97
	2	*Sphaeroma spp*	55.20 ± 42.54	*Macoma balthica*	6.13 ± 5.57
	3	*Golfingia vulgaris*	1.10 ± 1.97	*Sphaeroma spp*	2.75 ± 3.81
	4	*Mytilus edulis*	0.60 ± 0.97	*Venerupis philippinarum*	1.25 ± 1.39
	5	*Carcinus maenas*	0.30 ± 0.48	*Crepidula fornicata*	0.75 ± 2.12

See "Appendix 3" for taxonomic details and complete species list

[a] Total species number and

[b] Mean species/number per 0.1 m^2 quadrat

upper part of the mid-littoral zone with a long period of exposure of the *Sabellaria* reef. We identify 38 taxa in our samples from the Champeaux site, but our results are based on a more extensive sampling campaign.

Nevertheless, on the west coast of Cotentin, the TR appears to vary between different sites and structures, being higher on the platforms than on the reefs, and higher outside than inside the reef (Tables 3, 4, 8; Figs. 4, 6). This could be due to the fact that *S. alveolata* has developed as a flourishing reef monopolizing the area and volume by imposing a strong competition with other species. In this way, *S. alveolata* has occupied all the available space, where its density reaches and can exceed several thousands of individuals per square metre (Gruet 1971, 1982, 1986). Moreover, Porras et al. (1996), Dubois et al. (2002), and Desroy et al. (2011) pointed out that, in degraded reefs, including eroded reefs during the destruction phase, the TR is much higher than during the other phases of reef evolution. Well-developed reefs show the lowest levels of polychaete TR at several locations such as in Galicia, Spain (Anadon 1981), in the Valencia Gulf (Porras et al. 1996) and in the Tyrrhenian Sea (La Porta and Nicoletti 2009). High TR could be explained by fragmentation of the bio-constructions (Gruet 1970, 1971, 1972a, b, 1977, 1981, 1982, 1986) which leads to a greater structural complexity (Porras et al. 1996). The heterogeneity of the substrate due to the presence of dead or living reef structures gives it an irregular nature with few crevices, which favours the colonization of *Sabellaria* bio-constructions by species from soft- and hard-bottom surrounding habitats. Indeed, during the growth of reef structures, slumps and cracks are formed which create numerous more or less concealed cavities providing shelter for many animals (Gruet 1982). Moreover, since the structures do not evolve synchronously—as in the case of the Champeaux reef—this leads to the persistence of reefs in this area. Because of this, the associated benthic communities always find a favourable place to settle and the reef becomes colonized by species from the surrounding hard-bottom and soft-bottom habitats.

Furthermore, as highlighted by Dubois et al. (2006) the *S. alveolata* bio-constructions show a high TR since the faunal assemblages are composed of associations of taxa typically found on various hard and soft-bottom substrates. Thus, the TR within bio-constructions gives rise to a wide variety of trophic patterns making up a food chain involving not only suspension feeders and detritivores, but also scavengers (Gruet 1982). On the Lingreville site, we note the absence of *S. alveolata* associated with high abundances of *Porcellana platycheles*. According to Gruet (1982), *P. platycheles*, like *Carcinus maenas*, would be one of the main predators of *S. alveolata*.

The environmental conditions associated with a given bio-construction also play an important role in controlling diversity and abundance. In fact, one of the factors producing faunal changes is the position of the structure in the intertidal zone, between the upper and lower part of the mid-littoral zone (Gruet 1982). Indeed, at the four sites studied here, bio-constructions are not all at the same elevation with respect to sea level. The structures at Champeaux are developed in the upper part of the mid-littoral zone, at the foot of a 20-m-high cliff, while the structures of Lingreville, Blainville-sur-Mer and Saint-Germain-sur-Ay are located on the middle part of the mid-littoral zone. In addition, the exposure of the coast to hydrodynamic action, including tidal currents, swell and waves, also plays a major role in controlling the TR found within bio-constructions. Indeed, Gruet (1971 and 1982) observed higher values of TR in the bays, while exposed areas were less favourable for the development of high TR. As regards the present study, Champeaux is located in a more sheltered area compared with open sites exposed to higher energy hydrodynamic conditions such as Lingreville, Blainville-sur-Mer and Saint-Germain-sur-Ay.

The age of the biogenic formation also influences the TR developed on a given structure: this ranges from 5 to 8 years on the western coast of Cotentin. Indeed, Gruet (1971, 1982) pointed out that a certain lapse of time is required for a benthic community to settle, grow and (theoretically) reach equilibrium or a certain degree of maturity. In this context, the TR would be initially low, reaching a stable value indicating equilibrium of the community, while the highest TR would then be recorded along reefs. The time-evolution of TR would appear to be mainly due to the heterogeneity of the habitat and the age of the reef construction (minimum of 3–5 years).

During the 2014 sampling campaign, the surface-area of the platform and reef formations was of the same order magnitude as in 2010–2011: 2.28 km^2 in 2010–2011 as against 2.48 km^2 in 2014 (Basuyaux 2011; Lecornu 2014; Lecornu et al. 2016). At the scale of the four studied sites, the surface-area has remained stable at SGSA (0.11 km^2 in 2010–2011, as against 0.12 km^2 in 2014), but is increasing at CHAM (from 0.31 to 0.37 km^2). There has been a marked decrease in the area covered by bio-constructions at the two other sites (falling from 0.80 to 0.61 km^2 at BLSM and from 0.18 to 0.10 km^2 at LING). At these two latter sites, there has also been an increase in the area covered by degraded reef. Destruction has been observed at BLSM since 2011 (Lecornu 2014; Lecornu et al. 2016) and is continuing up to the present (Dauvin, personal observation): the disappearance of reef-type and degraded platform bio-constructions is probably due to high sedimentation rates, with high-energy hydrodynamics favouring the transport of sediment and *Ruditapes* clams into the same area (Beck et al. 2015). This decline in the *Sabellaria* population was observed in the 2014 survey of BLSM, so the decrease in

abundance of the honeycomb worm reflects a rapid local change between the middle of the winter and the summer, during a destruction phase, followed by colonization by algae (Table 4 and "Appendix 2").

Moreover, recreational fishing for shrimps, crabs and other target species is concentrated on the low mid-littoral and infralittoral fringe on the west coast of Cotentin, whereas *Sabellaria* bio-constructions are located on the middle and upper mid-littoral zones. Reef deterioration caused by human activities is very limited on this part of the coastline and does not represent the same challenge for preservation of the natural heritage as the reefs in the Bay of Mont-Saint-Michel (Desroy et al. 2011). The degradation of the reefs is mainly due to natural factors, such as the hydrodynamic regime and sediment transport in an area with strong tidal currents, and the frequent occurrence of severe winter storms along the Atlantic and English Channel coastlines since the beginning of the 2010 s, especially in 2014. These extreme events could be the consequence of climate changes linked to the anthropogenic increase in atmospheric carbon dioxide.

The importance of *Sabellaria alveolata* (Linnaeus 1767) (Polychaeta: Sabellariidae) reefs has led to their classification as a remarkable natural habitat (listed in Annex I of the Habitats Directive 92/43/EEC; Natura 2000). Thus, *Sabellaria alveolata* reefs are characterized by their great importance for the conservation of natural heritage and marine biodiversity in Europe. The French national inventory of natural heritage (INPN) has recognized *Sabellaria alveolata* reefs (Habitat code 1170-4; Bensettiti et al. 2004) as representing a highly original and localized habitat with high diversity, including rare species. Bensettiti et al. (2004) stresses that a maximal protection of reefs is desired to ensure their sustainability. These authors suggest that the monitoring of water quality is essential for the conservation of these reefs and that human trampling is to be avoided.

The Bay of Mont-Saint-Michel is classified as a Special Zone of Conservation and is a RAMSAR zone (https://inpn.mnhn.fr/docs/natura2000/fsdpdf/FR2500077.pdf). Consequently, the Champeaux and the Sainte-Anne reefs are included in this Marine Protected Area. Monitoring studies have been carried out on these reefs for two decades (Dubois et al. 2002, 2006; Desroy et al. 2011). Farther north, there is no specific MPA and no management measures have been implemented concerning honeycomb worm reefs. In this area, there is a project to set up a Natural Marine Park (http://www.aires-marines.fr/L-Agence/Organisation/Missions-d-etude-de-parc/Golfe-normand-breton), which will involve the mapping and management of natural habitats including *S. alveolata* reefs. In this process, the presence of temporary *S. alveolata* reefs merits special attention.

Conclusions

The objective of this study is to estimate the macrofaunal TR associated with *Sabellaria* bio-constructions (platform and reef types) on hard substrates along the west coast of the Cotentin Peninsula. Spatial analysis allows us to distinguish three groups among the studied sites. Champeaux is different from the other sites because the reef has developed on a soft substrate and the platform is located in the upper part of the mid-littoral zone. Lingreville is characterized by the presence of dead reef, which clearly reflects a degraded phase. The sites of Blainville-sur-Mer and Saint-Germain-sur-Ay are located in the north of the study area, and show similar patterns. The different study sites are found to display highly variable states ranging from a flourishing reef at Champeaux to a completely degraded reef at Lingreville. Some reef destruction is also observed at Blainville-sur-Mer. These results highlight a difference in TR between platforms and reefs, with platforms showing higher TR. Such variability supports the reef effect proposed in previous studies, i.e. a decrease in the TR of other resident macrofauna species in zones more intensely colonized by the honeycomb worm *Sabellaria alveolata*. Therefore, well-developed reefs in a flourishing state do not represent the most diversified habitats in terms of TR. This is because *S. alveolata* occupies all the space, inhibiting the creation of crevices, fissures and pits which offer the best refuges for TR in mosaic habitats developed during the construction and destruction phases of a reef. The project for the creation of a Natural Marine Park should be an opportunity to recognize and manage the natural heritage interest of such temporary reefs on hard bottom habitats along the western coast of Cotentin.

Authors' contributions

ES carried out the field work and identified the species, with the help of AB who assisted in the drafting of figures. ES analysed the results and drafted the manuscript. BL assisted with field sampling and identification of the species. JPP carried out the statistical analyses. JCD and OB designed the studies. JCD coordinated the drafting of the manuscript. All authors read and approved the final manuscript.

Author details

[1] UNICAEN, UNIROUEN, UMR M2C, CNRS 6143, Normandie Univ, 24 Rue des Tilleuls, 14000 Caen, France. [2] CREC, Station Marine, Université de Caen Normandie, 54 Rue du Docteur Charcot, BP 49, 14530 Luc-sur-Mer, France. [3] SMEL, Centre Expérimental, ZAC Blainville-sur-Mer, 50560 Blainville-sur-Mer, France.

Acknowledgements

The authors thank all their colleagues who helped during the field work. This study was funded by the GEDANOR programme of the *'Conseil Régional de Basse-Normandie'* entitled '*Evolution et interactions des* Sabellaria *en secteur conchylicole*' with the financial support of the '*Conseil Départemental*' (Funding is 100 % public). We also thank Michael Carpenter for editing the English style and grammar, and the three anonymous reviewers for their useful comments on the two first versions of the manuscript.

Competing interests

The authors declare that they have no competing interests.

Appendix 1

See Table 9.

Table 9 Species abundances (mean per 1/32 m^2 ± SD) of macrofauna associated with *Sabellaria alveolata* structures

Taxa	Platform type				Reef type			
	CHAM	LING	BLSM	SGSA	CHAM	LING	BLSM	SGSA
Sabellaria alveolata	1182.88 ± 676.30	1.50 ± 2.07	130 ± 53.86	80.00 ± 31.21	771.88 ± 265.52	0.15 ± 0.35	115.75 ± 140.50	242.75 ± 77.12
Polychaete—35 taxa								
Amphitritides gracilis	–	–	0.13 ± 0.35	0.38 ± 1.06	–	–	–	–
Aonides oxycephala	–	–	–	0.50 ± 1.07	–	–	–	0.25 ± 0.71
Arabella iricolor	–	–	–	–		0.13 ± 0.35	–	–
Branchiomma lucullanum	–	–	0.13 ± 0.35	0.63 ± 1.19	–	–	0.13 ± 0.35	0.63 ± 1.41
Capitella sp	2.38 ± 4.47 **[5]**	–	–	–		–	–	–
Caulleriella sp	–	–	–	0.13 ± 0.35	–	–	–	–
Cirratulus cirratus	0.75 ± 1.16	0.13 ± 0.35	–	–	–	–	–	2.63 ± 7.42 **[3]**
Eteone longa	0.13 ± 0.35	–	–	–	–	–	–	–
Eulalia ornata	5.63 ± 4.27 **[1]**	–	0.38 ± 0.52	–	0.13 ± 0.35	–	–	–
Eumida sanguinea	1.88 ± 1.36	0.63 ± 0.92	–	0.63 ± 1.06	0.75 ± 0.89	0.38 ± 0.74	0.25 ± 0.71	0.75 ± 1.04
Glycera tridactyla	0.25 ± 0.46	0.13 ± 0.35	–	–	0.13 ± 0.35	–	–	–
Goniadella bobrezkii	0.38 ± 0.74	0.13 ± 0.35	–	–	–	–	–	–
Hesionidae	–	0.25 ± 0.71	–	–	–	–	–	–
Hilbigneris gracilis	–	–	0.50 ± 0.53	1.38 ± 2.13	–	–	0.13 ± 0.35	0.13 ± 0.35
Lanice conchilega	–	–	–	3.50 ± 2.98 **[5]**	–	–	–	0.13 ± 0.35
Lysidice ninetta	–	–	–	–	–	–	–	0.13 ± 0.35
Lysidice unicornis	–	–	–	–	–	–	–	0.13 ± 0.35
Malacoceros fuliginosus	2.75 ± 4.30 **[3]**	1.75 ± 2.19 **[5]**	0.13 ± 0.35	0.63 ± 1.119	–	–	–	0.38 ± 1.06
Maldanidae	–	–	0.13 ± 0.35	0.13 ± 0.35	–	–	–	0.13 ± 0.35
Malmgreniella ljungmani	–	–	0.13 ± 0.35	0.25 ± 0.46	–	–	–	–
Marphysa sanguinea	–	–	0.13 ± 0.35	–	–	–	–	–
Nereis caudata	–	–	–	0.13 ± 0.35	–	–	–	–
Notomastus latericeus	0.13 ± 0.35	0.13 ± 0.35	0.13 ± 0.35	6.63 ± 6.30 **[3]**	–	–	–	0.50 ± 0.76
Paraonidae	–	–	0.13 ± 0.35	–	–	–	–	–
Perinereis cultrifera	3.75 ± 4.03 **[2]**	0.25 ± 0.46	1.13 ± 1.81 **[3]**	1.00 ± 1.41	0.13 ± 0.35	0.63 ± 0.52	1.00 ± 1.41 **[4]**	1.50 ± 1.51 **[5]**
Pholoe inornata	0.13 ± 0.35	–	–	–	–	–	–	–
Phyllodoce laminosa	–	–	–	–	0.13 ± 0.35	–	–	0.13 ± 0.35
Phyllodoce mucosa	0.25 ± 0.46	0.25 ± 0.46	–	–	–	–	–	–
Platynereis dumerilii	–	–	0.88 ± 0.99 **[5]**	1.63 ± 1.60	–	–	–	0.38 ± 0.52
Polycirrus medusa	0.13 ± 0.35	–	0.38 ± 0.74	1.25 ± 2.38	–	–	–	0.50 ± 1.07

Table 9 continued

Taxa	Platform type				Reef type			
	CHAM	LING	BLSM	SGSA	CHAM	LING	BLSM	SGSA
Schistomeringos neglecta	–	0.13 ± 0.35	–	–	–	–	–	–
Spio sp	0.63 ± 0.92	–	–	0.38 ± 0.74	–	0.13 ± 0.35	–	0.13 ± 0.35
Spirobranchus triqueter	0.25 ± 0.71	–	1.00 ± 1.07 **[4]**	1.88 ± 2.42	0.50 ± 0.76	–	–	1.13 ± 1.13
Sthenelais boa	–	–	–	0.13 ± 0.35	–	–	–	–
Syllidae	2.00 ± 2.00	0.13 ± 0.35	0.25 ± 0.46	0.38 ± 0.74	0.25 ± 0.46	–	–	0.63 ± 1.19
Mollusca—18 taxa								
Acanthochitona crinita	–	–	1.25 ± 1.39 **[2]**	0.50 ± 0.53	–	–	0.13 ± 0.35	0.50 ± 0.53
Cerastoderma edule	0.13 ± 0.35	–	–	–	–	–	–	–
Crassostrea gigas	–	–	0.13 ± 0.35	–	–	–	–	–
Crepidula fornicata	–	0.13 ± 0.35	–	–	–	–	–	–
Gibbula cinneraria	–	0.13 ± 0.35	–	0.50 ± 0.76	–	–	–	0.13 ± 0.35
Gibbula pennanti	–	1.00 ± 1.31	–	0.63 ± 1.19	–	–	0.38 ± 0.74	0.75 ± 1.16
Gibbula umbilicalis	0.13 ± 0.35	2.25 ± 2.82 **[4]**	0.25 ± 0.71	5.75 ± 3.41 **[4]**	–	3.00 ± 1.85 **[4]**	7.13 ± 7.85 **[1]**	1.38 ± 1.77
Goodallia triangularis	–	0.13 ± 0.35	–	–	–	0.13 ± 0.35	–	–
Littorina littorea	–	–	–	–	–	–	0.25 ± 0.71	–
Littorina obtusata	–	–	–	–	–	–	0.25 ± 0.46	–
Mytilus edulis	0.63 ± 0.74	3.13 ± 2.47 **[3]**	–	0.63 ± 1.06	0.50 ± 1.41	1.13 ± 1.25	0.25 ± 0.46	0.88 ± 1.46
Nassarius reticulatus	–	0.25 ± 0.46	–	0.38 ± 1.06	–	–	–	0.63 ± 1.06
Nucella lapillus	–	0.25 ± 0.71	–	–	–	–	–	–
Ocenebra erinaceus	0.13 ± 0.35	–	–	–	0.25 ± 0.46	–	–	–
Ruditapes philippinarum	0.13 ± 0.35	–	0.13 ± 0.35	–	0.13 ± 0.35	–	–	–
Spisula solida	–	–	–	–	0.38 ± 0.74	–	–	–
Trivia monacha	–	–	–	–	–	–	–	0.13 ± 0.35
Venerupis corrugata	0.13 ± 0.35	0.25 ± 0.46	0.75 ± 1.04	0.75 ± 0.46	0.25 ± 0.46	0.38 ± 0.52	0.63 ± 0.52 **[5]**	0.63 ± 0.74
Arthropoda—18 taxa								
Ampithoe rubricata	–	0.25 ± 0.71	0.13 ± 0.35	0.88 ± 1.81	–	0.25 ± 0.71	–	0.13 ± 0.35
Cancer pagurus	–	–	–	–	0.25 ± 0.71	–	–	0.13 ± 0.35
Carcinus maenas	0.38 ± 0.74	0.75 ± 0.71	0.13 ± 0.35	0.88 ± 0.83	1.00 ± 1.07	0.25 ± 0.46	0.13 ± 0.35	1.13 ± 0.83
Cheirocratus spp	–	0.25 ± 0.46	–	–	–	–	–	0.13 ± 0.35
Cyathura carinata	–	–	–	0.13 ± 0.35	–	1.13 ± 1.13	–	–
Dynamene bidentata	–	–	–	0.38 ± 0.52	–	–	0.25 ± 0.46	0.25 ± 0.46
Gnathia dentata	–	–	0.13 ± 0.35	–	0.13 ± 0.35	0.63 ± 1.41	–	–
Idotea granulosa	–	0.13 ± 0.35	–	–	–	–	–	–
Melita palmata	–	1.13 ± 0.64	–	0.13 ± 0.35	0.25 ± 0.46	0.88 ± 0.99	–	1.50 ± 1.41

Table 9 continued

Taxa	Platform type				Reef type			
	CHAM	LING	BLSM	SGSA	CHAM	LING	BLSM	SGSA
Monocorophium acherusicum	–	0.88 ± 0.35	–	–	–	0.63 ± 0.52	–	0.25 ± 0.46
Nymphon sp	–	–	–	–	–	–	–	0.38 ± 0.74
Orchomene humilis	–	0.13 ± 0.35	–	–	–	–	–	–
Palaemon elegans	–	0.25 ± 0.71	–	–	–	–	–	–
Pilumnus hirtellus	–	–	0.38 ± 0.52	1.88 ± 2.03	0.13 ± 0.35	–	0.25 ± 0.71	1.25 ± 1.75
Porcellana platycheles	–	17.25 ± 26.72 **[1]**	0.63 ± 0.92	11.88 ± 14.79 **[2]**	15.75 ± 37.17 **[2]**	7.88 ± 13.25 **[2]**	2.13 ± 2.23 **[2]**	32.50 ± 30.16 **[1]**
Sphaeroma serratum/monodi	2.63 ± 5.07 **[4]**	140.5 ± 55.63	0.38 ± 0.74	1.88 ± 1.64	100.13 ± 66.25 **[1]**	24.38 ± 10.32 **[1]**	0.13 ± 0.35	0.63 ± 1.41
Vaunthompsonia cristata	0.13 ± 0.35	–	–	–	–	0.13 ± 0.35	–	–
Chordata—2 taxa								
Ascidiidae	–	–	–	0.25 ± 0.71	0.88 ± 2.47	–	–	0.38 ± 1.06
Blenniidae	–	0.25 ± 0.71	–	–	–	0.13 ± 0.35	–	0.25 ± 0.46
Sipuncula—1 taxon								
Golfingia (Golfingia) vulgaris	0.25 ± 0.46	0.63 ± 1.06	12.25 ± 8.41 **[1]**	16.13 ± 6.77 **[1]**	5.38 ± 9.53 **[3]**	1.75 ± 2.38 **[5]**	1.25 ± 1.49 **[3]**	14.13 ± 11.57 **[2]**
Nemertea—1 taxon								
Nemertea	1.88 ± 4.55	4.75 ± 3.54 **[2]**	0.38 ± 0.52	0.75 ± 1.04	1.50 ± 2.78 **[5]**	5.88 ± 13.04 **[3]**	0.13 ± 0.35	1.88 ± 1.73 **[4]**
Bryozoa—1 taxon								
Electra pilosa	–	0.13 ± 0.35	–	–	–	–	–	–
Cnidaria—1 taxon								
Actiniaria	2.00 ± 2.07	0.38 ± 0.52	–	–	3.50 ± 5.40 **[4]**	0.75 ± 1.16	–	0.13 ± 0.35
Echinodermata—1 taxon								
Amphipholis squamata	–	0.13 ± 0.35	–	0.13 ± 0.35	–	0.13 ± 0.35	–	0.38 ± 0.74
Insecta—1 taxon								
Axelsonia littoralis	–	–	–	–	0.13 ± 0.35	–	–	–

Bold numbers in brackets are ranks of the top five species (excluding *S. alveolata*)

CHAM Champeaux, *LING* Lingreville, *BLSM* Blainville-Sur-Mer, *SGSA* Saint-Germain-Sur-Ay

Appendix 2

See Table 10.

Table 10 Species abundances (mean per 1/32 m^2 ± SD) of macrofauna associated with *Sabellaria alveolata* on each date at Blainville-sur-Mer

Taxa	Platform type			Reef type		
	February	June	August	February	June	August
Sabellaria alveolata	130 ± 53.86 **[1]**	51.63 ± 44.42 **[1]**	84.38 ± 54.22 **[1]**	115.75 ± 140.50 **[1]**	42.63 ± 38.63 **[1]**	16 ± 16.09 **[1]**
Polychaete—16 taxa						
Amphitritides gracilis	0.13 ± 0.35	–	0.38 ± 0.52	–	–	–
Aonides oxycephala	–	–	0.38 ± 0.74	–	–	–
Eulalia ornata	0.38 ± 0.52	–	0.5 ± 1.07	–	–	0.25 ± 0.71
Eumida sanguinea	–	0.5 ± 1.07 **[5]**	–	0.25 ± 0.71	0.5 ± 0.53 **[5]**	0.13 ± 0.35
Lanice conchilega	–	0.38 ± 0.74	1.88 ± 1.73	–	0.25 ± 0.71	–
Lysidice ninetta	–	–	0.13 ± 0.35	–	–	–
Malacoceros fuliginosus	0.13 ± 0.35	–	–	–	–	–
Maldanidae	0.13 ± 0.35	–	0.25 ± 0.46	–	–	–
Marphysa sanguinea	0.13 ± 0.35	–	–	–	–	–
Nereis caudata	–	0.13 ± 0.35	–	–	0.25 ± 0.46	–
Notomastus latericeus	0.13 ± 0.35	–	2.38 ± 1.69 **[5]**	–	–	–
Perinereis cultrifera	1.13 ± 1.81 **[3]**	–	0.88 ± 1.25	1 ± 1.41 **[4]**	–	2.75 ± 1.49 **[5]**
Platynereis dumerilii	0.88 ± 0.99 **[5]**	–	3.25 ± 4.89 **[3]**	–	–	0.38 ± 0.52
Polycirrus medusa	0.38 ± 0.74	–	–	–	–	–
Spirobranchus triqueter	1 ± 1.07 **[4]**	0.25 ± 0.71	0.38 ± 0.52	–	0.13 ± 0.35	–
Syllidae	0.25 ± 0.46	–	0.38 ± 0.74	–	–	–
Mollusca—11 taxa						
Acanthochitona crinita	1.25 ± 1.39 **[2]**	0.38 ± 0.74	1.13 ± 1.13	0.13 ± 0.35	0.38 ± 0.74	–
Crassostrea gigas	0.13 ± 0.35	–	–	–	–	–
Gibbula cineraria	–	–	–	–	0.13 ± 0.35	–
Gibbula umbilicalis	0.25 ± 0.71	2 ± 1.60 **[3]**	4.88 ± 4.36 **[2]**	7.13 ± 7.85 **[2]**	6.5 ± 3.66 **[2]**	12.38 ± 12.83 **[2]**
Littorina littorea	–	–	0.13 ± 0.35	0.25 ± 0.71	0.13 ± 0.35	0.75 ± 1.39
Littorina obtusata	–	–	–	0.25 ± 0.46	–	–
Mytilus edulis	–	–	0.13 ± 0.35	0.25 ± 0.46	0.13 ± 0.35	0.13 ± 0.35
Nassarius reticulatus	–	–	0.13 ± 0.35	–	–	–
Nucula hanleyi	–	–	0.38 ± 0.74	–	–	–
Ruditapes philippinarum	0.13 ± 0.35	–	–	–	–	0.13 ± 0.35
Venerupis corrugata	0.75 ± 1.04	0.38 ± 0.74	0.75 ± 0.71	0.63 ± 0.52 **[5]**	0.75 ± 1.03 **[3]**	0.13 ± 0.35
Arthropoda—11 taxa						
Ampithoe rubricata	0.13 ± 0.35	–	–	–	–	0.63 ± 1.41
Cancer pagurus	–	0.13 ± 0.35	–	–	–	0.13 ± 0.35
Carcinus maenas	0.13 ± 0.35	–	2.5 ± 2.51 **[4]**	0.13 ± 0.35	0.13 ± 0.35	1.75 ± 2.05
Cyathura carinata	–	0.25 ± 0.71	0.38 ± 1.06	–	–	8.38 ± 6.16 **[3]**
Dynamene bidentata	–	1.5 ± 1.60 **[4]**	0.25 ± 0.46	0.25 ± 0.46	0.25 ± 0.71	0.88 ± 1.25
Gnathia dentata	0.13 ± 0.35	0.13 ± 0.35	–	–	–	0.13 ± 0.35
Idotea granulosa	–	–	0.13 ± 0.35	–	–	–
Melita palmata	–	–	–	–	–	0.13 ± 0.35
Monocorophium acherusicum	–	–	–	–	–	0.13 ± 0.35
Pilumnus hirtellus	0.38 ± 0.52	–	–	0.25 ± 0.71	–	0.13 ± 0.35
Porcellana platycheles	0.63 ± 0.92	2.88 ± 5.36 **[2]**	1.38 ± 2.33	2.13 ± 2.23 **[3]**	0.63 ± 1.06 **[4]**	4.38 ± 3.25 **[4]**

Table 10 continued

Taxa	Platform type			Reef type		
	February	June	August	February	June	August
Cnidaria—1 taxon						
Actiniaria	–	–	–	–	0.13 ± 0.35	2.13 ± 3.23
Echinodermata—1 taxon						
Amphipholis squamata	–	0.13 ± 0.35	0.13 ± 0.35	–	–	–
Insecta—1 taxon						
Axelsonia littoralis	–	–	0.13 ± 0.35	–	–	–

Bold numbers in brackets are ranks of top five species in each studied area

Appendix 3

See Table 11.

Table 11 Species abundances (mean 0.1 m^2 ± SD) of macrofauna associated with *Sabellaria alveolata* reef and outside reef

Taxa	Inside Reef			Outside Reef		
	CHAM	BLSM	SGSA	CHAM	BLSM	SGSA
Sabellaria alveolata	99.00 ± 58.93 **[1]**	43.40 ± 24.36 **[1]**	22.90 ± 15.62 **[1]**	–	–	–
Mollusca—21 taxa						
Acanthochitona crinita	–	0.20 ± 0.63	0.10 ± 0.32	–	0.10 ± 0.32	0.20 ± 0.63
Crepidula fornicata	–	–	–	0.75 ± 2.12 **[5]**	–	–
Gibbula cineraria	–	0.70 ± 2.21 **[4]**	0.30 ± 0.67 **[4]**	–	5.50 ± 12.34 **[3]**	6.90 ± 6.21 **[3]**
Gibbula pennanti	–	1.70 ± 3.68 **[3]**	1.10 ± 1.66 **[3]**	–	8.50 ± 11.31 **[1]**	3.00 ± 2.91
Gibbula umbilicalis	–	7.80 ± 7.39 **[2]**	3.50 ± 3.31 **[2]**	–	5.70 ± 7.04 **[2]**	11.00 ± 11.87 **[1]**
Glycymeris	–	–	–	0.50 ± 1.07	–	–
Lepidochitona cinerea	–	–	–	–	0.10 ± 0.32	–
Littorina littorea	–	0.20 ± 0.42	–	–	0.30 ± 0.95	2.70 ± 3.16
Littorina obtusata	–	–	–	–	0.40 ± 0.97	0.50 ± 0.97
Macoma balthica	–	–	–	6.13 ± 5.57 **[2]**	–	–
Mytilus edulis	0.60 ± 0.97 **[4]**	–	0.20 ± 0.63	–	–	–
Nassarius reticulatus	–	0.60 ± 0.84 **[5]**	–	0.13 ± 0.35	0.60 ± 0.84	0.30 ± 0.67
Nucella lapillus	–	–	–	–	0.50 ± 0.85	3.80 ± 4.80
Nucula hanleyi	–	–	–	–	0.20 ± 0.42	–
Ocenebra erinaceus	–	–	–	–	0.10 ± 0.32	–
Patella intermedia	–	–	–	–	1.80 ± 3.49	1.80 ± 1.99
Patella ulyssiponensis	–	–	–	–	3.40 ± 3.37 **[5]**	4.70 ± 3.33 **[4]**
Patella vulgata	–	–	–	–	3.40 ± 3.50 **[4]**	4.50 ± 5.04 **[5]**
Spisula solida	–	–	–	6.38 ± 2.97 **[1]**	–	–
Venerupis decussata	–	–	–	0.13 ± 0.35	0.10 ± 0.32	–
Venerupis philippinarum	–	–	0.10 ± 0.32	1.25 ± 1.39 **[4]**	–	–
Polychaeta—12 taxa						
Boccardia polybranchia	–	–	–	–	–	10.90 ± 27.62 **[2]**
Cirratulus cirratus	–	–	–	0.25 ± 0.71	–	–
Eumida sanguinea	–	–	–	–	–	0.10 ± 0.32
Glycera tridactyla	–	–	–	0.25 ± 0.71	–	0.10 ± 0.32
Malacoceros fulginosus	–	–	–	–	–	0.10 ± 0.32
Nephtys cirrosa	–	–	–	0.13 ± 0.35	–	–
Nephtys hombergii	–	–	–	0.13 ± 0.35	–	–

Table 11 continued

Taxa	Inside Reef			Outside Reef		
	CHAM	BLSM	SGSA	CHAM	BLSM	SGSA
Notomastus latericeus	–	–	–	0.13 ± 0.35	–	–
Perinereis cultrifera	–	0.10 ± 0.32	0.10 ± 0.32	–	–	–
Platynereis dumerilli	–	–	0.10 ± 0.32	–	–	–
Spirobranchus sp.	–	–	0.10 ± 0.32	–	–	–
Syllidae	–	–	–	–	–	0.20 ± 0.63
Arthropoda—8 taxa						
Balanus spp	–	–	–	++	++	++
Cancer pagurus	0.10 ± 0.32	–	–	–	0.10 ± 0.32	–
Carcinus maenas	0.30 ± 0.48 **[5]**	–	0.20 ± 0.42	–	–	0.40 ± 0.52
Cyathura carinata	–	0.10 ± 0.32	0.10 ± 0.32	–	–	0.10 ± 0.32
Leucothoe incisa	–	–	0.20 ± 0.63	–	–	–
Melita palmata	–	–	0.10 ± 0.32	–	–	–
Porcellana platycheles	0.10 ± 0.32	0.20 ± 0.42	–	–	–	–
Sphaeroma spp	55.20 ± 42.54 **[2]**	–	0.10 ± 0.32	2.75 ± 3.81 **[3]**	0.10 ± 0.32	0.50 ± 1.58
Sipunculidae—1 taxon						
Golfingia vulgaris	1.10 ± 1.97 **[3]**	0.10 ± 0.32	0.10 ± 0.32	–	–	–
Cnidaria—1 taxon						
Actiniaria	0.20 ± 0.42	–	–	–	–	–
Sagartia troglodytes	–	–	–	0.13 ± 0.35	–	0.10 ± 0.32
Chordata—1 taxon						
Ascididae	–	–	0.20 ± 0.63	–	–	–
Porifera—1 taxon						
Porifera	–	0.20 ± 0.63	–	–	–	–

Bold numbers in brackets are ranks of top five species

CHAM Champeaux, *BLSM* Blainville-Sur-Mer, *SGSA* Saint-Germain-Sur-Ay

Appendix 4

See Table 12.

Table 12 List of species and taxa identified during the study

Scientific name	Author	Scientific name	Author
Polychaete		*Nucula hanleyi*	Winckworth, 1931
Amphitritides gracilis	(Grube, 1860)	*Ocenebra erinaceus*	(Linnaeus, 1758)
Aonides oxycephala	(Sars, 1862)	*Patella intermedia*	Pennant, 1777
Arabella iricolor	(Montagu, 1804)	*Patella ulyssiponensis*	Gmelin, 1791
Boccardia polybranchia	(Haswell, 1885)	*Patella vulgata*	Linnaeus, 1758
Branchiomma lucullanum	Delle Chiaje, 1828	*Ruditapes philippinarum*	(Adams & Reeve, 1850)
Capitella sp	Blainville, 1828	*Spisula solida*	(Linnaeus, 1758)
Cauleriella sp	(Southern, 1914)	*Trivia monacha*	(da Costa, 1778)
Cirratulus cirratus	(O. F. Müller, 1776)	*Venerupis corrugata*	(Gmelin, 1791)
Eteone longa	(Fabricius, 1780)	*Venerupis decussata*	(Linnaeus, 1758)
Eulalia ornata	Saint-Joseph, 1888		
Eumida sanguinea	(Örsted, 1843)	**Arthropoda**	
Glycera tridactyla	Schmarda, 1861	*Ampithoe rubricata*	(Montagu, 1818)
Goniadella bobrezkii	(Annenkova, 1929)	*Balanus* spp.	Costa, 1778
Hesionidae	**Grube, 1850**	*Cancer pagurus*	Linnaeus, 1758

Table 12 continued

Scientific name	Author	Scientific name	Author
Hilbigneris gracilis	Ehlers, 1868	*Carcinus maenas*	(Linnaeus, 1758)
Lanice conchilega	(Pallas, 1766)	*Cheirocratus spp*	Norman, 1867
Lysidice ninetta	Audouin & Milne-Edwards, 1833	*Cyathura carinata*	(Krøyer, 1847)
Lysidice unicornis	(Audouin & Milne Edwards, 1833)	*Dynamene bidentata*	(Adams, 1800)
Malacoceros fuliginosus	(Claparède, 1870)	*Gnathia dentata*	(Sars G.O., 1872)
Maldanidae	Malmgren, 1867	*Idotea granulosa*	Rathke, 1843
Malmgrenia ljungmani	(Malmgren, 1867)	*Leucothoe incisa*	(Robertson, 1892)
Marphysa sanguinea	(Montagu, 1815)	*Melita palmata*	(Montagu, 1804)
Nephtys cirrosa	(Ehlers, 1868)	*Monocorophium acherusicum*	(Costa, 1853)
Nephtys hombergii	Savigny in Lamarck, 1818	*Nymphon* sp	Fabricius, 1794
Nereis caudata	(Della Chiaje, 1828)	*Orchomene humilis*	(Costa, 1853)
Notomastus latericeus	Sars, 1851	*Palaemon elegans*	Rathke, 1837
Paraonidae	**Cerruti, 1909**	*Pilumnus hirtellus*	(Linnaeus, 1761)
Perinereis cultrifera	(Grube, 1840)	*Porcellana platycheles*	(Pennant, 1777)
Pholoe inornata	Johnston, 1839	Sphaeroma spp	Latreille, 1802
Phyllodoce laminosa	Savigny in Lamarck, 1818	*Vaunthompsonia cristata*	Bate, 1858
Phyllodoce mucosa	Örsted, 1843		
Platynereis dumerilii	(Audouin & Milne Edwards, 1834)	**Chordata**	
Polycirrus medusa	*Grube, 1850*	*Ascidiidae*	***Herdman, 1882***
Sabellaria alveolata	*(Linnaeus, 1767)*	*Blenniidae*	***Rafinesque, 1810***
Schistomeringos neglecta	*(Fauvel, 1923)*		
Spio sp	Fabricius, 1785	**Sipuncula**	
Spirobranchus triqueter	(Linnaeus, 1758)	*Golfingia (Golfingia) vulgaris*	de Blainville, 1827
Sthenelais boa	(Johnston, 1833)		
Syllidae	Grube, 1850	**Nemertea**	
		Nemertea	
Mollusca			
Acanthochitona crinita	(Pennant, 1777)	Bryozoa	
Cerastoderma edule	(Linnaeus, 1758)	*Electra pilosa*	(Linnaeus, 1767)
Crassostrea gigas	(Thunberg, 1793)		
Crepidula fornicata	(Linnaeus, 1758)	**Cnidaria**	
Gibbula cineraria	(Linnaeus, 1758)	Actiniaria	
Gibbula pennanti	(Philippi, 1846)	*Sagartia troglodytes*	(Price in Johnston, 1847)
Gibbula umbilicalis	(da Costa, 1778)		
Goodallia triangularis	(Montagu, 1803)	**Echinodermata**	
Glycymeris glycymeris	(Linnaeus, 1758)	*Amphipholis squamata*	(Delle Chiaje, 1828)
Lepidochitona cinerea	(Linnaeus, 1767)		
Littorina littorea	(Linnaeus, 1758)	**Insecta**	
Littorina obtusata	(Linnaeus, 1758)	*Axelsonia littoralis*	(Moniez, 1890)
Macoma balthica	(Linnaeus, 1758)		
Mytilus edulis	Linnaeus, 1758	**Porifera**	
Nassarius reticulatus	(Linnaeus, 1758)	Porifera	Grant, 1836
Nucella lapillus	(Linnaeus, 1758)		

Received: 24 November 2015 Accepted: 20 July 2016
Published online: 05 August 2016

References

Anadon N (1981) Contribucion al connocimiento de la fauna bentonico de la ria de Vigo. III. Estudio de los arrecifes de *Sabellaria alveolata* (L.) (Polychaeta, Sedentaria). Invest Pesq 45:105–122
Ayata SD, Ellien C, Dumas F, Dubois S, Thiébaut E (2009) Modelling larval dispersal and settlement of the reef-building polychaete *Sabellaria alveolata*: Role of hydroclimatic processes on the sustainability of biogenic reefs. Cont Shelf Res 29:1605–1623
Basuyaux O (2011) Etude et cartographie de *Sabellaria alveolata* sur la côte ouest du département de la Manche—Focus sur les abords de Granville. Rapport SMEL/CE-env/2011-01, 38 pp
Beck F, Pezy JP, Baffreau A, Dauvin JC (2015) Effects of clam rake harvesting on the intertidal *Ruditapes* habitat of the English Channel. ICES J Mar Sci 72:1663–1673
Bensettiti F, Bioret F, Roland J, Lacoste JP (2004) «Cahiers d'habitats» Natura 2000. Connaissance et gestion des habitats et des espèces d'intérêt communautaire. Tome 2 - Habitats côtiers. MEDD/MAAPAR/MNHN (eds) La Documentation française, Paris, p 399
Commito JA, Rusignuolo BR (2000) Structural complexity in mussel beds: the fractal geometry of surface topography. J Exp Mar Biol Ecol 225:133–152
Delhay JB (2010) Communautés macrobenthiques intertidales du havre et de l'estran de Blainville-sur-Mer (côte ouest du Cotentin) : exemple de l'endofaune des sédiments meubles du havre et des récifs d'hermelles. Rapport de Master 1, Université de Lille 1, France, 46 pp
Desroy N, Dubois SF, Fournier J, Ricquiers L, Le Mao P, Guerin L, Gerla D, Rougerie M, Legendre A (2011) The conservation status of *Sabellaria alveolata* (L.) (Polychaeta: Sabellaridae) reefs in the Bay of Mont Saint-Michel. Aqua Conserv Mar Fresh Ecosyst 21:462–471
Dias AS, Paula J (2001) Associated fauna of *Sabellaria alveolata* colonies on the central coast of Portugal. J Mar Biol Assoc U K 81:169–170
Dubois S, Retière C, Olivier F (2002) Biodiversity associated with *Sabellaria alveolata* (Polychaeta: Sabellaridae) reefs: effects of human disturbances. J Mar Biol Assoc U K 82:817–826
Dubois S, Commito JA, Olivier F, Retière C (2006) Effects of epibionts on *Sabellaria alveolata* (L.) biogenic reefs and their associated fauna in the Bay of Mont Saint-Michel. Estuar Coast Shelf Sci 68:635–646
Gruet Y (1970) Faune associée des récifs édifiés par l'annélide Sabellaria alveolata (Linné) en baie du Mont Saint-Michel: banc des Hermelles. Mém Soc Sc Cherbourg 54:1–21
Gruet Y (1971) Morphologie, croissance et faune associée des récifs de *Sabellaria alveolata* (Linné) de la Bernerie-en-Retz (Loire Atlantique). Tethys 3:321–380
Gruet Y (1972a) Aspects morphologiques et dynamiques de constructions de l'annélide polychète *Sabellaria alveolata* (Linné). Rev Trav Inst Pêch Marit 36:131–161
Gruet Y (1972b) Faune associée de 'récifs' d'Hermelles Polychète Sabellaridé: *Sabellaria alveolata* (Linné): cas de récifs morts à Crève cœur (La Bernerie, Loire Atlantique). Bull Soc Sc Bretagne 47:69–80
Gruet Y (1977) Peuplements de la côte rôcheuse de Sion-sur-l'Océan (Vendée) et faune associée aux « récifs » d'hermelles [*Sabellaria alveolata* (Linné), Annélide Polychète]. Bull Ecol 8:37–55
Gruet Y (1981) Peuplements de l'estran rocheux sur la côte normande de la baie du Mont Saint-Michel à Champeaux: situation et conditions générales. Bull Soc Linn Normandie 109:21–32
Gruet Y (1982) Recherches sur l'écologie des récifs d'Hermelles édifiés par l'Annélide Polychète *Sabelllaria alveolata* (Linné). PhD thesis. Université des Sciences et Techniques, Nantes, France
Gruet Y (1986) Spatio-temporal changes of Sabellarian reefs built by the sedentary polychaete *Sabellaria alveolata* (Linné). P S Z N I: Mar Ecol 7:303–319
Gruet Y, Bodeur Y (1997) Les récifs d'Hermelles. In Les biocénoses marines et littorales françaises des côtes Atlantique, Manche et Mer du Nord, synthèse, menaces et perspectives Collection Patrimoine naturel, IEGB/MNHN Paris/France 28:168–176
Guillaumont B, Hamon D, Lafond LR, Le Rhun J, Levasseur J, Piriou JY (1987) Etude régionale intégrée du Golfe Normano-Breton. Carte biomorpho-sédimentaire de la zone intertidale au 1/25000 Côte Ouest du Cotentin et Baie du Mont Saint-Michel. Notice Explicative. Rapport Ifremer, Direction Environnement et Recherches Océaniques Département Environnement Littoral. Les Presses Bretonnes, St-Brieuc, France, 50 pp + 7 cartes dépliantes couleur
Heip C, Herman PMJ, Soetaert K (1988) Data processing, evaluation and analysis. In: Higgings P, Thiel H (eds) Introduction to the study of meiofauna. Smithsonian Institute Press, Washington DC, pp 197–231
Hill MO (1973) Diversity and evenness: a unifying notationand its consequences. Ecology 54:427–432
Hommeril O (1967) Etude locale (Gouville-sur-mer, Manche) de la retenue des sédiments par deux polychètes sédentaires: *Sabellaria alveolata* (Hermelle) et *Lanice conchilega*. Cah Océanogr (XIVe année) 4:245–257
Hommeril P, Larsonneur C (1963) Quelques effets morphologiques du gel intense de l'hiver 1963 sur le littoral bas-normand. Cah Océanogr (XVe année) 9:638–649
La Porta B, Nicoletti L (2009) *Sabellaria alveolata* (Linnaeus) reefs in the central Tyrrhenian Sea (Italy) and associated polychaete fauna. Zoosymposia 2:527–536
Lecornu B (2014) Suivi de l'évolution des habitats de l'espèce *Sabellaria alveolata* (Linné) sur la côte ouest de la Manche et étude de la biodiversité associée aux récifs. Mémoire de Master 2 AQUACAEN Science des environnements continentaux et côtiers, Université de Caen, France, 95 pp
Lecornu B, Schlund E, Basuyaux O, Dauvin JC (2016) Dynamics (2010–2014) of the *Sabellaria alveolata* reefs on the west coast of Cotentin (France). Reg Stud Mar Sci. doi:10.1016/j.rsma2016.07.004
Porras R, Bataller JV, Murgui E, Torregrosa T (1996) Trophic structure and community composition of Polychaetes inhabiting some *Sabellaria alveolata* (L.) reefs along the Valencia gulf coast, Western Mediterranean. P S Z N I: Mar Ecol 17:583–602
Shannon CE (1948) A mathematical theory of communications. Bell Syst Tech J 27:379–423
Simpson EH (1949) Measurment of diversity. Nature, London 163:688
Wilson DP (1974) *Sabellaria* colonies at Duckpool, North Cormwall, 1971–1972. J Mar Biol Assoc U K 54:393–436

Submit your manuscript to a SpringerOpen journal and benefit from:

- ► Convenient online submission
- ► Rigorous peer review
- ► Immediate publication on acceptance
- ► Open access: articles freely available online
- ► High visibility within the field
- ► Retaining the copyright to your article

Submit your next manuscript at ► springeropen.com