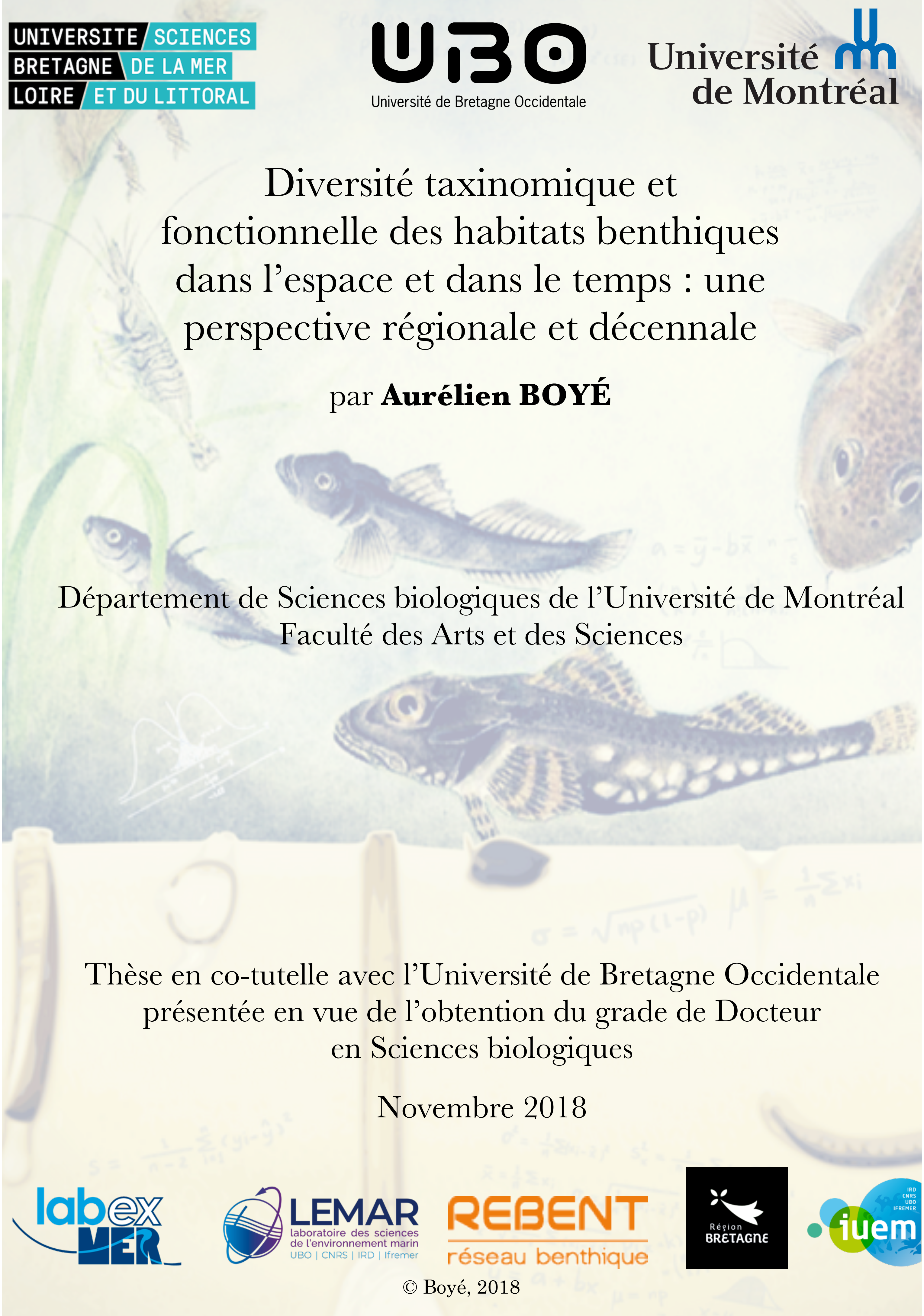

UNIVERSITE BRETAGNE LOIRE / SCIENCES DE LA MER ET DU LITTORAL

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Diversité taxinomique et fonctionnelle des habitats benthiques dans l'espace et dans le temps : une perspective régionale et décennale

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Merci ![1]

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INTRODUCTION

1. Les écosystèmes côtiers

a) Importance à l'échelle globale

Les eaux côtières, à l'interface entre océan et continent, sont des zones de transition reconnues pour leur intérêt majeur à l'échelle globale tant sur un plan écologique que socio-économique (Costanza et al. 1997, Agardy et al. 2005). Les eaux côtières sont des zones très productives avec une production primaire nette comparable à celle de forêts tempérées et même supérieure à celle de forêts équatoriales dans les régions marines les plus riches comme les zones d'*upwelling* (Suchanek 1994, Frontier et al. 2008). Malgré le fait qu'elles n'occupent que 7% de la surface globale des océans et qu'elles constituent moins de 5% de la surface de la planète, les eaux côtières représenteraient près de 20% de la production primaire océanique, 17% de l'assimilation de CO_2 par les océans, 80% de l'enfouissement de matière organique et 90% de la reminéralisation sédimentaire des océans (Gattuso et al. 1998, Agardy et al. 2005, Cai 2011). À cela s'ajoutent les nombreux services écosystémiques qu'elles fournissent comme l'approvisionnement en matières premières et en nourriture, la stabilisation des sédiments et la protection des côtes face à l'érosion, la régulation du cycle des nutriments, ou encore la bioremédiation de polluants (Barbier et al. 2011, Liquete et al. 2013).

Les eaux côtières fournissent aussi des habitats, lieux de vie des espèces (Odum 1953), essentiels pour de nombreuses espèces commerciales (Seitz et al. 2014) qui représenteraient plus de 90% des captures des pêcheries mondiales (Agardy et al. 2005). Ces zones contribueraient ainsi à plus de 70% de la valeur économique estimée de la biosphère (Costanza et al. 1997, Martínez et al. 2007). En outre, les zones côtières recèlent de systèmes extrêmement diversifiés et hétérogènes en termes de climat, de géomorphologie, d'hydrographie ou de géochimie (Spalding et al. 2007, Greenlaw et al. 2011). Cette diversité et cette hétérogénéité promeuvent une grande biodiversité[2] à l'échelle de la planète (Hay & Fenical 1996, Gray 1997, Tittensor et al. 2010, Sanford & Kelly 2011). À titre d'exemple, la facette la plus mesurée de la biodiversité marine est la richesse spécifique (Sala & Knowlton 2006) et celle des eaux côtières représenterait près de 80% de la diversité des espèces marines (Ray 1991).

b) Les habitats biogéniques benthiques: essentiel pour la diversité et le fonctionnement des eaux côtières

La diversité des espèces marines est majoritairement concentrée au niveau des fonds marins (Gray 1997, Snelgrove 1999). Ces derniers recèlent une grande variété d'habitats qui favorise la diversité des organismes vivant dans ou à proximité des fonds marins, le *benthos* (Ray 1991, Ellingsen 2002, Gray 2002). Cette diversité d'habitats provient de l'interaction entre l'importante hétérogénéité environnementale des eaux côtières (Ray 1991, Ellingsen 2001) et la présence au niveau des sédiments de structures physiques générées par certaines espèces benthiques (Thrush & Dayton 2002, Hewitt et al. 2005). Les coraux, les herbiers, les marais salants, ou encore les bancs de maërl ou d'huitres créent des habitats, dits *biogéniques*, dont la présence est reconnue de manière quasi-unanime pour favoriser la diversité des espèces et l'abondance des organismes qu'hébergent les fonds marins (Kovalenko et al. 2012, Sunday et al. 2017). En cela, ces espèces sont considérées comme des espèces « fondatrices » (*sensu* Dayton 1972) et leur étendue spatiale est communément utilisée comme indicateur de l'évolution de la biodiversité à l'échelle globale (Butchart et al. 2010). Mais leur importance ne se restreint pas à leur apport à la biodiversité car ces espèces sont aussi considérées comme des ingénieures autogéniques de l'écosystème (*sensu* Jones et al. 1994). Les ingénieures *autogéniques* sont des espèces qui modifient les conditions de leur milieu environnant *via* leurs propres structures physiques et se distinguent ainsi des ingénieures *allogéniques* qui

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[2] Le terme *biodiversité* se réfère ici à l'ensemble des variations biologiques existantes parmi les organismes vivants et les systèmes écologiques auxquels ils appartiennent, des variations génétiques intra-spécifiques à la diversité d'espèces et d'écosystèmes (Harper & Hawksworth 1994).

transforment leur environnement proximal par leurs activités (*p. ex. Arenicola marina* et son activité de bioturbation). Les espèces formant des habitats biogéniques modifient en effet profondément le fonctionnement des écosystèmes côtiers et la majorité des services écosystémiques que fournissent les eaux côtières serait directement ou indirectement dépendante de ces espèces ingénieures (Barbier et al. 2011, Salomidi et al. 2012). La protection des côtes face aux problèmes d'érosion, le cycle des nutriments avec l'atténuation des problèmes d'eutrophisation, ou encore le support des eaux côtières aux pêcheries, reposent en grande partie sur la présence d'habitats tels que les herbiers, les marais salants, les coraux ou les bancs de maërl (Heck Jr. et al. 2003, McGlathery et al. 2007, Barbier et al. 2011, Duarte et al. 2013, Seitz et al. 2014). Ces habitats constituent en outre des puits de carbone (Duarte et al. 2010) et jouent ainsi un rôle majeur dans la séquestration du carbone atmosphérique en le stockant plus ou moins durablement au sein des sédiments (Fourqurean et al. 2012, Pendleton et al. 2012, Lovelock et al. 2017). Enfin, ces habitats sont très productifs (Duarte & Chiscano 1999, Martin et al. 2005). Cette production bénéficie aux écosystèmes adjacents et est essentielle au fonctionnement des eaux côtières (Heck Jr. et al. 2008). Ainsi, ces habitats biogéniques sont essentiels à la fois à la biodiversité des océans mais aussi à leur fonctionnement et constituent de ce fait des priorités de conservation à l'échelle globale (Hoegh-Guldberg & Bruno 2010, Rice et al. 2012, Bernhardt & Leslie 2013, Duarte et al. 2013).

2. Des écosystèmes particulièrement menacés

La biosphère est aujourd'hui affectée à une échelle globale par l'empreinte des activités anthropiques qui engendrent depuis plusieurs décennies de profondes modifications des communautés naturelles et de leur environnement (Vitousek et al. 1997, Millenium Ecosystem Assessment 2005, Steffen et al. 2011). Néanmoins, l'impact des activités anthropiques sur les systèmes naturels et leur intensité n'est pas homogène sur l'ensemble de la planète (Hoekstra et al. 2005, Halpern et al. 2008). Les écosystèmes marins côtiers apparaissent parmi les plus sévèrement affectés (Lotze et al. 2006, Halpern et al. 2008, Jones et al.

2018). Les zones littorales concentrent en effet de fortes activités anthropiques puisqu'il est estimé aujourd'hui que près de 40% de la population mondiale vit le long des côtes, une proportion pouvant atteindre plus de 80% selon les pays (Martínez et al. 2007). À titre de comparaison, des estimations datant du début du siècle évaluaient que l'Homme utilisait environ 8% de la production primaire des océans alors que ce chiffre s'élève jusqu'à 35% pour les systèmes côtiers tempérés (Vitousek et al. 1997).

a) Multiplicité des pressions affectant les écosystèmes côtiers

Du fait de leur position à l'interface entre océan et continent, les eaux côtières sont soumises à la fois aux influences anthropiques d'origine terrestre et aux pressions affectant directement le milieu marin (Halpern et al. 2008, Crain et al. 2009, Bowler et al. 2018). Ainsi, les écosystèmes marins côtiers sont affectés par les rejets issus des bassins versants. Ces derniers engendrent notamment des problèmes d'eutrophisation liés au rejet massif de nutriments dans les eaux côtières, problèmes qui se sont aggravés au cours des dernières décennies (Nixon 1995, Cloern 2001), menant à une augmentation de la fréquence des phénomènes d'hypoxie, voire d'anoxie (Diaz & Rosenberg 2008, Vaquer-Sunyer & Duarte 2008). À cela s'ajoutent les rejets de polluants chimiques et organiques qui affectent la physiologie des organismes (Islam & Tanaka 2004). Les communautés ont de plus été profondément affectées par une surexploitation des ressources liée à l'intensité des efforts de pêches en zone côtière depuis plusieurs décennies (Jackson et al. 2001, Lotze et al. 2006). De surcroît, les eaux côtières sont les zones les plus touchées à l'échelle de la planète par les problèmes liés aux introductions d'espèces non-indigènes invasives, principalement par les vecteurs du transport maritime et de l'aquaculture (Grosholz 2002, Drake & Lodge 2004). Enfin, ces écosystèmes subissent directement les conséquences des changements globaux qui se manifestent par l'élévation des températures et l'acidification des eaux côtières, par l'élévation du niveau de la mer, ainsi que par des modifications des conditions hydrodynamiques (Harley et al. 2006).

b) La biodiversité marine face à l'homogénéisation des fonds marins

À l'ensemble de ces pressions s'ajoutent en milieu benthique les effets de l'urbanisation croissante des littoraux ainsi que les dégâts physiques qu'imposent les méthodes de pêche invasives comme le dragage ou le chalutage, qui ont provoqué des transformations rapides et profondes des fonds marins côtiers (Hall-Spencer & Moore 2000, Thrush & Dayton 2002, Airoldi & Beck 2007). Les habitats biogéniques apparaissent parmi les plus sensibles à ces multiples pressions (Airoldi & Beck 2007, Bouma et al. 2009, Sunday et al. 2017), avec pour conséquence majeure un « aplanissement » des fonds marins et une homogénéisation des paysages marins benthiques (Thrush et al. 2006, Airoldi et al. 2008). La disparition de ces espèces ingénieures affecte profondément le fonctionnement des écosystèmes côtiers (Coleman & Williams 2002, Bouma et al. 2009) et bouleverse l'ensemble du couplage bentho-pélagique (Cloern et al. 2015, Griffiths et al. 2017). En outre, la disparition de ces espèces « fondatrices » affecte la grande diversité des espèces qui leur sont associées (Hughes et al. 2009, Hoegh-Guldberg & Bruno 2010). Si les espèces vivant dans ces habitats biogéniques ne dépendent pas toutes exclusivement de ces derniers, la disparition de ces habitats est néanmoins considérée comme le deuxième facteur responsable de l'extinction des espèces marines dans les eaux côtières (Lotze et al. 2006).

c) Des interactions complexes à appréhender

Si l'ensemble de ces pressions a d'ores et déjà de profonds impacts sur les communautés marines et le fonctionnement des eaux côtières, il reste aujourd'hui difficile d'appréhender les changements qui découleront de leur continuelle intensification (Halpern et al. 2015, Cloern et al. 2015). La majorité des zones côtières sont affectées par plusieurs facteurs anthropiques (Halpern et al. 2008, Bowler et al. 2018) et il est aujourd'hui évident que toutes ces pressions ne peuvent être considérées ni gérées de manière isolée du fait de leurs interactions (Brook et al. 2008). En effet, leurs effets ne sont pas simplement additifs mais agissent le plus souvent de manière synergique ou antagoniste (Crain et al. 2008, Darling & Côté 2008). Ces interactions rendent le devenir des communautés difficile à appréhender et génèrent des « surprises écologiques » (Paine et al. 1998). Elles constituent d'ailleurs les principales sources d'incertitudes qui limitent notre capacité actuelle à prédire le devenir de la biodiversité (Sala et al. 2000).

À cela s'ajoute la diversité des échelles auxquelles se produisent les réponses des communautés. Ces réponses intègrent des changements aux niveaux génétique, physiologique, écologique et comportemental, ainsi que des changements à l'échelle des communautés et des écosystèmes (Bernhardt & Leslie 2013). Comprendre les réponses à chacun de ces niveaux représente un défi en soi (*p. ex.* Gunderson et al. 2016), auquel s'ajoute celui d'appréhender les interactions qui existent entre ces différentes échelles (Heffernan et al. 2014, Soranno et al. 2014). Des changements, même minimes, peuvent se trouver magnifiés au travers d'interactions entre les différentes échelles, générant ainsi des dynamiques non linéaires complexes dont les exemples sont nombreux en milieu marin (Levin & Lubchenco 2008, Hewitt, Ellis, et al. 2016, Giron-Nava et al. 2017). Ainsi, les processus opérant à une certaine échelle peuvent induire des propriétés émergentes à d'autres (Snelgrove et al. 2014), ce qui rend difficile de prédire comment un changement à un niveau peut se répercuter à d'autres échelles. L'une des difficultés majeures est ainsi la capacité de transférer les connaissances acquises à une échelle donnée vers les échelles supérieures ou inférieures (Mouquet et al. 2015).

Ces problématiques d'échelles prennent tout leur sens lorsque l'on veut appréhender l'évolution temporelle et spatiale des biocénoses de différents habitats car ceux-ci ne réagissent ni aux mêmes facteurs, ni avec la même dynamique. Par exemple, un habitat biogénique tel qu'un herbier est formé par une espèce qui peut être sensible à la température (Nejrup & Pedersen 2008) alors qu'un habitat géologique tel qu'un substrat rocheux ou sédimentaire ne l'est pas. Cela induit notamment des interactions complexes entre changements globaux et perte des habitats (Opdam & Wascher 2004, Mantyka-pringle et al. 2012). De même, alors que les plantes formant les herbiers ont une croissance qui varie entre 20 et 50 cm par an (Marbà & Duarte 1998, Boese et al. 2009), les algues rouges calcaires formant les bancs de maërl ont une croissance inférieure à 0.05 mm par an (Littler et al. 1991). Les temps de réponse et de recouvrement après une perturbation ne seront donc pas les mêmes et sont susceptibles d'avoir d'importantes répercussions sur les biocénoses associées. Enfin, toutes les espèces au sein d'un même habitat ne répondent pas de manière identique aux variations de l'habitat ou hydro-climatiques (Tomas et al. 2015). Appréhender les variations des biocénoses de différents habitats soumis à un ensemble de conditions environnementales qui ne les affectent pas forcément de la même façon est une problème complexe, qui nécessite d'être élucidée en prenant en compte un ensemble d'échelles de variations le plus exhaustif possibles (González-Megías et al. 2007).

3. Étendre les échelles d'étude des communautés benthiques

a) *Les échelles d'étude actuelles en milieu marin benthique*

L'accessibilité des communautés benthiques à l'observation est restreinte (McArthur et al. 2010). Cela a un impact sur les échelles d'études de la diversité marine. En effet, la majorité des connaissances sur les processus qui structurent les communautés marines est à ce jour issue d'études menées à des échelles spatiales et temporelles limitées (Duarte 1999, Witman et al. 2015). Witman et al. (2015) rapportent par exemple que 65,3% des 311 expériences *in situ* qu'ils ont recensées n'étaient conduites qu'en un seul site. Ces expérimentations ou observations à fine échelle ne peuvent rendre compte que d'un sous-ensemble des processus écologiques qui influencent les communautés (Whittaker et al. 2001) et ne peuvent représenter leur entière complexité et variabilité (Witman et al. 2015). De fait, ces résultats ne peuvent pas être directement extrapolés à des échelles supérieures sans générer d'importantes incertitudes et ont donc besoin d'être complémentés par des études à plus grandes échelles propres à prendre en compte les propriétés émergentes entre les différents niveaux d'organisation biologique (Snelgrove et al. 2014, Edgar et al. 2016). Ces études à plus grandes échelles sont aussi nécessaires pour combler le décalage existant entre les connaissances écologiques qui se concentrent à fines échelles et les actions de conservation qui opèrent à des échelles bien plus importantes (Cadotte et al. 2017).

b) L'intérêt des suivis biologiques à grandes échelles spatiales et temporelles

Il y a souvent un compromis à faire entre l'étendue d'un échantillonnage et le grain des observations *c.-à-d.* la taille de l'unité d'échantillonnage (Wiens 1989, Legendre & Legendre 2012). Les études à grandes échelles spatiales en milieu benthique doivent pour ces raisons souvent faire appel à des méthodes télémétriques qui ne donnent accès qu'à des mesures très intégratives des communautés comme l'étendue de certains habitats ou des estimations de biomasses (Edgar et al. 2016). Or, une majeure partie des variations biologiques sont masquées à ces niveaux d'observation (Edgar et al. 2016). Les suivis et inventaires biologiques peuvent offrir un compromis intéressant entre étendue et grain d'étude (Mouquet et al. 2015, Edgar et al. 2016). Le suivi biologique dans le temps de plusieurs sites répartis dans l'espace permet en effet d'intégrer les variations des communautés à des échelles locales, information nécessaire pour pleinement caractériser les relations entre les communautés et leur environnement (Costello 2009), sur de plus ou moins grandes échelles spatiales et temporelles. Cela permet de prendre en compte l'effet de multiples sources de variabilités à de multiples échelles (Ricklefs 2004, Edgar et al. 2016). En outre, ce type de suivi est nécessaire pour faire le lien entre les changements de communautés à des échelles locales et leurs effets à des échelles supérieures, celle des actions de conservation (Cadotte et al. 2017). Ils permettent notamment d'observer si les changements temporels des communautés sont homogènes sur l'ensemble d'une zone d'étude ou si au contraire il existe une interaction espace-temps (Legendre & Gauthier 2014). Cette information est vitale pour savoir si les actions de conservation menées à grandes échelles sont adéquates ou s'il faudrait, au contraire, mettre en œuvre une gestion site-spécifique. Les inventaires biologiques peuvent ainsi complémenter les études expérimentales en apportant des informations à des échelles différentes mais essentielles au maintien des communautés (Whittaker et al. 2001). En outre, ils permettent avec les outils statistiques actuels d’identifier et de guider les observateurs vers les mécanismes structurant potentiellement la diversité à ces échelles (Chase & Myers 2011, Legendre & Gauthier 2014, Hawkins et al. 2017).

Les études à courte durée ne permettent pas de saisir les variations graduelles et lentes qui peuvent s’opérer dans les communautés et qui dégagent une image statique là où un « présent invisible » est à l’œuvre, selon les termes de Magnuson (1990). Ces changements peuvent être masqués par la variabilité naturelle des écosystèmes et provoquer à terme des changements brutaux et de grande ampleur qui ne peuvent être anticipés et prédits sans études à plus longues durées (Scheffer & Carpenter 2003, Hewitt & Thrush 2007, Clare et al. 2017). Les suivis à long terme permettent d’identifier les tendances à long-terme, de les séparer des cycles récurrents et des fluctuations passagères, et de distinguer les effets des impacts anthropiques de la variabilité naturelle des écosystèmes (Luo et al. 2011, Sukhotin & Berger 2013). Ils représentent donc un outil particulièrement pertinent pour l’étude des écosystèmes côtiers qui sont reconnus pour leur nature dynamique et dont la multiplicité des processus et des interactions est difficile à démêler (Mann & Lazier 2006, Cloern & Jassby 2012). Ces suivis offrent aussi l’opportunité de détecter les phases de latence entre un processus et sa réponse (Lindenmayer et al. 2012) et sont nécessaires pour caractériser les nombreux processus non linéaires qui gouvernent le milieu marin (Hewitt, Ellis, et al. 2016, Giron-Nava et al. 2017). Ils fournissent des points de référence précieux pour évaluer l’efficacité d’actions de conservation ou de remédiation (Magurran et al. 2010, Cloern & Jassby 2012).

Les suivis à grandes échelles spatiales sont eux nécessaires pour relier les patrons locaux des communautés aux patrons de diversité à plus grandes échelles, et pour comprendre les facteurs qui régissent ces liens (Ellingsen 2002, de Juan & Hewitt 2011, Zajac et al. 2013). Une grande emprise spatiale permet d’accroître la probabilité d’avoir des facteurs orthogonaux et d’ainsi pouvoir distinguer les effets de différentes variables explicatives (Verheyen et al. 2017). De surcroît, la variabilité spatiale naturelle des communautés peut servir de laboratoire pour étudier comment les communautés actuelles se comportent face à tels ou tels changements environnementaux et ainsi envisager leur devenir (Rustad 2008). Certains sites peuvent par exemple présenter des conditions proches de conditions prévues dans le futur et représenter des *analogues spatiaux* (Carter et al. 2007) dont l'étude peut fournir de précieuses informations sur la capacité d'adaptation et de résilience des communautés (Wogan & Wang 2017).

Il y a souvent un compromis à trouver entre la dimension temporelle et spatiale des études des communautés (Hewitt & Thrush 2007). En effet, du fait des contraintes logistiques et financières des suivis biologiques, ces derniers doivent souvent prioriser l'étendue et l'intervalle d'échantillonnage soit dans le temps (*p. ex.* Hewitt et al. 2016, Lefcheck et al. 2017) soit dans l'espace (*p. ex.* Ellingsen 2002, de Juan & Hewitt 2011). Or, les relations existant entre les espèces et les variables environnementales qui les affectent dans l'espace ne sont pas forcément les mêmes que celles qui s'observent dans le temps (Oedekoven et al. 2017). De plus, les relations qu'ont les espèces avec leur environnement dans l'espace peuvent aussi varier dans le temps (Wlodarska-Kowalczuk et al. 2014, Zuckerberg et al. 2016). Il est donc important de prendre en compte les deux dimensions simultanément (Hewitt & Thrush 2007, Zajac et al. 2013). Cela est d'autant plus critique qu'il y a une relation positive entre les échelles spatiales et temporelles de variations des communautés (Wiens 1989). Ainsi, les variations spatiales à grande échelle des communautés doivent de préférence être intégrées sur de longues périodes pour appréhender l'ensemble des processus qui les génèrent. À ce jour, les études combinant de grandes échelles spatiales et temporelles restent peu nombreuses. Pour ces raisons, de nombreux auteurs prônent encore aujourd'hui une expansion des échelles d'études des communautés pour permettre l'amélioration à la fois de nos connaissances théoriques et de notre capacité de gestion et de conservation du milieu marin (Lawton 1999, Witman et al. 2015, Edgar et al. 2016, Verheyen et al. 2017).

4. Prendre en compte l'ensemble des facettes de la diversité benthique

a) Les variations des communautés et la composante β de la diversité

Dans le but de caractériser différents aspects de la diversité des communautés, Whittaker (1960, 1972) a été le premier à proposer de partitionner la diversité en trois composantes α (*alpha*), β (*beta*) et γ (*gamma*). La diversité α représente la diversité locale des communautés (*p. ex.* la diversité d'un site). La diversité γ est mesurée de manière similaire mais à une échelle supérieure, elle représente la diversité entière d'une région ou d'une zone géographique d'intérêt et est le plus souvent estimée à partir de l'agrégation de l'ensemble des observations faites dans cette zone géographique (Legendre et al. 2005). La diversité β est mesurée différemment puisqu'elle est définie comme une variation des assemblages d'espèces. Cette notion de diversité β regroupe à la fois les changements directionnels des communautés *c.-à-d.* leur *turnover* le long de gradients environnementaux, spatiaux, ou temporels, et les variations non-directionnelles des communautés *c.-à-d.* la variation des communautés parmi les unités d'étude au sein de la zone géographique ou de la fenêtre temporelle d'intérêt (Legendre et al. 2005, Anderson et al. 2011).

L'étude de la diversité β des communautés a connu un essor au début du siècle (Anderson et al. 2011) après avoir été longtemps négligée, notamment en milieu marin où la majorité des études étaient confinées à des mesures de richesse locale des communautés (Gray 2000). Or, la connaissance de la diversité α ne donne qu'une vision partielle des communautés qui ne permet pas d'appréhender pleinement leur structure spatiale et temporelle, ni les processus qui les gouvernent (Figure 1; McGill et al. 2015, Socolar et al. 2016a). L'identité des espèces et leurs variations dans le temps ou l'espace doivent être pris en compte pour saisir les changements qui affectent les communautés (Magurran & Henderson 2010). La diversité β fait ainsi le lien entre la diversité aux échelles locales (α) et le réservoir régional d'espèces (γ) en révélant les dissimilarités de composition entre les différents assemblages locaux de la région et leur potentielle complémentarité (Cornell & Lawton 1992, Loreau 2000). Elle permet d'analyser l'effet de gradients environnementaux et d'appréhender et quantifier les sources de variations des communautés qu'elles soient spatiales ou temporelles (Anderson et al. 2011). Elle permet enfin de baser les actions de conservation non seulement sur la diversité locale des communautés mais aussi sur l'unicité des assemblages dont les sites recèlent (Mumby 2001, Legendre & De Cáceres 2013). En cela, la diversité β représente un lien clé pour intégrer les actions de conservation à toutes les échelles (Socolar et al. 2016a).

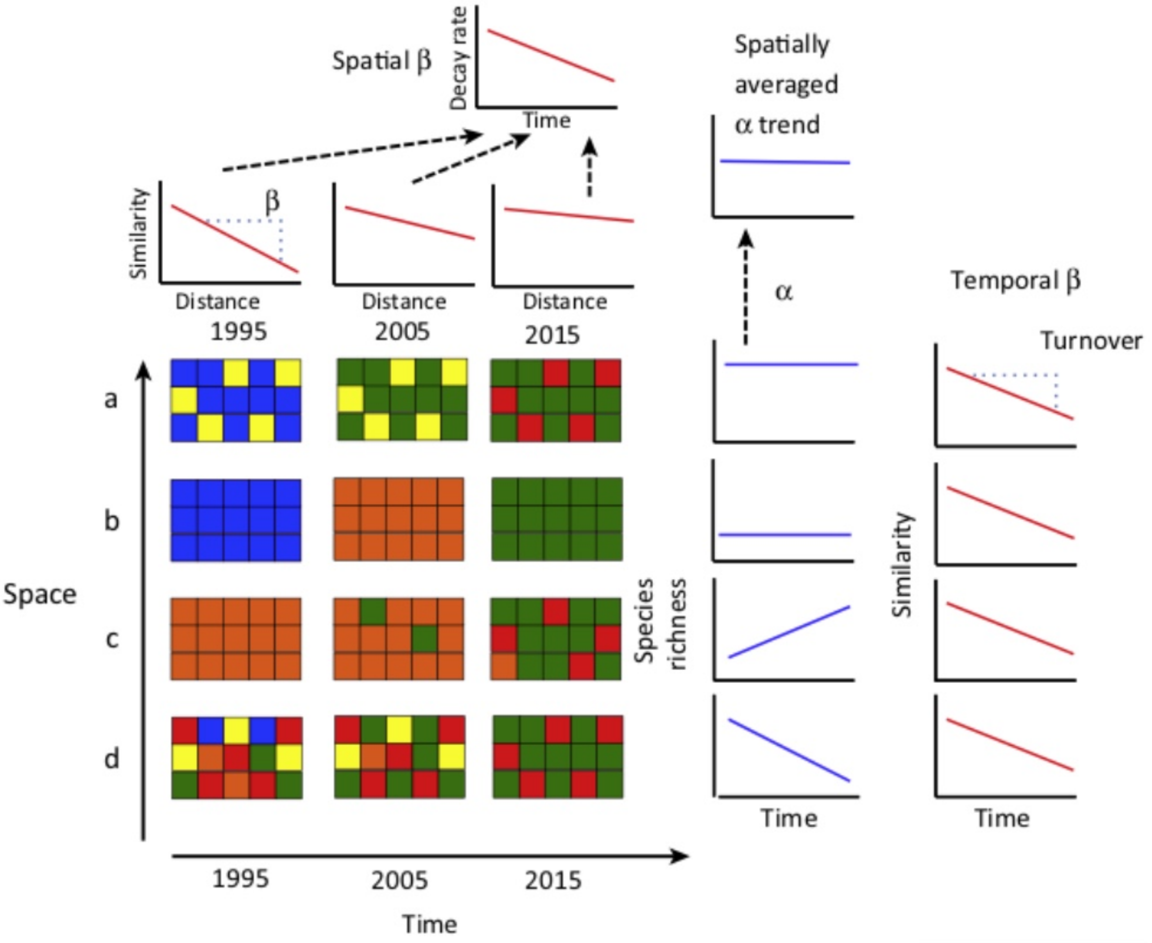

Figure 1. *Illustration des différentes relations existantes dans l'espace et le temps entre la diversité α et β, extraite de McGill et al. (2015). La richesse locale de deux communautés peut être similaire malgré des compositions d'espèces différentes. De ce fait, une communauté peut apparaître stable dans la temps au regard de sa richesse taxinomique, tout en ayant subit des modifications de sa composition c.-à-d. de l'identité des espèces qui la compose. Ces différences doivent être prises en compte pour appréhender comment les modifications locales des communautés se répercutent à de plus plus grandes échelles spatiales.*

b) L'homogénéisation benthique et ses effets sur les différentes facettes de la diversité

Du fait du parallèle qui peut être dressé avec ce qui a été observé en milieu terrestre (McKinney & Lockwood 1999), l'homogénéisation benthique est généralement reconnu comme la menace la plus sérieuse portant sur la biodiversité marine à l'avenir (Gray 1997, Hoegh-Guldberg & Bruno 2010, McCauley et al. 2015). Cette homogénéisation est l'illustration de l'effet que peuvent avoir les activités anthropiques aux différentes échelles qui génèrent et structurent la diversité (Figure 2). Les habitats structurellement complexes sont ceux qui disparaissent en priorité. Or, ils sont reconnus pour favoriser la diversité α des communautés (Kovalenko et al. 2012, Sunday et al. 2017). Mais la menace que leur disparition représente pour la diversité ne peut se résumer à cette perte locale de diversité (Airoldi et al. 2008). En effet, de nombreuses études montrent que la diversité et l'hétérogénéité des habitats qui couvrent les fonds marins favorisent la diversité β, et corollairement la diversité γ (Ellingsen 2002,

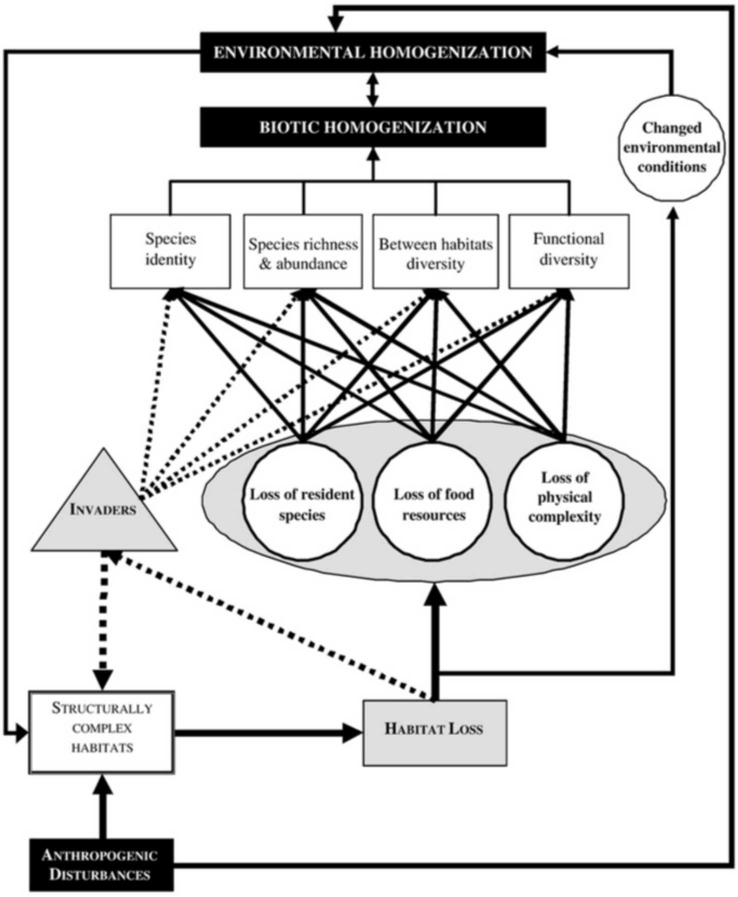

Figure 2. *Illustration des liens entre les impacts anthropiques, la perte des habitats benthiques les plus complexes et les différentes facettes de la diversité des communautés ainsi que des possibles interactions entre ces différentes processus résultant* in fine *à l'homogénéisation biotique des fonds marins (extraite de Airoldi et al. 2008)*

Hewitt et al. 2005, de Juan et al. 2013, Zajac et al. 2013). L'homogénéisation des fonds marins mène ainsi à une disparition de la faune caractéristique de chaque habitat, menaçant les espèces les plus spécialistes au profit d'espèces généralistes (Thrush et al. 2006). Cela se traduit par une augmentation de la similarité entre les biocénoses de différentes localisations ou régions, induisant un appauvrissement de la diversité des espèces à de grandes échelles spatiales du fait de la réduction de la diversité β (Olden & Rooney 2006).

Cette homogénéisation des communautés benthiques ne tient pas son origine à la seule perte des habitats biogéniques et à l'aplanissement des fonds marins. Cela semble en effet être l'une des conséquences les plus répandue des multiples pressions anthropiques qui affectent les écosystèmes aquatiques (Balata et al. 2007, Airoldi et al. 2008, Donohue et al. 2009, Quillien et al. 2015a). Or, les patrons de diversité β des communautés benthiques, dans le temps et l'espace, restent grandement inexplorés ce qui nous empêche d'évaluer pleinement l'empreinte des activités anthropiques sur la diversité des communautés (Olden & Rooney 2006, Airoldi et al. 2008). Caractériser cette composante de la diversité demeure une priorité de recherche, particulièrement à grandes échelles spatiales et temporelles (McGill et al. 2015). Airoldi et al. (2008) soulignaient ainsi le manque de programmes de suivi des communautés à grandes échelles spatiales et temporelles en zones tempérées et le déficit des connaissances qui en découlait relatif aux patrons de diversité inter-habitats. Rares en effet sont les études décrivant les patrons de diversité β entre habitats benthiques à une échelle régionale *c.-à-d.* > 100 km (Hewitt et al. 2008, de Juan & Hewitt 2011). Les efforts récents pour caractériser la diversité β entre différents habitats benthiques restent encore restreints à l'échelle de baies ou d'estuaires *c.-à-d.* < 10^{aine} km (*p. ex.* Hewitt et al. 2005, Josefson 2009, Törnroos et al. 2013, Zajac et al. 2013, Urra et al. 2017). De plus, les variations qui peuvent exister intra-habitat, notamment à grandes échelles spatiales (*p. ex.* Boström et al. 2006), sont souvent négligées dans les études de diversité β inter-habitats à ce jour (Törnroos et al. 2013). Ces variations intra-habitats ont le potentiel d'affecter notre appréciation des patrons spatiaux de diversité si elles ne sont pas prises en compte de manière adéquate, ce qui peut entraver notre capacité à cartographier et gérer la diversité à grandes échelles spatiales (Ferrier 2002, Fraschetti et al. 2008).

Une amélioration des connaissances sur les patrons de diversité des communautés à grandes échelles spatiales et temporelles est aujourd'hui nécessaire pour réconcilier les échelles auxquelles se déterminent les actions de conservation et les échelles auxquelles les connaissances écologiques sont disponibles (Cadotte et al. 2017). Il s'agit là d'un besoin urgent pour les acteurs de la conservation du milieu marin (Goldsmith et al. 2015). La classification et la cartographie des habitats benthiques constitue un point focal des actions de conservation (Ward et al. 1999, Costello 2009, McArthur et al. 2010, Buhl-Mortensen et al. 2014). Utiliser la distribution des habitats benthiques comme indicateur de la diversité apparaît comme une méthode idoine pour optimiser le coût et les expertises nécessaires à la mise en place des stratégies de conservation (Dalleau et al. 2010) et ainsi combler les manques de données actuels sur la répartition de la diversité marine à grandes échelles (Costello et al. 2010). Cependant, les indicateurs de diversité utilisés jusqu'à présent en milieu marin ont souvent une faible congruence avec les patrons de diversité qu'ils sont censés décrire (Stevens & Connolly 2004, Mellin et al. 2011).

En effet, les habitats benthiques sont le plus souvent définis à partir des types de substrat qui caractérisent les fonds marins et notamment des structures physiques ou biologiques qui s'y trouvent (*p. ex.* herbier, maërl, champ de laminaires) ou de leurs caractéristiques abiotiques comme la topographie ou la granulométrie de sédiments (Allee et al. 2000, Airoldi & Beck 2007, Törnroos et al. 2013). Ces caractéristiques sont facilement accessibles et cartographiables et constituent donc des indicateurs pratiques pour évaluer la diversité des espèces à grande échelle spatiale (Fraschetti et al. 2008, Costello 2009). Mais cette définition de l'habitat comme « *l'environnement physique dans lequel vivent les espèces* » souvent utilisée en milieu marin (Costello 2009) est réductrice par rapport au concept écologique originel de l'habitat (Odum 1953). Elle correspond à une définition opérationnelle (Hall et al. 1997) mais n'intègre pas l'ensemble des conditions qui permettent la survie des espèces, le sens premier du terme habitat (Southwood 1977, Krausman 1999). Il y a ainsi de nombreux autres facteurs biotiques[3] et abiotiques qui gouvernent les communautés à de multiples échelles (Levin 2000, Whittaker et al. 2001). Il est donc nécessaire d'éprouver et de calibrer ces outils pour s'assurer de leur pertinence et de leur capacité à représenter pleinement les patrons écologiques des communautés (Dalleau et al. 2010, Ferraro 2013, Törnroos et al. 2013). Pour les utiliser comme des indicateurs de diversité adéquats et s'assurer qu'ils constituent des unités de gestion appropriées, il faut d'abord caractériser le lien communauté-habitat sous une variété de conditions environnementales et en prenant en compte à la fois les variations intra- et inter-habitats, ainsi que l'influence de l'ensemble des autres facteurs gouvernant les communautés benthiques. Cela passe par l'évaluation des communautés à des échelles locales mais sur une emprise spatiale suffisante pour prendre en compte les multiples échelles et sources de variation des communautés (Ricklefs 2004). Cette caractérisation des patrons de variation des communautés à grandes échelles, prenant en compte l'ensemble des facettes de leur diversité, est essentielle pour établir des scénarios réalistes du devenir des communautés benthiques face à l'homogénéisation des habitats (Airoldi et al. 2008).

5. Lien entre diversité des communautés et fonctionnement

Les habitats benthiques et les communautés qu'ils abritent jouent un rôle clé dans le fonctionnement des eaux côtières (Snelgrove et al. 2014) dont ils assurent une bonne partie des services écosystémiques (Barbier et al. 2011, Salomidi et al. 2012). S'il est important d'appréhender les patrons spatiaux et temporels de la diversité benthique, il est donc tout aussi essentiel d'en évaluer les conséquences sur le fonctionnement des eaux côtières. L'érosion de la diversité à l'échelle globale est l'un des facteurs majeurs mettant en péril le

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[3] La prédation, le parasitisme, le mutualisme, le partitionnement des ressources entre espèces et les exclusions compétitives, les variations liées au recrutement des organismes et à la connectivité entre les communautés, ainsi que la dérive liée aux processus démographiques stochastiques (Ricklefs 1987, Vellend et al. 2014).

fonctionnement des écosystèmes et les services écosystémiques qu'ils fournissent (Chapin et al. 2000, Cardinale et al. 2012, Hooper et al. 2012). Une plus grande diversité d'espèces favorise en général le fonctionnement, *c.-à-d.* la performance globale (*cf.* Jax 2005), des écosystèmes, qu'ils soient terrestres (Hooper et al. 2005, Tilman et al. 2014), ou marins (Worm et al. 2006, Stachowicz et al. 2007, Gamfeldt et al. 2015, Strong et al. 2015). La combinaison de deux mécanismes peut expliquer cette relation positive entre diversité et fonctionnement (Stachowicz et al. 2007, Cardinale et al. 2012). Le premier est la *complémentarité* entre les espèces. Une communauté diversifiée a une plus grande probabilité de contenir des espèces dont les caractéristiques biologiques soient variées, permettant une meilleure exploitation des ressources *via* des phénomènes de facilitation et de partition de niches écologiques[4]. Le deuxième est l'effet d'*identité*. Une communauté diversifiée a une plus grande probabilité de contenir une espèce dont l'effet sur le fonctionnement de l'écosystème soit fort. Ainsi, toutes les espèces ne sont pas égales. Le fonctionnement des écosystèmes ne dépend donc pas directement de la diversité taxinomique des espèces présentes dans une communauté mais des caractéristiques biologiques, des *traits fonctionnels,* qu'expriment ces espèces (Hooper et al. 2005, Petchey & Gaston 2006, Cardinale et al. 2012). Selon les caractéristiques de ces espèces, la relation entre diversité et fonctionnement pourra prendre différentes formes. Elle pourra être linéaire et positive si toutes les espèces diffèrent dans leur rôle et se complètent, saturer à un certain niveau de diversité si plusieurs espèces remplissent les mêmes fonctions (*redondance fonctionnelle ;* Naeem & Wright 2003), voire être négative selon les interactions entre les espèces (Stachowicz et al. 2007, Strong et al. 2015).

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[4] Hutchinson (1957) a définit la niche réalisable d'une espèce comme étant l'enveloppe de conditions (*c.-à-d.* un hypervolume où chaque dimension représente une ressource ou une variable environnementale) dans laquelle une espèce est capable de maintenir une population viable sur le long terme. La niche réalisée est l'espace de cette niche fondamentale que l'espèce est contrainte d'occuper du fait des compétitions avec les autres espèces.

Un *trait fonctionnel* est défini comme *toute caractéristique morphologique, physiologique ou phénologique mesurable à l'échelle d'un individu* (Violle et al. 2007) déterminant l'effet des organismes sur les processus d'un écosystème (*trait effet*) ou leur réponse à leur environnement (*trait réponse* ; Lavorel & Garnier 2002). Les mesures de *diversité fonctionnelle*, qui prennent en compte les distribution de ces traits au sein des communautés, mettent d'avantage en exergue la complémentarité et les différences entre les espèces que les mesures de diversité spécifique classiques, ce qui en font potentiellement de meilleurs prédicteurs des propriétés fonctionnelles des écosystèmes (Cadotte et al. 2011, Tilman et al. 2014). Les traits fonctionnels ne sont pas des mesures directes des processus d'un écosystème mais représentent des *proxys* efficaces de multiples fonctions écologiques (Thrush & Lohrer 2012, Villnäs et al. 2013, Bolam & Eggleton 2014). Analyser de multiples traits fonctionnels permet donc de considérer la *multifonctionnalité* des écosystèmes *c.-à-d.* comment les multiples processus des écosystèmes se comportent simultanément, ce qui est primordial pour appréhender le fonctionnement des écosystèmes (Hector & Bagchi 2007, Gamfeldt et al. 2008, Lefcheck et al. 2015). Ces données sur la multifonctionnalité des écosystèmes sont actuellement manquantes (Manning et al. 2018), tout comme les informations à grandes échelles spatiales et temporelles qui puissent intégrer l'hétérogénéité, la variabilité naturelle et les interactions des processus écologiques au sein des écosystèmes marins (Stachowicz et al. 2007, Snelgrove et al. 2014, Gamfeldt et al. 2015).

Les traits fonctionnels représentent un outil intéressant, et complémentaire aux manipulations expérimentales, pour relier les patrons taxinomiques aux processus qui gouvernent les écosystèmes et approfondir nos connaissances sur leur fonctionnement à grandes échelles spatiales et temporelles (Naeem & Wright 2003, Thrush & Lohrer 2012). De plus, s'il est souvent difficile d'identifier des processus écologiques par la seule observation des patrons taxinomiques qu'ils génèrent (Wagner & Fortin 2005), appréhender les variations des traits fonctionnels des espèces en lien avec les changements de leur environnement biotique et abiotique peut informer sur les mécanismes qui gouvernent les communautés (Beauchard et al. 2017, Cadotte & Tucker 2017). L'intérêt des approches par traits fonctionnels est ainsi double car elles permettent d'explorer 1) les mécanismes responsables des changements de communautés et 2) les conséquences de ces changements sur le fonctionnement des écosystèmes (Figure 3 ; Suding et al. 2008, Cadotte et al. 2011, Salguero-Gómez et al. 2018). Ces méthodes ont ainsi le potentiel d'apporter d'importantes informations pour permettre de mieux envisager les impacts fonctionnels de l'homogénéisation des paysages benthiques (Airoldi et al. 2008, Bremner 2008, Villéger et al. 2013).

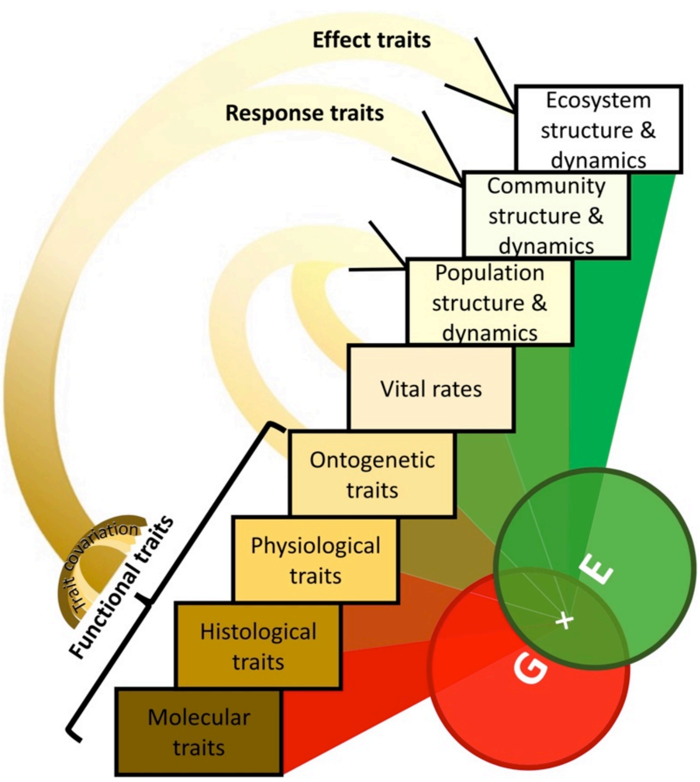

Figure 3. *Les approches par traits biologiques s'inscrivent dans un cadre conceptuel permettant de relier les mécanismes gouvernant la structure et la dynamique des populations et des communautés, de leurs déterminants génétiques (G) à leurs réponses à l'environnement (E), à leurs effets sur le fonctionnement des écosystèmes (Figure extraite de Salguero-Gómez et al. 2018).*

6. Contexte et objectifs de la thèse

a) Description de la région d'étude : la Bretagne

La Bretagne est une zone de transition biogéographique (Dinter 2001, Gallon et al. 2017) qui se partage entre deux régions marines : la Manche-Mer du Nord et le golfe de Gascogne (Figure 4). Un front hydrologique important séparant des eaux stratifiées au sud et des eaux plus homogènes au nord constitue la démarcation entre ces deux zones biogéographiques (Derrien-Courtel et al. 2013, Quillien et al. 2015b). De par cette caractéristique, la Bretagne représente une limite de distribution pour de nombreuses espèces benthiques

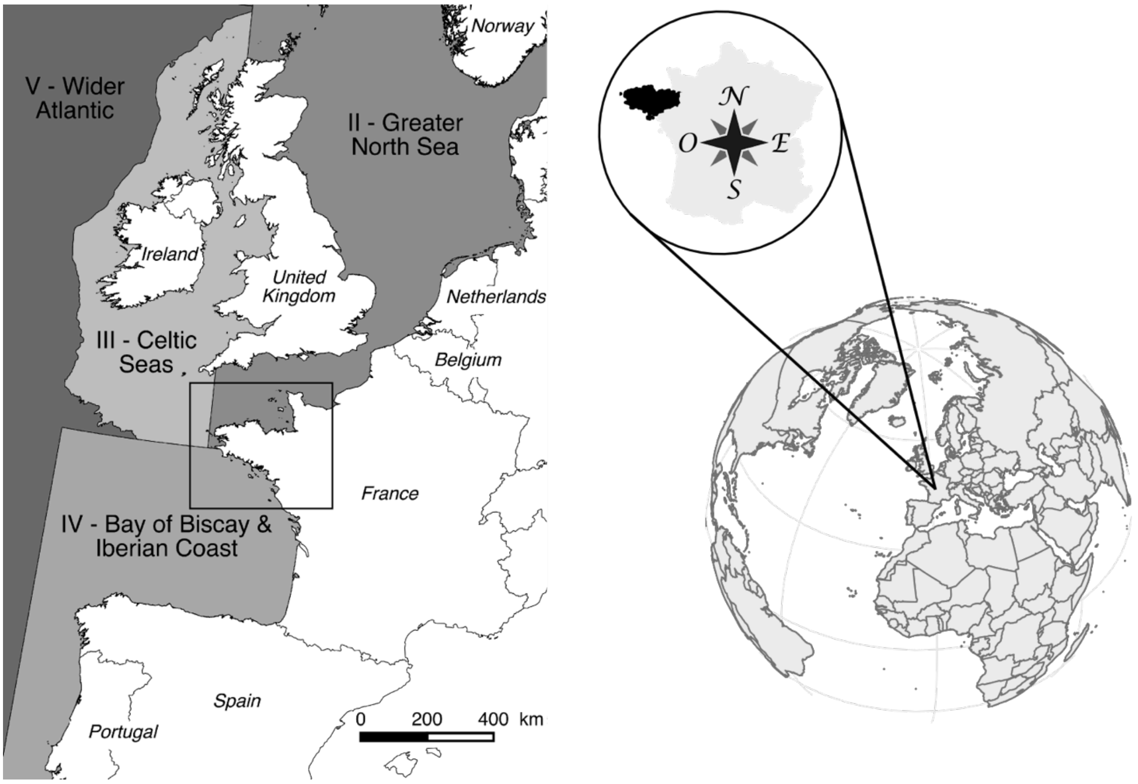

Figure 4. *La Bretagne, encadrée en noir dans la carte de gauche, est située dans l'Atlantique Nord Est et constitue une zone de transition biogéographique entre deux régions marines définies par la commission OSPAR (Dinter 2001) : la région II au nord de la Bretagne formée par la Manche et la mer du Nord, et la région IV au sud de la Bretagne constituée par le Golfe de Gascogne.*

(Dauvin et al. 2006, Duff & Grall 2012, Quillien et al. 2012). Elle constitue donc une zone de suivi d'un grand intérêt face aux changements climatiques et aux changements de distribution des espèces (Derrien-Courtel et al. 2013). Cette région se distingue aussi par la diversité et l'hétérogénéité des conditions topographiques et hydrodynamiques qu'elle abrite : allant des estuaires, des golfes ou des baies abritées, à des îles exposées, en passant par tout un éventail de conditions semi-exposées. Cela se traduit par une grande variété de conditions hydrologiques et sédimentaires, d'eaux turbides aux fortes influences d'eau douce et aux sédiments vaseux, à des eaux pleinement marines aux sédiments plus ou moins grossiers (Derrien-Courtel et al. 2013, Gallon et al. 2017). La diversité et l'hétérogénéité de ces conditions semblent favoriser une grande richesse spécifique à l'échelle régionale, faisant de la Bretagne une région remarquable par sa diversité macrobenthique particulièrement élevée (un *hotspot* de diversité; Gallon et al. 2017). En outre, cette région est d'un intérêt particulier pour ses systèmes intertidaux car elle est soumise à un régime macrotidal avec un marnage en période de vives eaux généralement compris entre 4 et 8 m selon les localisations, avec certaines zones pouvant même être considérées comme mégatidales (*p.ex.* en baie du Mont Saint-Michel avec près de 12 m ; Garcia 2010, Quillien et al. 2015b).

b) La macrofaune comme objet d'étude

Cette thèse se concentrera sur la *macrofaune* qui constitue une part importante de la diversité des fonds marins (Snelgrove 1998). Elle est définie comme l'ensemble des invertébrés marins benthiques de taille supérieure à 1 mm, vivant dans le sédiment *c.-à-d. endofaune*, ou sur un substrat de manière attachée ou libre, *c.-à-d. épifaune*. Ces organismes revêtent un rôle clé dans le transport et la transformation de la matière organique, dans le cycle des nutriments, dans l'enfouissement et l'épuration des polluants, dans la production secondaire et dans les réseaux trophiques marins (Snelgrove 1998, Levin et al. 2001, Mermillod-Blondin 2011). Ils sont de ce fait essentiels au couplage bentho-pélagique qui régit le fonctionnement des écosystèmes marins côtiers (Frontier et al. 2008, Griffiths et al. 2017). La macrofaune possède aussi une valeur économique, esthétique, culturelle et récréative importante en région Bretagne en raison de l'importance des pratiques de pêche à pied dans la région (Hitier et al. 2010). Du fait de leur grande importance dans le fonctionnement des fonds marins et de la grande diversité d'espèces et de réponses possibles qu'ils intègrent, ces organismes sont communément utilisés pour évaluer l'état de santé des écosystèmes marins (Dauer 1993, Diaz et al. 2004, Beauchard et al. 2017). Ils constituent donc d'excellents modèles pour étudier les variations des communautés et leur lien avec le fonctionnement des écosystèmes, et améliorer à la fois nos connaissances théoriques mais aussi notre capacité de gestion des écosystèmes marins (Pearson & Rosenberg 1978, Bremner et al. 2003).

c) Les habitats suivis

Quatre habitats ont été étudiés dans cette thèse : les herbiers intertidaux et les bancs de maërl subtidaux, deux habitats biogéniques structurellement complexes et menacés par l'homogénéisation des fonds marins, ainsi que les

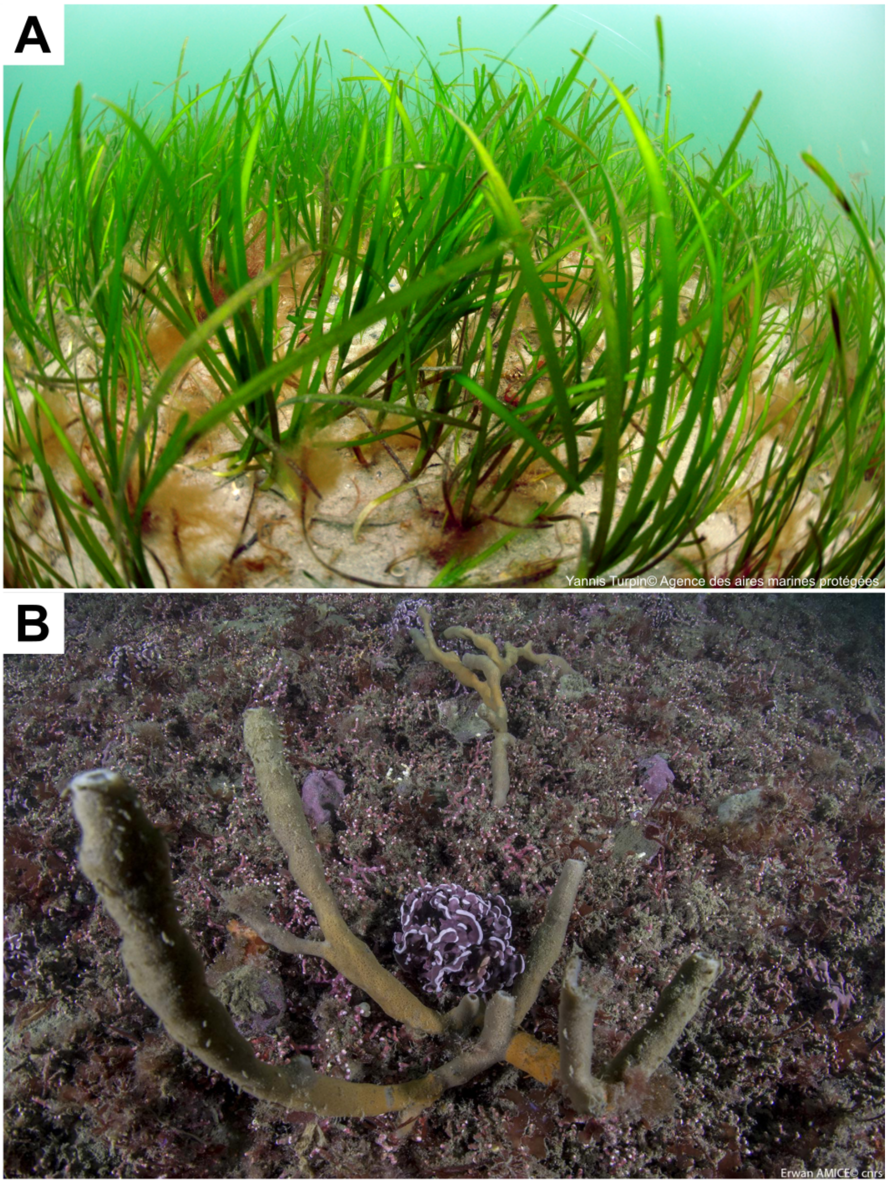

Figure 5. A*. Photographie d'un herbier de Zostère marine (*Zostera marina*) ; crédit: Yannis Turpin, Agence des aires marines protégées.* ***B****. Photographie d'un bancs de maërl; crédit: Erwan Amice, Centre National de la Recherche Scientifique.*

sédiments nus associés en zone intertidale et subtidale. Les herbiers sont assimilables à des prairies marines (Figure 5.A) et sont formés par des phanérogammes marines. En Bretagne, ils sont formés le plus souvent de bancs monospécifiques de *Zostera marina,* la Zostère marine, et sont parfois accompagnée de la Zostère naine, *Zostera noltii* (Green & Short 2003). Ces plantes ont fait l'objet d'un important intérêt de recherche dont l'état des connaissances est détaillés dans plusieurs revues récentes (Orth et al. 2006, Cullen-Unsworth & Unsworth 2013, Unsworth et al. 2014, Davey et al. 2016). Les herbiers sont reconnus comme des habitats essentiels pour la diversité et le fonctionnement des eaux côtières (Hily & Bouteille 1999, Duffy 2006, Heck Jr. et al. 2008). Les bancs de maërl sont quant à eux formés par des accumulations d’algues rouges calcaires vivant librement sur les fonds marins (Figure 5.B). Le terme réunit plusieurs espèces d’algues différentes (Hall-Spencer et al. 2010), toutes formant des structures complexes qui abritent une grande richesse floristique et faunistique (Barbera et al. 2003, Grall et al. 2006, Peña et al. 2014). En Bretagne, les bancs de maërl sont formés par au moins deux espèces : *Lithothamnion corallioides* and *Phymatolithon calcareum* (Riosmena-Rodríguez et al. 2017). Ces accumulations mettent des centaines d’années à se développer du fait de leur croissance très lente (Littler et al. 1991, Barbera et al. 2003) ce qui les rend particulièrement vulnérables aux dégâts physiques tels qu’imposés par le dragage (Hall-Spencer & Moore 2000, Barbera et al. 2003, Airoldi & Beck 2007). La formation de ces habitats, leur distribution, et les services écosystémiques qu’ils fournissent sont notamment détaillés dans Barbera et al. (2003), Barbier et al. (2011) et Foster (2001). En outre, les facteurs influençant la complexité structurelle des bancs de maërl en Bretagne ont été décrits par Dutertre et al. (2015). Les plages sédimentaires intertidales dominent les côtes de la planète (Barboza & Defeo 2015) et sont parmi les habitats marins en contact le plus direct avec les activités humaines (Schlacher et al. 2007). Ces habitats sont caractérisés par des gradients physiques importants qui structurent fortement leurs communautés (Raffaelli et al. 1991). Les communautés de macrofaune associées à ces habitats sont à ce jour assez bien documentés (Defeo et al. 2009, McLachlan & Brown 2010, Barboza & Defeo 2015), notamment en région Bretagne (Quillien et al. 2015a, Quillien et al. 2015b, Quillien et al. 2016). Leurs pendants subtidaux font aussi l’objet d’un corps de littérature développé (Davis 1978, Gray 1981, Snelgrove 1999, Gray & Elliott 2009).

d) Objectifs

L’objectif principal de cette thèse est de mieux appréhender le rôle des habitats biogéniques dans la diversité et le fonctionnement des fonds marins côtiers et ainsi de fournir des connaissances permettant de mieux prédire le devenir des communautés benthiques face à leur éventuelle dégradation.

S’appuyant sur un suivi temporel de plus d’une décennie couvrant une échelle spatiale régionale ainsi qu’une large gamme d’environnements abiotiques, cette thèse a pour ambition de relier et d’intégrer les connaissances théoriques et empiriques existantes à différentes échelles sur l’écologie des communautés benthiques aux échelles supérieures auxquelles s’intéressent la gestion et la conservation de ces habitats.

Pour cela, différentes composantes de la diversité benthique ont été prises en compte (Figure 6). Au-delà des variations de diversité locale α entre les communautés, la diversité β des sédiments marins a été évaluée à une large gamme d’échelles : dans l’espace entre les habitats d’un même site, nommée ici β_1, au sein d’un même habitat entre différents sites β_2, entre différents habitats de différents sites, β_3, ainsi que dans le temps pour chaque communauté, β_T. De surcroît, la diversité de ces communautés benthiques a été caractérisée à la fois d’un point de vue taxinomique et fonctionnel, par le bais d’une approche par traits biologiques des espèces.

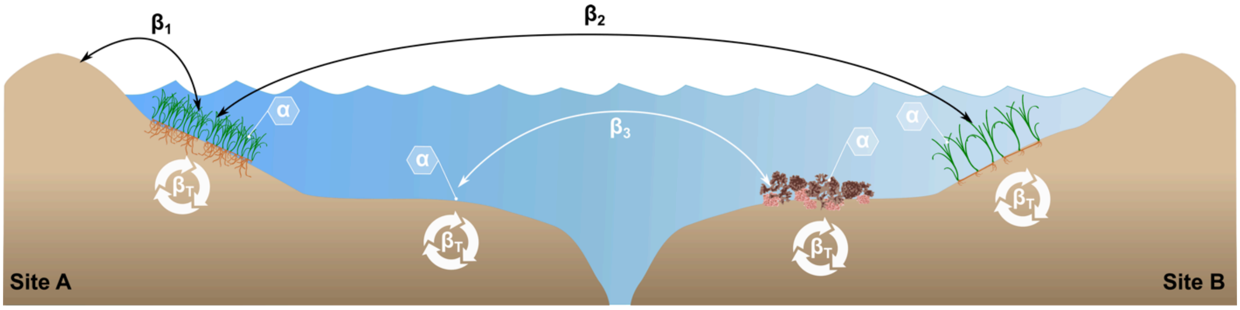

__Figure 6.__ Différentes composantes de la diversité qui doivent être prises en compte pour caractériser la diversité des communautés benthiques et pleinement appréhender l'impact de l'homogénéisation benthique.

Pour aborder chacune de ces composantes, ce travail a été subdivisé en trois chapitres qui examinent les communautés benthiques à différentes échelles et se concentrent sur différentes facettes de leur biodiversité. Un quatrième chapitre est consacré aux rôles des suivis à grandes échelles spatiales et temporelles dans notre compréhension de la biodiversité et des facteurs qui la gouvernent. Ainsi, ce travail de thèse se décompose de la façon suivante:

i. Le premier chapitre de cette thèse est consacré à la caractérisation des variations intra-habitat à grandes échelles spatiales et temporelles.

Les variations dans l'espace (β_2) et le temps (β_T) qui peuvent exister au sein des herbiers de Zostères ont été examinées dans le but de mieux appréhender 1) les conséquences sur la diversité benthique associées à leur dégradation à l'échelle mondiale, et, 2) leur cohérence taxinomique à une échelle régionale afin de mieux guider les actions de conservation. Cette étude prend ainsi en compte les communautés d'endofaune et d'épifaune associées aux herbiers et caractérise leurs variations sur 5 années dans 8 herbiers répartis le long des côtes bretonnes.

ii. Le deuxième chapitre vise à mieux comprendre le rôle des habitats biogéniques dans le fonctionnement et la résilience des communautés benthiques à une échelle régionale

Par le bais de l'analyse des traits biologiques des espèces de polychètes, cette étude s'est employée à décrire les mécanismes qui gouvernent la diversité des communautés benthiques et à appréhender comment les habitats biogéniques pouvaient moduler ces processus. En prenant en compte les variations spatiales (β_1, β_2 *et* β_3) et temporelles (β_T), ainsi que les facettes taxinomique et fonctionnelle de 50 assemblages de polychètes sur 3 années, cette étude vise ainsi à fournir un savoir théorique et mécanistique sur le rôle que jouent les habitats biogéniques dans le fonctionnement et la résilience des communautés benthiques à une échelle régionale. Deux habitats biogéniques ont été considérés, à savoir, des herbiers intertidaux et des bancs de mäerl subtidaux, qui sont comparés à des sédiments nus (dépourvu d'espèces ingénieures) se trouvant dans les mêmes franges tidales.

iii. Le troisième chapitre aborde le rôle des habitats biogéniques dans la dynamique temporelle à moyen terme des communautés benthiques et dans la stabilité de leur structuration spatiale

Par la caractérisation sur 9 ans des trajectoires dans le temps de 42 communautés et l'examen de leur lien avec les conditions environnementales, cette étude fournit une approche taxinomique permettant d'appréhender 1) la relative importance des variations intra- et inter-habitats dans le temps et l'espace (β_1, β_2, β_3 *et* β_T), ainsi que 2) les variations des patrons spatiaux des communautés à l'échelle de la région sur près d'une décennie, et enfin 3) l'importance des contraintes abiotiques, des habitats biogéniques et des facteurs historiques dans la dynamique et la structure actuelle des communautés benthiques côtières étudiées.

iv. Le quatrième chapitre vise à fournir un retour d'expérience sur les suivis à grandes échelles spatiales et temporelles et discute des opportunités et défis associés à l'exploitation des données qui en sont issues

En s'appuyant sur l'expérience acquise au cours de cette thèse par l'exploitation des données issues du suivi REBENT (*Réseau Benthique ;* http://www.rebent.org), ce chapitre 1) discute de la place des suivis à grandes échelles dans notre compréhension de la biodiversité et pour la conservation des écosystèmes, 2) identifie les principaux écueils pouvant limiter l'exploitation des données issues de ces suivis et 3) discute des pratiques et outils permettant d'optimiser l'exploitation de ces suivis.

7. Outline and objectives of the thesis (English version)

The main objective of this thesis is to better apprehend the role of biogenic habitats in the diversity and functioning of benthic communities at broad spatial and temporal scales.

Biogenic habitats have experienced severe losses over the past decades (Airoldi & Beck 2007), and this is considered to be one of the major threats facing the biodiversity of marine coastal ecosystems (Hoegh-Guldberg & Bruno 2010, McCauley et al. 2015). However, important shortfalls remain in our understanding of the mechanisms through which biogenic habitats affect the diversity of marine sediment (Kovalenko et al. 2012, Bulleri et al. 2015) and of their repercussions at broad spatial scale in terms of within- and among-habitat β diversity (Airoldi et al. 2008). Resolving these knowledge gaps is key to better envision the role biogenic habitats may play in the responses of benthic communities to future changes of the seafloor and of the marine environment in general (Bulleri et al. 2018).

For this purpose, this thesis takes advantage of broad-scale monitoring data on the benthic communities associated to two biogenic habitats (intertidal *Zostera marina* meadows and subtidal maerl beds; Figure 5), and to bare sediment at similar tidal levels, to deepen our understanding of the main drivers of benthic diversity at broad scales. Thereby, this thesis aims to upscale available empirical and theoretical knowledge on benthic communities to broader scales that are in agreement to those at which society manages and benefits from these natural ecosystems (Isbell et al. 2017).

This work is decomposed into four chapters, three addressing different scales and components of the variation of benthic communities (Figure 6) and different facets of their biodiversity (here taxonomic and functional), and a fourth chapter discussing the role of broad scale monitoring programmes in our understanding of biodiversity. In more details, this work is decomposed as follow:

i. Chapter 1 characterizes the community variations existing within biogenic habitats at broad spatial and temporal scales

The within-seagrass β diversity of benthic communities existing in space (β_2; Figure 6) and time (β_T; Figure 6) at broad scales was examined in order to better apprehend 1) the consequences of their worldwide decline on the biodiversity of coastal sediment at a regional scale, and 2) their taxonomic consistency at a regional scale, and thereby, the relevance of telemetric approaches in guiding the conservation of benthic diversity. For this purpose, this study characterizes the variation of epifaunal and endofaunl communities over 5 years and across 8 meadows distributed in contrasted environmental settings along the coast of Brittany.

ii. Chapter 2 aims to better apprehend the role of biogenic habitats in the functioning and resilience of benthic communities at a regional scale

By taking into account the spatial ($\beta_1, \beta_2, \beta_3$; Figure 6) and temporal (β_T; Figure 6) variations of 50 polychaete assemblages over 3 years in terms of both their taxonomic and functional (trait-based approach) facets, this study aimed at better understanding the mechnisms governing the diversity of benthic fauna in space and time, and evaluating the role of biogenic habitats in mediating these ecological processes. Additionnaly, the repercussions of these mechanisms at regional scale in terms of taxonomic and functional diversity, and in terms of the potential resilience of the communities are evaluated. For this purpose, two biogenic habitats are considered, namely intertidal seagrass meadows and subtidal maerl beds, and are compared to sediment devoid of foundation species at similar tidal levels.

iii. Chapter 3 adresses the role of biogenic habitats in the temporal dynamics of benthic communities and explores their potential role in mediating future environmental changes

This chapter characterizes the 9-year temporal trajectories of 42 endofaunal communities and examines their relationships with abiotic conditions in different benthic habitats (intertidal seagrass meadows, subtidal maerl beds, intertidal and subtidal bare sediment). In doing so, this study aims to 1) assess the relative importance of within- and among-habitat variation of endofaunal communities in space and time (β_1, β_2, β_3 and β_T; Figure 6), and 2) evaluate how the spatial structures of communities at a regional scale have varied over 9 years, and, 3) examine the relative importance of abiotic constraints, foundation species, and historical drivers in the temporal dynamic and the contemporary structure of the studied benthic communities.

iv. Chapter 4 aims to provide a first-hand feedback on the benefits and challenges associated to the exploitation of broad-scale monitoring data and discuss how monitoring programmes can contribute to our understanding of ecosystems

Building on the experience provided by the exploitation during this thesis of data from the REBENT monitoring programme (*Réseau Benthique;* http://www.rebent.org), this chapter aims to 1) highlight the questions broad scale monitoring programmes allow to address and discuss how these programmes can contribute to our understanding of biodiversity and its conservation, 2) identify key leverage points that may hinder their exploitation, and 3) delineate the tools and best practices to optimize their valorisation.

8. Matériels et méthodes

Ce travail de thèse est bâti autour de l'exploitation des données du suivi REBENT (*Réseau Benthique ;* http://www.rebent.org). La stratégie générale de ce suivi et les méthodes d'acquisition des données faunistiques sont résumées ci-dessous car elles forment une base commune à l'ensemble des chapitres. Cependant, afin de répondre aux différentes questions posées au cours de cette thèse, différents sous-ensembles des données du suivi REBENT ont été utilisés selon les chapitres, et ont pu être complémentés par des données acquises *a posteriori*. Les méthodes et spécificités propres à chacun des chapitres ne sont ici pas détaillées ici, l'intégralité des informations se trouvant dans chaque chapitre, mais les principales informations concernant les approches employées au sein de chacun des trois chapitres sont résumées dans le Tableau 1.

a) Stratégie générale du suivi

Mené conjointement par l'observatoire de l'Institut Universitaire Européen de la Mer (IUEM), et les stations biologiques de Roscoff et de Concarneau, le REBENT consiste en un suivi standardisé des communautés et de l'environnement de différents habitats sur l'ensemble de la Bretagne de 2003 à aujourd'hui (Figure 7.A). Chaque habitat est placé sous la responsabilité thématique d'un laboratoire. L'observatoire de l'IUEM a ainsi acquis et bancarisé les données concernant les herbiers (*Herbiers Intertidaux*), les sites de sédiments intertidaux (*Intertidal Meuble*), et les données de bancs de maërl (*Bancs de Maërl*) utilisées dans ces travaux. Les données portant sur les sédiments subtidaux (*Subtidal Meuble*) ont été fournies par Éric Thiébaut et Caroline Broudin qui coordonnent ce suivi à la station biologique de Roscoff. Les observations au sein de chaque habitat ont été effectuées à la fin de l'hiver lors des équinoxes de printemps ainsi qu'à celles d'automne. Les échantillonnages automnaux concernent l'ensemble des sites pour les premières années, puis n'ont été poursuivis que pour les sites situés au sein de la Zone Atelier Brest-Iroise (ZABrI, www.iuem.univ-brest.fr/zabri/fr). Dans le cadre de cette thèse, seules les données récoltées en fin d'hiver/début printemps ont été utilisées. Cet échantillonnage a lieu avant la période de recrutement printanier de la majorité des espèces benthiques dans la région (Dauvin et al. 2007) et correspond à la période de densité et de richesse faunistique minimale (Grall 2002). En outre, cet échantillonnage a lieu avant le début de la phase de croissance saisonnière de la Zostère, à la période de développement minimal de l'herbier (Moore & Short 2006). Ainsi, l'acquisition des données à cette période permet d'appréhender les variations interannuelles des communautés sans les facteurs confondants que pourraient représenter les variations interannuelles du recrutement des espèces ou du développement saisonnier de l'herbier.

Brièvement, chaque site suivi compte trois points de prélèvement fixes distants d'environ 200 mètres (Figure 7.B). Les communautés d'épifaune et/ou d'endofaune sont inventoriées pour chacun des points à l'aide de trois répétitions. L'endofaune des sites de sables intertidaux et d'herbiers de Zostères est échantillonnée sur chacun des trois points d'un site par trois prélèvements de 0,03 m^2 réalisés au carottier. Pour les sites de maërl et de sédiments subtidaux, l'endofaune est échantillonnée sur chaque point par 3 prélèvements effectués à l'aide d'une benne Smith de 0,1 m^2. Les prélèvements sont tamisés sur un tamis d'une maille de 1mm, et ensuite formolés en attendant leur analyse en laboratoire. La récolte de l'épifaune vagile n'est effectuée que pour les herbiers de Zostères et consiste pour chaque point d'un site en 3 traits d'haveneaux de 10 m^2 chacun. Il y a donc pour chaque compartiment (endofaune et épifaune), 3 prélèvements effectués aux 3 points de suivi d'un site, pour un total de 9 prélèvements par saison et par site.

Des variables biologiques complémentaires portant sur la plante elle-même sont mesurées pour les herbiers de Zostères. Pour les quatre habitats, la granulométrie et la teneur en matière organique du sédiment sont mesurées au moment de l'échantillonnage de la faune. Dans le cadre de cette thèse, des variables environnementales (climat, hydrologie, exposition, profondeur) et biologiques (traits d'histoire de vie) ont aussi été acquises *a posteriori*. Les méthodes d'acquisition et de traitement de ces données sont décrites dans les chapitres concernés par l'utilisation de ces variables (c.f. Tableau 1).

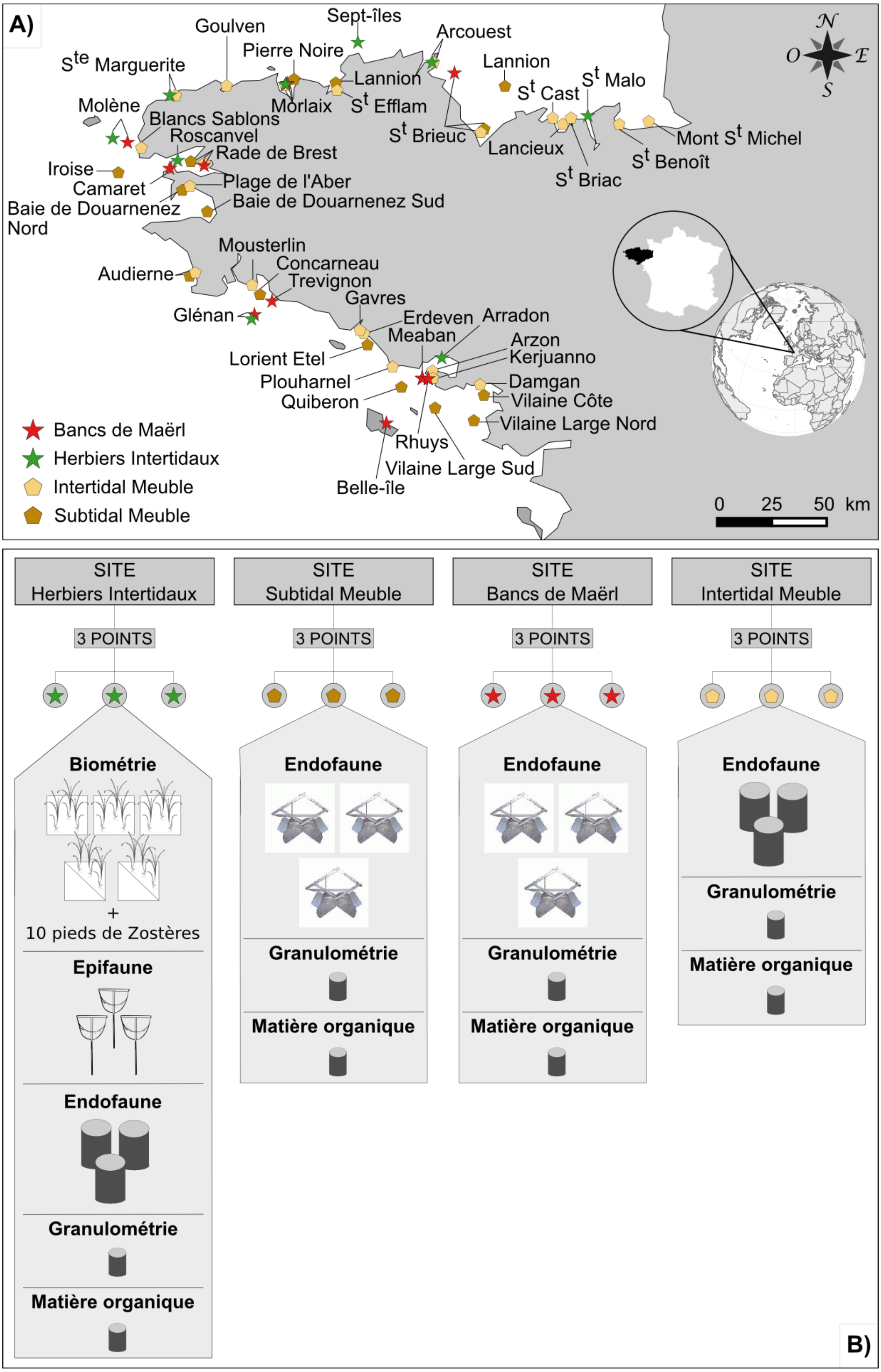

Figure 7. *A) Carte des sites échantillonnés pour les différents habitats suivis dans le cadre du Réseau Benthique (REBENT) mis en place en Bretagne depuis 2003 (www.rebent.org). B) Résumé schématique des protocoles d'échantillonnage d'un site pour chacun des quatre habitats.*

a) Validation et homogénéisation taxinomique de la base de données

Les données taxinomiques ont été acquises par différentes équipes de recherche et les organismes identifiés par différentes personnes. De plus, la taxinomie de certains groupes a pu évoluer au cours des plus de 10 ans du suivi. De ce fait, un des premiers travail de cette thèse a consisté à effectuer une validation et homogénéisation taxinomique sur l'ensemble de la base de données réunie afin de s'assurer 1) qu'une espèce ne change pas de nom en cours d'étude ou selon les experts, 2) que la même résolution taxonomique soit utilisée pour un même taxon tout au long de l'étude et sur les différents habitats, et qu'une diversification ou un appauvrissement au sein d'un groupe ne soit pas dû à des changements d'expert ou de littérature par exemple. En présence d'experts taxinomiques des différents organismes de recherche impliqués (Observatoire marin de l'IUEM et Station Biologique de Roscoff), la distribution dans le temps et l'espace de chaque espèce enregistrée a été examinée et les taxons dont les patrons ou la présence apparaissaient douteux ont été dégradés à des niveaux taxinomiques supérieurs (*p.-ex.* au genre). Nous avons favorisé la possibilité de sous-estimer la vraie diversité plutôt que de garder de potentiels artefacts. Ce travail a été mené sur l'intégralité de la base de données REBENT disponible au début de cette thèse et est commun à l'ensemble des trois chapitres.

b) Résumé des méthodes employées dans chacun des chapitres / Summary of the approaches used in each chapter (english version)

Addressing the questions asked in this thesis required different approaches, led at different scales and based on different methodologies. Detailed descriptions of materials and methods are found in each individual chapter and are therefore not given here. Furthermore, Table 2 provides a synthetic summary of the main characteristics of each chapter.

Tableau 1. *Résumé des objectifs, des échelles et des données utilisées dans chacune des trois études réalisées*

	Chapitre 1	**Chapitre 2**	**Chapitre 3**
Objectifs	Appréhender les variations de communautés intra-herbiers à grande échelle spatiale et temporelle	Appréhender l'effet des habitats biogéniques sur la diversité fonctionnelle des communautés benthiques	Appréhender l'effet des habitats biogéniques sur la dynamique et trajectoire temporelle des communautés benthiques
Habitat	Herbiers intertidaux	Intertidal Meuble Herbiers Intertidaux Subtidal Meuble Bancs de Maërl	Intertidal Meuble Herbiers Intertidaux Subtidal Meuble Bancs de Maërl
Compartiment faunistique	Endofaune et épifaune	Endofaune, polychètes seulement	Endofaune
Emprise temporelle	**5 ans** 2007, 2009, 2010, 2011, 2012	**3 ans** 2007, 2010, 2013	**9 ans** 2006 à 2014
Emprise spatiale	8 herbiers répartis le long des côtes Bretonnes	**50 communautés dans 42 sites répartis le long des côtes Bretonnes :** 18 sédiment nu intertidal 14 sédiment nu subtidal 9 herbiers intertidaux 9 bancs de maërl	**42 communautés dans 35 sites répartis le long des côtes Bretonnes :** 16 sédiment nu intertidal 10 sédiment nu subtidal 8 herbiers intertidaux 8 bancs de maërl
Facette de la diversité	Taxinomique	Taxinomique et fonctionnelle	Taxinomique
Données complémentaires		Traits d'histoire de vie	Données environnementales et biométriques de la Zostère

Tableau 2. *Summary of the aims, spatial and temporal scales, and data used in each of the three studies*

	Chapter 1	**Chapter 2**	**Chapter 3**
Aims	Apprehending the variability of communities within seagrass meadows at broad spatial and temporal scales	Apprehending the effects of biogenic habitats on the functional diversity of benthic communities at regional scale	Apprehending the effects of biogenic habitats on the dynamics and temporal trajectories of benthic communities
Habitat	Intertidal seagrass beds	Intertidal bare sediment Intertidal seagrass beds Subtidal bare sediment Subtidal maerl beds	Intertidal bare sediment Intertidal seagrass beds Subtidal bare sediment Subtidal maerl beds
Faunal compartment	Endofauna and epifauna	Enfodauna, polychaetes only	Endofauna
Temporal coverage	**5 years** 2007, 2009, 2010, 2011, 2012	**3 years** 2007, 2010, 2013	**9 years** 2006 à 2014
Spatial coverage	8 seagrass meadows across the whole region	**50 sites across the whole region including:** 18 intertidal bare sediments 14 subtidal bare sediments 9 seagrass beds 9 mearl beds	**35 sites across the whole region including:** 16 intertidal bare sediment 10 subtidal bare sediment 8 seagrass beds 8 maerl beds
Biodiversity facets	Taxonomic diversity	Taxonomic and functional diversity	Taxonomic diversity
Complementary data		Biological traits	Abiotic variables and biometric data on *Z. marina*

CHAPITRE 1

Variabilité des communautés d'herbiers à Zostères à une échelle régionale

1. Préambule

Les variations des communautés pouvant exister au sein des habitats habituellement définis en milieu benthique doivent être prises en compte dans les schémas de conservation et dans les scénarios de diversité envisageant les effets de l'homogénéisation des paysages benthiques (Airoldi et al. 2008, Fraschetti et al. 2008). Ces variations sont souvent négligées dans les comparaisons inter-habitats et ont le plus souvent été évaluées au travers de mesures de la diversité α. Ainsi, il n'existe pour les herbiers, qui sont pourtant parmi les habitats benthiques des zones tempérées les plus étudiés, qu'une seule étude à notre connaissance sur la diversité β intra-habitat à une échelle régionale (> 100 km ; Boström et al. 2006). Cette étude est de plus située en mer Baltique, une région aux conditions environnementales particulières et aux communautés appauvries en espèces. Dans ce chapitre, j'ai évalué la variabilité des communautés d'épifaune et d'endofaune à des échelles spatiales et temporelles inédites. Pour cela, j'ai analysé les données du suivi REBENT de huit herbiers répartis le long des côtes bretonnes sur cinq ans. Ces travaux ont fait l'objet d'une publication dans *Journal of Sea Research* (Boyé et al. 2017).

En résumé, nous avons mis en évidence une forte richesse spécifique au sein des herbiers à l'échelle de la Bretagne, celle-ci s'expliquant par la combinaison d'une forte diversité α de chacun des herbiers et d'une importante diversité β entre les herbiers. Tous les herbiers étudiés ont montré une contribution similaire à cette diversité β, ce qui retranscrit une grande complémentarité des communautés des différents sites à l'échelle de la région. Les communautés d'endofaune et d'épifaune ont montré des patrons spatiaux et temporels différents. Cette différence a pu en partie être expliquée par des différences dans leur relation aux conditions hydrologiques locales. Ces variations étaient constituées pour les deux compartiments par des changements d'espèces dominantes mais aussi par d'importantes variations des nombreuses espèces rares recensées. Nous avons pu aussi montrer que les changements de richesse spécifique entre les herbiers étaient faibles et que ces variations d'assemblages étaient avant tout liées au remplacement des espèces. Ainsi, malgré d'importantes variations des conditions locales, la richesse locale des herbiers s'est révélée particulièrement stable eut égard des importantes variations des communautés observées. Ces résultats, associés à la littérature existante, ont permis de proposer l'existence d'une capacité de charge des herbiers en termes de diversité spécifique. Les herbiers des différents sites étudiés partageraient ainsi des propriétés qui permettraient le maintien d'une richesse spécifique similaire malgré des conditions locales différentes.

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Constancy despite variability: Local and regional macrofaunal diversity in intertidal seagrass beds

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ABSTRACT

The importance of seagrass habitat for the diversity of benthic fauna has been extensively studied worldwide. Most of the information available is, however, about α diversity while little consideration has been given to β diversity. To fill the knowledge gaps regarding the variability of epifaunal and infaunal seagrass assemblages at large spatial and temporal scales, we scrutinized an extensive dataset covering five years of monitoring of eight intertidal *Zostera marina* meadows around Brittany (France). High species richness arose at the regional scale from the combination of high local diversity of the meadows and substantial among-meadows β diversity. Epifauna and infauna appeared as distinct self-communities as they displayed different spatial and temporal patterns and varied in their responses to local hydrological conditions. Infauna had higher total β diversity than epifauna due to a tighter link to the great variability of local environmental conditions in the region. Both exhibited substantial variations in species composition and community structure with variations of dominant species that were accompanied by extensive change in numerous rare species. The dominant epifaunal species were all grazers. Changes in species composition were induced mostly by species replacement and rarely by richness differences between meadows. Indeed, species richness remained within a narrow range for all seagrass beds, suggesting a potential carrying capacity for species richness of the meadows. Overall, all meadows contributed equally to the regional turnover of seagrass macrofauna, emphasizing high variability and complementarity among beds at the regional scale. The implications of this substantial within-seagrass variability for the functioning of benthic ecosystems at broad scale and for conservation purposes in habitat mosaics warrant further investigations but our results clearly advocate taking into account within-habitat variation when evaluating the diversity of benthic habitats and the potential effect of habitat loss.

1. Introduction

Seagrasses are marine flowering plants thriving along the world's coastlines from temperate to sub-Antarctic and Arctic regions (Green and Short, 2003). They form widespread meadows that have gained increasing recognition in the past decades as some of the most valuable ecosystems in the biosphere (Costanza et al., 1997; Duarte et al., 2008; Dewsbury et al., 2016). Indeed, seagrasses act as ecosystem engineers (*sensu* Jones et al., 1994). As such, they fulfil key ecological roles in coastal ecosystems and provide high-value ecosystem services including coastal protection and erosion control, carbon sequestration, key contributions to nutrient cycling associated with water purification capabilities, provision of raw materials and food, and maintenance of important commercial fisheries (Barbier et al., 2011; Fourqurean et al., 2012; Cullen-Unsworth and Unsworth, 2013). Furthermore, they transform bare and relatively homogeneous sediment into structurally more complex, productive and diverse habitats (Hemminga and Duarte, 2000; Duffy, 2006). They provide stable hydrological and sedimentary conditions, abundant resources, higher available surface area and ecological niches, and protection against predation to their associated fauna (Fonseca et al., 1983; Orth et al., 1984; Attrill et al., 2000; Larkum et al., 2006; Heck et al., 2008). Accordingly, seagrasses are typically inhabited by richer and more diverse fauna than bare substrata (*e.g.* Edgar, 1990; Boström and Bonsdorff, 1997; Hily and Bouteille, 1999).

Preventing loss of complexity and homogenisation of benthic

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landscape has now become one of the main priorities and challenges for marine biodiversity conservation (Airoldi and Beck, 2007; Airoldi et al., 2008). This concern particularly applies to seagrass meadows as they rank among the most threatened marine habitats (Orth et al., 2006). Indeed, seagrasses are facing increasing pressures from both natural (storms, overgrazing, diseases) and anthropogenic sources (eutrophication, physical damages, over-exploitation, global change; Short and Wyllie-Echeverria, 1996; Duarte, 2002; Orth et al., 2006). This ongoing ecological degradation of coastal waters has led to dramatic shrinkage of seagrass coverage worldwide (Waycott et al., 2009). This has become a major issue as it affects the whole functioning of coastal waters by disrupting the essential linkages between seagrass beds and other habitats and altering the ecological services they provide (Airoldi et al., 2008; Heck et al., 2008; Hughes et al., 2009).

The plethora of studies comparing vegetated bottoms and bare sediment only allow to ambiguously forecast the effects of seagrass loss as they do not fully account for the diversity and variability of seagrass communities (Bell et al., 2006; Airoldi et al., 2008; Boström et al., 2011). By focusing on among-habitat patterns, traditional assessments of seagrass communities have often neglected within habitat variability. Clear evidences of communities variability have however been documented at all spatial scales: within single meadows (Webster et al., 1998; Blanchet et al., 2004; Bologna, 2006; Wong and Dowd, 2015), at the landscape scale (Hovel et al., 2002; Bell et al., 2006; Boström et al., 2011; Carr et al., 2011) and among different locations (Boström and Bonsdorff, 1997; Boström et al., 2006; Borg et al., 2010; Barnes, 2014). Such variability can affect our appreciation of biodiversity distribution and ecosystem functioning and need to be accounted to adequately preserve seagrass biodiversity (Airoldi et al., 2008; Fraschetti et al., 2008; Törnroos et al., 2013).

The need for long-term monitoring and broad scale comparisons is increasingly advocated to apprehend the diversity and variability of seagrass systems and the consequences of their broad spatial and temporal scale disappearance (Duarte, 1999; Airoldi et al., 2008; Boström et al., 2011; Edgar et al., 2016). Broad scale comparisons of seagrass communities among different locations are however scarce with the exception of the Baltic Sea (Boström and Bonsdorff, 1997; Boström et al., 2006). Furthermore, the majority of spatial datasets are “snap shot” that do not include the temporal component of seagrass variability over long periods (Boström et al., 2011). Because there is a positive relationship between the spatial and the temporal scales of variation of ecological phenomena (Wiens, 1989), information on the broad spatial scale variability of seagrass communities should preferably be integrated over long periods. There is increasing evidence that inter-annual variations can be as important as and even blur seasonal patterns (Duarte et al., 2006; Douglass et al., 2010). Inter-annual variations need to be assessed in particular to reveal the long-term effects of wave exposure, tidal currents, or of long-term changes in temperature, salinity or turbidity on seagrass and their communities (Rasheed and Unsworth, 2011; Potouroglou et al., 2014; Lefcheck et al., 2017a, 2017b). These environmental factors can have strong structuring effects on local communities, prone to induce important variability among meadows at broad spatial scale (Boström and Bonsdorff, 1997; Boström et al., 2006; Borg et al., 2010). Yet, most studies have limited spatial and/or temporal extents, often covering between 1 and 50 km^2 or with durations limited to 1 or 2 years (Duarte, 1999; Boström et al., 2011). Therefore, they cannot be used to infer quantitatively how local conditions may shape diversity patterns at regional scale (De Juan and Hewitt, 2011). There are indeed compelling evidences that patterns arising at one scale often do not translate directly at others (Bell and Westoby, 1986; Turner et al., 1999; Balestri et al., 2003; Kendrick et al., 2008). Measuring diversity at regional scales is necessary to guide conservation actions (De Juan and Hewitt, 2011) but the links between regional diversity, local diversity and ecosystem processes requires further studies in seagrass meadows (Duffy, 2006).

One major impediment to our knowledge of seagrass biodiversity at broad scale is that community assessments have traditionally been biased towards the assessment of the local diversity of seagrass meadows (α diversity; Whittaker, 1960), while little interest has been given to the spatial and temporal differentiation and renewal of their communities (β diversity; Whittaker, 1972; Gray, 1997, Airoldi et al., 2008). Yet, assessment of this neglected component is necessary to properly estimate the role of seagrass in promoting coastal diversity and functioning and to adequately define management actions at large spatial scales (Airoldi et al., 2008; Fraschetti et al., 2008; Törnroos et al., 2013). Assessment of β diversity patterns helps in capturing the potential complementarity of communities (Bond and Chase, 2002) and in revealing fundamental facets of community structure and their underlying processes (Whittaker, 1972; Legendre and De Cáceres, 2013). Structurally complex habitats are recognized to favour among-habitat β diversity in comparison to their less complex counterparts (Hewitt et al., 2005; Airoldi et al., 2008). The importance of this facet of within-habitat diversity remains however largely unknown, especially at large spatial and temporal scales. In particular, while the relative contributions of epifauna (organisms living on the surface of the sediment or the seagrass) and infauna (living within the sediment) to the local diversity of seagrass meadows and to among-habitat patterns have previously been described (Boström and Bonsdorff, 1997; Duffy, 2006), there exists no previous assessment of their broad scale patterns and relative importance to within-seagrass β diversity.

In this study we used innovative statistical analysis to scrutinize an extensive dataset arising from a regional survey of intertidal *Zostera marina* beds in order to fill the knowledge gaps regarding β diversity and within-seagrass variability of macrofaunal communities at broad spatial and temporal scale. Data on the epifaunal and infaunal assemblages of eight *Zostera marina* meadows were collected during five years along Brittany as part of the REBENT (Réseau Benthique) monitoring programme. Being a biogeographical transition zone between the North Sea and the Bay of Biscay (Fig. 1), Brittany is of particular interest for its high benthic macrofaunal diversity that is enhanced by the great range of hydrological conditions found in this region (Gallon et al., 2017, this issue). Like most of the eastern Atlantic, Brittany has been severely affected by seagrass disappearance over the last century (Airoldi and Beck, 2007; Godet et al., 2008). The diversity and functioning of these meadows however, have only been locally characterised (Hily and Bouteille, 1999; Hily et al., 2004; Martin et al., 2005). As part of the REBENT programme, molecular approaches have highlighted the variability of Brittany meadows and their communities (Becheler et al., 2010, 2014; Cowart et al., 2015) but their spatial and temporal variation and their underlying structuring mechanisms remain largely to be determined.

In this context, we aim at assessing at the scale of this rich region the α, β, and γ (regional) diversities of seagrass macrofauna and at identifying the sources of community variation within this habitat such as richness differences, species replacement, as well as the role of abundance patterns and the importance of rare species. Barnes (2014) highlighted substantial variations of the infaunal assemblages among

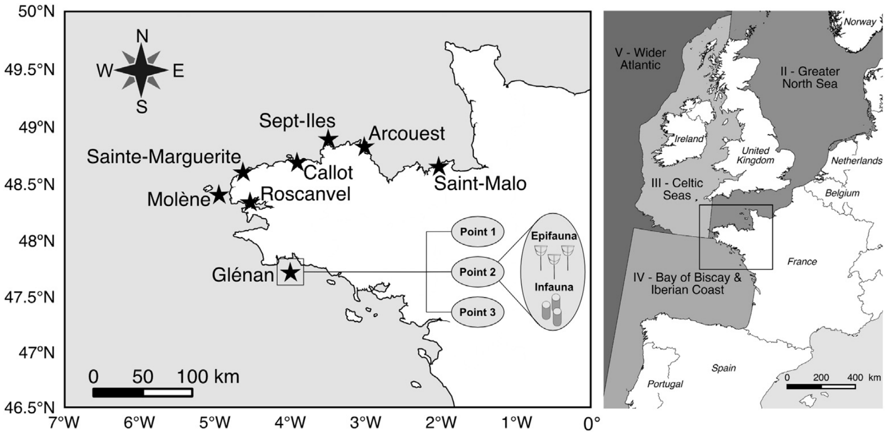

Fig. 1. Localities of the eight *Zostera marina* meadows (black stars) monitored by the RÉseau BENThique (REBENT) in Brittany in 2007 and from 2009 to 2012. Each meadow was sampled at three points located 200 m apart for epifauna (using three dip nets) and infauna (using three sediment cores), as exemplified in the figure for the Glénan meadow. Brittany waters (encompassed by the rectangle in the right-hand map) constitute a marine biogeographical transition zone between two marine regions defined by the OSPAR commission: region II of the Greater North Sea (northern Brittany) and region IV of the Bay of Biscay and the Iberian coast (southern Brittany).

three sheltered intertidal meadows of different geographical areas (Australia, South-Africa and United Kingdom) but pointed out that common assemblage structures were found in all three. We hypothesise however, that the capacity of seagrass meadows to promote similar assemblage structures is unlikely in highly contrasted environments (Barnes, 2016), as present in the Brittany region. We expect indeed strong spatio-temporal variability of all components of epifauna and infauna diversity, along with site-specific dynamics. Both compartments are also hypothesised to respond differently (Leopardas et al., 2014). An exploration of the role of the hydrologic regimes, assessed here using sediment characteristics as proxy, will also provide a first insight into the influence of local environmental conditions on the patterns observed.

2. Material and methods

2.1. Sampling and processing protocols

In the context of the REBENT monitoring programme, eight intertidal *Zostera marina* beds were sampled in 2007 and from 2009 to 2012 along the coast of Brittany, France (Fig. 1). These eight meadows were chosen to encompass the spectrum of environmental settings in which intertidal *Zostera marina* meadows can be found in Brittany: from sheltered bays and turbid waters to exposed areas and fully marine conditions, through semi-opened habitats (Hily et al., 2003). As a consequence, the eight meadows differ in terms of underlying sediment, densities, biomasses, and distribution areas, which may contribute to the variability of their associated macrofauna. Sampling was consistently performed for all beds around the spring equinox of each year, between the end of February and the beginning of May (Appendix 1). This sampling season correspond to the season of minimum canopy development and was set to limit inter-annual variability that may arise from variation in the growth phase of *Zostera marina* during the spring/summer season (Moore and Short, 2006). This sampling season also follows the winter storms and is therefore the period of minimum macrofaunal densities and diversities in the region (Grall, 2002). Inter-annual variability induced by the seasonal variations of macrofauna and their development or recruitment processes is limited at this time of year.

Three fixed sampling points distributed 200 m apart were visited within each seagrass bed. At each point, epifauna was sampled by three 10 m horizontal hauls of a 1 m width dip net (1 mm mesh size) shortly before low tide. These three samples were pooled to estimate abundances at the point level (illustrated for the Glénan meadow in Fig. 1). Likewise, at each point infauna was sampled using three sediment cores of 0.03 m^2 that were also pooled to estimate abundances at the point level. Accordingly, macrofaunal densities were estimated based on the 30 m^2 and 0.09 m^2 surface sampled per points for epifauna and infauna respectively. Sediment cores were then sieved over 1 mm mesh and fixed in 4% formalin in the laboratory until sorting and morphological identification to the lowest taxonomic levels possible. Despite a constant scientific supervision of the monitoring programme by one of the author (J. Grall) for the duration of the study, several field and laboratory personnel were involved in data acquisition over the years. Hence, to ensure that a consistent taxonomic resolution was used in the study, the distribution in time and space of each recorded species was scrutinized by experts in benthic taxonomy. Degradation to higher taxonomic levels was undertaken for doubtful identifications, safeguarding against major misidentification, differences in identification among operators, or changes in time in given taxonomic groups due to updates in the taxonomic literatures. Particular care was taken for rare species and decision on their taxonomic degradation was made according to the robustness of the criteria discriminating the species, the level of expertise needed to discern them, and the likelihood of their presence in the studied area given their known distribution range. We favoured the possibility of underestimating the true diversity over that of keeping potential artificial patterns.

Another sediment core was collected at each point for grain size distribution assessment and organic matter content. Sediments were dried in an oven (24 h at 60 °C), separated into 15 fractions (< 63 μm, 63, 80, 100, 125, 160, 200, 315, 500, 800, 1250, 2000, 3150, 5000 and > 10,000 μm) whose masses were measured. Fractions were afterwards grouped into gravels (> 2 mm), sand (63 μm to 2 mm) and silt and clay (< 63 μm; Fournier et al., 2012). Organic matter content was estimated by mass loss after combustion at 450 °C for 5 h.

2.2. Data analyses

Species richness, abundance of individuals and Simpson's inverse (1/λ), which is Hill (1973) diversity number N_2, were calculated for

Table 1
Spatial and temporal variability of species richness, Simpson's inverse (1/λ) and abundance per m^2 for epifauna (Epif.) and infauna (Inf.). Mean values are displayed with their standard deviations.

Site		Total species richness	Mean species richness per point						Mean diversity (1/λ) per point						Mean abundance per m^2
			2007	2009	2010	2011	2012	Mean	2007	2009	2010	2011	2012	Mean	
Saint-Malo	Epif.	108	30	33	30	38	34	33 ± 5	8.8	9.3	8.1	7.4	8.0	8.3 ± 1.5	30 ± 26
	Inf.	119	43	27	32	30	26	32 ± 8	8.9	9.3	13.6	12.8	9.0	10.7 ± 3.4	3196 ± 1862
Arcouest	Epif.	142	40	53	53	46	36	46 ± 10	12.7	8.4	6.8	10.8	3.3	8.4 ± 4.4	40 ± 22
	Inf.	132	43	33	37	39	33	37 ± 5	9.0	7.6	8.7	7.6	10.6	8.7 ± 3.5	4775 ± 1451
Sept-Iles	Epif.	91	22	30	29	29	37	29 ± 7	4.4	4.8	5.6	5.8	4.7	5.1 ± 1.4	31 ± 13
	Inf.	134	47	19	37	38	33	35 ± 12	7.6	5.3	6.7	6.4	6.6	6.5 ± 2.1	6842 ± 4736
Callot	Epif.	155	53	44	50	70	56	55 ± 9	12.9	4.5	3.2	3.4	6.4	6.1 ± 4.2	55 ± 19
	Inf.	187	70	47	51	52	51	54 ± 10	14.0	12.3	13.7	14.5	12.4	13.4 ± 2.9	6609 ± 3161
Sainte-Marguerite	Epif.	127	37	49	36	57	41	44 ± 9	5.4	5.6	5.3	3.1	3.6	4.6 ± 1.4	131 ± 61
	Inf.	118	25	38	30	42	42	36 ± 9	2.1	3.6	3.4	4.3	4.6	3.6 ± 1.3	19429 ± 10457
Molène	Epif.	140	48	41	44	47	43	45 ± 9	13.1	17.8	7.8	18.2	4.9	12.4 ± 5.8	36 ± 28
	Inf.	139	41	29	45	35	40	38 ± 8	4.9	4.4	6.6	5.4	4.7	5.2 ± 2.1	12629 ± 4907
Roscanvel	Epif.	139	39	32	21	49	47	38 ± 14	5.9	4.4	3.2	5.3	5.0	4.8 ± 1.4	40 ± 21
	Inf.	163	59	66	34	51	29	48 ± 16	16.3	16.5	12.3	17.4	8.5	14.2 ± 4.1	6628 ± 3620
Glénan	Epif.	153	45	43	45	65	36	47 ± 14	10.0	6.1	4.5	8.1	5.3	6.8 ± 3.3	66 ± 54
	Inf.	136	42	48	34	38	32	39 ± 7	2.2	1.9	2.9	2.2	1.4	2.1 ± 0.8	24304 ± 12695

each sampling point of each seagrass bed for the 5 years of the study to characterise the α diversity of epifauna and infauna and its spatial and temporal variations. Simpson's inverse was chosen for its property to down-weight rare species (Hill, 1973) as these species may not have been properly sampled in such a monitoring programme with large spatial and temporal extents. Additionally, β diversity for each pair of observations was first estimated from presence-absence data, using the Jaccard dissimilarity (Jaccard, 1908), computed for each macrofaunal compartment separately. This is the simplest and the most frequently used of the measures of β diversity described in Table 1 of Koleff et al. (2003). To test whether spatial and temporal variations of epifauna and endofauna composition were predominantly induced by changes of species identity or fluctuations of species richness, β diversity among each pair of samples was partitioned into two components, namely species replacement ($\beta_{\text{Replacement}}$) and richness difference (β_{RichDiff}) following Legendre's (2014) re-description of the Podani family indices (Podani and Schmera, 2011):

$$\beta_{\text{Replacement}} = \frac{2\min(b, c)}{a + b + c}$$

and

$$\beta_{\text{RichDiff}} = \frac{|b - c|}{a + b + c}$$

with, for any two samples S_j and S_k, a being the number of species found in both samples, b the number of species unique to S_j and c the number of species unique to S_k. $\beta_{\text{Replacement}}$ and β_{RichDiff} sum to the Jaccard dissimilarity, $(b + c) / (a + b + c)$, hence they represent a full decomposition of that index of β diversity. Calculation and decomposition of the Jaccard dissimilarity was performed for each faunal compartment 1) between all samples (all pairwise comparisons possible), 2) between samples belonging to the same sites (within-site variation), 3) between samples belonging to different sites (among-site variation), 4) between samples belonging to the same sampling year (within year), 5) between samples belonging to different sampling years (among years).

In order to account for the species relative importance in the communities, patterns of species abundances were visualised using Principal Component Analysis (PCA) of the Hellinger-transformed data. Hellinger transformation allows for the use of Euclidean-based methods on abundance data and also has, as for the Simpson concentration, the desirable property of not giving excessive weight to the rare species (Legendre and Gallagher, 2001). Additionally, the spatial and temporal patterns observed were quantified using multivariate analysis of variance (MANOVA), which allowed us to test the null hypotheses of no difference among the macrofaunal communities through space and time. The MANOVA was computed by redundancy analysis (RDA; Rao, 1964) on the Hellinger-transformed abundances of epifauna and infauna separately and tested by permutations (Legendre and Anderson, 1999; Legendre and Legendre, 2012). Sites, years and their interaction were coded by Helmert contrasts (Legendre and Gauthier, 2014); homogeneity of multivariate dispersions was tested at the $\alpha = 0.05$ significance level prior to this analysis (Anderson, 2006). Interaction between space and time was measured and tested to estimate if temporal variations were similar across all sites; or expressed differently, if the spatial patterns were constant through time.

Macrofaunal patterns were related to sediment characteristics of the seagrass meadow visually, using triangular plots of the three granulometric fractions defined above. As well, the relationship between macrofauna and granulometric conditions was quantified separately for epifauna and infauna using redundancy analysis with the Hellinger-transformed species abundances. Among the explanatory variables for this analysis, only the sand and the silt and clay fractions were used, as the gravel fraction is highly collinear with the other two. Median grain size and the Sorting-Index, $So = \sqrt{Q_{25}/Q_{75}}$ with Q_{25} and Q_{75} the first and third quartiles of the distribution, were calculated to describe the position and dispersion of the granulometry and were also included in the RDA as explanatory variables along with organic matter content. Missing organic matter data for two points of Roscanvel in 2007 and one

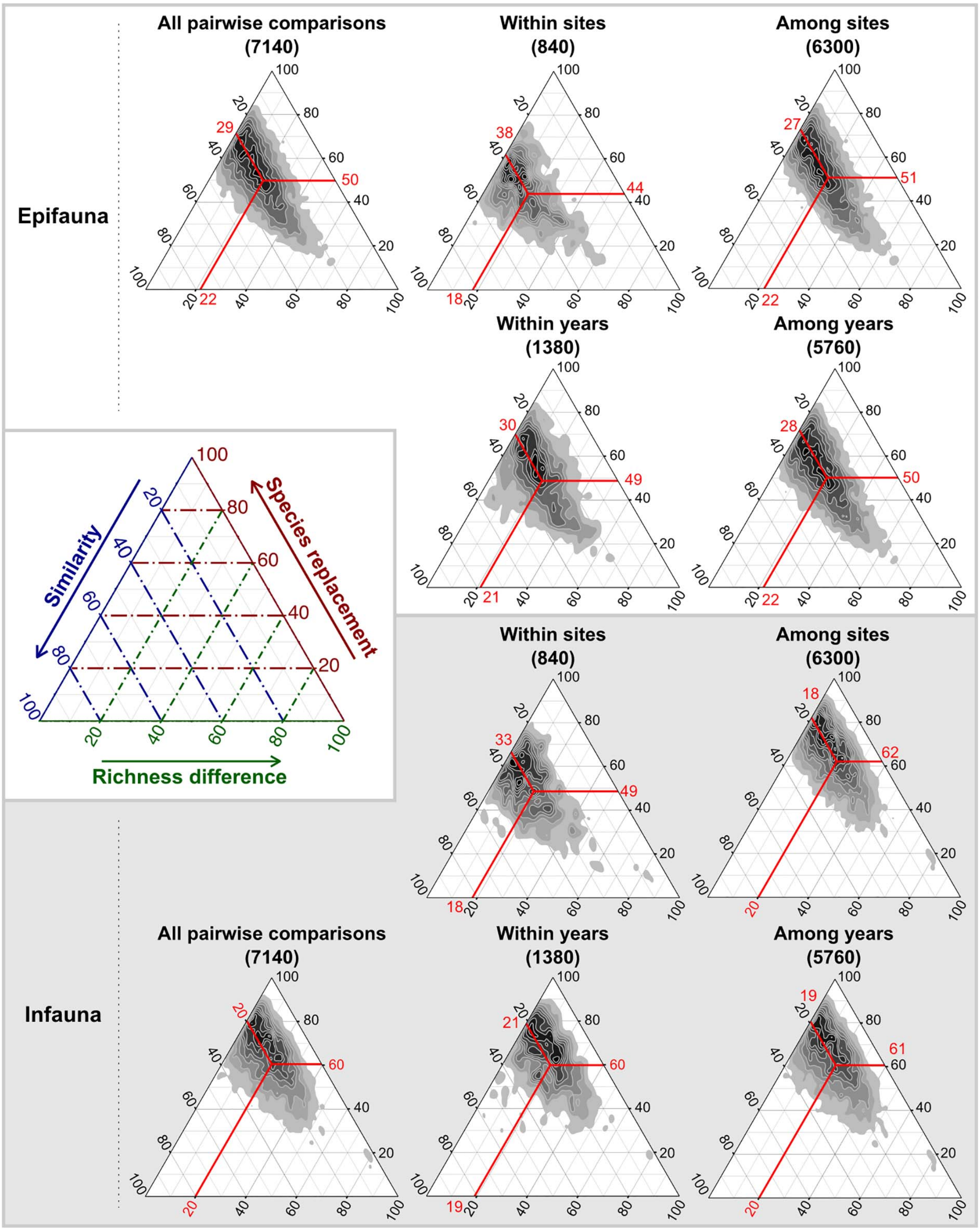

Fig. 2. Triangular plots illustrating the spatial and temporal variations of the Jaccard dissimilarity between the species composition (presence/absence data) of the eight seagrass beds over the five years of the study, and its decomposition into similarity, richness difference (*i.e.* variation in species richness) and species replacement (*i.e.* variation in species identity). Contributions were calculated for each compartment (epifauna and infauna) separately, for all pairwise comparisons and for comparisons between samples belonging: to the same meadow (within site), to different meadows (among sites), to the same year (within year), to different years (among years). Due to the high number of pairwise comparisons, the density of points was estimated by two-dimensional kernel estimations and was represented with darker colour for higher numbers of comparisons. Numbers in parentheses indicate the number of pairwise comparisons used for kernel estimation. Red lines indicate the centroid value for each graph with its associated mean values for the three components of dissimilarity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

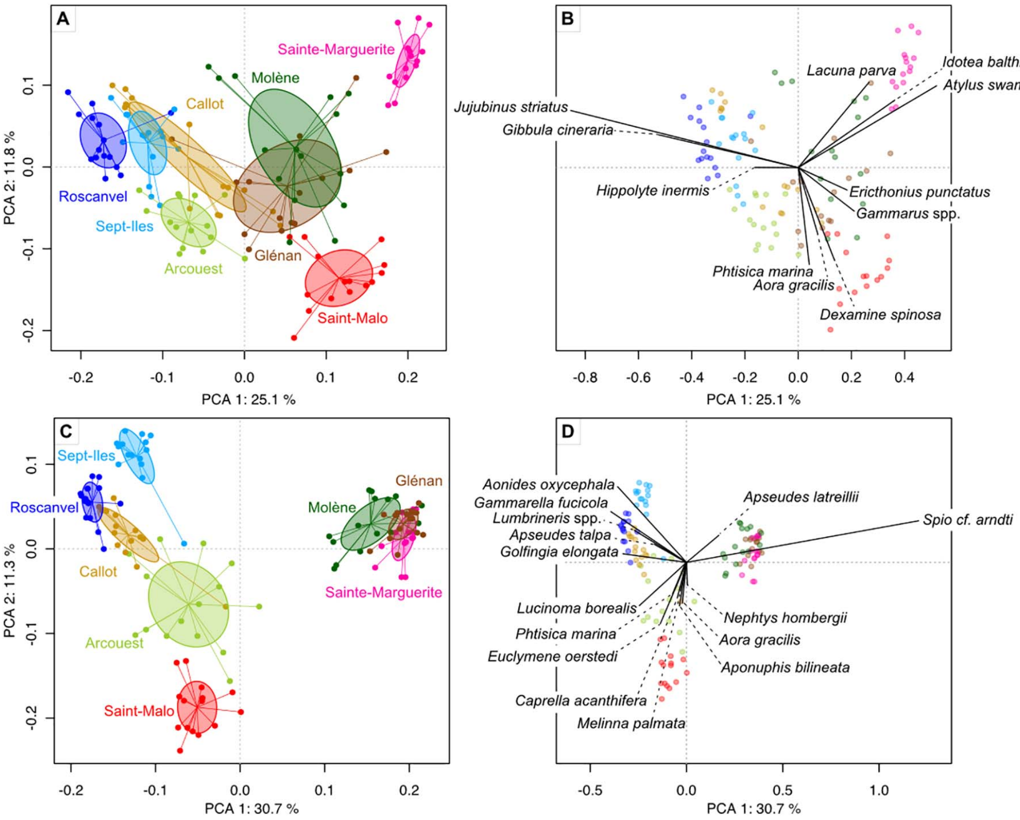

Fig. 3. Principal component analyses of the Hellinger-transformed abundances for the epifauna (A and B) and the infauna (C and D) of the eight *Zostera marina* beds over the five years of the study. The first two axes represent 36.9% and 43% of the total variation of epifaunal and infaunal communities respectively. A and C: the sites for each point sampled during the 5 years of the study with their 95% confidence dispersion ellipses. Within-site dispersions represent temporal variability and variation of the communities among the three points sampled per year. B and D: positions of the species for which the two first axes represented at least 40% (cumulative R^2) of their variance, ensuring that these species were well represented and contributed to the patterns observed in the ordination. A and C are represented in scaling 1 (distance biplot) preserving the distances among the sites. B and D are represented in scaling 2 (correlation biplot) preserving the covariances among the species. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

point of Glénan in 2010 were estimated beforehand using k-Nearest neighbour imputation (Acuña and Rodriguez, 2004). This prevented the removal of entire sites or years of the analysis while giving neutral weights to these observations.

Finally, total beta diversity (BD_{TOTAL}) was estimated for each faunal compartment as the total variance of the Hellinger-transformed community matrix and expressed as a percentage of the maximum possible value, reached only if all sites have completely different community compositions, which is $BD_{max} = 1$ for this coefficient (Legendre and De Cáceres, 2013). Contributions of individual sampling units to this total β diversity was measured for each point-site-year combination for epifauna and infauna separately using LCBD indices (Local Contributions to Beta Diversity; Legendre and De Cáceres, 2013). LCBD indices indicate the uniqueness of a community sample; they were used to evaluate the relative contribution of each seagrass meadow to the total β variation of each of the faunal compartments (epifauna and infauna) at the regional scale and over the five years of the study.

All statistical analyses were conducted using R (R Core Team, 2015) and relied on the G2Sd (Fournier et al., 2014), VIM (Templ et al., 2015), vegan (Oksanen et al., 2016), adespatial (Dray et al., 2016) and ggtern (Hamilton, 2016) packages.

3. Results

3.1. Spatial and temporal patterns of α diversity in seagrass communities

During the five years of this study, a total of 120 samples were collected in the eight *Zostera marina* meadows. They contained a total of 306,566 individuals within 460 species. Epifauna and infauna shared a total of 190 species while 113 and 157 species were respectively unique to epifauna and infauna. Species retrieved in only one sampling unit over the 120 of this study represented 17% (78/460) of the total number of recorded species. Species represented by a single individual represented 3.5% (16/460) while 179 species (39% of total richness) were represented by 10 specimens or less.

All eight seagrass beds had substantial overall richness over the five years of the study with > 200 species recorded in each of them (Table 1). On average, one sampling point contained between 30 and

55 species for each compartment with epifauna and infauna contributing similarly to total richness. Contrary to species richness that displayed comparable values among seagrass meadows, marked spatial differences were observed for Simpson's inverse and total abundances. Indeed, densities (individuals/m^2) revealed the striking predominance of infaunal organisms compared to epifaunal ones and at the regional scale, a factor of 8 was found between the infaunal abundances of the least populated site (infauna, Saint-Malo) and the most crowded meadow (infauna, Glénan). Similarly, high amplitude variations were observed between meadows for Simpson's inverse with most values found between 2 and 13 for both epifauna and infauna. Meadows that displayed high diversity for a compartment rarely exhibited concomitant high values for the other. Overall, all three community measures displayed major temporal variations. They mostly exhibited punctual and abrupt changes and their year-to-year variations often differed between the two compartments of the same meadow and for the same compartment in different meadows. Furthermore, temporal variations of Simpson's inverse (Table 1) appeared unrelated to changes observed in species richness or in abundances (Appendix 2).

3.2. Quantification and decomposition of the variation of species compositions among meadows

The β diversity of the macrofauna of *Zostera marina* meadows was first investigated with presence/absence data through pairwise comparisons between the 120 samples of each compartment (Fig. 2). Calculation and decomposition of the Jaccard dissimilarity between samples belonging to the same site provided information on within-site variations: temporal variation of the community at the site on the one hand, and variation among the three points sampled within the meadow on the other hand (Fig. 2 – Within sites). Calculation between samples belonging to the same year provided information on the spatial variations of the communities within each time step (Fig. 2 – Within years). Finally, among-years comparisons provided information on overall temporal variation, regardless of sampling site, and among-sites comparisons provided information on overall spatial variation, regardless of sampling year (Fig. 2 – Among years & Among sites).

Over the whole spatial and temporal extent of this study, epifaunal communities shared on average 29% of their species, with most pairwise similarities lying between 20 and 50% shared species (Fig. 2 – All pairwise comparisons). Comparatively, infaunal communities displayed higher compositional changes with an average of only 20% shared species over the whole extent of the study. Similarity values among the infaunal communities ranged mostly from 10 to 40% shared species. Substantial changes in species composition were observed within sites with mean similarity values of 38% shared species for epifauna and 33% for infauna (Fig. 2 – Within sites). Hence there is, on average, more similarity (less dissimilarity) within sites for epifauna than for infauna albeit the difference is not very large and both compartments mostly ranged from 20% to 60% of shared species within meadows. The amplitude of these similarity values indicated important differences among meadows in terms of their fine-scale heterogeneity and/or temporal variability. Yet, despite these low proportions of shared species within meadows, within-site comparisons still displayed higher similarities than among-site comparisons, indicating even more extensive variations of species composition among meadows. The importance of the spatial variation of community compositions was confirmed by the low similarities observed for within-year comparisons with mean values of 30% shared species for epifauna and 21% for infauna. Hence again, there is, on average, more similarity (less dissimilarity) within years for epifauna than for infauna, indicating more important compositional changes among sites for infauna. Ultimately, this substantial spatial variation emerged as dominant compared to the temporal variation as, for both compartments, within- and among-years comparisons displayed the same patterns.

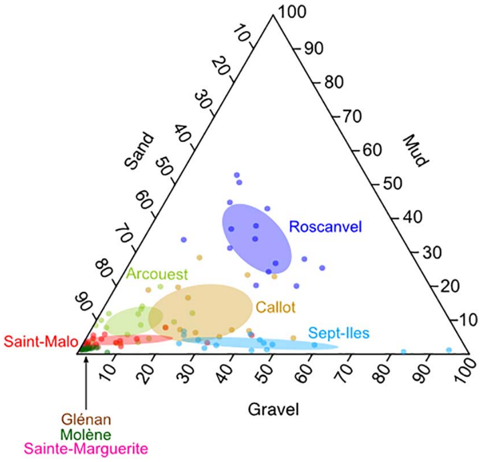

Fig. 4. Granulometry of the points sampled on each of the eight *Zostera marina* beds during the five years. 95% confidence ellipses are drawn for the points corresponding to each site. Within-site dispersion represents temporal variability during the 5 years of the study and variability among the three points sampled per year. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Relative contributions of species replacement and richness difference to species composition renewal in space (Fig. 2 – Within years) were comparable with those for temporal changes (Fig. 2 – Within sites). On average, when considering all pairs of epifaunal assemblages together, 70% of the species were found in only one assemblage: 50% of them changed in terms of species identity (replacement) and 20% were unique to the richest assemblage and thus linked to the richness difference (Fig. 2 – All pairwise comparisons). Likewise, for all pairs of infaunal assemblages, on average 80% of the species were found in only one assemblage with 60% changing identity due to species replacement and 20% linked to richness differences. The contributions of richness difference were on average similar in both compartments albeit they appeared more variable in epifaunal than in infaunal communities. Indeed, more comparisons implying extremely important changes of species richness were observed for epifaunal communities than for infauna. Yet, for each compartments, richness differences constituted > 60% of the dissimilarity in > 2% of the total pairwise comparisons. In all these cases, it involved comparisons with few specific samples where important drops in richness had occurred such as in Roscanvel 2010 for the epifauna or in one point of Sept-Iles in 2009 for the infauna. Overall, variations of species composition within and among seagrass meadows were mostly driven by changes in species identity and were rarely induced by important changes in species richness.

3.3. Variations of the community structures of seagrass epifauna and infauna and relationship with sediment conditions

Principal component ordinations of the Hellinger-transformed abundances confirmed extensive spatial and temporal variations of the

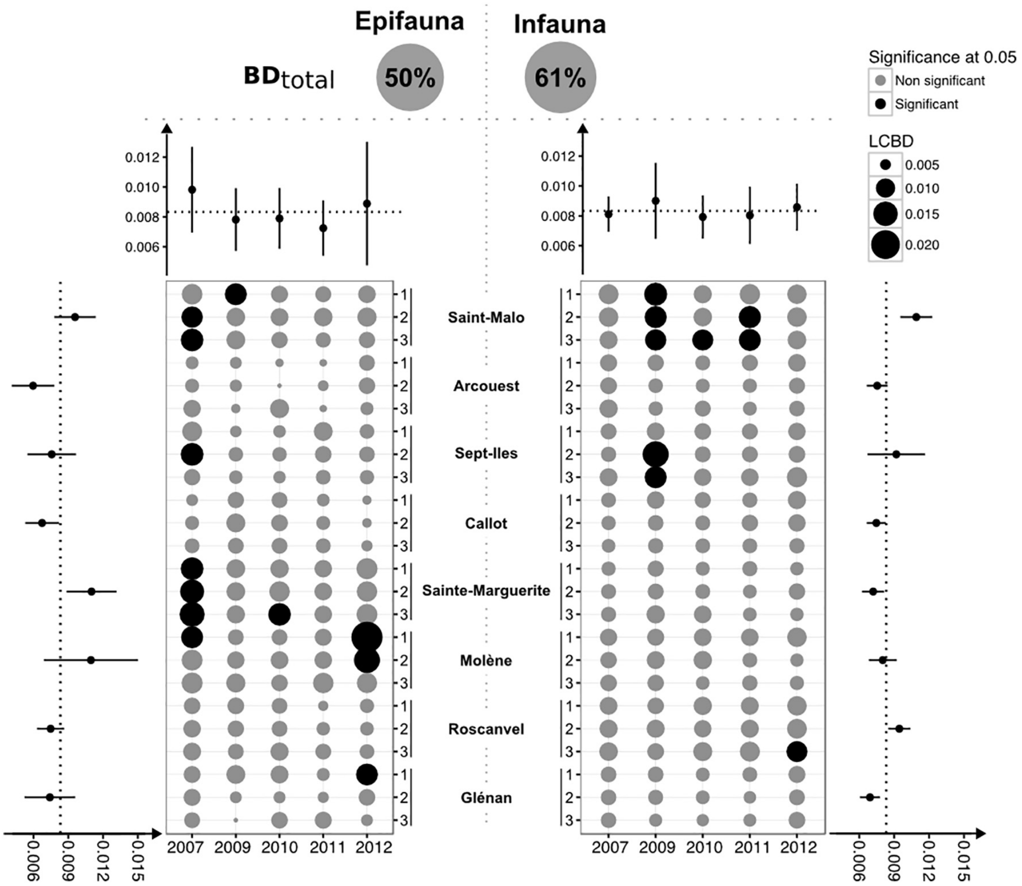

Fig. 5. Spatio-temporal map of the Local Contributions to Beta Diversity (LCBD) of the three points of each site for the 5 years of the study. LCBD values were calculated using Hellinger-transformed data for the epifauna (on the left) and the infauna (on the right) separately. They indicate the extent to which each local community is unique in terms of its composition. Circle surface areas are proportional to the LCBD values. Circles in black indicate significant LCBD indices at the $\alpha = 0.05$ significance level. Marginal diagrams indicate mean LCBD values associated with their standard deviations per year (upper margin) and per site (left margin for epifauna and right margin for infauna). Dashed line in marginal diagrams indicates the expected LCBD value if all samples contributed equally (*i.e.* 1/120). Total β diversity, quantified as the variance of the Hellinger-transformed abundance data, is expressed in the upper panel as the percentage of its maximum possible value for Hellinger-transformed data, which is 1.

seagrass macrofaunal assemblages (Fig. 3). These patterns were consistent with those obtained with presence-absence data (Appendix 3). Besides, removing the 179 species represented by < 10 specimens over the whole study had little impact on the observed patterns, even for presence/absence analyses (Appendix 4). Overall, predominance of spatial over temporal variation and differences in spatio-temporal structures between epifauna and infauna emerged from the two PCAs. Spatial and temporal variations were further tested and quantified with two-way MANOVAs in which significant space-time interactions were found for both compartments. The interaction was more important for the epifaunal communities ($F = 4.05$, $p = 0.001$, $R^2 = 27\%$) than that of their infaunal counterparts ($F = 2.47$, $p = 0.001$, $R^2 = 18\%$), confirming the visual conclusions drawn from the PCA. Indeed, Glénan, Molène and Callot meadows exhibited extensive within-site variation in terms of epifauna whereas, comparatively, infaunal communities showed more homogeneous within-site variation with the exception of the Arcouest meadow. Furthermore, epifauna and infauna not only displayed different heterogeneity level among meadows in terms of their temporal variations but also exhibited distinct spatial patterns. Epifaunal assemblages expressed a main gradient that separated the sites of Roscanvel and Sept-Iles on one side from the meadows of Sainte-Marguerite and Saint-Malo on the other. Further differences were also found between the communities of the latter two meadows on the second axis. The main gradient observed in epifaunal communities was also retrieved in infauna but was eclipsed by the important differences of the three meadows of Glénan, Molène and Sainte-Marguerite with the other beds. Consequently, the gradient between the infaunal communities of Sept-Iles and Saint-Malo was relegated to the second axis.

The main gradient within epifaunal assemblages of the seagrass meadows was mainly expressed through changes in the dominant grazers. It particularly opposed the trochid-dominated meadows of Roscanvel and Sept-Iles, highly dominated by *Jujubinus striatus*, *Gibbula cineraria* and *Gibbula pennanti*, to communities dominated by other mesograzers. Identity of these other mesograzers was also at the basis of the distinction between Sainte-Marguerite, displaying high abundances of *Lacuna parva*, *Idotea balthica* and *Atylus swammerdami*, and Saint-Malo's epifauna, exhibiting instead high abundances of *Dexamine spinosa*, *Phtisica marina*, *Aora gracilis* and of *Gammarus* species. The singularity of the infaunal communities of the Glénan, Sainte-Marguerite and Molène meadows arose from the high dominance of *Spio cf. arndti* that represented respectively 36%, 14% and 9% of the total abundances observed in these sites during the five years of the study. Comparatively, this polychaete represented < 0.5% of the total abundances in the other sites. The lower abundances of *Golfingia elongata* contributed to their distinction as well. All other meadows displayed weaker dominance. The seagrass beds of Sept-Iles and Roscanvel were characterised by high abundances of the polychaetes *Aonides oxycephala* and of the *Lumbrineris* genus, the amphipod *Gammarella fucicola* and the tanaid *Apseudes talpa*, which distinguished them from the communities of Arcouest and Saint-Malo. The latter were differentiated by high relative abundances of the polychaetes *Euclymene oerstedi*, *Melinna palmata*, *Aponuphis bilineata* and *Nephtys hombergii*, the two bivalves, *Lucinoma borealis* and *Loripes lacteus*, and the amphipods *Phtisica marina*, *Caprella acanthifera and Aora gracilis*.

Sediment granulometry displayed a gradient similar to the one retrieved for the epifauna and infauna between the meadows of Roscanvel and Sept-Iles on one side and of Sainte-Marguerite and Saint-Malo on the other (Fig. 4). Indeed, it separated the sites with heterogeneous sediments, with high contents of silt and clay or gravel, from the meadows composed of well-organized and homogenous sediments characterised by high sand content. Particularly, the important distinction of the infauna of Glénan, Molène and Sainte-Marguerite matched with the uniqueness of their sediment as all three displayed extreme sandy characteristics over the 5 years of the study. In comparison, all other sites displayed greater variability in time and more heterogeneity. Overall, redundancy analysis (RDA) of the community data against sediment properties explained 27.1% of the variation of infaunal communities (adjusted R^2, $F = 9.8$, $p = 0.001$) whereas 18.0% only of the epifaunal variation was related to the sediment conditions of the seagrass beds (adjusted R^2, $F = 6.2$, $p = 0.001$). Hence, variation among the macrofaunal communities could not be entirely explained by sediment properties alone. This is especially the case for the two sites of Roscanvel and Sept-Iles, which displayed similar communities while having completely opposed granulometry with a dominance of fine and coarse sediments, respectively. Moreover, within-site community variability did not coincide with sediment variability of the sites, especially in terms of epifauna as exemplified by the Molène meadow.

3.4. Contributions to overall β diversity

The contribution of each meadow to the overall spatial and temporal renewal of seagrass macrofaunal communities was evaluated using LCBD indices calculated for each of the faunal compartments separately (Fig. 5). Infaunal communities displayed greater overall variation than epifauna with a BD_{total} reaching 61% of its maximum possible value while it was 50% for epifaunal communities. Contributions to total β diversity displayed little variation across the different meadows or the different years, albeit the variation was more pronounced for epifauna than for infauna. Indeed, mean contributions for the five years were similar for infauna and lied near their expected mean if all communities had equal contributions. Comparatively, the years 2007 and 2012 contributed more than the three others for the epifauna, mainly due to high contributions in these two years of the Saint-Malo, Sainte-Marguerite and Molène communities. All meadows did not contributed equally to the total variation of epifauna but higher average contributions of some meadows mainly arose from punctual events. For instance, Molène's contribution appeared mainly linked with the high and significant LCBD scores registered in 2012 and related to the drop of diversity – as recorded by Simpson's inverse – observed in that year. The 11 significant LCBD scores observed among the 120 sampling units represent a 9% rejection rate that remains near the expectation level of type I error for a significance threshold of 5% if all LCBD values were drawn from the same statistical population. This also applies to the 9 significant LCBD scores observed for the infauna, which represent a 7.5% rejection rate albeit the highest LCBD scores were repeatedly found in the Saint-Malo meadow. With the exception of the latter bed, similar average LCBD contributions were observed across the different sites with values near the expected mean for most of the infaunal communities. As for epifauna, punctual high contributions could be related to important drops of diversity such as in Sept-Iles in 2009 or in Roscanvel in 2012, but overall, contributions to total β diversity of infauna were even more homogenously distributed across sites and across years than for the epifauna.

4. Discussion

Local studies can only evidence a subset of ecological patterns. Apprehending the general laws that underlie diversity structures in ecosystems often requires the combination of a variety of observations at various scales of analysis (Whittaker et al., 2001). For that reason, authors increasingly advocate the expansion of the scales of ecological studies for both marine conservation and theoretical purposes (Witman et al., 2015; Edgar et al., 2016). Here, using an extensive dataset covering eight seagrass meadows surveyed during five years, we provide the first estimation of the substantial spatial and temporal variability of the species-rich macrofaunal communities in mid-Atlantic meadows at a regional scale.

Seagrass meadows form a highly productive habitat (Heck et al., 2008). We observed important densities of macrofaunal organisms, which correspond to values reported from both sides of the Atlantic and from the Baltic and Mediterranean seas (mostly ranging from 2000 to 50,000 ind·m^{-2}; Orth, 1973, Blanchet et al., 2004, Boström et al., 2006; and references therein). Mean species richness in these *Zostera marina* beds was higher than in the meadows of the Baltic Sea (often < 10 species in 0.002 m^2 samples with 0.5 mm mesh size; Boström and Bonsdorff, 1997, Boström et al., 2006) but were comparable to values reported for infauna in the North-Eastern and Western Atlantic (mostly from 10 to 60 species in samples ranging from 0.004 to 0.27 m^2 with 0.5 or 1 mm mesh size; Orth, 1973, Stoner, 1980, Edgar et al., 1994, Blanchet et al., 2004 and references therein). In addition to this high local richness often reported for individual seagrass meadows (Hemminga and Duarte, 2000), our estimates of BD_{total} (Fig. 5) indicate extensive variation of communities at the regional scale. Hence, regional richness was enhanced by a combination of high α and β diversities, in agreement with the recent description of Brittany waters as a hotspot for macrobenthic richness in Western Europe (Gallon et al., 2017, this issue).

The invertebrate communities differed among sites and years although the 120 sampling units (8 sites × 3 points × 5 years) presented the kind of variation in composition expected for sampling units drawn from a large statistical population such as the broad-scale meta-community of invertebrates of the *Zostera* beds of Brittany with year-to-year variation. There is indeed strong variation in community composition and α diversity among sites and years. These changes were both dependent on the meadow and the faunal compartment considered. In particular, extensive variations of species composition were observed among sites, confirming that faunal composition of seagrass meadows is not a fixed or constant attribute. Similar variations among meadows were indeed observed in the Baltic Sea by Boström and Bonsdorff (1997), with Jaccard similarity ranging from 0.32 to 0.72 for both the epifauna and infauna associated with *Zostera marina* beds. Likewise, Edgar et al. (1994) found Jaccard similarities ranging from 0.1 to 0.59 among seagrass infauna of different sites in South East Australia.

Removing the 179 species represented by < 10 specimens over the whole study had little impact on the major patterns described by the ordinations, even when considering presence/absence data. However, the β diversity decompositions, computed with all species, indicated extensive species turnover even within meadows with renewals often > 50%, which primarily suggests important fluctuations of the numerous rare species observed in this study. Marine datasets usually contain large numbers of rare species that may partly be attributed to sampling methodology (Gray et al., 2005). Yet, they may also be favoured by the increased niche availability and surface area provided by structurally complex habitat such as seagrass (Boström and Bonsdorff, 1997; Attrill et al., 2000; Lürig et al., 2016). Rare species are often characterised by limited niche breadth, and studies with large spatial and temporal extents – such as the present study – encompass large-scale environmental gradients that inherently favour the discovery of rare species (Gaston and Kunin, 1997; Legendre and Legendre, 2012). As these rare species may be of prime functional importance (Hooper et al., 2005; Ellingsen et al., 2007; Mouillot et al., 2013), further work is needed to disentangle whether they may be attributed to sampling methodology or to underlying ecological causes (Chase and Myers, 2011) and evaluate to what extent the important compositional changes may affect seagrass functioning.

Interestingly, despite important community composition changes, species richness remained within narrow limits. Indeed, species replacement predominated while richness differences were of limited extent, implying that changes in species composition were induced by simultaneous gain and loss of species among meadows. A similar case of varying assemblage composition accompanied by constancy in associated diversity measures was previously reported over 1.5 ha of an intertidal meadow in South Africa (Barnes, 2013) but this is the first report at such broad spatial scale and across such contrasted environments. Barnes (2013) suggested extending the theoretical framework for temporal constancy of biodiversity measures to the spatial context of seagrass meadows. This would require constant levels of productivity and resource availability despite spatially variable environmental conditions, and an open system with opportunity for compensatory mechanism among species to exploit all resource spectra while withstanding varying conditions (Brown et al., 2001; Barnes, 2013). Provided that similar functional spaces are available across the different meadows, the rich regional pool of species available to colonise these North-East Atlantic meadows may provide foundation for portfolio effects (Schindler et al., 2015). Indeed, spatial and/or temporal stability of community's organisations may theoretically arise from independent dynamics among species that perform similar ecosystem functions (Tilman et al., 1998; Schindler et al., 2015). Such ecological equivalence may arise at regional scale among species that only vary subtly in their ecological niches such that their partially overlapping niches make believe that they fulfil similar roles in the communities at such scales of study (Shmida and Wilson, 1985; Munoz and Huneman, 2016). Biogenic habitats often harbour similar functional groups across different locations while displaying high levels of redundancy within each groups (Hewitt et al., 2008; Barnes and Hamylton, 2015). For instance, several mesograzers can coexist through micro-habitat partitioning in seagrass (Lürig et al., 2016), nonetheless they are generally regarded as occupying equivalent trophic positions and feeding niches (Duffy, 2006). Accordingly, we observed important local changes in the identity and preferences of dominant mesograzers among beds but their functional space was invariably occupied. Thus, in a species-rich region such as Brittany, some are able to thrive in the different local conditions while occupying similar functional spaces. High species replacement together with low richness differences may indicate that the studied meadows share essential properties in terms of niche and resource availability despite varying local conditions (Cornell and Lawton, 1992). These shared properties may constrain their diversity and the narrow range of species richness described in this study may therefore correspond to the species richness carrying capacity for seagrass (*sensu* Hansen et al., 2011).

Ecological equivalence among species may have a large stochastic component (Munoz and Huneman, 2016) so that the processes underlying this apparent richness constancy remain unclear (Barnes and Hendy, 2015). Accordingly, efforts should be made to disentangle the biotic and abiotic structuring factors of epifaunal and infaunal communities. Seagrasses form intricate structures that vary at a series of hierarchical levels, generating complex interplay between the scales at which their associated fauna responds (Turner et al., 1999). This study confirms that the structuring factors underlying epifauna patterns may differ from those shaping infauna, as shown at more local spatial scale than the present study by Leopardas et al. (2014). Indeed, PCAs showed that epifauna and infauna did not display the same patterns and MANOVA results revealed that these patterns where different with respect to space and time. Hence, despite sharing a substantial number of species, epifauna and infauna may not respond in similar ways and be sensitive to the same prevailing forces. Both compartments have considerable amount of unique species that are most likely the ones inducing the differences observed. A community is most often defined as group of interacting species occurring together in space and time (Stroud et al., 2015). Accordingly, the differences between epifauna and infauna spatial and temporal patterns described here support the hypothesis that they may be considered as distinct self-communities (Hemminga and Duarte, 2000; Törnroos et al., 2013; Leopardas et al., 2014). This statement however, does not preclude that these two communities may be closely linked in their fate and depend on their respective functional roles, nor does it challenge the trophic relationships that may exist between some of the species composing the two communities (Orth et al., 1984).

Epifauna was characteristically dominated by grazers (Duffy, 2006). Variation of epifauna was partly related to sediment characteristics implying a relationship between local hydrological conditions and aboveground communities. This relationship may operate through direct effects of currents on epifauna (Hovel et al., 2002), or through indirect effects *via* modification of the *Z. marina* beds' architecture and characteristics under the influence of substrate and hydrodynamic conditions (Frederiksen et al., 2004; Moore and Short, 2006). For instance, epifauna has often been related to variation in seagrass aboveground biomass (Attrill et al., 2000; Leopardas et al., 2014). The present epifaunal assemblages were dominated by trochids and crustacean mesograzers that generally feed on epiphytic algae associated with *Z. marina* blades but have different feeding behaviour (Hily et al., 2004; Duffy, 2006; Rueda et al., 2008; Mancinelli, 2012). These behaviours may induce different responses to variations in epiphyte availability linked with seagrass biomass as well as to differences that may exist among beds in terms of epiphytic composition (Saunders et al., 2003; Borg et al., 2010). They may also be influenced by external phenomena such as provision of transient food sources. Accumulation of drifting algae may represent an important food supply for benthic invertebrates (Norkko et al., 2000). Such input was for instance commonly observed in the Sainte-Marguerite meadow since the beginning of its monitoring by the REBENT programme in 2004. This can explain the dominance of species such as *Idotea balthica* in this meadow, as these isopods are often associated with drifting algae (Duffy, 2006). The role of environmental variables not accounted for in the present analysis such as temperature, salinity or primary productivity (Snelgrove, 1998) remain however to be unveiled. In particular, *Zostera marina* displays a large phenotypic plasticity in Brittany (Becheler et al., 2010). Variation in seagrass morphology can certainly influence associated macrofauna but the role of seagrass structure has mostly been explored in terms of among-habitat patterns (Airoldi et al., 2008). Its influence on within-seagrass community variability remain however to be fully apprehended, in particular regarding its relative importance compared to abiotic factors and its underlying mechanisms (Attrill et al., 2000; Sirota and Hovel, 2006; Ávila et al., 2015). Likewise, the influences of dispersal patterns, of historical events and macroevolutionary processes, and of local scale processes such as predation, facilitation, resource partitioning and competitive exclusion are largely unknown at such scales (Ricklefs, 1987; Wagner and Fortin, 2005; Boström et al., 2010).

Sediment conditions and the forces that shape them are often the main factors structuring infaunal communities (Gray, 1974). The Glénan, Sainte-Marguerite and Molène communities were clearly distinguished by the great dominance of *Spio cf. arndti* that is characteristic of fine sand conditions (Dauvin, 1989). All other meadows displayed more heterogeneous sediments with characteristic species such as *Golfingia elongata* (Gibbs, 2001) and *Nematonereis hebes* (George and Hartmann-Schröder, 1985). While the effects of local conditions on epifauna may be dampened by their adult dispersal capabilities (Thrush and Whitlatch, 2001), infauna is more sedentary and often displays a tight relationship with its proximate environment (Pearson and Rosenberg, 1978). Accordingly, infauna showed a stronger response to the local hydrological characteristics of the meadows than epifauna and therefore displayed a higher BD_{total}. As hypothesised by Gallon et al. (2017), the great range of local hydrological conditions found in Brittany may explain the important spatial renewal observed for infaunal communities, promoting high overall richness at the regional scale. Thus, while seagrass epifauna has been described as an important local addition to infauna diversity and as playing an important role in among-habitat diversity (Boström and Bonsdorff, 1997), the present study reveals that infauna may be more variable at the regional scale and thus contribute more importantly to within-habitat β diversity of seagrass communities. Further work is needed to refine our understanding of the relative roles of epifauna and infauna on regional diversity in habitat mosaics, taking into account the within-habitat contribution of the infauna.

Management actions should vary, for sites with similar local α diversity, depending on their local contributions to β diversity (Noss, 1983). Despite a growing interest in measuring and understanding β diversity (Koleff et al., 2003; Legendre et al., 2005; Anderson et al., 2011; Legendre and De Cáceres, 2013), only a few studies have explicitly focused on spatial or temporal turnover of marine communities. These studies mainly concerned fish communities (*e.g.* Belmaker et al., 2008; Lamy et al., 2015) and macrofauna of rocky habitats (*e.g.* Balata et al., 2007) and soft sediments (*e.g.* Hewitt et al., 2005; Josefson, 2009; Zajac et al., 2013). High β diversity was observed in the PCAs and LCBD analyses, implying that the studied *Zostera marina* meadows differed markedly from one another, each one containing but a small fraction of the regional richness (Koleff et al., 2003). Exceptional contributions to β diversity were only punctual and these high LCBD values were mostly related to drops in local diversity. These drops may be linked to catastrophic events such as the sand dune movement that covered the Molène meadow in 2012 (personal observation) but this remains to be determined for the other high LCBD scores, and in particular for the Saint-Malo meadow that repeatedly had significant LCBD scores. Overall, all seagrass meadows had fairly similar contributions to the high β diversity. They consequently have equivalent conservation values (Legendre and De Cáceres, 2013). This conclusion is strengthened by the weak species richness differences observed among the sites, while the substantial community replacement among meadows confers them high complementarity. Future work will need to evaluate the relevance of this extensive within-seagrass variation in a multi-habitat context. This variability, however, undoubtedly needs to be accounted for in management schemes to fully preserve the regional diversity (Fraschetti et al., 2008; Törnroos et al., 2013). In particular, a significant space-time interaction was found, indicating that spatial patterns have changed over time or, conversely, that the year-to-year variations of the meadows were location-specific (Legendre et al., 2010). These spatial and temporal interactions seem to be a common feature in seagrass (Boström et al., 2011; Carr et al., 2011). Accordingly, to preserve this high regional diversity, management actions should focus on site-specific rather than broad-scale measures. These measures should foster the maintenance of the local diversity of meadows but also their complementarity at broad scale. If local diversity seems to be a good predictor of the functioning of seagrass meadows (Duffy et al., 2015), the important variations observed in species composition, and especially of rare species, and the equal contribution of the different meadows to regional diversity, raise questions about their functional complementarity at regional scale (Bond and Chase, 2002). Life trait analysis of these seagrass communities would be of particular interest to deepen our understanding of the processes underlying their apparent carrying capacity for species richness. It may give insights into the role of species and on how functional space may vary among these meadows in relation to environmental filters (Villéger et al., 2011; Mason et al., 2013).

Large scale analyses of marine biodiversity have traditionally focused on surrogates of species-level pattern such as mapping habitat feature (Ferrier, 2002; Fraschetti et al., 2008). The ability of these approaches to grasp the biodiversity of different seagrass species have however been challenged in previous work (Hamilton et al., 2012). In agreement, we illustrate here, through an important monitoring effort, the existence of not negligible ecological patterns among meadows that remained concealed with these approaches (Edgar et al., 2016). In the context of benthic homogenisation and loss of complexity on the sea floor, this study argues for a better consideration of all components of diversity in marine studies (Gray, 1997; Airoldi et al., 2008). It emphasizes in particular the importance of taking β diversity patterns into account to fully grasps the richness of benthic habitat at broad scale (De Juan and Hewitt, 2011; De Juan et al., 2013). Efforts in the broad scale acquisition of ecological data have long been thwarted by various logistical or methodological impediments (Edgar et al., 2016). However, appropriate analytical tools are becoming increasingly available and the present study illustrates the potential contributions of broad spatial and temporal monitoring programmes combined with innovative statistical analyses. Further broad scale analyses in contrasted environments will help to deepen our understanding of biodiversity patterns and their underlying ecological processes, and in turn will help guide management actions.

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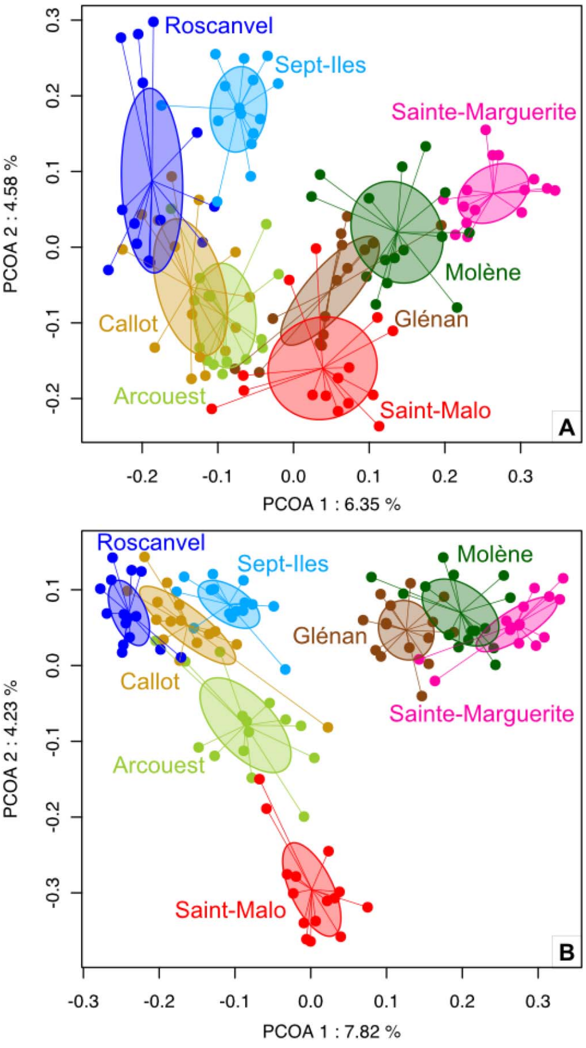
Appendix 1. Sampling dates of each site in the 5 years of the study. Date format: day/month/year (DD/MM/YY). Sampling dates may vary from one year to another due to tide conditions or logistic constraints.

Sites	Sampling dates
Arcouest	2/19/2007
Arcouest	3/12/2009
Arcouest	3/1/2010
Arcouest	3/22/2011
Arcouest	4/4/2012
Callot	2/21/2007
Callot	3/11/2009
Callot	3/2/2010
Callot	4/19/2011
Callot	4/8/2012
Glénan	4/17/2007
Glénan	3/11/2009
Glénan	4/20/2010
Glénan	4/18/2011
Glénan	5/7/2012
Saint-Malo	2/20/2007
Saint-Malo	3/28/2009
Saint-Malo	4/1/2010
Saint-Malo	4/18/2011
Saint-Malo	3/8/2012
Sainte-Marguerite	2/20/2007
Sainte-Marguerite	2/12/2009
Sainte-Marguerite	2/3/2010
Sainte-Marguerite	3/19/2011
Sainte-Marguerite	3/9/2012
Molène	4/18/2007
Molène	2/11/2009
Molène	2/2/2010
Molène	3/22/2011
Molène	5/8/2012
Roscanvel	4/17/2007
Roscanvel	2/10/2009
Roscanvel	2/1/2010
Roscanvel	3/21/2011
Roscanvel	3/8/2012
Sept-Iles	4/18/2007
Sept-Iles	3/10/2009
Sept-Iles	3/1/2010
Sept-Iles	3/21/2011
Sept-Iles	5/7/2012

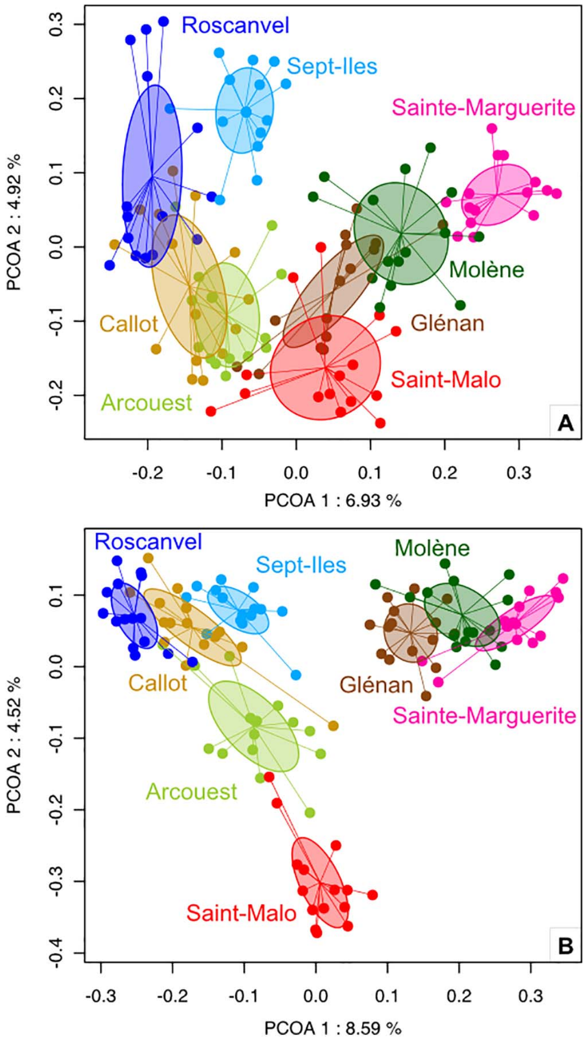
Appendix 2. Total abundances per m^2 per site (sum over the 3 points) in the 5 years of the study. Epifauna (Epif.) and Infauna (Inf.)

Site		Mean abundance per point				
		2007	2009	2010	2011	2012
Saint-Malo	Epif.	11	78	20	17	24
	Inf.	5889	4193	2444	1981	1470
Arcouest	Epif.	15	48	62	36	40
	Inf.	6422	4541	4807	5378	2726
Sept-Iles	Epif.	31	39	33	19	30
	Inf.	13,763	2156	8156	5522	4611
Callot	Epif.	42	40	86	55	51
	Inf.	12,289	5296	5615	3585	6259
Sainte-Marguerite	Epif.	76	188	96	203	94
	Inf.	32,178	26,000	9578	7944	21,444
Molène	Epif.	26	19	73	12	48
	Inf.	13,141	12,630	16,511	7441	13,422
Roscanvel	Epif.	22	28	38	67	45
	Inf.	8422	12,274	4348	5267	2840
Glénan	Epif.	37	89	32	144	27
	Inf.	18,185	41,941	6696	25,830	28,867

Appendix 3. Principal coordinates analyses (PCoA) of presence/absence data based on the square root of Jaccard dissimilarity. The square root of Jaccard dissimilarity was used because distances calculated in this way are fully embeddable in Euclidean space and the distance matrix does not produce negative eigenvalues (Legendre and Legendre, 2012). The analysis of epifaunal communities is represented in panel A and of the infauna in panel B. The first two axes represent 10.9% and 12.1% of the total variation of epifaunal and infaunal community compositions respectively. 95% confidence ellipses are drawn for the points corresponding to each site. Within-site dispersions represent temporal variability during the 5 years of the study and variation of the communities among the three points sampled per year.



Appendix 4. Principal coordinates analyses of presence/absence data based on Jaccard dissimilarity. Species represented by < 10 specimens over the whole study (representing 179 species over the epifauna and infauna together) were removed from these analyses. The square root of Jaccard dissimilarity was used because distances calculated in this way are fully embeddable in Euclidean space and the distance matrix does not produce negative eigenvalues (Legendre and Legendre, 2012). The analysis of epifaunal communities is represented in panel A and of the infauna in panel B. The first two axes represent 11.9% and 13.1% of the total variation of epifaunal and infaunal community compositions respectively. 95% confidence ellipses are drawn for the points corresponding to each site. Within-site dispersions represent temporal variability during the 5 years of the study and variation of the communities among the three points sampled per year.



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2. Perspectives

Les résultats de ces travaux offrent plusieurs perspectives de recherche. La première est d'appréhender l'effet de variables environnementales non prises en compte dans cette étude sur la diversité α et β des communautés. En particulier, il serait intéressant d'examiner l'influence de la structure morphologique de la Zostère sur les communautés associées. Distinguer en conditions naturelles les effets directs de l'environnement des effets indirects, *via* la réponse de la Zostère à son environnement et les modifications de la structure physique des herbiers qui s'ensuit, pourrait fournir de précieuse informations sur le devenir des communautés face à la dégradation des herbiers de Zostères. Cet aspect est en partie exploré dans le 3ème chapitre de cette thèse qui relie les variations des communautés d'endofaune de différents habitats, dont les herbiers, aux variations environnementales. Deuxièmement, nous avons mis en évidence et caractériser l'importante variabilité des communautés de macrofaune associées aux herbiers. Il semble alors pertinent d'évaluer les implications de cette variabilité dans un contexte multi-habitats afin de tester la cohérence taxinomique des habitats en prenant en compte ces importantes variations. Ces implications sont évaluées dans le 2ème et 3ème chapitre de cette thèse. La troisième perspective qu'ouvrent ces travaux est d'appréhender le rôle fonctionnel des nombreuses espèces rares observées dans les herbiers et d'évaluer l'influence de leur important *turnover* dans le fonctionnement des habitats complexes. Cette question des liens entre diversité β, notamment des espèces rares, et fonctionnement est l'objet du 2ème chapitre de cette thèse.


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CHAPITRE 2

Les suivis biologiques à travers le prisme des traits d'histoires de vie afin de réconcilier théorie et conservation

1. Prélude

L'un des freins majeurs à l'efficacité des mesures de conservation de la biodiversité est le décalage existant entre les échelles auxquelles s'appliquent les actions de conservations, et celles auxquelles sont produites les connaissances écologiques théoriques et empiriques concernant le fonctionnement des communautés (Cadotte et al. 2017, Isbell et al. 2017). Dans le but d'établir ce lien et de mieux appréhender les conséquences fonctionnelles de la dégradation des habitats biogéniques à l'échelle mondiale, ce chapitre se propose d'analyser la diversité α et β des communautés benthiques d'une part sous un angle taxinomique et d'autre part à travers le prisme des traits d'histoires de vie des espèces. En se concentrant uniquement sur le groupe des polychètes, rassemblant des espèces aux stratégies écologiques extrêmement diversifiées (Giangrande 1997, Rouse & Pleijel 2006, Jumars et al. 2015) et constituant une part importante de la diversité et biomasse des communautés benthiques (Hutchings 1998), cette étude explore les mécanismes qui gouvernent les communautés au sein de différents habitats, leurs répercussions sur la diversité taxinomique et fonctionnelle à une échelle régionale, et, finalement, leurs implications en ce qui concerne la résilience des communautés benthiques sur le long-terme.

En résumé, cette étude met en évidence le rôle prépondérant des habitats biogéniques dans la diversité des communautés benthiques et leur résilience à long-terme et insiste ainsi sur l'importance de leur conservation. Ces habitats favorisent la diversité locale des communautés, à la fois taxinomique et fonctionnelle, et en cela promeuvent une plus grande redondance fonctionnelle au sein des assemblages de polychètes. Ainsi, ils fournissent une sorte d'assurance dans l'espace et le temps, facilitant le maintient des fonctions écologiques auxquelles contribuent ces espèces. Cette redondance n'est pas retrouvée dans les assemblages de sédiment nu, bien que, selon les résultats de cette étude, ceux-ci abritent à l'échelle de la région une diversité de niches écologiques tout aussi grande que les habitats biogéniques. En effet, contrairement aux attentes qui pourraient être formulées face à leur faible richesse locale relative, les assemblages de sédiment nu contribuent de manière similaire à la diversité fonctionnelle de la région grâce à leur importante diversité β. Cela met en exergue l'importance de préserver l'hétérogénéité de ces habitats, un aspect de conservation jusqu'à présent probablement sous-évalué.

Enfin, cette étude a mis en lumière les mécanismes qui semblent gouverner les communautés dans ces différents habitats. Les assemblages de sédiment nu sont principalement contraints par les forçages abiotiques alors que les habitats biogéniques réduisent l'emprise qu'ont les conditions environnementales sur les communautés qui leurs sont associées. Les résultats de ce chapitre montrent également que les mécanismes qui régissent les assemblages de polychètes au sein des bancs de mäerl et des herbiers diffèrent largement et sont associés à différentes vulnérabilités des communautés qu'ils abritent. Ainsi, la forte diversité taxinomique et fonctionelle des bancs de maërl semble provenir de l'importante hétérogénéité à fine échelle de cet habitat. Cette hétérogénité promeut une grande diversité de niches écologiques et favorise une importante redondance fonctionnelle. Au contraire, la forte diversité taxinomique et fonctionnelle qu'abritent les herbiers semble en grande partie dépendante de l'apport d'espèces rares provenant d'autres habitats. Seuls certains rôles écologiques avantagés par l'abondance des resources détritiques au sein des herbiers (*p.ex.* les déposivores) semblent bénéficier d'une redondance importante. Ainsi, la protection de la diversité fonctionnelle des herbiers nécessite de prendre en compte les paysages benthiques dans lequels ils s'intégèrent et leur connectivité avec d'autres communautés. Par le bais d'une approche par traits biologiques, cette étude intègre ainsi les connaissances empiriques et théoriques existantes sur ces communautés à grandes échelles spatiales et temporelles et permet donc d'émettre des recommandations pour mieux guider la conservation de la diversité associée à ces habitats afin d'assurer l'intégrité fonctionnelle des fonds marins sur le long terme.

From theory to conservation priorities for the functioning of marine benthic systems across habitats: trait-based approach to monitoring data along 500 km of coastline

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2. Abstract

β diversity relationships with ecosystem functioning remain poorly documented. This impedes our capacity to predict how local community changes affect ecosystem functioning at scales relevant for conservation. Combining a trait-based approach to monitoring data covering a 7-year period and 500 km of coast, we evaluate the functional implications of on-going seafloor changes by characterizing the α and β diversities in different benthic habitats currently threatened by biotic homogenization. We describe the taxonomic and functional diversity of habitats associated with two different types of foundation species, intertidal seagrass and subtidal maerl beds, compared to bare sediment at similar tidal level and link the mechanisms underlying their α diversities to their repercussions at regional scale. Foundation species appear as a major factor governing community composition and locally promote taxonomic and functional α diversity, reinforcing the conservation value of biogenic habitats. However, our results reveal that these species act through different mechanisms and that the functional diversity of biogenic habitats is associated to different vulnerabilities whose implications for conservation are discussed. Maerl fine-scale heterogeneity promotes niche diversity and leads to high functional redundancy for the whole subtidal compartment at regional scale, providing insurance for seafloor functioning at long-term. In contrast, seagrass diversity is associated with redundancy for only a few functions because their functional diversity relies on transient species and mass effects. Maintaining the seascapes in which seagrass are embedded seems essential to ensure their long-term functioning. At regional scale, the locally poorer bare sediment harbored similar functional richness as biogenic habitats because of higher within-habitat β diversity, stressing a potential underrated conservation value for benthic ecosystem functioning. We show here that coupling trait-based approaches to monitoring data can help link broad-scale β-diversity to their underlying drivers, bringing local mechanistic understanding closer to the scales at which biodiversity loss and management actions occur.

Keywords:

Functional diversity - Beta diversity - Broad scale monitoring - Community assembly – Ecosystem engineers – Biotic homogenization - Habitat loss - Coralline algae - *Zostera marina*

3. Introduction

Earth is profoundly marked by the imprints of anthropic activities (Steffen et al., 2011). In particular, anthropogenic impacts on natural ecosystems are causing a massive decline of biodiversity at global scale (Pimm et al., 2014). This imperils the functioning of ecosystems (Naeem et al., 2012) and, thereby, the goods and services derived from them (Cardinale et al., 2012). Quantitatively, consequences of biodiversity loss on ecosystem functioning rival those attributable to the direct effect of global change stressors such as climate warming, acidification or nutrient pollution (Duffy et al., 2017; Hooper et al., 2012). Therefore, there is an increasing demand for conservation policies to account not only for biodiversity changes but also for their outcomes on ecosystem functioning and on the delivery of ecosystem services (Isbell et al., 2017). However, relationships between biodiversity and ecosystem functioning are currently best understood at fine spatial and temporal scales (Duffy et al., 2017; Gamfeldt et al., 2015). There is now a growing consensus that measures of local diversity alone (α diversity, Whittaker, 1960) cannot fully capture current biodiversity trends (Hillebrand et al., 2017). Patterns of biodiversity changes are indeed scale-dependent and are more pervasive and consistent at broader spatial scales (Jarzyna & Jetz, 2018; McGill et al., 2015). As such, there is a mismatch between the fine scales of our understanding of biodiversity relationships with ecosystem functioning, and the broad scales at which anthropogenic stressors and conservation policies operate (Isbell et al., 2017).

Despite the large consensus on threats associated with the loss of local diversity for ecosystem functioning (Cardinale et al., 2012), current biodiversity changes may not systematically involve the loss or direct modification of α diversity (Hewitt et al., 2010; Primack et al., 2018). Indeed, constant α diversity may hide substantial changes in community composition and structure in space and time (Dornelas et al., 2014), termed β diversity (Whittaker, 1972). β diversity determines how local changes scale-up to affect biodiversity at broader scales and understanding it is critical to assist conservation planning (Socolar et al., 2016). β diversity patterns are increasingly modified by anthropogenic stressors with, in particular, a tendency for increasing similarity of communities at broad scale (Socolar et al., 2016). This decline in β diversity worldwide, termed “biotic homogenization”, appears as the main component of biodiversity loss at global scale (Olden & Rooney, 2006; Primack et al., 2018). Yet, patterns of β diversity remain poorly documented (McGill et al., 2015) and their roles in ecosystem functioning have received little attention compared to that of local (α) diversity (Mori et al., 2018). Therefore, a better appraisal of the linkages between patterns of β diversity and ecosystem functioning is needed to predict the effects of biodiversity changes that may emerge at broader scales (Burley et al., 2016; Mori et al., 2018).

It is now clear that both α and β diversities interact to determine the performance of ecosystems at broad scale (Hautier et al., 2017) but their relative importance in particular ecosystems remains to be clarified (Barnes et al., 2016). Nonetheless, available evidence suggests that loss of β diversity alone directly imperils the performance of ecosystems at broad spatial scale (Hautier et al., 2017; Pasari et al., 2013; Plas et al., 2016) and poses latent threats to their long-term functioning by weakening their resilience capacity (Isbell et al., 2018; Oliver et al., 2015). Apprehending these direct and indirect threats requires an understanding of the relationship between the susceptibility of a species to be lost and its role in the functioning of an ecosystem (Bracken et al., 2008), and in its resilience (Clavel et al., 2011).

Species influences on ecosystem properties and their responses to their environment are mediated by physiological, morphological, phenological and behavioral characteristics, referred to as functional traits (Violle et al., 2007). Trait-based approaches therefore offer an integrative framework to apprehend both the causes and functional consequences of current biodiversity changes (Suding et al., 2008) and provide an appealing tool to apprehend the role of community variation in the functioning of ecosystems at broad scales (Burley et al., 2016; Violle et al., 2014). There is increasing evidence that spatial patterns of taxonomic and functional (trait-based) β diversity may be decoupled and that neither can serve as proxy for the other (Devictor et al., 2010; Loiseau et al., 2016). As such, while temporal changes in functional β diversity may track taxonomic variation (Brice et al., 2017; Naaf & Wulf, 2012), functional homogenization has been shown to exceed the extent of taxonomic homogenization in some instances (Mori et al., 2015; Villéger et al., 2014) whereas in others, modification of species assemblages did not lead to pervasive changes in functional structure and composition (Sonnier et al., 2014; White et al., 2018). While the functional outcomes of biotic homogenization remain largely underexplored hitherto (Clavel et al., 2011; Olden et al., 2018), these findings prompt an urgent need to identify when and where species changes might greatly impact the functional characteristics of communities and to provide risk assessment and conservation priorities regarding the functional diversity of ecosystems (Cadotte & Tucker, 2018). The consequences of habitat degradation on ecosystem functioning have, in this respect, received increasing attention in terrestrial ecosystems (Liu et al., 2018). Although there are many parallel issues in benthic systems (Snelgrove et al., 2014), available data remain scant in marine systems and warrant further research (Mazor et al., 2018).

Benthic communities are essential components of the functioning of coastal ecosystems (Snelgrove et al., 2014). They rank amongst the most affected ecosystems of the planet (Halpern et al., 2008) and continue to face increasing anthropogenic pressures (Halpern et al., 2015). In particular, coastal benthic ecosystems are facing dramatic losses of their most diverse and productive habitats (Airoldi & Beck, 2007). These are mostly biogenic, formed by ecosystem engineers (Jones et al., 1994) and most often by foundation species (*sensu* Dayton, 1972) such as seagrasses, macroalgae or biogenic reefs, and are acutely vulnerable to current environmental changes (Airoldi & Beck, 2007). The degradation of crucial foundation populations is recognized as a major threat to marine faunal populations (McCauley et al., 2015) and imperils both the high local diversity they harbor and the among-habitat β diversity they create (Airoldi et al., 2008). In addition, the effects of ecosystem engineers may be variable in space and time (Crain & Bertness, 2006), potentially leading to high within-habitat β diversity (Boyé et al., 2017). However, this variability remains largely neglected when evaluating the effect of ecosystem engineers on species diversity (Romero et al., 2015). As such, while current understanding of the role of biogenic habitats in the functional diversity of communities is focused on their contribution to the α diversity of the sediment, it rarely accounts for their contribution to within- and among-habitat β diversity (Airoldi et al., 2008). This leads to great uncertainties when extrapolating the potential consequences of their broad scale degradation (Snelgrove et al., 2014).

Here we assess the main sources of taxonomic and functional diversity of benthic communities at regional scale in 2007, 2010 and 2013, and discuss their importance in relation to the potential vulnerability of these communities. In particular, we focus on the role of two biogenic habitats, intertidal *Zostera marina* meadows (Figure 1. D) and subtidal maerl beds (unattached coralline red algae) formed by at least two species in Brittany, *Lithothamnion corallioides* and *Phymatolithon calcareum* (Riosmena-Rodríguez et al., 2017; Figure 1. E). These two biogenic habitats are under substantial threats (Grall & Hall-Spencer, 2003; Waycott et al., 2009). We compare their taxonomic and functional α and β diversities to those from bare sediment using monitoring data covering the whole Brittany seaboard (France; Figure 1. A), a highly diverse environmental mosaic (Boyé et al., 2017). We explore the mechanisms governing community assembly in these different habitats and their variability in space and time, and assess how each habitat contributes to the functional diversity at regional scale. For this purpose, the present study focuses on *Polychaeta* (Phylum Annelida), a phylogenetically diverse class comprised of a great diversity of species exhibiting a wide range of ecological strategies (Giangrande, 1997; Jumars et al., 2015; Rouse & Pleijel, 2006) and having a critical role in ecosystem functioning through activities such as bioturbation (Queirós et al., 2013).

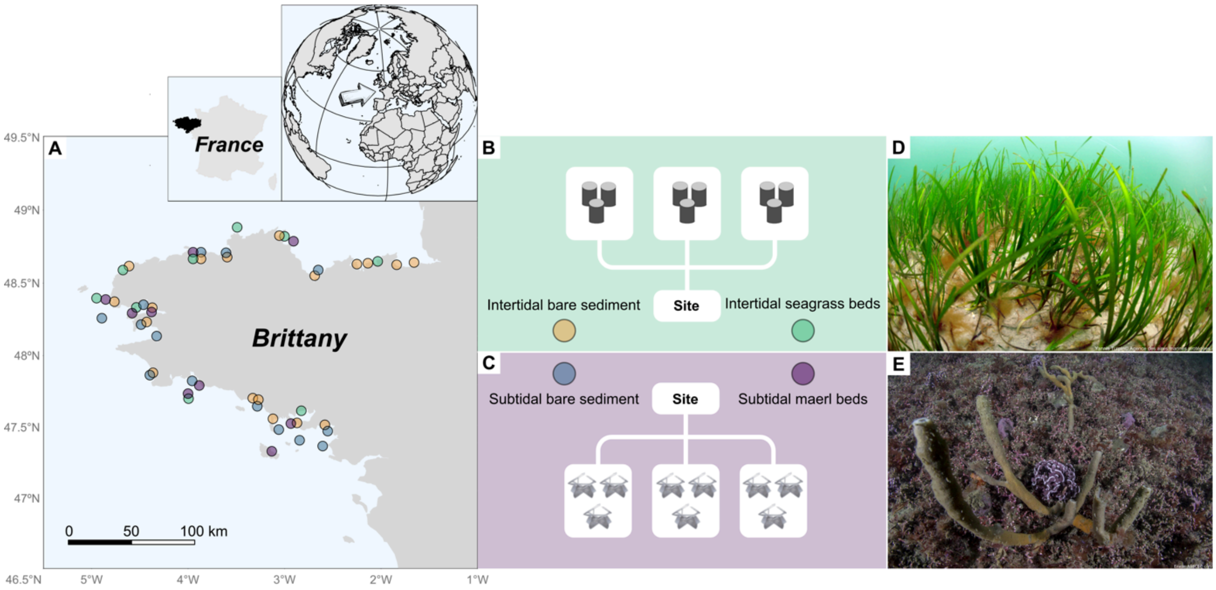

Figure 1. *A. Map of the monitored sites. B. For intertidal habitats, three points are sampled at each site using three sets of three sediment cores, each cylinder representing one such set. C. For subtidal habitats, three points are sampled at each site using three Smith-McIntyre grabs. The nine cores or grabs were then pooled to estimate abundances at the site level. Accordingly, macrofaunal densities were estimated based on 0.27* m^2 *and 0.9* m^2 *surfaces sampled per site for the intertidal and subtidal sites respectively. D. Photography of a Zostera marina meadow; photography credit: Yannis Turpin, Agence des aires marines protégées. E. Photography of a maerl bed; photography credit: Erwan Amice, Centre National de la Recherche Scientifique.*

4. Sampling and Methods

a) Field sampling

In the context of the on-going REBENT (*Réseau Benthique*) monitoring programme started in 2003 (http://www.rebent.org), 50 benthic communities were monitored yearly across 42 sites covering the whole Brittany seaboard (Figure 1. A), representing four habitats: 9 intertidal seagrass beds and 9 subtidal maerl beds for the biogenic habitats, 18 intertidal sandy beaches and 14 locations of subtidal sediment devoid of biogenic habitats (respectively referred to as intertidal and subtidal bare sediment thereafter). These sampling locations were chosen to encompass most of the environmental settings that can be found along Brittany's coasts. Thereafter, we will use the term *site* to describe a given habitat in a given location. The terms *observation* and *assemblage* respectively refer to a sampling occasion and to the polychaete composition of a given site at a given year.

This study focuses on three years of the REBENT monitoring (2007, 2010 and 2013), chosen to maximize the spatial and temporal coverage of the data, and ensure similar temporal resolution for all sites (data are only missing for two sites in 2010; see Supplementary material, Figure 1). Sampling was consistently performed for all sites between the end of February and the beginning of May, before the recruitment of most species (Dauvin et al., 2007), using a standardized protocol summarized in Figure 1. B and C and more fully described in the Supplementary material. Note however, that sampling gears differ between intertidal and subtidal sites so that comparisons are fully meaningful within a given tidal level, while comparisons between the two tidal levels may bear methodological imprint.

b) Trait collection

For the purpose of this study, we focused only on species belonging to the *Polychaeta* class. We collated data on the 234 polychaetes species found during this survey for 11 traits that were divided into a total of 44 categories. These traits characterized the maximum size, the feeding and reproductive ecology of the species, their mobility, and their bioturbation potential (Table 1) and were chosen to reflect key ecological processes (Table 1 of the Supplementary material). Trait data were collected from the publicly available database Polytraits (http://polytraits.lifewatchgreece.eu), reviews specific to the reproduction and feeding ecology of polychaetes (Giangrande, 1997; Jumars et al., 2015; Rouse & Pleijel, 2006) and to the bioturbation potential of benthic species (Queirós et al., 2013), primary literature on specific species or genera, or from expert knowledge. Information was collected at the lowest possible taxonomic level and inferred when missing from data available from other species from the same genus, or in the most extreme cases from knowledge available at the family level (only for feeding-related traits and mobility types and for families showing low variability for these traits). For reproduction frequency, development mode and sexual differentiation, data were missing for 9% (21 species), 7% (17), and 1% (3) of the species respectively. Missing values were imputed as described in the Supplementary material. Species were scored for each trait modality based on their affinity using a fuzzy coding approach (Chevenet et al., 1994). The coding procedure, detailed in the Supplementary material, allowed for the incorporation of within-species variability.

The observation-by-trait matrix containing the total abundances of each modality within the assemblages was calculated using the matrix product of the observation-by-species matrix (usually referred to as site-by-species), containing the abundances of the species in the assemblages, with the filled species-by-trait matrix, containing the relative expression of trait modalities by species after standardization of the scores to 1 per trait and per species. This procedure partitions, for each trait, the abundances of the species into the different modalities they expressed. For example, if an assemblage contains a single species with 10 specimens and this species is indifferently predator and scavenger (therefore coded 0.5 for both modalities after standardization), this assemblage has 5 predators and 5 scavengers in the assemblage-by-trait matrix. In this matrix, the sum of each trait for an observation is the total abundance of the species found in the assemblage.

c) Data analyses

Differences among habitats in terms of local diversity were explored using several complementary indices describing different aspects of the taxonomic and functional α diversity of the assemblages. In addition to the total abundance and the species richness of the assemblages, taxonomic diversity was characterized by the Simpson diversity index, calculated as (Greenberg, 1956):

$$D = 1 - \sum_{i=1}^{S} p_i^2$$

with S being the species richness of the assemblage and p_i the relative abundance of species i. This index was used because of its relationship with Rao's quadratic entropy (Rao, 1982) that was used to measure functional diversity in the null model approach developed in this study (see below). It is indeed a specific case of Rao's index where all species are considered maximally different from each other (Botta-Dukát, 2005). Simpson's index also has the desirable property of down-weighting rare species (Hill, 1973) as these species may not have been properly sampled in such a monitoring programme with large spatial and temporal extents. The functional structure of the assemblages was characterized using four indices: *functional richness* ($FRic$), *functional evenness* ($FEve$), *functional divergence* ($FDiv$), and *functional dispersion* ($FDis$, Laliberté & Legendre, 2010; Villéger et al., 2008). These four indices were chosen for their complementarity and capacity to depict different facets of the functional structure of communities (Mouchet et al., 2010). A brief description of these indices and their complementarity is provided in the Supplementary material, along with details of their calculation method.

We used a null model approach to assess whether the observed functional diversity of communities was lower or higher than expected if community assembly was independent of species traits. Prevalence of trait divergence (higher diversity than expected), convergence (lower diversity than expected), or random distribution among the assemblages of each habitat was then used to evaluate how biogenic habitats influenced assembly mechanisms (Perronne et al., 2017). For that, we calculated Rao's quadratic entropy for each assemblage, both using all traits simultaneously and for each trait separately, to account for the fact that assembly processes may act contrastingly on different traits (Spasojevic & Suding, 2012). Rao's metric is adequate for detecting trait convergence or divergence (Botta-Dukát & Czúcz, 2016). We then compared these values to those of simulated communities using randomizations of the site-by-species matrices within each tidal level separately, i.e. randomizing species across bare and seagrass habitats in the intertidal, and across bare and maerl habitats in the subtidal, but not across intertidal and subtidal assemblages. The randomization procedure was constrained to keep constant: 1) the observed species richness of communities, 2) the number of occurrences (number of samples where the species occur) of each species at the regional scale and within each tidal level, and 3) the total abundance of each species at the regional scale and within each tidal level. This procedure was implemented using the *trial-*

swap method of the *randomizeMatrix* function provided in the *picante* package in R (Kembel et al., 2010) and was used to simulate 1000 randomly assembled communities. For each simulation, 100 000 trial-swaps were done. To compare the observed values to the results of these null models, we calculated the Standard Effect Size (SES, Gotelli & McCabe, 2002) for each community, defined as:

$$SES = \frac{RaoQ_{observed} - \mu_{nullmodels}}{\sigma_{nullmodels}}$$

with $RaoQ_{observed}$ the observed functional diversity, $\mu_{nullmodels}$ the mean of the null distribution of the functional diversity, and $\sigma_{nullmodels}$ its standard deviation. Positive SES values indicate trait divergence whereas negative values suggest trait convergence. Near zero values indicate random distribution.

Patterns of taxonomic and functional β diversity were characterized using Principal Component Analysis (PCA) of the Hellinger-transformed species and trait modality abundances. Hellinger transformation allows for the use of Euclidean-based methods on frequency data and has the desirable property of not giving excessive weight to the rare species (Legendre & Gallagher, 2001). The extent of β diversity within each habitat at the regional scale was also quantified using the overall variance of the Hellinger-transformed assemblage-by-species and assemblage-by-modalities matrix for each habitat separately, following the measure of total β diversity (BDtot) proposed by Legendre & De Cáceres (2013). Again, these values of BDtot are only comparable within the same tidal level due to the previously raised methodological constraints. This regional scale within-habitat variability from both a taxonomic and functional trait perspectives were then put in relation with the contribution of each habitat to the functional richness of the region. The latter was assessed through their percentage occupancy of the regional trait space, calculated following McWilliam et al. (2018) as the convex hull volume occupied by the species of one or several assemblages, divided by the global convex hull, defined as the volume (functional richness) of the species-by-trait matrix containing all species found over the whole study (all sites and the three years of data). The relative importance of the α and β diversities of each habitat in their contribution to regional functional richness was assessed by comparing the average contribution of the assemblages of the habitats (volume occupancy of the species found in each assemblage) to the total contribution of the habitats at the regional scale (volume occupancy of all the species found within each habitat over the whole study). Lastly, the relationships between taxonomic variation of communities and changes in trait composition were assessed using co-inertia analyses (Dolédec & Chessel, 1994) between the PCA of Hellinger-transformed species and trait abundances, both within each habitat, and across all samples. The RV coefficient (Robert & Escoufier, 1976), a multivariate generalization of the squared Pearson correlation (Legendre & Legendre, 2012), was used to quantify these relationships.

All statistical analyses were performed using *R* (*R* Core Team, 2017). Simpson diversity and Rao's quadratic entropy were calculated using the *rao.diversity* function of the *SYNCSA* package (Debastiani & Pillar, 2012). $FRic$, $FEve$, $FDiv$, and $FDis$ were calculated using the *dbFD* function of the *FD* package (Laliberté et al., 2014). All other analyses relied on the *vegan* package (Oksanen et al., 2017).

5. Results

a) Taxonomic α and β diversity patterns

The main gradient in polychaete composition, materialized by the first axis of the PCA of polychaete abundances (Figure 2), separates bare sediment assemblages (left) from those found in biogenic habitats (right). These differences account for more than 14% of the total variance of the assemblages and surpass the distinctions between intertidal and subtidal areas, reflected partly on the second axis of the unconstrained ordination. For these differences however, it is

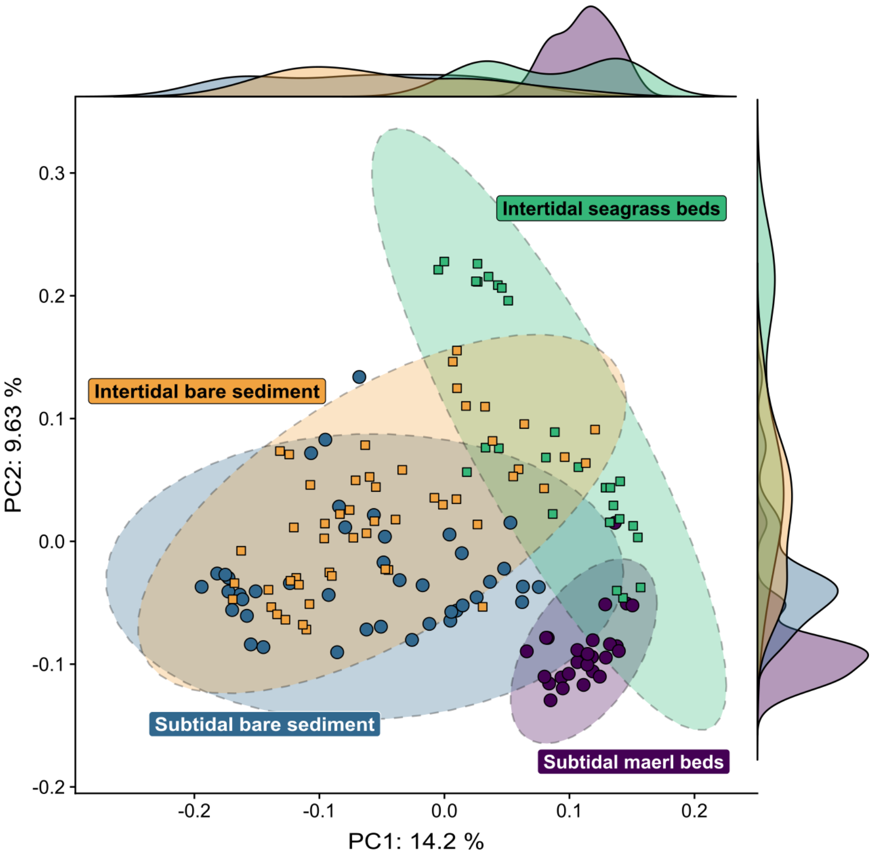

Figure 2. *Principal component analysis of Hellinger-transformed polychaete abundances. Samples are displayed in scaling 1 in the central panel. The shapes of the points reflect differences in the tidal levels and sampling methods: squares represent intertidal habitats sampled using sediment cores and circles represent subtidal habitats sampled using Smith-McIntyre grabs (see Figure 1). The densities of points for each habitat along the first and second axis are displayed as curves in the outer panels. Within-habitat variability comprises of both spatial and temporal variations (see Supplementary material, Figure 1). The first two PCA axes represented account together for 23.83% of the total variance of Hellinger-transformed polychaete composition. The species scores associated with this analysis are represented in Supplementary material Figure 5.*

impossible to separate the influence of ecological determinants from differences due to variation in sampling gear between the intertidal and subtidal compartments. Notwithstanding, differences between bare sediment assemblages and those of biogenic habitats emerged irrespectively of the sampling methods. This observation reinforces the conclusion of a strong structuring effect of foundation species upon polychaete assemblages composition.

The effects of biogenic habitats are also conspicuous on the α diversity of polychaete assemblages (Figure 3). Within tidal levels, their presence consistently increases the species richness of assemblages. However, differences between bare and biogenic habitats in terms of abundance or Simpson diversity were less consistent and of lesser extent overall. In terms of richness, maerl beds hosted, by far, the richest assemblages with an average richness of 53 species (± 2.1; standard error). They harbored at least 32 species and reached a maximum of 73 species. These values exceed those found in subtidal bare sediment (average richness of 29 ± 2.2 se, maximum of 68 but minimum as low as 6 species). Likewise, seagrass meadow richness exceeded values found in intertidal bare sediment. With an average richness of 25 (± 1.7; se), a maximum of 50 and hosting at least 10 species, seagrass meadows maintained in intertidal areas levels of richness similar to those observed in subtidal bare sediment. Comparatively, bare sediment in intertidal areas displayed richness ranging from 1 to 29 species with an average of 12 species (± 1.0; se). Abundance on the other hand was on average higher in bare sediment in subtidal areas than in maerl beds, and in seagrass meadows in intertidal areas than in bare sediment, mostly due to a higher variability and some extreme values in these habitats.

Simpson diversity did not show major differences among habitats of similar tidal levels.

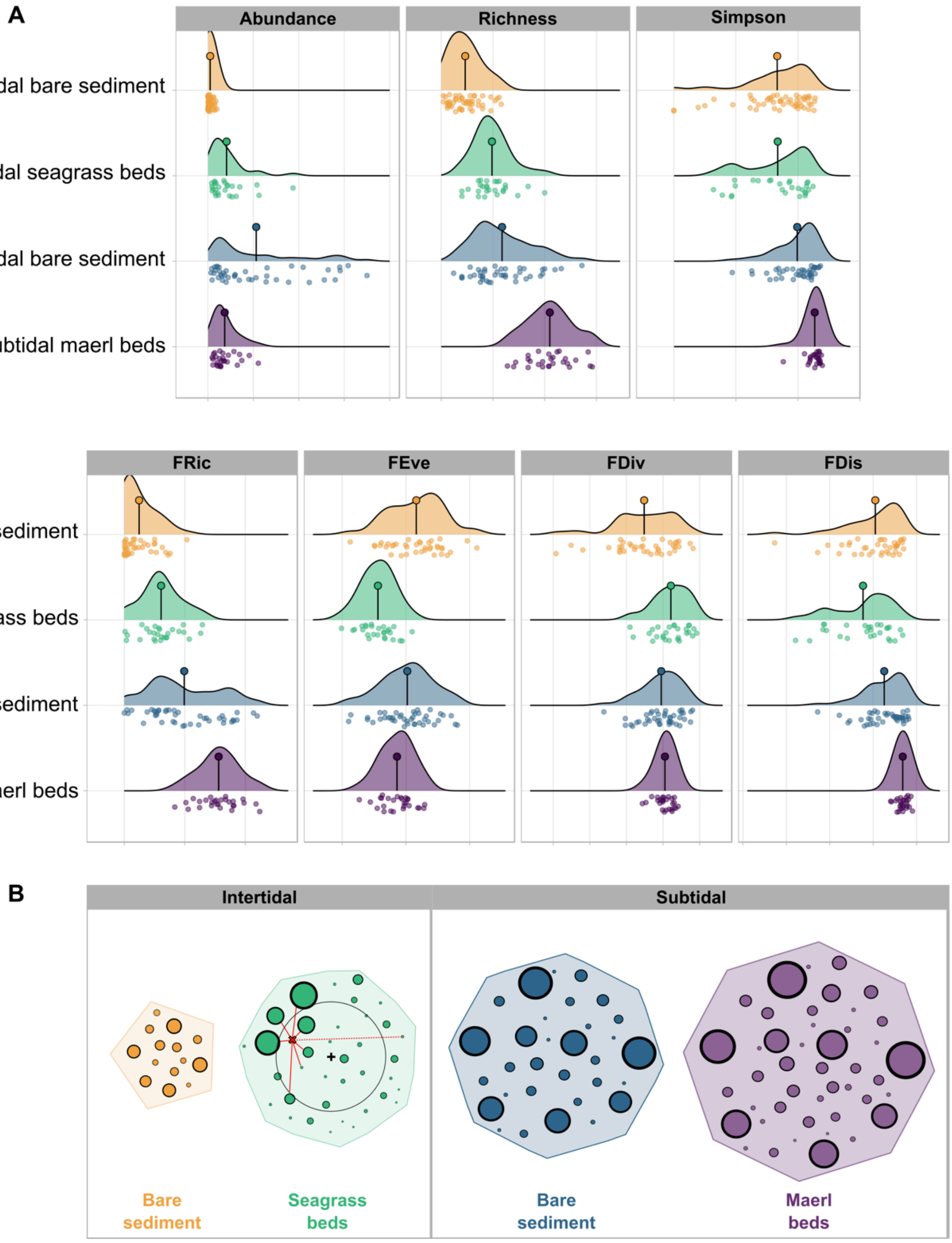

Figure 3. A. *Distribution of taxonomic and functional* ***α****-diversity indices among the four habitats.* ***B.*** *Schematic view derived from these indices of the functional spaces representing an average assemblage of each habitat.* ***A.*** *For each habitat, the distributions include the values of the different sampled sites with, for each site, values for the three years (2007, 2010, 2013). The mean value for each of these indices is represented by the point pinned on each distribution. Abundance corresponds to the total abundance of each assemblage (one site for one habitat at one year). Richness corresponds to the species richness of the assemblage. Simpson corresponds to Simpson's diversity index.* ***FRic****,*

FEve, *and* ***FDiv*** *correspond to the functional richness, the functional evenness and the functional divergence respectively, and were calculated on 5 PCOA axis representing 66% of the original species dissimilarity matrix.* ***FDis*** *corresponds to the functional dispersion.* ***B.*** *Conceptual representation of species abundances in functional space (following representations from Boersma et al., 2016; and Mouillot et al., 2013b) integrating the insights provided by the different functional indices to depict the average functional structure of each of the four habitats. Circle size reflects the relative abundance in each trait space of each particular traits combination. The convex polygons represent in two dimensions the volume of the trait space, larger surfaces representing higher FRic. The center of gravity of the functional space (black cross) and the abundance-weighted centroid (red cross) are schematically represented for the seagrass trait space to illustrate our conceptual explanation for how lower functional dispersion than in bare sediment can emerge despite higher FRic and FDiv. The black circle represents the hypothetic mean functional distance from the center of gravity. It is high if all abundant species are found at the extreme part of the trait space, as in the representation where all are clustered on the edge of the trait space. The red dotted lines represent the distances of some species to the abundance-weighted centroid. All distances are weighted by abundances and averaged in the calculation of FDis. Therefore, FDis can be low despite high FRic and FDiv if, as represented, the abundance-weighted centroid is close to the abundant species when these are all clustered together at the edge of the trait space and if all species far from the centroid are rare and have therefore low weights in the averaging of the distances during the calculation of FDis.*

b) Functional structure and diversity at local scale

The positive effect of biogenic habitats on species richness translated into higher functional richness values in seagrass and maerl beds compared to the bare sediment of the same tidal levels (Figure 3. A; FRic). Interestingly, the other facets of functional diversity were not affected in similar ways by these two types of foundation species when compared to their bare counterparts. In subtidal environments, maerl associated assemblages displayed similar average functional evenness (Figure 3. A; FEve), functional divergence (Figure 3. A; FDiv) and functional dispersion (Figure 3. A; FDis) to those found in sediment devoid of foundation species, albeit a slightly lower mean for the latter that is related to the lower functional richness found in bare sediment. The spatial and temporal variability of these indices however, differed between the two subtidal habitats, with more stable values found in maerl beds (less dispersed distributions). In contrast, seagrass meadows deeply modified the functional α-diversity profiles exhibited by the polychaete assemblages of intertidal environments. Seagrass presence tended to reduce the functional evenness of the assemblages while promoting higher functional divergence. Functional dispersion also tended to be lower in seagrass although values remained in comparable ranges and with similar distribution shapes than those observed in bare sediment.

To integrate the results provided by the α diversity indices, the functional structure of an average assemblage of each habitat was derived from the different taxonomic and functional indices and schematically represented in Figure 3. B. An average assemblage in intertidal bare sediment has few species within a small functional space (low FRic), with abundances evenly distributed within it (high FEve). In comparison, seagrass promotes a broader functional space but at the expense of lower evenness, indicating more clustered abundances in trait space. The high functional divergence indicates that higher abundances are found in the extreme part of the trait space. Together with lower functional dispersion occurring despite higher functional richness, and lower evenness than in bare sediment, it suggests that all abundant species in seagrass tend to cluster in the same area located near the edge of the trait space. This means that dominant species share similar characteristics that are fairly different from all other species (mainly microphageous suspensive and deposit feeders and sessile tube builders, see section IV.d), and that a large part of the broad functional space is occupied by rare species with rare traits. In subtidal areas, maerl hosts more species and promotes larger functional space (higher FRic and FDis) than bare sediment but within these functional spaces, abundances are distributed in a similar fashion (similar FEve and FDiv).

c) Assembly mechanisms: trait convergence/divergence

To assess to what extent the differences in local diversity of the habitats could be explained by their trait composition and by differences in assembly mechanisms, we compared observed functional diversity to null expectations (Figure 4). This approach revealed differences between biogenic and bare habitats, but also between the assemblages of the two types of foundation species (Figure 4. A). First, in bare sediment, and irrespective of tidal level, SES values appeared

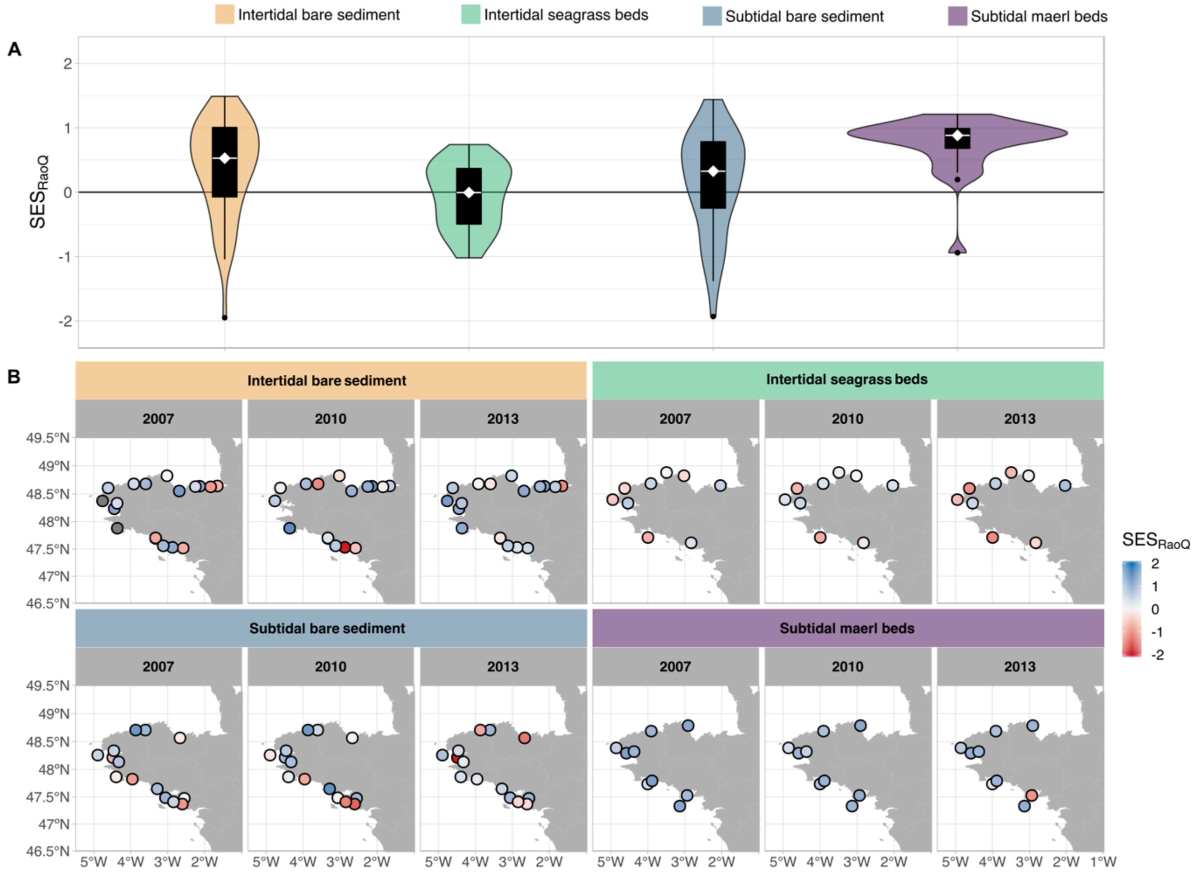

Figure 4. A. *Distribution of the Standard Effect Size (SES) values within each habitat.* ***B.*** *Maps of the spatial distribution of SES values for each habitat and for the three years. Positive SES values indicate trait divergence and negative values trait convergence. Values near zero indicate random distribution. We did not test for the significance of each individual value as our interest lied in characterizing the distribution of SES values at the scale of the four habitats. Nonetheless, note that SES values below −1.96 or higher than 1.96 are often interpreted as being statistically significant with the implicit assumption that z-ratios follow a normal distribution (Veech, 2012). However, normality of the null distributions was not verified here. Black dots in 2007 for intertidal bare sediment corresponds to two samples with only one species. Hence, for these samples RaoQ diversity is 0 and SES values cannot be calculated because the richness of the sites are kept constant in the trialswap model, always giving a functional diversity of 0 for these sites.*

highly variable in both space and time (Figure 4. A and B), a pattern also found when considering traits individually (Supplementary material Figure 3). They varied from highly positive, i.e. higher functional diversity than expected, reflecting strong trait divergence, to highly negative, i.e. lower functional diversity than expected, reflecting strong convergence, through near-zero values, not departing from the null models. Notably, the assemblages with the highest trait divergences in intertidal bare sediment were those with the lowest abundances and species richness within this habitat while these two factors appeared unrelated to the SES values within subtidal bare sediment (Supplementary material Figure 2). Comparatively, both biogenic habitats SES values were more stable but, as previously observed for the functional indices, the two types of engineers differed in their signatures (Figure 4. A). Maerl beds assemblages consistently displayed higher functional diversity than expected, a pattern that was consistent across locations and stable among the three years of monitoring (Figure 4. B). This divergence was also found when considering each individual trait separately with the exception of reproduction frequency (Supplementary material Figure 3). This trait seems to converge due to the high dominance of iteroparous species and the consistently low abundance of semelparous polychaetes in maerl assemblages (Supplementary material Figure 4). In comparison, SES values of seagrass assemblages were confined between −1 and 1, indicating that trait dispersion in seagrass meadows cannot be distinguished from random expectations under the constraints of the randomization procedure. This absence of strong departure from the null models is consistent over the whole region and the three years. Furthermore, SES values for both maerl and seagrass beds appeared unrelated to the abundance and richness of the assemblages (Supplementary material Figure 2). Overall, SES values revealed extremely variable assembly mechanisms in bare sediment while they appeared more stable in biogenic habitats. However, the two types of foundation species acted differentially on trait dispersion patterns, with seagrass assemblages consistently matching with null expectations and maerl beds promoting trait divergence, irrespectively of the location and underlying environment.

d) Functional β diversity: quantification and description

The greater variability of local assembly mechanisms highlighted by SES in bare sediment translates into a greater β diversity in these habitats, both in terms of taxonomic and trait composition (BDtot, Table 2). The two-fold increase in total variance of trait composition in bare sediment is also apparent on the first two axis of the PCA on trait abundances (Figure 5). Interestingly, this high taxonomic and subsequent functional β diversity compensates at the scale of the region the lower local diversity of these assemblages. Indeed, within tidal levels, bare habitats harbor a similar regional functional richness as biogenic habitats (Total occupancy of regional trait space; Table 2). The species found in intertidal and subtidal bare sediment respectively represent 62% and 82% of the total functional space formed by the regional species pool (all species found in this study). In comparison, species associated with seagrass and maerl beds respectively cover 64% and 86% of the regional trait space. However, different patterns underlie these similar total occupancies of regional trait space. Indeed, on average, a single intertidal bare sediment assemblage occupies three times

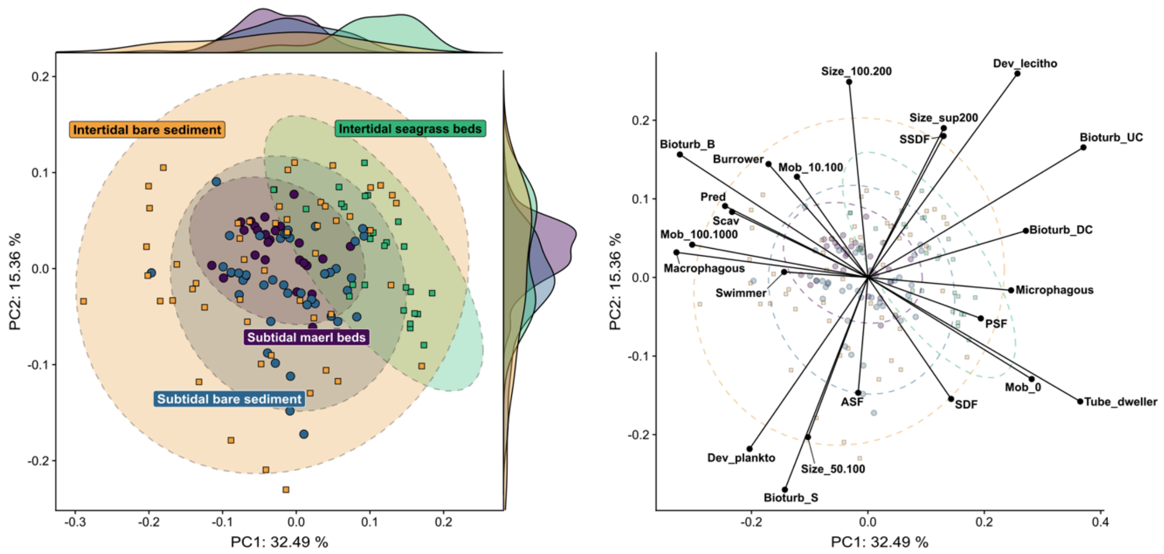

Figure 5. *Principal Component Analysis (PCA) of Hellinger-transformed trait modality abundances. Left panel: Samples are displayed in scaling 1 in the central panel. The shapes of the points reflect differences in the tidal levels and sampling methods: squares represent intertidal habitats sampled using sediment cores and circles represent subtidal habitats sampled using Smith-McIntyre grabs (see Figure 1). The densities of points for each habitat along the first and second axis are displayed in the corresponding margins. Within-habitat variability is comprised of both spatial and temporal variations (see Supplementary material, Figure 1). The first two PCA axes represented account together for 47.85% of the total variance of Hellinger-transformed trait composition. Right panel: modalities whose variances along these two axes represent more than 30% of their total variances (assessed with the function goodness; vegan). For abbreviations, please refer to Table 1.*

less space than that of a seagrass meadow, and a subtidal assemblage in bare sediment covers two times less space than that of a maerl bed (Average occupancy; Table 2). Similar results are obtained in terms of taxonomic richness, although there are some quantitative differences in the contribution of each habitat, in particular for subtidal bare sediment (Table 2).

The different ways in which bare and biogenic habitats reach similar regional functional richness are well illustrated in the PCA of trait composition (Figure 5). Indeed, the centroid of subtidal maerl and bare sediment assemblages and of intertidal bare sediment assemblages are located near the origin of the PCA space, indicating that all modalities are equivalently represented in these habitats at the regional scale. This observation was confirmed by the examination of the third and fourth axes of the PCA (not shown). However, all maerl assemblages are located near the origin, stressing that each of these assemblages is functionally rich and harbors all the modalities relatively equivalently. On the other hand, assemblages of intertidal bare sediment are extremely variable in their trait composition, from assemblages with high proportions of mobile macrophagous predators and scavengers with mostly biodiffusing actions on the sediment (on the left of the PCA) to assemblages with opposite characteristics, dominated by sessile microphagous suspensive and deposit feeders (on the right), through assemblages dominated by large active suspension feeders and by species with planktotrophic development which mainly modify the surficial sediment layers (bottom of the ordination plot). Taken together, these different local functional assemblages allow for a representation of all modalities in intertidal bare sediment at the regional scale. Subtidal bare sediment assemblages are intermediate between these two extremes with both functionally rich assemblages but also a higher variability than in maerl beds, as previously shown by the BDtot values (Table 2). Seagrass assemblages, on the other hand, display a different and more internally consistent and specialized trait signature with positions shifted on the first axis towards higher relative proportions of microphagous suspensive and deposit feeders and sessile tube builders. In particular, and in contrast with intertidal bare sediment, seagrass assemblages also tend to be dominated by species with similar sediment reworking activities, either upward- or downward conveyors. Seagrass assemblages are also characterized by a lower relative proportion of macrophagous mobile predators and scavengers. Therefore, in contrast with the other habitats, seagrass assemblages have a clear trait signature and are consistently dominated by similar modalities.

e) Relationship between taxonomic and functional β diversity

The main patterns of within- and among habitats trait variation highlighted by the PCA (Figure 5) appear different from those observed in terms of taxonomy (Figure 2). The RV coefficient computed between the two ordinations – despite the lack of independence of the data – is only 0.62, which confirms the difference between the two facets. Actually, the strength of the taxonomy-trait composition relationship varies among habitats. Indeed, this relationship is stronger in seagrass beds (RV = 0.85) and, to a lesser extent, in subtidal bare sediment (RV = 0.71), while it is fairly weak in intertidal bare sediment (RV = 0.56) and maerl beds (RV = 0.54). Compared to all other assemblages, multivariate dispersion of seagrass communities are nearly identical with regard to taxonomy and functional traits (Figure 6). This also applies, albeit to a lesser extent, to subtidal bare sediments. In contrast, while having similar average positions in the two multidimensional spaces compared to the other habitats, intertidal bare sediment assemblages are more dispersed in trait space that in terms of taxonomy (Figure 6). In agreement, values of functional BDtot for this habitat are 1.5 to 4 times that of other habitats (Table 2). On the contrary, maerl assemblages display similar dispersions in the two multidimensional spaces, confirming their high stability in terms of traits and species compositions (Figure 6; Table 2). The decoupling between taxonomic and trait facets in this habitat is clearly illustrated by the shift of the centroid position of the assemblages (Figure

6). This suggests that differences between maerl assemblages and those of other habitats are of lesser extent in terms of trait composition than they are in terms of taxonomy. In agreement, while maerl assemblages have distinct taxonomic composition compared to other habitats (Figure 2), they lie at the center of the trait-based ordination (Figure 5).

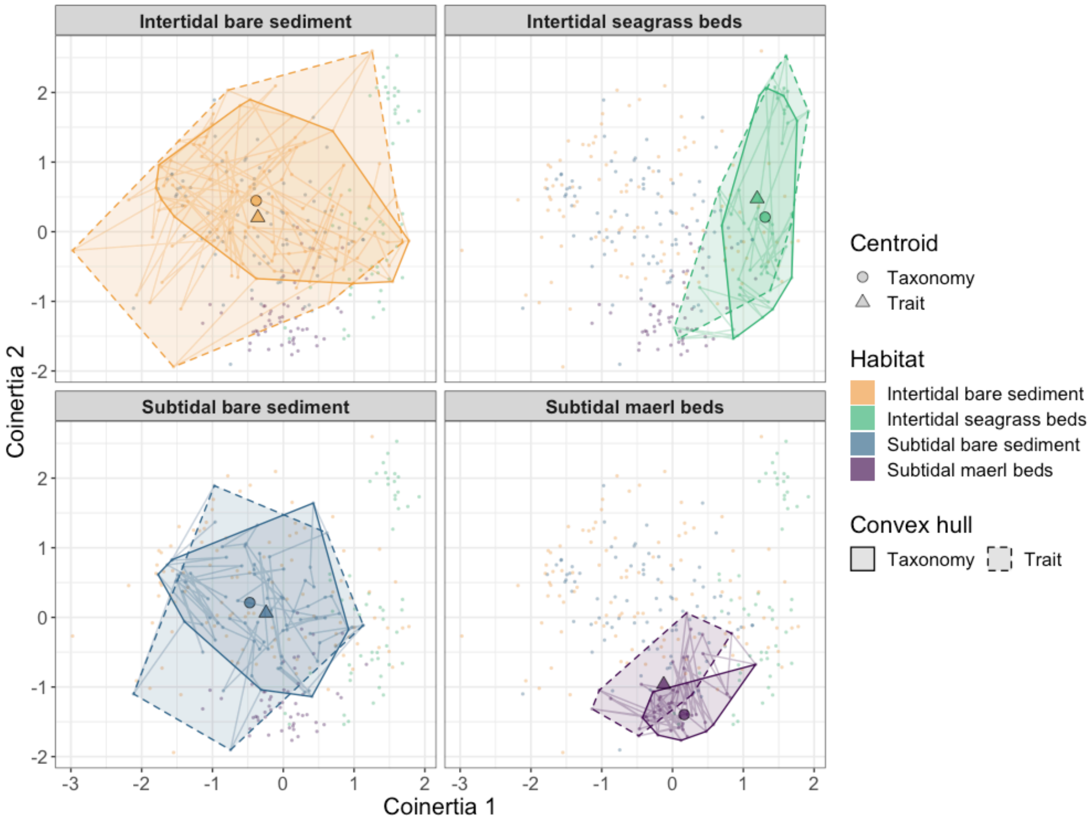

Figure 6. *Coinertia analysis between the taxonomic **β** diversity patterns represented in Figure 2 and the trait-based patterns of Figure 5. Five axes of each ordination were kept for the coinertia analysis; the RV coefficient between the two ordinations was 0.62. The four panels highlight the two-dimensional convex hull covered in the coinertia ordination by the assemblages of each habitat in terms of taxonomy (plain border) and trait composition (dashed border). All four panels are based on a single coinertia analysis involving all samples, represented in the background of each panel with colors corresponding to the four habitats. The centroid positions of the assemblages of each habitat in terms of trait and species composition are represented by distinctive symbols. Lines link the two points representing a sample in the species and trait spaces respectively.*

6. Discussion

a) Processes underlying local diversity and influence of biogenic habitats

Apprehending the mechanisms governing species coexistence and their spatial and temporal variability is becoming increasingly critical to envision how community structure and diversity could respond to future changes (Kuczynski & Grenouillet, 2018). SES values were highly variable in bare sediment, suggesting important variation across this environmentally heterogeneous region in the prevalence of abiotic and biotic drivers in the absence of biogenic structure. Trait convergence generally reflects the signature of environmental filters while divergence may arise in less stringent environments from competitive interactions (Perronne et al., 2017). Some types of intertidal bare sediment (IBS) are recognized for their harsh conditions, which require unique adaptations of species to establish themselves and persist (Defeo & McLachlan, 2005). Alternatively, competitive interactions are rather weak in soft-bottom environments but they may be fairly strong among polychaetes and are likely a key driver of coexistence in sheltered subtidal (Wilson, 1990) and intertidal bare sediment (Defeo & McLachlan, 2005). Over-dispersion was only observed in the IBS with the lowest richnesses and abundances, however. Such small assemblages with high niche specialization and functional evenness evoke initial successional stages (Song & Saavedra, 2018) that may result from the strong disturbance regimes of intertidal environments, which constantly resets communities (Defeo & McLachlan, 2005). Therefore, SES variability in IBS is likely to reflect different “ecological ages” of assemblages (Bracewell et al., 2017), rather than different assembly mechanisms, abiotic constraints largely governing the community of these IBS (Quillien et al., 2015b).

SES distribution in bare sediment reflects variation in the degree of environmental severity and indicates an important role of the local context. On the contrary, the stability observed in biogenic habitats highlights the presence of consistent mechanisms across different seagrass or maerl beds governing their associated assemblages. This stability and the absence of strong trait convergence confirm their role as refugia from abiotic constraints (Bulleri, 2018), and their capacity to buffer the effects of broad-scale environmental gradients (Jurgens & Gaylord, 2017). This is further supported by the SES values showing a strong association between iteroparity and maerl beds (MB). Indeed, iteroparity is associated with long-lived polychaetes with life cycle less related to environmental variation than semelparous species relying on environmental cues to reproduce synchronously (Giangrande, 1997). As a result, biogenic habitats emerged as a major factor governing the structure and composition of polychaete assemblages at the regional scale and they consistently promoted their α diversity across disparate environments. These results confirm patterns previously reported worldwide and reaffirm the conservation value of seagrass and maerl beds (Hemminga & Duarte, 2000; Riosmena-Rodríguez et al., 2017). Interestingly however, we show here that different mechanisms underlie their diversity.

MB assemblages consistently exhibited trait over-dispersion, which indicates niche differentiation promoting mechanisms among species across environmental gradients (Perronne et al., 2017). This over-dispersion may arise from the effects of biotic interactions whose strength may be enhanced by the more stable abiotic conditions provided by maerl beds. However, it may alternatively be the symptom of a fine-scale heterogeneity encompassed in our sampling grain (D'Andrea & Ostling, 2016). While fine-scale heterogeneity is generally trivial in soft sediment and stems principally from bioturbation (Gray & Elliott, 2009), MB provides the foundation for the establishment of a whole range of epiphytes (Peña et al., 2014). This in turn creates a great diversity of living spaces for polychaetes through a hierarchy of facilitative interactions called "habitat cascade" (Thomsen et al., 2010). This process results in high heterogeneity at fine-scale (Figure 1. E) and is associated with great niche diversity (Grall et al., 2006). Rather than competitive interactions, we therefore hypothesize that this sequential habitat formation is the main driver underlying the high taxonomic and functional richness of MB, the 3D structure of MB promoting secondary foundation species such as epiphytes (Thomsen et al., 2018).

In contrast, in seagrass beds (SB), high local richness was linked to abundances concentrated in some specific trait combinations. Resource-rich environments may favor a small number of optimal suites of traits when competition is focused around a few limiting resources (Perronne et al., 2017). Such competitive dominance may occur in SB; the substantial amount of detrital material fueling seagrass food webs (Ouisse et al., 2012) may indeed act as a core resource (Ricklefs, 2012) leading to the consistent dominance of sessile microphagous suspensive and deposit feeders. Contrary to expectations (Perronne et al., 2017), however, competitive dominance did not translate into functional convergence in our case, trait dispersion matching random expectations. This is potentially linked to the substantial contribution of rare species with rare traits that points towards an important presence in SB of transient species that have a large stochastic component (Umaña et al., 2017). Seagrass patches mitigate low tide exposure and provide refugia of lower hydrodynamic intensity, which constitute sink areas for larvae and organisms in highly hydrodynamic settings such as intertidal environments (Boström & Bonsdorff, 2000; Bouma et al., 2009). This may lay foundations for mass effects, allowing the persistence of numerous rare, and potentially maladapted, species dispersing from neighboring sites and habitats (Hillebrand et al., 2008). Such source-sink dynamics are supported by the high species replacement observed in space and time among the whole community of these SB while their local species richness remain fairly unchanged in a near-neutral dynamic equilibrium fashion (Boyé et al., 2017). Similar β diversity patterns have been reported in other meadows and for other taxonomic groups (Barnes, 2013; Iacarella et al., 2018), which suggests that this large stochastic component of SB diversity is not limited to the meadows under study. It further emphasizes the important contribution of transient species to the diversity of aquatic systems (Sgarbi & Melo, 2018; Snell Taylor et al., 2018). We therefore propose a mechanism involving a mix of competitive dominance and mass effect encompassing the different effects of seagrass engineering process (Bouma et al., 2009), which would explain the preservation of similar functional structure and dominant functional entities across geographically distant intertidal seagrass meadows despite a high stochastic component (Barnes & Hendy, 2015).

b) Scaling-up to regional scale: component promoting regional diversity and their vulnerability

It is increasingly clear that not all functions can be maximized concomitantly in any given place, by any given species or community, due to inevitable trades-off in the provisioning of these functions (Meyer et al., 2018). Here, changes in taxonomic composition across sites and years were strongly associated to changes in trait composition in SB and SBS according to the coinertia analysis and RV coefficients. In IBS, functional changes were exacerbated when compared to taxonomic changes, which suggests strong functional specialization of communities in space and time, in particular for bare habitats for which both taxonomic and functional β diversity were high. This suggests a functional complementarity of communities at broad scale (Bond & Chase, 2002), which is confirmed by values of functional richness at regional scale. Indeed, the functional volume occupied by species is similar for bare sediment and biogenic habitats at regional scale despite lower local functional richness in bare sediment. The latter are indeed compensated by higher β diversity. Such functional complementarity has been shown to enhance the functioning of ecosystems in heterogeneous landscapes because different species best perform different functions in different environments (Hautier et al., 2017). Therefore, while conservation policies largely focus on local community diversity and their taxonomic complementarity (Bush et al., 2016), we emphasize the need to consider their contribution to both taxonomic and functional β diversity and apprehend their functional complementarity (Mori et al., 2018). Indeed, the extent of the functional consequences of the homogenizing effects of eutrophication on intertidal bare sediment assemblages (Quillien et al., 2015a, 2016) may be as large as the loss of seagrass-associated endofauna based on our estimates on polychaetes.

Preserving β diversity is also critical to ensure the stability and maintenance of ecosystem functioning in the face of changing environments (Isbell et al., 2018; Pasari et al., 2013). Indeed, spatial and temporal β diversity provides insurance for the long-term functioning of ecosystems as it allows different species to become increasingly dominant when and where they perform best (Wang & Loreau, 2014). In this perspective, preserving environmental heterogeneity and ensuring the maintenance of a mosaic of benthic habitats is critical (Airoldi et al., 2008). Important anthropogenic impacts such as bottom trawling or eutrophication threaten the heterogeneity of the seafloor, in particular through adverse effects on biogenic habitats (Airoldi et al., 2008). Yet, our results suggest that maintenance of biogenic habitats is essential to ensure the long-term maintenance of benthic ecosystem functioning. In particular, while in other habitats variation of trait composition either match taxonomic patterns (SB and SBS) or were even exacerbated as compared to taxonomic variation (IBS), RV coefficient and coinertia analysis showed a decoupling between MB taxonomic and functional patterns. Maerl-associated assemblages were characterized by distinct taxonomic composition at regional scale compared to the other habitats. However, coinertia showed that these taxonomic differences were not traduced by as much differences in terms of trait composition. This suggests that, despite taxonomic differences, there is a degree of functional redundancy between maerl assemblages and those of other habitats.

The central positions of MB assemblages in the trait-based PCA and their average occupancy of the regional trait space of 30% suggest that, irrespective of taxonomic composition, their high richness ensures that many of the functional entities of the region are found within each MB assemblage. This functional richness is not an argument in favor of the selective protection of a few beds to preserve the whole diversity of subtidal soft-bottoms; it is on the contrary a strong case in favor of the protection of multiple beds across the region. Indeed, in contrast with bare sediment, MB promote stable assemblages across space and time, both in terms of taxonomy and functional composition. MB rich assemblages therefore provide functional redundancy for bare sediment assemblages across different environments and as such, they may serve as sources of species over the whole Brittany seaboard to replenish any of the functional entities that may be lost in subtidal sediments. The functional redundancy associated with MB across the region provide spatial and temporal insurance for benthic ecosystem functioning and the loss of biogenic structures may in consequence have high potential to lead to regime shifts (Hewitt & Thrush, 2010).

However, not all highly diverse systems are associated with high functional redundancy (Mouillot et al., 2013a, 2014). This depends on the linkages between the functional rarity of species and their rarity in terms of abundances and occurrences in the communities (Violle et al., 2017). As highlighted here in the differences between MB and SB, the relative contribution of dominant and rare species to functional redundancy may vary among benthic environments (Mouillot et al., 2013a; Ellingsen et al., 2007). SB promote species with specific trait combinations, which provide stability and redundancy for the functions associated with the promoted species. For instance, the stability of sedimentary processes within SB (Bernard et al., 2014) may arise from the consistent upward and downward conveying activities of the microphageous species favored through competitive dominance. However, variation of assemblages led, as in bare sediment, to differences in SB functional composition because transient species with rare traits make up most of the functional richness of SB. Therefore, SB high taxonomic diversity is associated with redundancy of a few functions only. This over-redundancy (Mouillot et al., 2014) implies that SB functional diversity remains highly vulnerable to species loss. In addition, while rare species may have a substantial role in the performance of ecosystems (Soliveres et al., 2016), it remains unclear to what extent transient species are directly involved in ecosystem functioning in the case of SB (Umaña et al., 2017). Nonetheless, transient species are critical in providing insurance for the functioning of benthic habitats (Hewitt et al., 2016). Indeed, while dominant species often govern the short-term resilience of ecosystems, rare species could determine their long-term dynamics (Arnoldi et al., 2018). Because their presences are dependent on mass effect, ensuring the long-term functioning of SB requires not only maintenance of the meadows themselves, but also of the heterogeneity of the seascape in which they are embedded. The differences observed between maerl and seagrass beds emphasize the need to understand the ecological processes associated with different foundation species to appropriately predict and manage the functional consequences of future biodiversity changes (Pessarrodona et al., 2018).

Some limitations of this study likely make these highlighted contribution conservative estimates. Firstly, although the considered functional traits are interesting proxies of benthic ecosystem functioning (Bolam & Eggleton, 2014; Villnäs et al., 2017), the trait-function links can vary with environmental context (Snelgrove et al., 2014). Our fuzzy coding procedure only roughly accounts for intra-specific variability that may yet be an important component of benthic functioning (Wohlgemuth et al., 2017). Secondly, by focusing solely on polychaetes, an arguably important and diversified taxonomic group, we only accounted for some of the indirect effects of biogenic habitats on ecosystem functioning. Other taxonomic groups, and in particular epifaunal species, would further add to the contribution of biogenic habitats to ecosystem functioning (Duffy, 2006). Foundation species have other indirect effects as they modify the fluxes and physical characteristics of the environment, and also directly contribute to ecosystem functioning (Alsterberg et al., 2017; Liu et al., 2018) so that their estimated contributions extend beyond those highlighted here. Nonetheless, by filling important gaps in the understanding of benthic functional diversity and of the role of β diversity in regional diversity patterns (Airoldi et al., 2008), our study provides key elements to guide the conservation of the seafloor in coastal marine areas.

In particular, our results highlight an overall decoupling between taxonomic and functional β diversity that is increasingly recognized (Devictor et al., 2010; Loiseau et al., 2016). The latter was previously described for bare soft sediment (Bremner et al., 2003) but we show here that the relationship between these two biodiversity facets may depend on the habitat. As a consequence, functional priorities may not always match conservation priorities stemming from other biodiversity facets. This supports the need to directly incorporate functional aspects in the design of conservation schemes in order to achieve the implementation of a multi-faceted conservation of biodiversity (Cadotte & Tucker, 2018; Pollock et al., 2017), capable of enhancing the resilience of ecosystems in the face of current environmental changes (Thrush & Dayton, 2010). In this process, our results provide important guiding elements for preserving the integrity of benthic functioning depending on the target objectives (see Table 3).

We show here that biogenic structures are important structuring factors of polychaete assemblages at the regional scale. They enhance local diversity and provide spatial and temporal insurance to the functioning of benthic system at local and broad spatial scale that is absent in bare sediment. Preserving the integrity of foundation populations is therefore key to mitigate biodiversity loss on the long-term (Bulleri, 2018). However, our results show that different mechanisms govern each habitat's diversity. They are associated with different vulnerabilities of the assemblages that should be taken into account in the planning of management actions. Additionally, although locally poorer, bare sediment assemblages have similar contributions to the functional richness of the region because of their high spatial and temporal β diversity. As such, significant threats to the functioning of benthic ecosystems may emerge at broad scale from their homogenization. In light of these results, and given the substantial loss already experienced by biogenic habitats (Airoldi & Beck, 2007), important efforts should also be devoted to the understanding and conservation of the β diversity of bare sediment.

Maintaining high β diversity is key to ensure the functional complementarity of communities at broad scale and the long-term stability of ecosystem functioning in the face of environmental changes (Burley et al., 2016; Isbell et al., 2018). Our study reinforces the need for a better incorporation of β diversity patterns in conservation policies for preserving species diversity over broad spatial scales (Socolar et al., 2016) and ensuring the short- and long-term maintenance of ecosystem functioning (Mori et al., 2018). The mismatch between the fine spatial and temporal scales of most marine ecological studies (Witman et al., 2015) and the broad scales of the threats facing biodiversity is a major limit to our forecasting abilities regarding the fate of ecosystems (Isbell et al., 2017) and impedes the successful transitioning of current knowledge into applied solutions for the management of ecosystem (Cadotte et al., 2017). The broad-scale monitoring data used in this study allowed us to bridge knowledge of communities across scales, linking the mechanisms governing diversity at local scales to the vulnerability of ecosystems at regional scale. This further highlights the key role of such monitoring programmes that allow ecologists to bring the conclusions of theoretical and fine-scale experimental studies closer to the spatial and temporal scales at which biodiversity is lost and at which society manages and benefits from nature (Isbell et al., 2017).

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8. Tables

Table 1*. Traits and modalities used in this study along with their abbreviations in Figure 5.*

Trait	Modalities	Abbreviations
Maximum size (mm)	<2	Size_inf2
	2 to 5	Size_2-5
	5 to 10	Size_5-10
	10 to 50	Size_10-50
	50 to 100	Size_50-100
	100 to 200	Size_100-200
	>200	Size_sup200
Feeding method	Subsurface deposit feeder	SSDF
	Surface deposit feeder	SDF
	Active suspension feeder	ASF
	Passive suspension feeder	PSF
	Grazer	Grazer
	Predator	Pred
	Scavenger	Scav
	Parasitic	Parasitic
Food size	Microphagous	Microphagous
	Macrophagous	Macrophagous
Adult preferred substrate position	Infaunal	Infaunal
	Epibenthic	Epibenthic
Living habit	Tube dweller	Tube_dweller
	Burrower	Burrower
	Crawler	Crawler
	Swimmer	Swimmer
	Attached	Attached
Daily adult movement capacity	None (0m)	Mob_0
	<10m	Mob_inf10
	10-100m	Mob_10-100
	100 - 1000m	Mob_100-1000

Bioturbation	None	Bioturb_N
	S Surficial modifiers	Bioturb_S
	B Biodiffusors	Bioturb_B
	UC Upward conveyors	Bioturb_UC
	DC Downward conveyors	Bioturb_DC
	R Regenerators	Bioturb_R
Sexual differentiation	Hermaphrodite	Hermaphrodite
	Gonochoric	Gonochoric
Development mode	Asexual	Dev_asex
	Direct	Dev_direct
	Indirect - planktotrophic	Dev_plankto
	Indirect - lecithotrophic	Dev_lecitho
Reproduction frequency	Iteroparous	Iteroparous
	Semelparous	Semelparous
Life span	Short (< 2 years)	Short_life_span
	Medium (2 to 5 years)	Medium_life_span
	Long (> 5 years)	Long_life_span

Table 2. *Variability of species and trait community compositions within each habitat at regional scale, in relation with the proportion of regional functional space and species richness found in each habitat, either on average per assemblage, or in total at regional scale. Within-habitat **β** diversity was measured using the total variance of the observation-by-species matrix of each habitat (termed BDtot for total **β** diversity, sensu Legendre & De Cáceres, 2013), both in terms of species (Taxonomic BDtot) and trait composition (Functional BDtot). The percentage of occupancy of the regional multidimensional trait space was measured based on the first 6 axes of the PCA of the species-by-trait matrix, which contained 70.36 % of total variance. It was calculated as the percentage of the volume formed by all the species found in this study (regional richness) that is represented by the volume formed by all the species found in each habitat at the regional scale, considering all sites and all years (total occupancy), or by the volume formed by all the species found in each assemblage, which was then averaged per habitat (average occupancy ± standard deviation). The same approach was applied for the taxonomic richness of polychaete species with the percentage of the regional species pool found in each habitat, in total and on average per assemblage.*

Habitat	Taxonomic BDtot	Functional BDtot	Total occupancy of regional trait space (%)	Average occupancy of regional trait space (%) ± sd	Total contribution to regional taxonomic richness (%) ± sd	Average contribution to regional taxonomic richness (%) ± sd
Intertidal bare sediment	0.75	0.13	61.77	2.76 ± 4.02	40.20	4.96 ± 3.21
Intertidal seagrass beds	0.52	0.06	64.14	9.34 ± 6.52	47.00	10.50 ± 3.83
Subtidal bare sediment	0.60	0.06	82.27	15.67 ± 12.88	60.30	12.60 ± 6.16
Subtidal maerl beds	0.47	0.03	86.10	28.24 ± 7.93	77.80	22.40 ± 4.67

Table 3. *Recommended actions at regional scale based on our results, as a function of the conservation targets.*

Conservation targets	Proposed actions based on our results
Preserving current taxonomic diversity	Preserve biogenic habitats across the region, ideally through protection of several maerl and seagrass beds encompassing contrasted environments
Preserving current functional diversity	Preserve any single maerl bed, a few beds selected for their complementarity may protect most of the regional diversity
	Preserve seagrass associated β diversity at the regional scale
	Preserve bare sediment β diversity at the regional scale, including their temporal asynchrony in intertidal environments
Ensuring the maintenance of functional diversity on the long-term	Preserve maerl beds and their β diversity all over the region
	Protect landscapes in which intertidal seagrass beds are embedded

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10. Supplementary material

a) Sampling protocol

In each site, three points located approximately 200 meters apart were sampled (Figure 1. B and C of the article). In the intertidal, each point was sampled using three sets of three sediment cores totaling 0.03 m^2 while in the subtidal, macrofauna was collected at each of the three points using three Smith-McIntyre grabs of 0.1 m^2. These nine cores or grabs were then pooled to estimate abundances at the site level. Accordingly, macrofaunal densities were estimated based on 0.27 m^2 and 0.9 m^2 surfaces sampled per site for the intertidal and subtidal sites respectively. The exact number of sediment cores or grabs used for each sampling occasion is summarized in Figure 1 of the Supplementary material. Each core and grab sample was sieved over 1 mm mesh and fixed in 4% formalin until sorting and morphological identification to the lowest possible taxonomic levels in the laboratory. Homogenization of the taxonomy was performed as described in Boyé et al. (2017) to ensure a consistent taxonomic resolution across sites and years.

b) Ecological processes associated to each trait

Table 1. *List of traits and associated ecological processes*

Trait	Ecological processes associated
Maximum size (mm)	Resource acquisition, habitat use, species interaction (competition, predation), nutrient cycling, secondary production (Törnroos & Bonsdorff 2012, Degen et al. 2018)
Feeding method	Resource utilisation, energy transfer, nutrient cycling (Törnroos & Bonsdorff, 2012)
Food size	Resource utilisation, energy transfer, nutrient cycling (Törnroos & Bonsdorff, 2012)
Adult preferred substrate position	Resource acquisition, habitat use, species interaction, nutrient cycling (Norling et al., 2007; Törnroos & Bonsdorff, 2012)
Living habit	Colonisation, recolonisation, dispersal, nutrient cycling (Norling et al. 2007, Queirós et al. 2013)
Daily adult movement capacity	Colonisation, recolonisation, dispersal (Törnroos & Bonsdorff, 2012)
Bioturbation	Nutrient cycling, sediment oxic-anoxic boundaries and chemical properties (Norling et al. 2007, Queirós et al. 2013) ; species interaction (Bouma et al., 2009)
Sexual differentiation	Reproductive success, recolonisation, dispersal, secondary production (Törnroos & Bonsdorff, 2012)
Development mode	Reproductive success, recolonisation, dispersal, secondary production (Törnroos & Bonsdorff, 2012)
Reproduction frequency	Reproductive success, recolonisation, dispersal, secondary production (Törnroos & Bonsdorff, 2012)
Life span	Secondary production, recolonisation, dispersal (Degen et al. 2018)

c) Description of the coding scheme with examples

In our coding procedure, a species expresses each modality of a given trait on a scale from 0 to 4, with 4 being an exclusive affinity for a modality (all other modalities of the trait being 0 for that species), 3 a strong affinity for a modality, 2 a mean or uncertain affinity for a modality, 1 an occasional behavior or observed value for the species, and 0 for the absence of the modality. When the species expressed several modalities of a trait without marked preferences, or with unknown preferences, it was coded 2 for all modalities expressed and 0 for those not expressed. On the other hand, when species expressed marked preferences for some modalities of a trait while expressing others occasionally, the preferred modalities were coded 3, the occasional modalities were coded 1 and those not expressed were coded 0. This coding procedure accounts to some extent for the plasticity of species and allows the incorporation of within-species variability in the functional analysis.

Table 2. *Practical examples of the fuzzy coding procedure used in this study*

Known affinity of the species	Modality A	Modality B	Modality C	Modality D
Only modality A expressed	4	0	0	0
Affinity shared between modality A and B without marked or known preferences	2	2	0	0
Mainly expresses modality A (strong affinity), and occasionally expresses modality B	3	1	0	0
Mainly expresses modality A but also modality B, with a preference less marked that in the case above	3	2	0	0
Mainly expresses modality A, but occasionally expresses modality B and C	3	1	1	0
Mainly expresses modality A, but also modality B, and occasionally modality C	3	2	1	0

d) Imputation of missing trait data

Overall, data on maximum life span were missing for half of the species so that it was removed from analyses. For the reproduction frequency, development mode, and sexual differentiation, data were missing for 9% (21 species), 7% (17), and 1% (3) of the species respectively. For these traits, we imputed missing values using nearest neighbour imputation relying on Gower dissimilarity that accommodates missing data. Missing traits were inputed based on the median value of the functionally closest species for which the trait was known as well as those falling within a threshold dissimilarity of 0.01 times the dissimilarity between this closest species and the species to be inferred. This procedure gave similar results to imputation based on the 5 nearest neighbours using the kNN function of the VIM package in R (Kowarik & Templ, 2016). The species used to infer each missing data were then verified by experts of benthic taxonomy to ensure the ecological soundness of this imputation procedure.

e) Functional α diversity indices

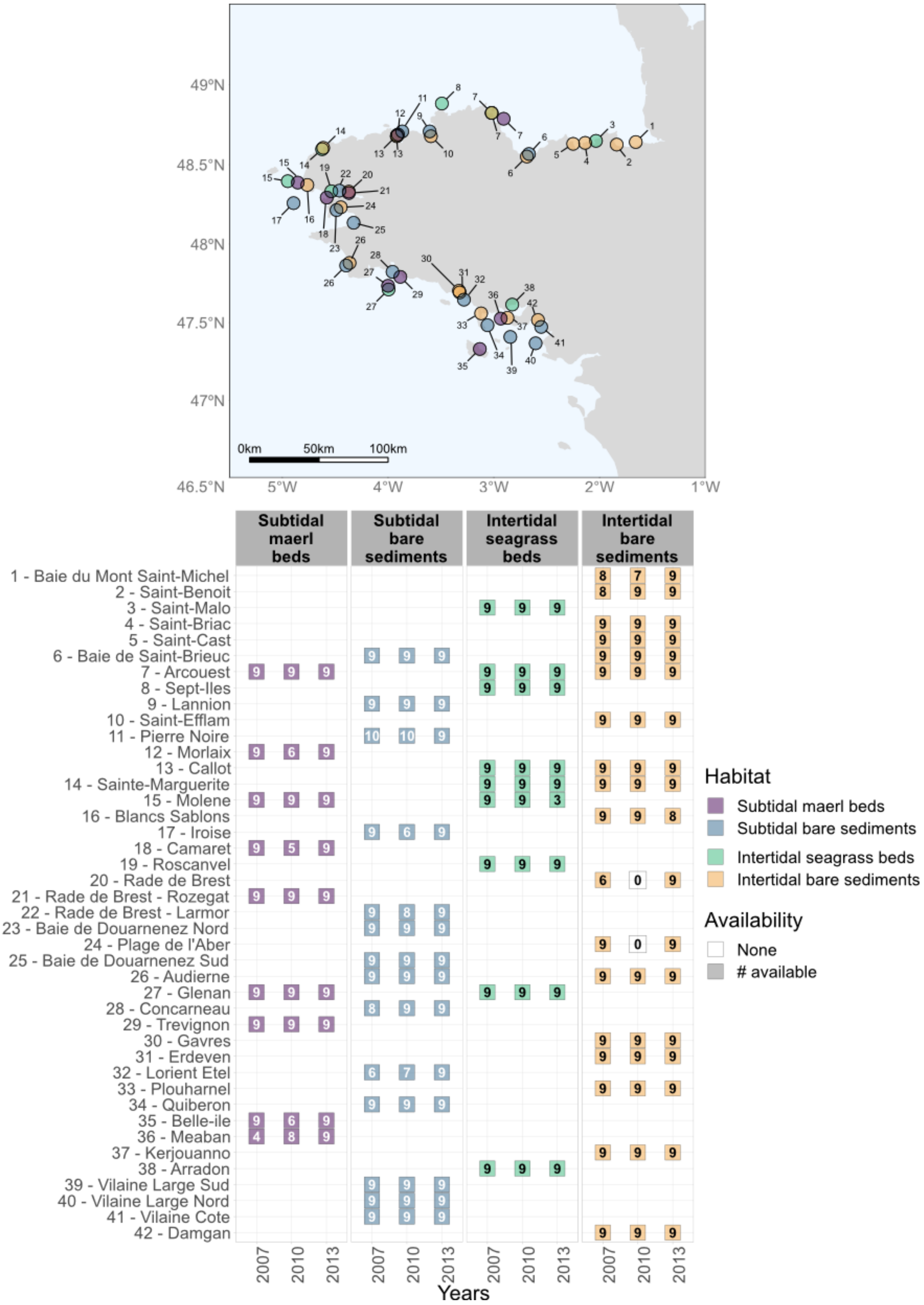
i) Description of the functional indices and their complementarity

The $FRic$ corresponds to the convex hull volume occupied by the species of an assemblage in the multidimensional trait space, which is used as a measure of the size of the niche space occupied by an assemblage (Blonder, 2017; Cornwell et al., 2006). It is the multidimensional equivalent of the trait range, and is unaffected by species abundances (Schleuter et al., 2010; Villéger et al., 2008). The three other indices on the other hand, inform on abundances distribution in the trait space. $FEve$ measures the regularity of species abundances within the convex hull volume, accounting for both the evenness of abundance distribution among species and for the regularity of the functional distances among species (Villéger et al., 2008). $FDiv$ is the abundance-weighted deviations of species to the species' mean distance to the centre of gravity of the convex hull (Schleuter et al., 2010). It describes wether high abundances are distributed in the centre or in the external part of the trait space occupied by the assemblage, or in other words, wether the most abundant species have the most extreme traits or have on the contrary average characteristics. Two important properties of this index are that species abundances are not involved in the calculation of the coordinates of the centre of gravity of the convex hull and that the size of the functional space does not influence its value (Villéger et al., 2008). In contrast, $FDis$ accounts for the size of the functional space occupied by the assemblages and species abundances are involved in all steps of the calculation as it is defined as the abundance-weighted mean distance of species to their abundance-weighted centroid (Laliberté & Legendre, 2010). Therefore, these four indices are rather independent from each other and provide insights into different aspects of the functional structure of the assemblages (Laliberté & Legendre, 2010; Mouchet et al., 2010).

ii) Method used for their calculation

$FRic$, $FEve$, and $FDiv$ were computed on a subset of Principal Coordinates Analysis (PCoA) axes following Villéger et al. (2008) and Laliberté & Legendre (2010). Euclidean distance was computed on the standardised species-by-trait matrix and PCoA was performed after removing assemblages with less than 5 species, in order to keep 5 PCoA axes for the calculation of the indices. This allowed the calculation of the $FEve$ (at least three species are needed, Villéger et al., 2008) and resulted in a reduced-space that represented 66% of the original variance (quality of the representation measured with R^2-like ratio as described in Legendre & Legendre, 2012 p. 505-506). This reduction of dimensionality to 5 axes is often done to ease the calculation of convex hull volumes and has been suggested to be sufficient to characterise most ecological systems (Blonder, 2017).

f) Figures



	Subtidal maerl beds			Subtidal bare sediments			Intertidal seagrass beds			Intertidal bare sediments		
	2007	2010	2013	2007	2010	2013	2007	2010	2013	2007	2010	2013
1 - Baie du Mont Saint-Michel										8	7	9
2 - Saint-Benoit										8	9	9
3 - Saint-Malo							9	9	9			
4 - Saint-Briac										9	9	9
5 - Saint-Cast										9	9	9
6 - Baie de Saint-Brieuc				9	9	9				9	9	9
7 - Arcouest	9	9	9				9	9	9	9	9	9
8 - Sept-Iles							9	9	9			
9 - Lannion				9	9	9						
10 - Saint-Efflam										9	9	9
11 - Pierre Noire				10	10	9						
12 - Morlaix	9	6	9									
13 - Callot							9	9	9	9	9	9
14 - Sainte-Marguerite							9	9	9	9	9	9
15 - Molene	9	9	9				9	9	3			
16 - Blancs Sablons										9	9	8
17 - Iroise				9	6	9						
18 - Camaret	9	5	9									
19 - Roscanvel							9	9	9			
20 - Rade de Brest										6	0	9
21 - Rade de Brest - Rozegat	9	9	9									
22 - Rade de Brest - Larmor				9	8	9						
23 - Baie de Douarnenez Nord				9	9	9						
24 - Plage de l'Aber										9	0	9
25 - Baie de Douarnenez Sud				9	9	9						
26 - Audierne				9	9	9				9	9	9
27 - Glenan	9	9	9				9	9	9			
28 - Concarneau				8	9	9						
29 - Trevignon	9	9	9									
30 - Gavres										9	9	9
31 - Erdeven										9	9	9
32 - Lorient Etel				6	7	9						
33 - Plouharnel										9	9	9
34 - Quiberon				9	9	9						
35 - Belle-ile	9	6	9									
36 - Meaban	4	8	9									
37 - Kerjouanno										9	9	9
38 - Arradon							9	9	9			
39 - Vilaine Large Sud				9	9	9						
40 - Vilaine Large Nord				9	9	9						
41 - Vilaine Cote				9	9	9						
42 - Damgan										9	9	9

Figure 1. *Number of grab or core samples available for the different sites for the three years of the study. Only one site of bare subtidal sediments (Pierre Noire) did not follow the same protocol than other locations with the sampling of ten grabs located in a single point instead of nine grabs in three separated points.*

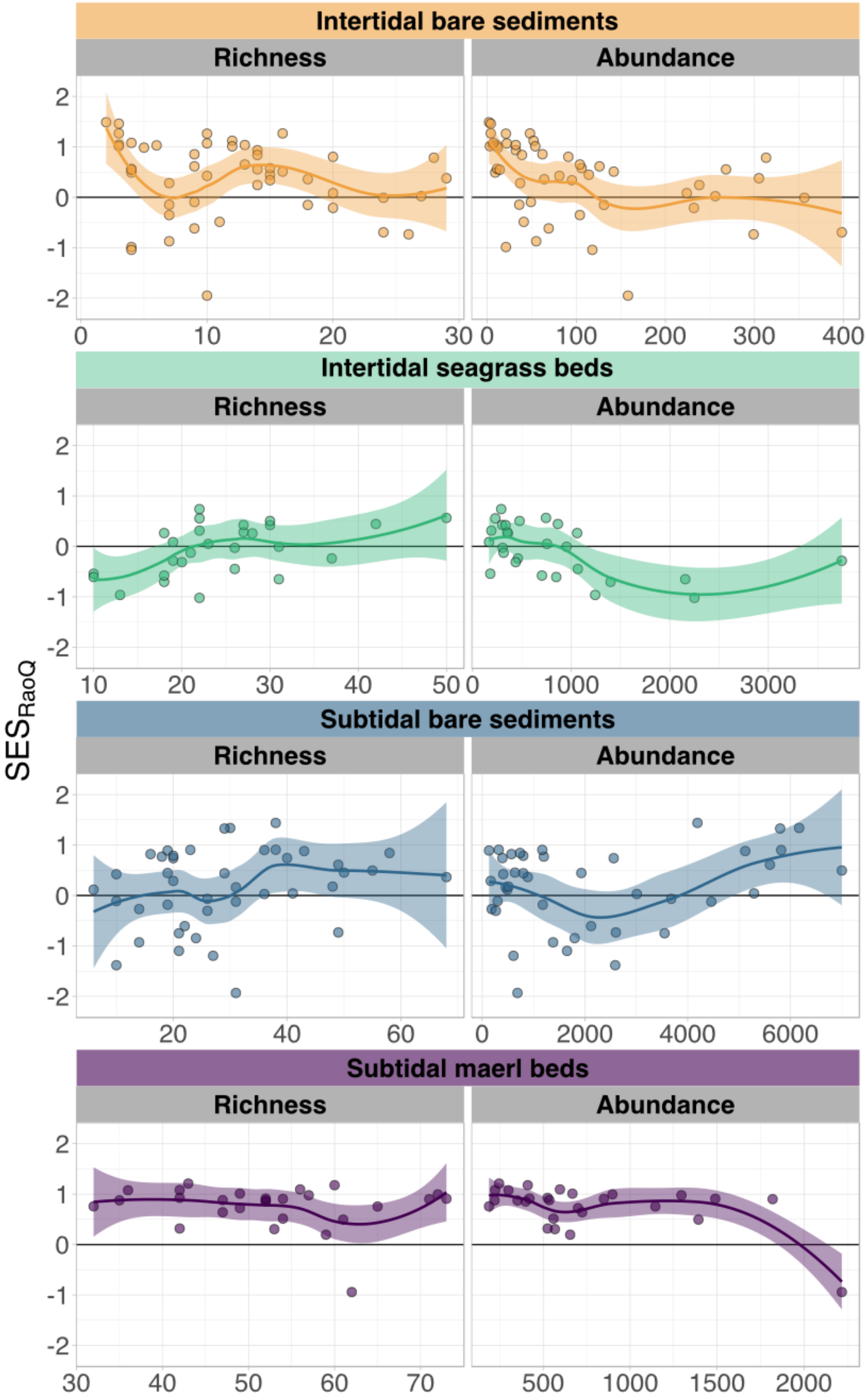


Figure 2. *Relationships between the* $\boldsymbol{SES_{RaoQ}}$ *and the richness or total abundance of the assemblages for the four habitats*

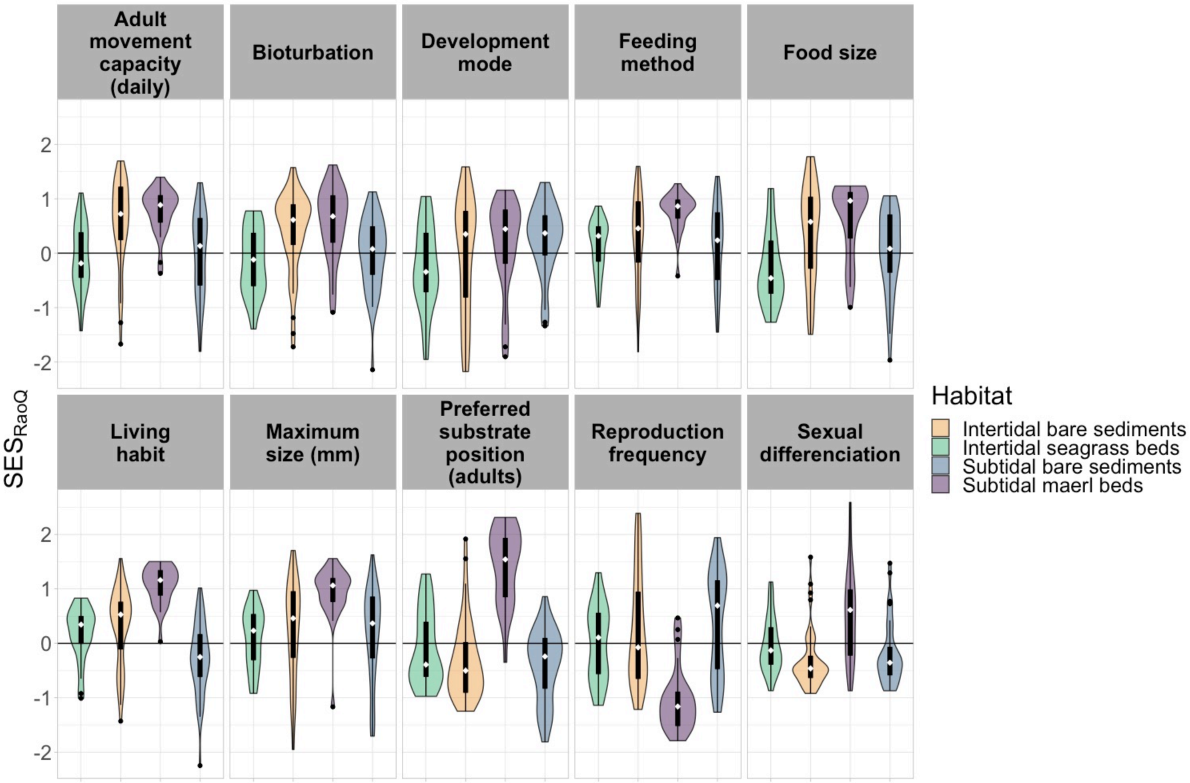


Figure 3. *Distribution of the SES values for each trait individually. Positive SES values indicate trait divergence, while negative values suggest trait convergence. Near zero values indicate random distribution. Values of Rao's quadratic entropy were calculated for each trait separetely and compared to null expectations using randomisation of the communities. For further details please refer to the Material and Methods section of the article.*

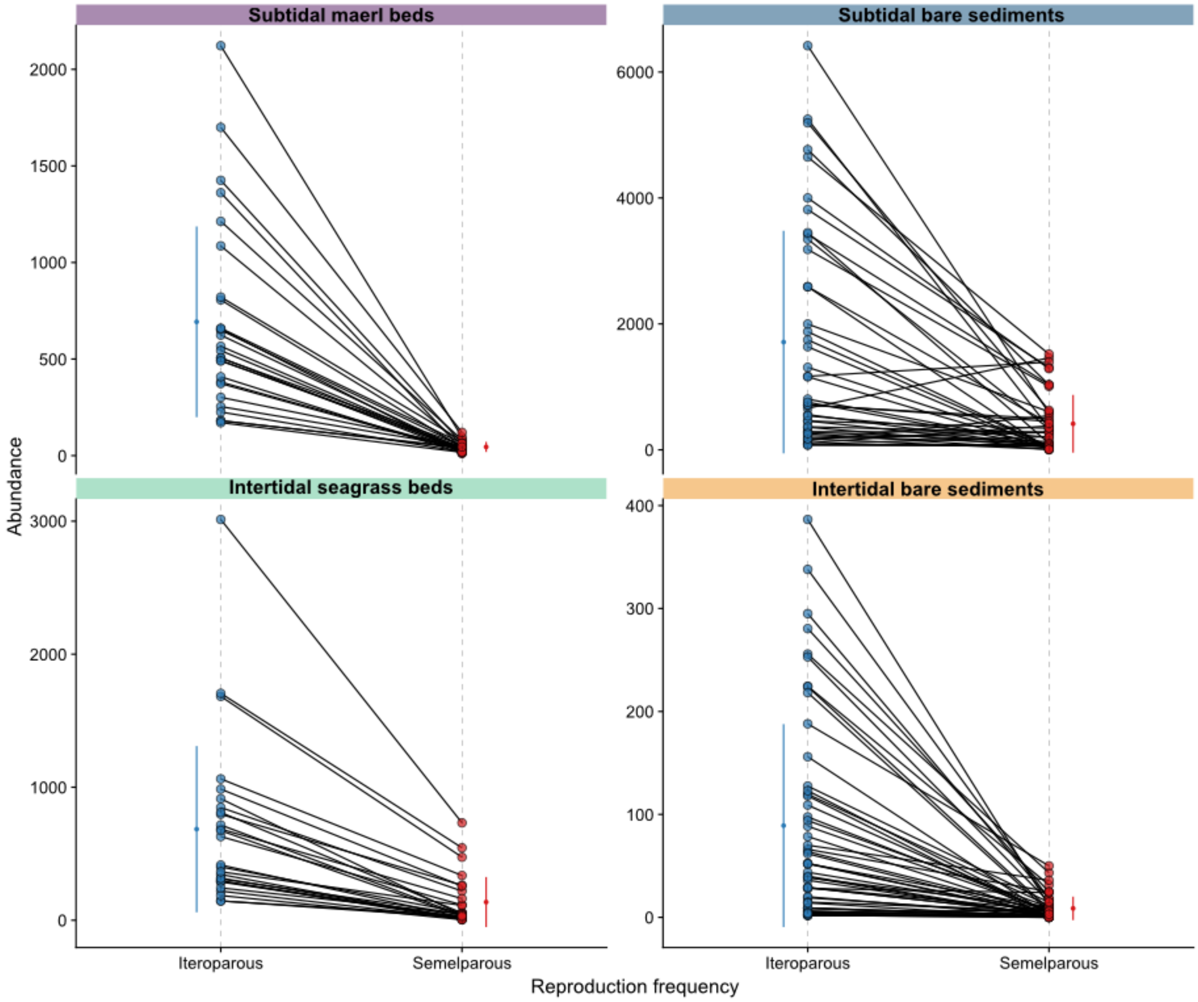


Figure 4. Abundances of the two modalities of reproduction frequency for the different assemblages of each habitat. The lines link the abundance of one modality to the abundance of the other for each assemblage. The mean and standard deviation of each modality for each habitat are plotted next to the points. For subtidal maerl assemblages, reproduction frequency consistently converge towards iteroparous species while the distribution of abundances among the two modalities is more variable and in general follow a random pattern in the other habitats (see Figure 3 of the Supplementary material)

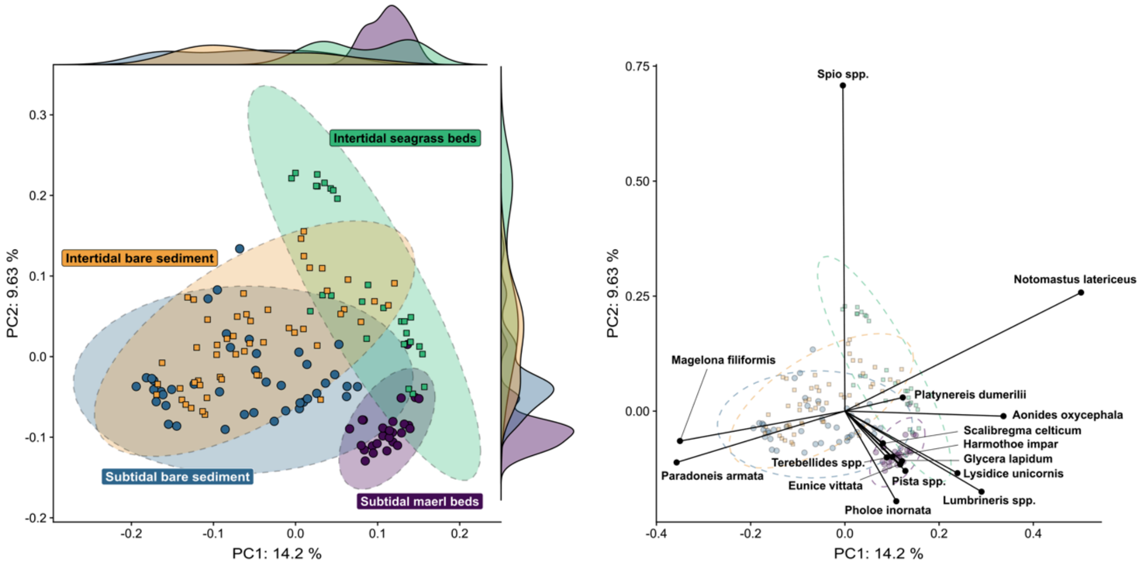


Figure 5. *Principal component analysis of Hellinger-transformed polychaete abundances. Left panel : Samples are displayed on the central panel in scaling 1 (this panel is the same figure shown in Figure 2 of the main article). The shapes of the points reflect differences in the tidal levels and sampling methods: squares represent intertidal habitats sampled using sediment cores and circles represent subtidal habitats sampled using grabs. The density of points for each habitat along the first and second axis are displayed in the outer panels. Within-habitat variability comprises of both spatial and temporal variations (see Supplementary Figure 1). The first two axes represented account for 23.83% of the total variance of polychaete composition. Right panel: only the species whose variance in these two axes represents more than 30% of their total variance are represented (assessed with the fonction goodness; vegan)*

g) References

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CHAPITRE 3

Contraintes abiotiques, espèces fondatrices, et histoires écologiques récentes : comprendre les déterminants de la diversité β régionale des communautés benthiques

1. Prélude

L'intensité des changements environnementaux et des impacts anthropiques auxquels font face les communautés côtières sont hétérogènes dans l'espace (Burrows et al. 2011, Halpern et al. 2015). L'un des défis majeurs auquel sont confrontées les politiques de conservation est ainsi d'appréhender et de préserver la biodiversité à une échelle régionale en gérant des dynamiques et des trajectoires de communautés qui pourront différer selon les sites, comme mis en évidence dans le chapitre 1. Dans ce contexte, il est important de déterminer les facteurs qui régissent les dynamiques locales des communautés ainsi que leur hétérogénéité dans l'espace. En effet, le chapitre 2 a mis en évidence que différents processus semblaient gouverner les communautés dans les différents types d'habitats benthiques (nus ou biogéniques, et selon l'identité de l'espèce fondatrice). De part leur rôle facilitateur, les espèces fondatrices sont à même d'influencer la réponse des communautés benthiques aux changements environnementaux (Bulleri et al. 2018). Cependant, notre compréhension de la direction, de l'intensité et de la variabilité de cette influence est empreinte d'importantes incertitudes et nécessite d'être clarifiée selon les espèces fondatrices (Bulleri et al. 2015).

Ce chapitre a ainsi pour objectif de mieux caractériser le rôle des deux types d'espèces fondatrices étudiées dans cette thèse (maërl et Zostère marine), et d'évaluer les implications que pourrait avoir les différents mécanismes mis en évidence dans le chapitre 2 sur la dynamique temporelle des communautés. Pour cela, cette étude a caractérisé la réponse des communautés d'endofaune aux changements environnementaux ayant eu lieu pendant 9 ans.

En résumé, les résultats de ce chapitre semblent confirmer que les habitats biogéniques joueront un rôle essentiel dans la médiation des effets des changements environnementaux sur les communautés benthiques. En particulier, ces résultats suggèrent que leur influence sur la dynamique des communautés s'effectue principalement par le biais d'une réduction de l'impact des évènements extrêmes sur les communautés. Les habitats biogéniques ne semblent en revanche pas affecter la réponse des communautés aux variations des conditions abiotiques moyennes. Néanmoins, cela semble permettre aux bancs de mäerl et aux herbiers de promouvoir la stabilité temporelle des communautés sur les 9 années étudiées, bien que les deux habitats agissent sur différents aspects des dynamiques temporelles des communautés. En particulier, les communautés intertidales ont montré une plus grande variabilité que les communautés subtidales sur ces 9 années d'études. Par ailleurs, la présence d'herbiers a permis le maintien de structures spatiales plus stables dans le temps à l'échelle de la région par rapport à celles observées dans les sédiments nus.

Enfin, malgré des variations dans le temps des communautés et l'occurrence d'évènements extrêmes tels que les tempêtes de 2008 et de 2014, les structures spatiales des communautés à l'échelle régionale sont apparues remarquablement préservées sur les 9 ans d'étude. Ces résultats révèlent ainsi une forte empreinte historique dans la structure spatiale régionale actuelle des communautés benthiques et montrent le rôle crucial que joue la fenêtre d'observation dans l'évaluation de l'étendue d'un changement observé. Cette étude met en exergue le rôle des suivis à long-terme pour fournir un état de référence des communautés qui ne soit pas une image statique mais une enveloppe de possibilités permettant de mieux juger l'importance de changements observés.

Abiotic constraints, foundation species and recent historical legacies: deciphering the prevailing drivers of marine benthic β-diversity at regional scale

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2. Abstract

Understanding what drives communities to exhibit different temporal dynamics and apprehending the consequences at broad spatial scales of heterogeneous responses of communities is a key challenge to predict and mitigate future biodiversity changes. Here, we address the role of foundation species in mediating the response of benthic communities to changes in abiotic conditions and assess how they affect the temporal dynamics of their associated communities at a regional scale. For this purpose, we explored the imprints of recent environmental changes on the temporal trajectories of 42 benthic communities over 9 years in two biogenic habitats, intertidal seagrass and subtidal maerl beds (calcifying red algae) and in bare sediment at similar tidal level across 35 locations differing in their local environmental conditions. Benthic communities exhibited similar predictable variation in relation to the environment in biogenic and bare habitats, suggesting that biogenic habitats may not buffer changes in mean environmental conditions. However, biogenic habitats promoted the temporal stability of communities compared to bare sediment by dampening the effect of extreme events. In particular, while regional diversity patterns of intertidal communities changed more quickly than subtidal ones, seagrass meadows mitigated this variability and maintained stable spatial β diversity through time. Overall, our results confirm the crucial role of biogenic habitats in mitigating future biodiversity changes of benthic communities but highlight that the ecological processes involved differ according to the foundation species and tidal level. Lastly, despite temporal variation of communities and occurrence of extreme events over the 9 years, spatial β diversity remain remarkably preserved, highlighting that only a long-term perspective can fully reveal the extent of biodiversity changes and provide appropriate baselines. In this perspective, our work present an application of innovative statistical analysis for the study of community temporal trajectory that may help revealing sites that have been recently diverging from the mean regional trend, even before that these changes become conspicuous in the spatial β diversity of communities.

Keywords:

Global changes – Community trajectory – Historical heritages – Benthic macrofauna – Facilitative interactions

3. Introduction

A hallmark of the past decades is undoubtedly the increasing pace and variance of environmental changes, imprints of continuously increasing anthropic activities (Lewis & Maslin, 2015). Marine ecosystems have, in particular, experienced rapidly changing environments over the past 50 years (Burrows et al., 2011; Hoegh-Guldberg & Bruno, 2010), especially in coastal areas that face high anthropogenic pressure (Halpern et al., 2015, 2008). These environmental modifications have profoundly altered coastal ecosystems (McCauley et al., 2015), raising important concern given the ecological importance and economic value of these marine areas (Martínez et al., 2007; Worm et al., 2006). Substantial efforts have been devoted to characterize the imprint of anthropic activities on coastal ecosystems and knowledge of individual and species-level responses, including phenological, demographic, or distribution changes, has greatly advanced in recent years (Poloczanska et al., 2013, 2016). However, community-level responses remain poorly understood and have been scarcely studied (Poloczanska et al., 2013). Response and resilience of coastal communities and ecosystems in the face of environmental changes involve a myriad of processes acting and interacting across multiple spatial and temporal scales, whose understanding poses important challenges (Bernhardt & Leslie, 2013; Cloern et al., 2015). As such, predicting how the effects of environmental changes at individual and population levels translate at higher organizational levels remains a key issue hampering the implementation of effective conservation actions (Harley et al., 2006).

A particular challenge facing biodiversity conservation is to apprehend and manage the broad-scale consequences of inconsistent and highly diverse local dynamics (McGill et al., 2015; Primack et al., 2018). Indeed, rates of abiotic changes and impacts of anthropic activities are heterogeneous across space (Burrows et al., 2011; Halpern et al., 2015), which may induce different community trajectories across locations (Hovel et al., 2017). These heterogeneities added to the variability of species responses across taxonomic groups and across locations are likely to induce substantial reorganization of marine ecosystems at broad spatial scales (Poloczanska et al., 2013, 2016). Hitherto, most of the available knowledge regarding the temporal dynamics and trajectories of communities is focused on local diversity (α diversity; Whittaker, 1960), which alone cannot fully capture such intricate biodiversity changes (Hillebrand et al., 2017). Indeed, there is strong evidence, in particular in marine environments, that over the last decades substantial temporal variation of the structure and composition of communities have occurred without important or consistent modifications of their richness (Dornelas et al., 2014; Gotelli et al., 2017; Magurran et al., 2018, 2015). These compositional variations, which are known as spatial or temporal β diversity (Whittaker, 1972), can explain the apparent paradox between the decline of species richness observed at global scale (Pimm et al., 2014) and the stable or even increasing diversity trends observed in some locations (Vellend, 2017). Therefore, while substantial shortfalls remain in our understanding of the spatial and temporal β diversity of communities (McGill et al., 2015), developing a better understanding of the variation of communities and their underlying drivers is an urgent need to guide the prioritization of conservation actions in the face of complex environmental and biodiversity changes (Mori et al., 2018; Socolar et al., 2016).

The need for a more comprehensive understanding of community β diversity is particularly conspicuous in relation to the on-going alterations of the seafloor (Airoldi et al., 2008). Benthic communities are essential components of the functioning of coastal ecosystems (Snelgrove et al., 2014). In particular, coastal seafloor harbor a wide range of foundation species (*sensu* Dayton, 1972) that form speciose habitats such as seagrass meadows, kelp forests or biogenic reefs (Sunday et al., 2017; Teagle et al., 2017). These biogenic habitats have experienced dramatic losses over the past decades (Airoldi & Beck, 2007) and their continuing alteration is heralded as one of the major threats posed to coastal biodiversity (Hoegh-Guldberg & Bruno, 2010; McCauley et al., 2015). Indeed, foundation species regulate multiple processes in the functioning of coastal ecosystems (Bouma et al., 2009) and as such, they may play a key role in mediating the responses of coastal communities to environmental changes (Bulleri, 2018; Sunday et al., 2017). Again however, most of the available knowledge regarding the effect of these coastal engineers (sensu Jones et al., 1994, 1997) concerns only α diversity (Romero et al., 2015) whereas important knowledge-gaps remain regarding how biogenic habitats affect the temporal dynamics of benthic communities and how their disappearance may affect the β diversity of marine coastal sediment (Airoldi et al., 2008; Bulleri et al., 2015).

Community dynamics are governed by intrinsic and extrinsic factors operating across multiple spatial and temporal scales (Leibold & Chase, 2017). Foundation species can influence the strength of many of these processes (Bulleri et al., 2015). In particular, biogenic habitats may mitigate the strength of abiotic constraints on communities by dampening environmental variation and alleviating the severity of harsh environments for their associated fauna (Bulleri, 2018; Bulleri et al., 2015). Foundation species also modify resource availability for benthic organisms (Duffy, 2006), altering species interactions (Bulleri et al., 2015), as well as dispersal patterns (Boström & Bonsdorff, 2000). The balance between the different processes through which biogenic habitats influence benthic communities will depend on the abiotic context and identity of the foundation species, and we currently lack comprehensive understanding of how these different influences of biogenic habitats integrate to regulate the temporal dynamics of their associated communities (Bulleri et al., 2015). Developing such an understanding is key to apprehend the role biogenic structures may have in the responses of coastal communities to environmental changes (Bulleri, 2018).

Long-term data on coastal communities are becoming increasingly available but hitherto, they remain most often restricted in their spatial extent (Buckley et al., 2018). This impedes our capacity to fully apprehend the effects of biogenic habitats on benthic communities and in turn their role in mediating future changes of coastal biodiversity. Here, using monitoring data covering 9 years and 35 sites distributed over 500 km of coasts in a wide range of environmental contexts, we address the effect of two types of foundation species on the spatial and temporal variability of benthic macrofauna. This study, conducted in Brittany (France; Figure 1 A), focuses on the role of two biogenic habitats: intertidal *Zostera marina* meadows and subtidal maerl beds (unattached coralline red algae) formed by at least two species *Lithothamnion corallioides* and *Phymatolithon calcareum* (Peña et al., 2014). Specifically, we quantify and characterize the spatial and temporal β diversity associated to these biogenic habitats compared to the β diversity of bare sediment at similar tidal levels. We also assess how these two types of foundation species modify the factors governing community by estimating for each of these four habitats the fraction of community variation that is explained by environmental variables compared to the spatially or temporally structured fractions that cannot be explained by these abiotic variables, or to the unexplained variation (see for example Soininen, 2014). Lastly, we assess how the ecological dynamics that have occurred over recent years may contribute to present-day spatial β diversity in these intertidal and subtidal environments. Indeed, given the pace of current environmental changes, the ecological changes to which the communities have been exposed over the last decade may strongly influence their contemporary composition (Jung et al., 2018; Perring et al., 2016). Therefore, in the last part of this study, we explore if and how the distinctness of the temporal trajectories of the assemblages over the preceding 8 years (2006-2013) can be linked to their distinctness in terms of composition and structure in the last year of our study (2014).

Based on available evidence, we have the following expectations regarding the effects of biogenic habitats on the β diversity of benthic communities:

Expectation #1: Lower spatial and temporal β diversity in biogenic habitats compared to bare sediment because of their dampening effects on environmental variation;

Expectation #2: Because of their dampening effects on environmental variation and of the more constant resource supply within biogenic habitats (Teagle et al., 2017), temporal β diversity should be mostly attributable to balanced abundance variation and species replacement rather than total abundance and richness variation in biogenic habitats, and conversely for bare sediment (Soininen et al., 2018);

Expectation #3: Potentially different effects of the biogenic habitats on the temporal β diversity of communities between the intertidal and the subtidal because of difference in the harshness of these environments (Crain & Bertness, 2006);

Expectation #4: Lower capacity to predict variation of communities using abiotic variables in biogenic habitats than in bare sediment; higher residual and pure spatial and temporal fractions in biogenic habitats due to a more important role of biotic interactions in these habitats compared to bare sediment assemblages that should be more strongly governed by abiotic constraints;

Expectation #5: Due to the higher abiotic dynamism of intertidal environments (Gray & Elliott, 2009), we expect intertidal communities to be governed over shorter terms than subtidal communities. Therefore, intertidal spatial β diversity patterns should be more related to the differences of temporal trajectories among the sites over the past 8 years than in the subtidal. This relationship may be mediated by biogenic habitats in ways difficult to predict.

4. Material and methods

a) Data acquisition

This study was conducted in Brittany (France; Figure 1 A), using data from the on-going REBENT (Réseau Benthique) monitoring programme (http://www.rebent.org). In the context of this monitoring, macrofaunal communities have been sampled yearly since 2003 in four habitats: intertidal seagrass beds and subtidal maerl beds for the biogenic habitats, and intertidal sandy beaches (referred to as intertidal bare sediment hereafter) and subtidal sediment devoid of biogenic structure (referred to as subtidal bare sediment hereafter) for the bare habitats. These habitats are found all along Brittany's seaboard and monitoring sites cover most of the environmental settings that can be found in the region. For the purpose of this study, only community monitoring series containing a minimum of 7 yearly observations between 2006 and 2014 were included (Figure 1 B). This yielded a total of 42 distinct series. However, as some sites (e.g. site 14 – Sainte-Marguerite) harbor more then one habitat type (e.g. intertidal bare sediment and seagrass bed in Sainte-Marguerite), the entire dataset covers a total of only 35 distinct monitoring sites (Figure 1 A).

Details for the sampling methodology of this monitoring programme can be found in the 2nd chapter of this thesis and in Quillien et al. (2015a) and Boyé et al. (2017) for intertidal habitats. Briefly, sampling was consistently performed for all sites between the end of February and the beginning of May, before the recruitment of most species (Dauvin et al., 2007). It consisted in each site in the sampling of three points located approximately 200 meters apart. Different sampling gears were used for intertidal and subtidal sites. As such, comparisons are fully meaningful within a given tidal level whereas comparisons between the two tidal levels may bear methodological imprint. In the intertidal, each point was sampled using three sets of three sediment cores totaling $0.03m^2$. In the subtidal, the three points were sampled using three Smith-McIntyre grabs of $0.1\ m^2$. In this study, analyses were performed at the site level so that

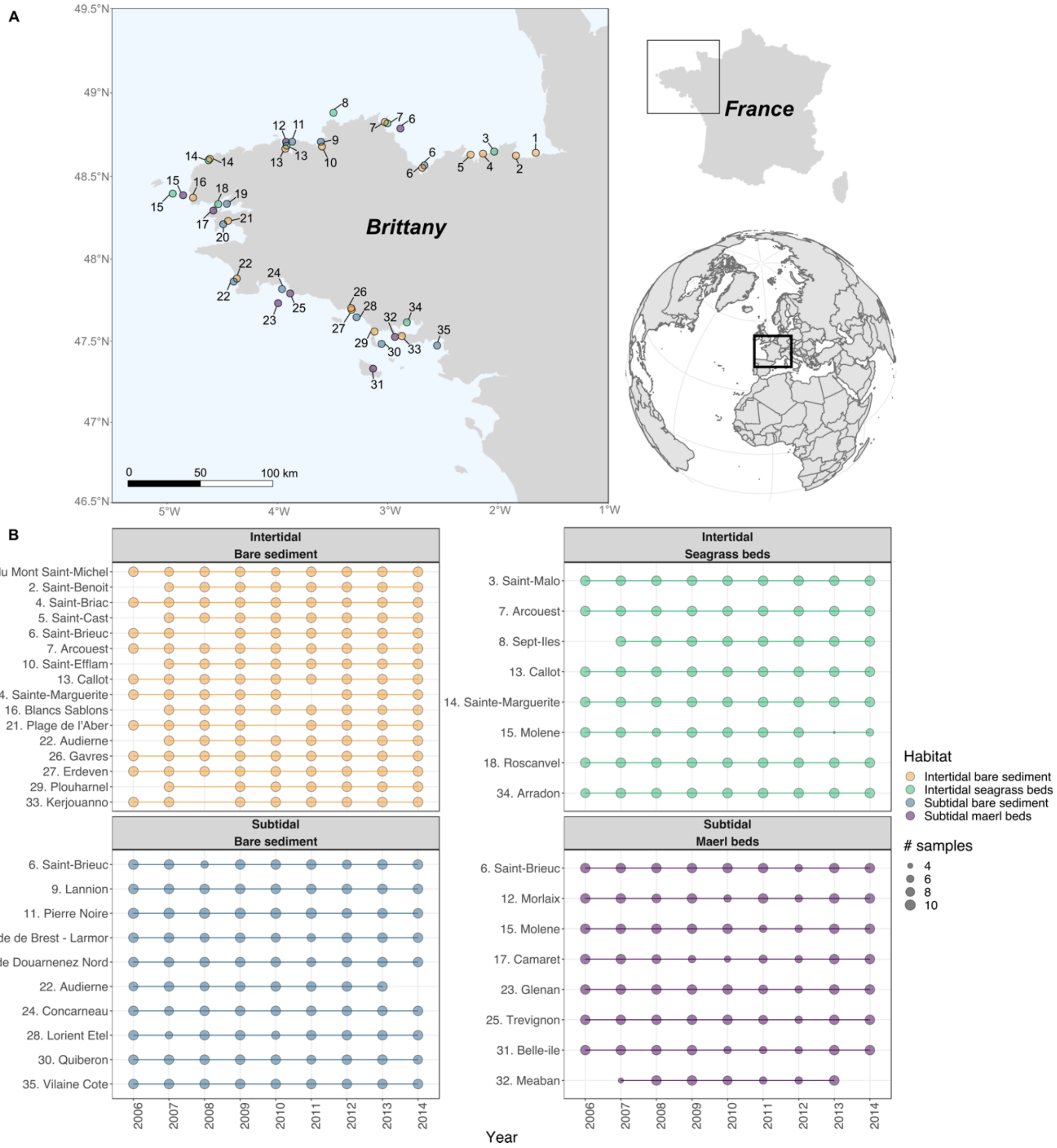

Figure 1. A. Map of the monitored sites. B. Data availability for each site from 2006 to 2014. The size of the points is proportional to the number of sediment core (intertidal) or grab (subtidal) samples aggregated to estimate abundances at the site level for each year. Some sites harbor more than one habitat (e.g. both an intertidal bare sediment and a seagrass bed are monitored at site 14 – Sainte-Marguerite)

abundances were estimated by aggregating the data of the three points (the nine cores or grabs) sampled per site. Accordingly, macrofaunal densities were estimated on 0.27 m^2 and 0.9 m^2 of surfaces for the intertidal and subtidal sites respectively. The exact number of grabs used for each sampling occasion as well as missing sampling occasions are summarized in Figure 1 B. Core and grab samples were sieved over 1 mm mesh and fixed in 4% formalin in the laboratory until sorting and morphological identification to the lowest possible taxonomic levels. Homogenization of the taxonomy was performed as described in Boyé et al. (2017) to ensure a consistent taxonomic resolution across sites and years.

Environmental variables were collected *in situ* or *a posteriori* to explain the patterns of community variation. For the intertidal, abiotic explanatory variables include meteorological information, in particular variables characterizing aerial temperature and wind velocity; hydrological data describing sea water temperature and salinity, as well as current velocity; granulometric data characterizing sediment properties; and average fetch, used as a proxy for the degree of exposure of the sites. For the subtidal, explanatory variables include hydrological and granulometric data, as well as depth. The complete list and acquisition details for all environmental variables are found in the Supplementary material.

b) Data analyses

i) Description of spatial and temporal β diversity patterns

The main spatial and temporal β diversity patterns of intertidal and subtidal communities were visualized using Principal Component Analyses (PCA) of the

Hellinger-transformed species density matrices for each tidal level separately. Hellinger transformation allows for the use of Euclidean-based methods on frequency data and has the desirable property of reducing the importance of the most abundant species while not giving excessive weights to the rare species (Legendre & Borcard, 2018; Legendre & Gallagher, 2001).

The temporal variability of communities at each site was quantified using the measure of total β diversity (BDtot) proposed by Legendre & De Cáceres (2013). It consists in measuring the overall variance of the abundance matrix containing the different years surveyed for each site. This was done in three different ways: 1) using the Hellinger-transformed density matrix, 2) using the Ružička difference index computed on density data, and 3) using the Jaccard dissimilarity on presence/absence data. In comparison to Hellinger distances, the total density of each site is taken into account by the Ružička dissimilarity index, which is the quantitative form of the Jaccard dissimilarity. The overall contributions of species replacement ($Repl_{Total}$) versus richness differences ($RichDiff_{Total}$) and of balanced abundance variation ($BalAbund_{Total}$) versus total abundance differences ($AbundDiff_{Total}$) to the total temporal β diversity of the assemblages were assessed by partitioning the Jaccard dissimilarity and the Ružička difference index respectively. This was done using the Podani-family decompositions (Podani & Schmera, 2011) described in Legendre (2014) using the *beta.div.comp* function (coef = “J”) of the R package *adespatial* (Dray et al., 2017). In this decomposition family, $BD_{Total(Jaccard)} = Repl_{Total} + RichDiff_{Total}$ and $BD_{Total(Ruzicka)} = BalAbund_{Total} + AbundDiff_{Total}$ so that the relative contribution of one component to the overall temporal variability of a community can be computed as $Repl_{Prop} = Repl_{Total}/BD_{Total}$ and $RichDiff_{Prop} = RichDiff_{Total}/BD_{Total}$ for presence absence data for example (Legendre, 2014). Differences between biogenic and bare habitats were assessed within each tidal level using Mann-Whitney-Wilcoxon tests.

ii) Explaining spatial and temporal β diversity

To assess the relationships between the temporal β diversity of the sites and their abiotic conditions, we tested, in the intertidal, for linear relationships between temporal BDtot values, and their components ($RichDiff_{Prop}$ and $AbundDiff_{Prop}$), with the degree of exposure of the sites (estimated using average fetch) for each habitat separately. Similarly, we tested for linear relationships with depth in the subtidal for each habitat separately. Average fetch and depth were estimated as described in the Supplementary material.

The variance of communities within each of the four habitats was partitioned through partial redundancy analyses (Borcard et al., 1992; Peres-Neto et al., 2006) among three sets of explanatory variables: space, time and abiotic constraints. This was done in a first analysis with the raw abiotic variables detailed in the Supplementary material (hereafter *Raw analysis*). In a second analysis, orthogonal polynomials of the second degree were calculated for all these abiotic variables and were included along the raw variables in the set of abiotic variables used in the variance partitioning (hereafter *Polynomial analysis*).

Spatial patterns were modeled and tested using (i) a bivariate linear geographic trend (sites coordinates were transformed into geodetic coordinates through the *geoXY* function of the *SoDA* package in R, Chambers, 2013), as well as (ii) distance-based Moran's Eigenvector Maps (dbMEM, Dray et al., 2006). For dbMEM eigenfunctions computation, distances among sites were calculated as the shortest paths along the coast following the methodology described in the Supplementary material. Similarly, temporal signals were modeled using a linear trend and dbMEM eigenfunctions among the nine years.

For seagrass habitat, and on top of conducting the analysis with the space, time and abiotic constraints, the variance of the assemblages was also partitioned among four sets of explanatory variables by adding a fourth set of variables describing the structural properties of the *Zostera marina* meadows (hereafter *Biometric variables*) to the previous partitioning analysis. These biometric variables on the *Zostera marina* meadows include in particular shoot density, size, above- and below-ground biomass and are fully described in the Supplementary material. This additional analysis was used to assess to what extent abiotic constraints on seagrass-associated endofauna may be mediated by modification of the structural properties of the *Zostera marina* meadows.

Within each set of explanatory variables, collinear variables were removed using variance inflation factors (VIF) with a threshold of 10. Redundancy analyses were then performed for each set of explanatory variables separately and tested for significance using 9999 permutations of the community data. When overall spatial/temporal/abiotic/biometric models were significant, selection of variables was performed within each explanatory set. Abiotic and biometric variables were selected using stepwise selection based on adjusted R^2 with p-values for adding and dropping variables of 0.05 and 0.1 respectively. Forward selections based on adjusted R^2 were also conducted for temporal and spatial dbMEM (Blanchet et al., 2008). Variance partitioning was then performed on the selected variables of each globally significant set of explanatory variables. All analyses were performed on Hellinger-transformed species abundances using the R packages *adespatial* (Dray et al., 2017) and *vegan* (Oksanen et al., 2017).

iii) Historical legacies in modern spatial β diversity patterns

LCBD indices (Local Contributions to Beta Diversity, Legendre & De Cáceres, 2013) were calculated using Hellinger distances for the intertidal and subtidal separately using the *beta.div* function in the *adespatial* package (Dray et al., 2017). They were used to estimate the uniqueness of communities in terms of structure and composition in 2014 and describe how each sampling location (one habitat in one site) contributes to the spatial β diversity in the last year of sampling considered in this study. To assess to what extent these “modern” contributions could be explained by the history of the communities, we characterized the uniqueness of the temporal trajectories of these communities over the preceding 8 years (from 2006 to 2014). For this purpose, we applied the framework recently proposed by De Cáceres et al. (2018) for the analysis of community trajectory using the R package *vegclust* (De Cáceres et al., 2010). We calculated the pairwise dissimilarities of community trajectories using the *directed segment path dissimilarity* (D_{DSP}) metric. D_{DSP} was symmetrized by averaging as proposed by De Cáceres et al. (2018). This was done using the *trajectoryDistances* function (distance.type = “DSPD”, symmetrization = “mean”) separately for the intertidal and subtidal. Trajectory dissimilarities were calculated for each tidal level separately based on a Principal Coordinates

Analysis (PCoA) of Hellinger distances between communities. This was done for both raw and centered trajectories. The latter were computed using the *centerTrajectories* function. Differences between raw and centered trajectories are illustrated and explained in Figure 2. As proposed by De Cáceres et al. (2018), LCBD indices were then calculated on the D_{DSP} dissimilarity matrices for both raw and centered trajectories to estimate Local Contributions to dynamic Beta Diversity (LCdBD). LCdBD values indicate how unique the temporal trajectory of a community is compared to that of the mean community trajectory of the region.

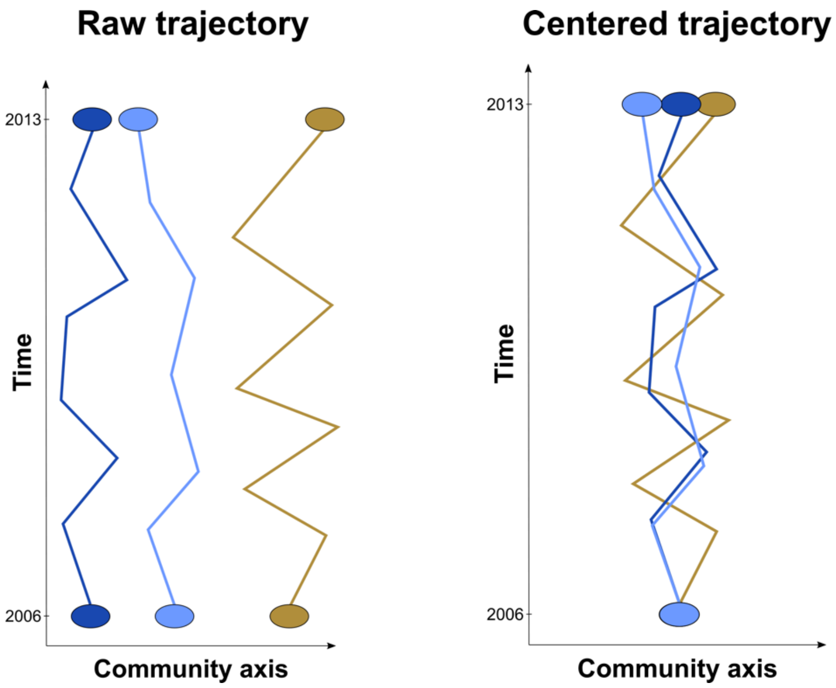

Figure 2. *Schematic representation of the difference between raw and centred trajectories. Raw trajectories account for differences in the position of communities in multidimensional space as well as for differences in their temporal trajectories. Therefore, they inform on both persistent spatial patterns and on the temporal variation over the years used to calculate the trajectories, in this case the 8 preceding years. Centered trajectory only account for differences of temporal trajectories and do not include the position of communities in multidimensional space in their calculation. Therefore, they only contain information on the relative path of communities during the 8 past years, regardless of their starting position, and LCdBD values of these trajectories (* $\boldsymbol{LCdBD_{cent}}$ *) represent the unicity of communities in terms of their recent temporal histories.*

LCdBD values of centered trajectories ($LCdBD_{cent}$) represent the unicity of communities in terms of their recent temporal histories while those on raw trajectories ($LCdBD_{raw}$) also include persistent spatial differences (Figure 2). We then tested for linear relationships between the LCdBD values computed on the trajectory distances and the contemporary LCBD values (calculated from 2014) to assess to what extent the degree of distinctness of the communities in terms of composition and structure in the last year of our study (2014) can be explained by the degree of distinctness of their temporal history (model I linear regressions predicting 2014 LCBD values from LCdBD values). Communities not sampled in 2014 were excluded from this analysis (one subtidal bare sediment at Audierne, site 22, and one subtidal maerl bed at Meaban, site 32; Figure 1 B).

Lastly, to quantify how spatial β diversity patterns within each of the four habitats have changed over time, we computed RV coefficients (Robert & Escoufier, 1976), a multivariate generalization of the squared Pearson correlation (Legendre & Legendre, 2012), between ordinations describing within-habitat spatial β diversity for pairs of years of observation. The idea here was to use RV coefficients in a within-habitat temporal correlogram reflecting changes or stability of spatial β diversity patterns between any two observation years. As sites were not all sampled each and every year, for a given comparison, ordinations – and thus RV coefficients – were calculated for all sites available for the two years considered. Although the maximum difference in years in this dataset is 8 years (2006-2014), this analysis was only performed for all pairs of surveys made from one year to a maximum of six years apart. This ensured a minimum of 10 pairwise comparisons per time distance class (time lag in years).

This procedure was performed for density data using PCA of the Hellinger-transformed species density, as well as for presence/absence data using PCoA on Jaccard dissimilarities.

All statistical analyses were performed using the R statistical language (R Core Team, 2017).

5. Results

a) β diversity in space and time: the role of biogenic habitats

PCA was used to illustrate the main sources of β diversity in this study (Figure 3). Presence or absence of biogenic habitat appears as a major factor governing community structure and composition, albeit this effect is more pronounced in the subtidal than in the intertidal. Indeed, the first axis of each PCA mostly materialize differences between biogenic and bare habitat and account for 18.4% of the total variance of the assemblages in the intertidal and 21.88% in the subtidal. However, while there is a clear distinction between maerl and bare habitat in the subtidal, distinction between seagrass and intertidal bare sediment in the PCA are fuzzier. In particular, sites 7, 13 and 14 harbor both biogenic and bare habitat (Figure 1) and the bare sediment assemblages of these sites are closer in the ordination to those of their neighboring seagrass beds than of the other bare sediment assemblages of the region. Notwithstanding, in both tidal levels communities are first differentiated through their habitat type and site whereas temporal variations, materialized by within-site dispersion, only rank third. This indicates that spatial β diversity is of greater extent than temporal β diversity in this study. Furthermore, the extent of temporal variation

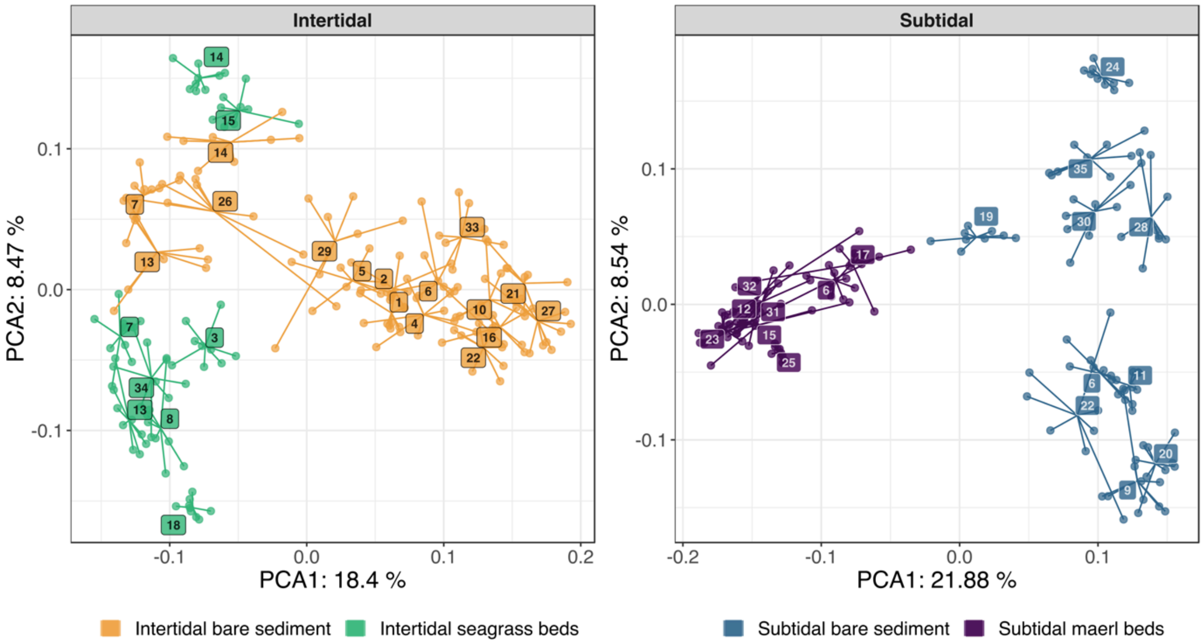

Figure 3. *Principal Component Analyses (PCA) of Hellinger-transformed densities. The two PCAs were performed separately for intertidal (left) and subtidal (right) assemblages. Samples are displayed in scaling 1 and species are omitted. A point represents the position of a community of a given site for a given year. The lines link the position of the communities of a site at each year to the centroid position of the same community across years. This illustrates within-site dispersion and represents the community's temporal variability. Colours correspond to the habitats. Sites are labelled as in Figure 1. The first two PCA axes presented together account for 26.87% and 30.42% of the total variance of Hellinger-transformed composition of intertidal and subtidal assemblages respectively.*

seems to vary among the sites, which is illustrated by differences of within-site dispersion in the PCA.

In the intertidal, temporal β diversity is significantly higher in bare sediment communities than in seagrass beds (Figure 4). This is true whether abundance or presence/absence data are considered. In both habitats however, temporal variations are primarily related to species replacement and the presence of seagrass does not significantly modify the extent of variation of the total richness and abundance of intertidal communities. In the subtidal on the contrary, presence of maerl does not significantly modify the overall temporal β diversity of the communities. Indeed, both habitats display similar BDtot values, albeit values are higher on average in maerl than in bare sediment when BDtot is measured using Hellinger distances.

However, the presence of maerl alters the main component of community temporal changes. Similar to the intertidal, community variations in time are mostly related to species replacement in these two subtidal habitats although the

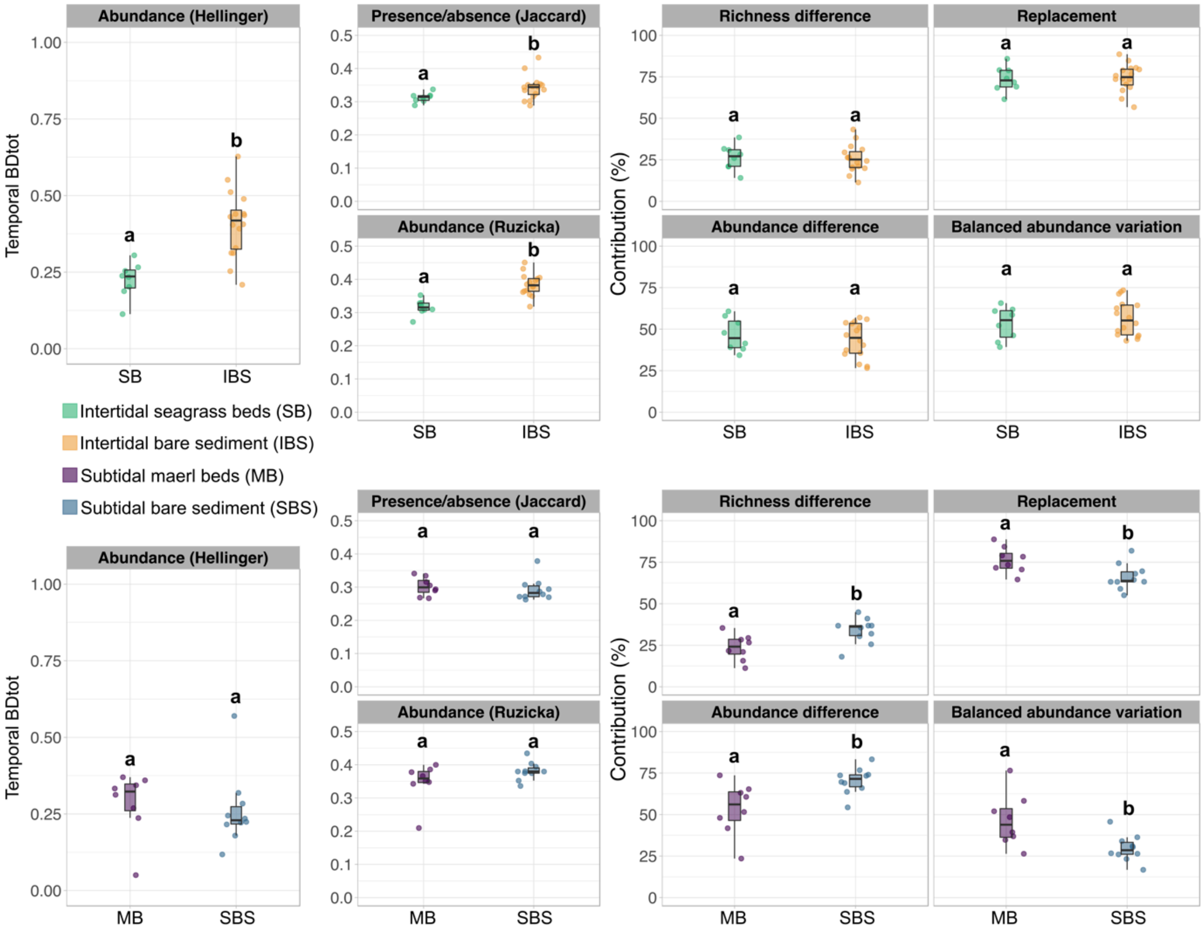

Figure 4. *Temporal variability of the assemblages according to the habitats. The overall temporal **β** diversity of each site (Temporal BDtot) was measured on species density data using Hellinger distances as well as the Ružička difference index and on presence/absence data using Jaccard dissimilarity. When all years contain a different set of species with no species in common, the maximum value that BDtot can take is 0.5 for the Jaccard dissimilarity and for its quantitative form, the Ružička difference index. This maximum value is 1 for the Hellinger distance. The overall contributions of species replacement (vs richness differences) and balanced abundance variation (vs total abundance differences) to the total temporal **β** diversity of the assemblages were assessed by partitioning the Jaccard dissimilarity and the Ružička difference index respectively. This was done using Podani-family decompositions as described in Legendre (2014). Contributions are represented as percentages of BDtot. Within each habitat, points were jittered along the x-axis to see them individually. Differences between biogenic and bare habitats were assessed within each tidal level using Mann-Whitney-Wilcoxon tests. Within each panel, significant differences at the* $\boldsymbol{\alpha} = \mathbf{0.05}$ *threshold are represented by different letters.*

extent of this pattern varies significantly between maerl and bare sediment. Higher replacement and lower species richness variation are observed in maerl communities. Likewise, while temporal variation in bare sediment are consistently dominated by changes in the total abundances of the communities, temporal variation of abundances appear more balanced in maerl communities on average. Overall, compared to bare sediment, maerl has different effects on the temporal β diversity of communities than that observed for seagrass beds in the intertidal.

b) Explaining community variation in space and time: the role of abiotic constraints

The extent of within-site temporal variability (temporal BDtot) of intertidal communities is not related to the degree of exposure of the sites – estimated using average fetch – neither in bare sediment nor in seagrass beds (Supplementary material Figure 1). Likewise the contribution of richness difference is not related to exposure. There is in contrast a relatively weak but significant positive relationship between the contribution of abundance difference to the temporal BDtot of the sites and their exposure in intertidal bare sediment. This trend is not observed in seagrass beds. In the subtidal, there is a significant linear negative relationship between depth and the temporal BDtot of bare sediment communities in terms of presence/absence (Supplementary material Figure 1). A similar relationship is found between depth and the extent of richness differences in time in this habitat. In contrast, these two relationships are not found in maerl communities. In both habitats, no link was found between depth and temporal BDtot values when measured on abundances.

Overall, no significant linear temporal trend was found using redundancy analysis within each habitat. Likewise, temporal dbMEM calculated on the 9 years did not model any significant temporal variation. As a consequence, no explanatory variables representing temporal variation were included in the final partition of the spatial and temporal variance of the communities of each habitat aiming to quantify the role of abiotic constraints (Figure 5).

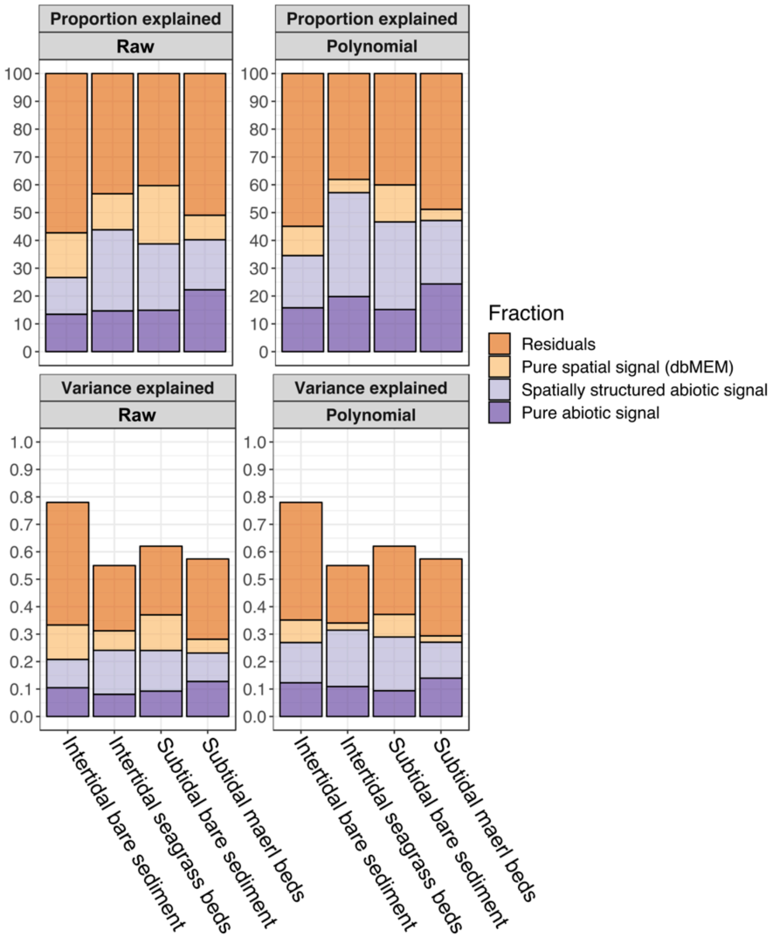

Figure 5. *Spatial and temporal variations of the assemblages of each habitat partitioned into pure abiotic signal, spatially structured abiotic signal, pure spatial signal and unexplained variance. Temporal signal was non significant for the four habitats and was not included in the final models presented here. Fractions are expressed in terms of the proportion of the total variance of the assemblages they represent using adjusted* $\boldsymbol{R^2}$ *(top panels) and in terms of total variance by multiplying adjusted* $\boldsymbol{R^2}$ *with the total spatial and temporal variance (BDtot) of the assemblages of each habitat (bottom panels). Hellinger-transformed abundances were used for these analyses so that the maximum possible value for BDtot is 1. This maximum value is reached if all communities of an habitat (in space and time) are completely different.*

Overall, between 40 and 60% of the community variation could be modeled with spatial and abiotic variables depending on the habitats (Figure 5, Proportion explained). In general, models including second-degree polynomes of abiotic variables have total predictive power similar to those containing only raw abiotic variables. However, in all cases including polynomial abiotic variables increases the variance explained by the set of abiotic variables. This variance remains in the "pure spatial" fraction otherwise. Including second degree polynomes increased the total fraction explained by abiotic variables from 27 to 35 in intertidal bare sediment (adjusted R^2), from 44 to 57 in seagrass beds, from 39 to 47 in subtidal bare sediment and from 40 to 47 in maerl beds. Irrespective of these considerations, abiotic variables explained a higher proportion of community variance in seagrass beds than in bare sediment. In seagrass, 40% of the total proportion of variance explained by abiotic conditions is shared with the set of variables characterizing the biometry of the seagrass meadows (Supplementary material Figure 2. A). In particular, most of the additional variance explained by polynomial abiotic variables is shared with biometric and spatial variables (Supplementary material Figure 2. A & B). In the subtidal, the fraction explained by abiotic variables is similar in the two habitats but the spatially structured abiotic signal is more important in bare sediment than in maerl beds (32% of the total variance in bare sediment with the polynomial model against 23% in maerl beds). Overall, spatially structured variation unexplained by abiotic variables are of lesser extent in biogenic habitat than in bare sediment for both tidal levels.

Although the proportion of total variance explained by spatial and abiotic variables varies among habitat, rescaling these results in terms of the amount of variance explained levels these differences (Figure 5, Variance explained). Indeed, biogenic habitats have lower total spatial and temporal variance than bare habitats with BDtot inferior to 0.6 while intertidal bare sediment reach 0.78. As such, the amount of variance explained in each habitat is fairly similar but, because bare sediment are more variable, a lower proportion of community variance is explained in these habitats. Examination of the residual correlations among species for each habitat suggested that 1) no obvious community structure was left unexplained in each habitat although there was some strong pairwise correlation remaining and 2) that the extent of residual variance that may be explained by biotic signal compared to purely random variation was not different among bare and biogenic habitats (Supplementary material Figure 3).

c) Historical legacies in benthic spatial β diversity patterns

To assess to what extent modern spatial β diversity patterns may bear historical imprints, we assessed the relationships between the uniqueness of assemblages in 2014 in terms of composition, measured using Local Contributions to Beta Diversity (LCBD), and the uniqueness of their temporal trajectories from 2006 and 2014, measured through Local Contributions to dynamic Beta Diversity (LCdBD). Spatial LCBD values of communities in 2014 are significantly ($p <$ 0.05) related to the uniqueness of their raw trajectory over the past 8 years ($LCdBD_{raw}$), this relationship being stronger in the subtidal (R^2 = 0.76) than in the intertidal (R^2 = 0.55; Figure 6). Examining this relationship with centered community trajectories ($LCdBD_{cent}$) yielded different results. Indeed, accounting only for the uniqueness of the temporal variation of communities over the past 8 years without accounting for their inherent differences existing before this period does not significantly explain the LCBD values observed in 2014 in the subtidal. In the intertidal however, LCBD values of 2014 remain significantly predicted by

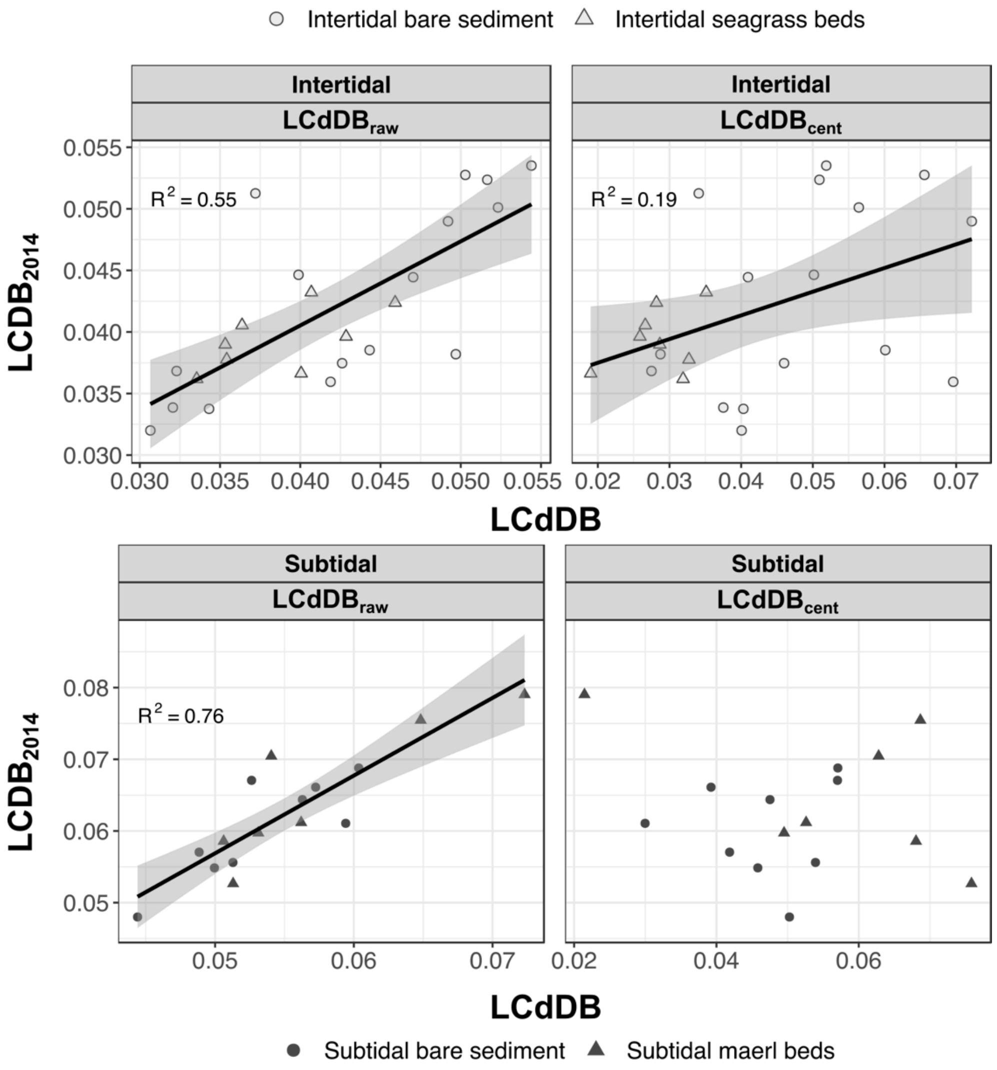

Figure 6. *Measured relationships between sites' Local Contributions to Beta Diversity (LCBD) in 2014 and the LCdBD of their temporal trajectory (i.e. their Local Contributions to dynamic Beta Diversity) from 2006 to 2013 for raw trajectories ($\boldsymbol{LCdBD_{raw}}$) and centered trajectories ($\boldsymbol{LCdBD_{cent}}$). LCBD values indicate the extent to which each local community is unique in terms of its compositionn, with higher $\boldsymbol{LCBD_{2014}}$ values indicating more unique assemblages in 2014. When calculated on temporal trajectories (LCdBD), they indicate how unique the temporal trajectory of the community is compared to that of the other communities of the region. Only significant linear relationship at the $\boldsymbol{\alpha = 0.05}$ threshold are shown. Model I linear regressions were fitted for the intertidal and subtidal separately without any distinction between the habitats within each tidal level.*

$LCdBD_{cent}$ values, albeit this relationship is much weaker than with raw trajectories ($LCdBD_{raw}$).

Overall, the strong relationship of 2014 LCBD with raw trajectory indicates that spatial patterns are well preserved in time, which is further confirmed by the RV coefficients calculated within-each habitat among different years and that remain mostly superior to 0.85 (Figure 7). Spatial β diversity patterns are particularly stable in seagrass beds, both in terms of presence/absence or abundances. Variation of community patterns from one year to another are greater in subtidal bare sediment and maerl beds, but only when considering abundance data for maerl beds. However, there is no obvious relationship in either of these three habitats between the number of years separating two surveys and the extent of their differences in terms of spatial configurations. In contrast, surveys separated by longer time lags show lower RV coefficients in intertidal bare sediment when considering abundance data. Therefore, in contrast with the three other habitats, intertidal bare sediment communities seem to exhibit directional changes to their spatial configurations through time. However this is not true when considering only presence/absence data. In addition, in intertidal bare sediment two consecutive years exhibit on average greater spatial differences than in any other habitats, particularly when considering presence or absence of taxa, highlighting a higher variability of the regional spatial patterns in this habitat at short term.

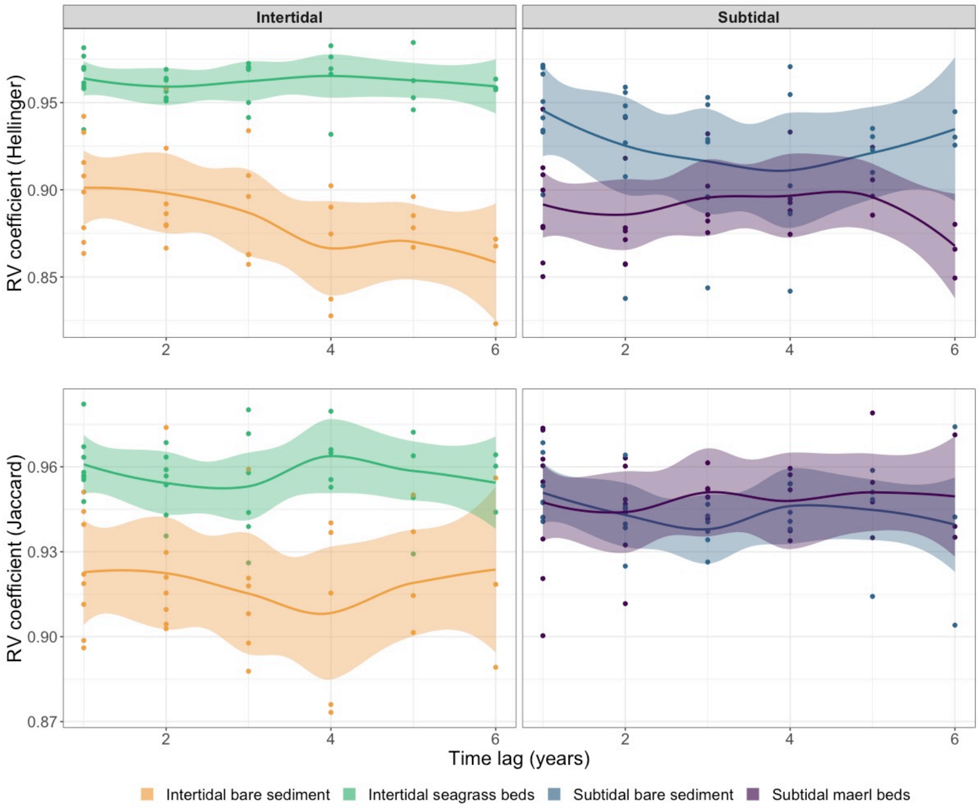

Figure 7. *Differences of spatial* $\boldsymbol{\beta}$ *diversity patterns within each habitat for different time lags between observations. In the graphs, the points represent a RV coefficient computed between two years, based on the ordinations of all the communities available for the two years in a given habitat. RV coefficient is a multivariate generalization of the squared Pearson correlation and here quantifies how close spatial* $\boldsymbol{\beta}$ *diversity patterns of the communities are between pairs of years. Calculations were performed within each habitat separately and two types of ordinations were used to calculate RV coefficients. To assess how abundance-based patterns have changed, Principal Component Analyses (PCA) were performed on Hellinger-transformed data (top two panels). For presence/absence-based patterns, Principal Coordinates Analyses (PCoA) were performed on Jaccard distances (bottom panels). A maximum lag of 6 years was considered to ensure a minimum of 10 pairwise comparisons per time lag. The lines represent the average trends of each habitat and was obtained through a loess (local polynomial regression fitting). The envelopes surrounding these average trends represent their 95% confidence interval.*

6. Discussion

As highlighted by the PCAs for both intertidal and subtidal environments, the spatial heterogeneity provided by the presence of both biogenic and bare habitats in the region appeared as the major source of β diversity in this study, in front of differences among locations and temporal variations. However, the extent of between-habitat community differences is variable, in particular in the intertidal. Sites harboring both bare and seagrass habitat, for instance, exhibited relatively similar communities. This may arise from the shared environmental conditions the communities are exposed to (site specific), as well as from the potential influence of seagrass beds on neighboring communities (Heck et al., 2008). Irrespective of the processes underlying the similarity of communities in these specific sites, these observations echoes previous work that have highlighted the context-dependency of the effect of structurally complex habitat (Bracewell et al., 2018; Watt & Scrosati, 2013). Addressing this variability across space, time and environments is a key step to develop a more predictive understanding of coastal ecosystems and guide their conservation (Bulleri et al., 2015; Crain & Bertness, 2006).

a) Different foundation species, different environments, different effects on community temporal dynamics

On the basis that biogenic habitats can dampen the effect of abiotic constraints on communities (Bulleri et al., 2015; Crain & Bertness, 2006), to the extent of overriding broad-scale environmental gradients (Jurgens & Gaylord, 2017), we hypothesized that the overall β diversity (spatial and temporal) of benthic communities would be lower within biogenic habitats than in bare sediment. In the intertidal, seagrass β diversity matched with expectation #1 with lower total β diversity and on average lower temporal β diversity of communities compared to bare sediment. In contrast, maerl beds only partially met this expectation. Indeed, although total spatial and temporal β diversity was lower within maerl habitat than in bare sediment, there was no significant difference in the extent of temporal β diversity among communities of the two substrates. Actually, temporal BDtot tended to be higher in maerl beds when not accounting for the temporal variation of community total density (using Hellinger dissimilarity). Indeed, in agreement with expectation #2, maerl beds dampened variation of the size of the communities in terms of total richness and density compared to bare sediment. Maerl temporal β diversity appeared more driven by balanced abundance variation and species replacement and the higher BDtot values obtained with Hellinger distance therefore indicate that maerl promotes higher replacement of species in time than in bare sediment, although they dampen other aspects of community temporal variation. In contrast, seagrass did not meet expectation #2 so that while they dampen the extent of temporal β diversity of intertidal communities, they do not seem to alter the components responsible for these variations.

The difference between how seagrass and maerl habitat met with expectations #1 and #2 may be partly explained by expectation #3, which posited a potential difference between the effect of foundation species in the intertidal and in the subtidal because of difference in the harshness of these environments (Crain & Bertness, 2006). For instance, Watt & Scrosati (2013) have shown experimentally that the positive effects of biogenic habitats on community richness was more pronounced higher in the intertidal, associated with stressful conditions, than lower on the shore in milder conditions. Crain & Bertness (2006) suggested that the effects of foundation species shifts from providing refuge from consumers or competitors in physically benign environments to providing refuge from limiting physical conditions in physically stressful environments. Therefore, while seagrass may modify resource supply to benthic communities compared to bare sediment (Ouisse et al., 2012), community size in terms of both richness and abundance remains largely driven by stochastic factors in intertidal meadows due to the physical constraints associated to these highly dynamic environments (Chapter 2; Barnes & Hendy, 2015). In the more stable subtidal environments on the other hand, the role of foundation species in mediating resource supply and species interaction may become more important in governing community size (Crain & Bertness, 2006). The higher resource availability and diversity of food sources in maerl beds (Grall et al., 2006) may ensure a more constant resource supply than in bare sediment while the high functional richness and redundancy of maerl-associated communities (Chapter 2) may promote more stable community size in time through compensatory dynamics and asynchronous species temporal variation within functional groups (Magurran & Henderson, 2018). This hypothesis is consistent with the findings in Chapter 2 of a well-preserved functional structure for the polychaetes inhabiting these maerl beds between 2007 and 2013 despite the high species replacement observed.

b) Bare and biogenic habitats : similar predictability, different strength of abiotic constraints

These results point towards a more important role of abiotic constraints in the intertidal than in the subtidal. Understanding the role of abiotic constraints is key in the current context of rapidly changing environments and variance partitioning have been increasingly used for this purpose (Cottenie, 2005; Soininen, 2014). The amount of variance explained by abiotic variables was similar in the four habitats, which contrasts with expectation #4 as well as with the results above. In the intertidal, this fraction was even proportionally higher in seagrass compared to bare sediment. Several factors may be invoked to explain the residual fraction of community variation and their higher values in bare habitats, which include the effects of unmeasured abiotic variables, differences in the relative strength of abiotic and biotic forcing, and also historical factors (Leibold & Chase, 2017). The set of variables included in our analysis is relatively exhaustive in regards of the main factors known to govern benthic communities, namely temperature, salinity, substrate properties, current velocity, exposure and depth (McArthur et al., 2010). Analysis of the residuals showed that most correlation structures among species were accounted for by our models and there was no difference in the residual correlation structures between biogenic and bare habitats. Additionally, the identity of the variables selected in the models was fairly similar between biogenic and bare habitats in their respective tidal levels (see Supplementary material). Regarding the relative strength of abiotic and biotic factors, Quillien et al. (2015a) have shown that a significant fraction of the variation of communities in the intertidal bare sediment under study was explained by the presence of green tides (stranding *Ulva* spp.). However, this fraction remained minor in comparison to the fraction attributable to abiotic variables and may not have a strong contribution to the difference of total β diversity observed between bare and seagrass habitat as seagrass meadows may also trap important amount of drifting algae (Boström & Bonsdorff, 2000). The similar residual correlation structures found between biogenic and bare habitats suggest that biotic forcing cannot explain their differences of total β diversity alone.

The rationale behind expectation #4 was that biogenic habitats influence the range of physical conditions under which species can persist (Bulleri et al., 2015). However, while they buffer climate variability and the severity of extreme events, biogenic habitats do not seem to alter mean environmental conditions (e.g. Jurgens & Gaylord, 2017). This may explain the absence of marked differences in the variance partitioning between biogenic and bare habitats. Although we accounted for some components of the variability of abiotic conditions through the minimum, maximum or standard deviation of the variables, our set of abiotic variables likely better represents the average conditions of the sites, and to some extent their average variability, than the occurrence of extreme events. Therefore, rather than highlighting a similar strength of abiotic constraints across the different habitats, results from the variance partitioning analyses more likely reveal that benthic communities have similar predictable variation in relation to the environment in these four habitats. The higher residual fraction observed in bare habitats however suggest that biogenic and bare habitat communities are differently affected by more punctual and unpredictable events. For instance, two important storms have affected Brittany during the studied period (2008 and winter 2013-2014, Fichaut & Suanez, 2011; Masselink et al., 2016). These extreme events were associated with massive erosion of intertidal bare sediment in the region (Masselink et al., 2016), which can lead organisms to be washed away, the extent of this effect depending on the physical characteristics of the sites (Harris et al., 2011). Accordingly, the trait-based approach led in Chapter 2 suggested that some of these intertidal bare sediment communities were in a recovery stage and hinted towards an asynchrony of their ecological ages (Bracewell et al., 2017) at the regional scale. This asynchrony may be due to different timing of disturbances or to different responses according to the locations, and likely contribute to the residual fraction of the total β diversity of these communities. This may explain the difference with seagrass habitat whose species diversity and density tends to benefit from wind disturbances (up to a certain threshold) because seagrass meadows provide refugia of lower hydrodynamic intensity, which constitute sink areas for larvae and organisms (Boström & Bonsdorff, 2000). In agreement, higher fetch was related to higher contribution of abundance difference in bare and not seagrass habitat, which indicate that more exposed bare sediment experienced more important variation of total densities while this was not true in seagrass meadows.

c) Historical legacies in benthic systems and time scale of community responses to abiotic changes

Benthic β diversity patterns may show remarkable constancy over long time period (Casebolt & Kowalewski, 2018; Tyler & Kowalewski, 2017) and contemporary diversity patterns may therefore have important historical legacies. Although increasingly acknowledged in terrestrial ecosystems (Ogle et al., 2015; Perring et al., 2016), the role of historical heritages has been seldom assessed in benthic systems. Here, we found that spatial β diversity structures were relatively stable since 2006 in all four habitats. The contemporary distinctness of communities was strongly related to their distinctness since 2006 but not to the distinctness of their temporal trajectory from 2006 and 2013. This suggests that spatial β diversity patterns at regional scale have persisted over the 9 years and that the recent trajectories of communities have a minor contribution to their present state, especially in the subtidal. Even the strong storms occurring just before the 2014 sampling (Masselink et al., 2016) did not break the LCBD/LCdBD relationship. This means that the temporal variations of communities over the nine years were of small extent and did not deviate communities much from their long-term baseline. Therefore, what may seem as important variation at a given time scale (e.g. the monthly variation of intertidal bare sediment Quillien et al., 2015b) might be insignificant from a long-term perspective. We show here that *baselines* or *reference states*, rather than static starting points, are better viewed as envelopes that are dependent on the temporal observation window, and that long-term monitoring is key to provide appropriate baseline to disentangle long-term from short-term changes and to reveal the full extent of biodiversity change (Hawkins et al., 2017; Hillebrand et al., 2017). Importantly, our results were not directly influenced by year-to-year variation in species recruitment and therefore provide appropriate long-term references to which compare future changes.

This stability of β diversity patterns does not imply the absence of environmental changes in the region over the studied period. Important lags between long-term temperature changes and the response of benthic fauna have been documented in the region under study (Gaudin et al., 2018; Hiddink et al., 2014). Intertidal communities have been shown to respond more quickly (Hawkins et al., 2009) than subtidal environments (Hinz et al., 2011), which matches with the more important temporal changes observed in the spatial β diversity of intertidal bare sediment over a 6 year period. It is also in agreement with the weak but significant relationship observed in the intertidal, but not the subtidal, between LCBD values in 2014 and the LCdBD on centered trajectories representing the temporal variation over the preceding 8 years. The different time scale of species responses and environmental changes may lead to non-linear responses of communities to environmental variations (Smith et al., 2009). Such responses are increasingly reported in benthic systems (Flanagan et al., 2018; Hewitt et al., 2016) and were also important in this study, in particular in seagrass habitat for which an important part of the variance explained by non-linear relationships with abiotic variables was shared with the biometric characteristics of the meadows. This suggests that abiotic effects on the communities are partly mediated by changes of the foundation species and lead to non-linear responses of the associated communities.

d) Conclusion

Modification of spatial β diversity can have profound consequences for the functioning of benthic ecosystems, with high potential to lead to regime shift (Fisher et al., 2015; Juan et al., 2013). We show here that the spatial β diversity of intertidal communities respond more quickly than in the subtidal but also that presence of seagrass meadows mitigate these variations and allows the maintenance of more stable regional spatial β diversity through time. Overall, the two biogenic habitats significantly altered the temporal dynamics of benthic communities. Thereby, we confirm the crucial role of biogenic habitats in mitigating future biodiversity changes of benthic ecosystems (Bulleri, 2018). Importantly, our results suggest that biogenic habitats may not buffer changes in mean environmental conditions but serve to dampen the effect of extreme events, whose effects are however expected to be greater than variation of mean conditions (Vasseur et al., 2014). We also highlighted that foundation species may act through different mechanisms and in contrasting ways on the temporal variability of communities (Bulleri et al., 2015) and that apprehending the ecological process associated with different foundation species is essential to better predict the consequences of future coastal ecosystems changes (Pessarrodona et al., 2018). Lastly, sites that have similar communities at a given time but are on opposite temporal trajectory may respond differently to future changes (Perring et al., 2016) and such dynamics cannot be predicted from spatial “snap shot” surveys. Approach such as LCdBD, especially when they are computed on centered trajectories, may help revealing sites that have been recently diverging from the mean regional trend. In this study, some sites have experienced distinct temporal trajectories compared to mean regional changes without this being directly visible in the contemporary spatial snapshot. The drivers underlying these trajectories will need to be resolved to apprehend their future dynamics and their potential for regime shifts.

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9. Supplementary material

a) Acquisition of explanatory variables

i) Spatial distances among sites

Distances among sites were calculated as the shortest paths along the coast using the SpatialLinesLengths and shortestPath functions of the gdistance package (Etten, 2017). This calculation relied on a transition layer that was build on a 100 meter resolution raster constructed from the same polygon layer used to calculate fetch (see details below). The translation layer was computed using the raster (Hijmans, 2017) and maptools (Bivand & Lewin-Koh, 2018) packages in the R statistical language (R Core Team, 2017).

ii) Environmental variables

(1) Fetch

Fetch was calculated using land polygon data made available by OpenStreetMap (http://openstreetmapdata.com/data/land-polygons; downloaded on October, 28, 2017) and the fetchR package (Seers, 2018). Land polygons were modified to correct for invalid polygons using the gSimplify (with a tolerance of 0.00001) and gBuffer functions (byid=TRUE, width=0) from the rgeos package (Bivand & Rundel, 2018). The average wind fetch, referred hereafter to as “fetch”, was calculated in kilometers as the average length of nine radiating fetch segments (one every 10 degrees) with a maximum distance for any fetch segment set to 300 km.

(2) Depth

Depth was retrieved at the coordinates of each subtidal sites using the mean depth bathymetry layer of 1/8 by 1/8 arc minutes resolution (ca. 230 * 230 meters grid cells) made available by the EMODnet bathymetry portal (EMODnet Bathymetry Consortium, 2016).

(3) Meteorological data

Meteorological variables were retrieved for each site from the nearest Météo France (http://www.meteofrance.com/) meteorological station (Figure 8 of the Supplementary material). They include the daily minimum, mean and maximum air temperature measured in a shelter, the daily temperature range, daily frost duration, the daily average wind speed at 10 meters height and the daily maximum instantaneous wind speed.

These meteorological data were integrated from the first day of the year to the sampling dates of the sites to characterize weather conditions at each site:

- Minimum, Mean and Maximum air temperatures (°C)
- Standard deviation of the daily mean temperature (°C)
- Mean and Maximum daily range of air temperature (°C)
- Cumulative frost duration over the period (minutes)
- Cumulative rainfall over the period (mm) and Standard deviation of daily cumulative rainfall (mm)
- Maximum and mean wind velocity over the period ($m.s^{-1}$) and Standard deviation of the daily maximum wind velocity over the period ($m.s^{-1}$)

(4) Hydrological data

Water temperatures (°C), salinities (PSU) and current velocities ($m.s^{-1}$) were obtained from the publicly available PREVIMER database (http://www.previmer.org/) based on the MARS3D model (2.5 km grain, 40 depth levels). All variables were extracted daily for the years under study at midday near the sediment surface. Variables were estimated at the site level by extracting and averaging data in a radius of 3.75 km of the focal coordinates (representing at most 9 grid cells of the model: the focal cell, the 4 adjacent cells and the 4 diagonal cells). When needed, extraction coordinates of intertidal sites were shifted away from the coast to avoid model edge effect. Salinity and temperature data measured *in situ* during the sampling campaign of 2017 or available from the literature and from environmental monitoring programme such as the Service d'Observation en Milieu Littoral (SOMLIT;

http://somlit.epoc.u-bordeaux1.fr/fr/) and the Réseau d'observations Conchylicoles (RESCO; https://wwz.ifremer.fr/lerpc/Ressources-aquacoles/RESCO) were used to adjust the coordinates and methodology of data extraction from the model. Seawater temperatures, salinities and current velocities were then characterized by their distribution from the first day of the year to the sampling dates of the sites, with the minimum and maximum, the first and third quartile, the mean and the standard deviation.

(5) Granulometric data

In the intertidal for both bare and seagrass habitat, a sediment core was collected at each point for grain size distribution and organic matter content assessment. Core samples were dried in an oven (24 h at 60°C) and separated into 15 fractions (<63 µm, 63, 80, 100, 125, 160, 200, 315, 500, 800, 1250, 2000, 3150, 5000 and >10000 µm) whose masses were measured. In subtidal bare habitat, sediments were also collected at each point for grain size distribution assessment and organic matter content. However, after being dried in an oven (24 h at 60°C), sediments from subtidal bare habitat were separated into different fractions, namely <63 µm, 63, 125, 250, 500, 1000 and >2000 µm. Subtidal maerl beds followed the same protocol as in the intertidal so that for comparisons with subtidal bare sediment, fractions were aggregated to match as closely as possible with fractions of the subtidal bare sediment. As a result, the following fraction were used in maerl beds for the calculation of granulometric indices: <63 µm, 63, 125, 200, 500, 800, 1250 and >2000 µm. Therefore, there are slight differences between the fractions used in the two habitats, but granulometric data for subtidal bare sediment and maerl beds are never used together in a single analysis (analysis were performed for each habitat separately).

These data were used to calculate the following summary indices:

- mean of the grain-size distribution (logarithmic Folk and Ward method, mm scale)
- median of the grain-size distribution (logarithmic Folk and Ward method, mm scale)
- the Trask or Sorting Index defined as $\frac{D25}{D75}$ with D25 the 25th percentile and D75 the 75th percentile of the grain-size distribution
- kurtosis of grain-size distribution (logarithmic Folk and Ward method, mm scale)

Lastly, fractions were grouped into gravels (> 2 mm), sand (63 µm to 2 mm) and silt and clay (<63 µm, Fournier et al., 2012), and used in the models along the summary statistics described above.

Overall, data were missing for 10 observations out of 375. They were imputed by k-Nearest neighbor imputation using the median value of the 5 closest neighbors based on Gower distance. This imputation procedure was performed for each habitat separately on the complete abiotic matrix (containing the identity of the site and year of the samples, the hydrological data, the meteorological data and the fetch in the intertidal, and the depth in the subtidal). This was done using the `kNN` function of the VIM packages (Kowarik & Templ, 2016) in the R statistical language (R Core Team, 2017).

Organic matter content was estimated by mass loss after combustion at 450°C for 5 hours. Data were missing for 16 observations out of 375 and imputed as described above.

iii) *Zostera marina* biometric data

At each of the three points of a seagrass meadow site, all shoots in two quadrats of 0.05 m2 were collected to measure densities (shoot.m^{-2}), overall aboveground (leaves and sheaths) and belowground (rhizomes) biomasses (g.m^{-2}), and describe each shoot's morphology with measures of sheath height (mm), leaves length (mm) and width (mm) as well as the number of leaves per shoot. Associated drifting algae biomasses were also measured in each quadrat (g.m^{-2}).

Sheath height was measured from the first node to the separation mark of the leaves. The length of each leaf was measured from the first node to the apex. The number of broken leaves was counted and expressed as a percentage of the total number of leaves found in each quadrat. One leaf of median length was used to estimate the leaf width for each shoot. Leaves and sheaths, rhizomes, and brown, red and green algae biomasses were estimated as dry weight after 24 hours desiccation at 60°C for each quadrat. Total *Zostera marina* aboveground and belowground biomasses, *Z. marina* densities and algae biomasses were scaled up and expressed per square meter for the two quadrats. An above-to-belowground biomass ratio was also calculated within each quadrat based on the total above- and belowground biomasses measured in each. For all other variables (densities, sheath height, leaf length and width, number of leaves per shoot, proportion of broken leaves), mean values were calculated for each of the two quadrats. The six values available per sites for each variable, two per quadrat values for the three points, were then averaged to estimate all the variables at the site level.

Overall, between one and two values were missing according to the variables. They were imputed by k-Nearest neighbor imputation using the median value of the 5 closest neighbors based on Gower distance. This imputation procedure was performed using the matrix containing the identity of the site and year of the samples along the biometric data. This was done using the `kNN` function of the VIM packages (Kowarik & Templ, 2016) in the R statistical language (R Core Team, 2017).

b) Summary of all variables included for stepwise selection after removal of collinear variables

i) Intertidal bare sediment

(1) Meteorological

Minimum, Mean and Maximum air temperatures (°C) - Mean and Maximum daily range of air temperature (°C) - Cumulative frost duration (minutes) - Cumulative rainfall (mm) - Mean and maximum wind velocity over the period ($m.s^{-1}$) & Standard deviation of the daily maximum wind velocity over the period

(2) Hydrological

Maximum & minimum current velocity over the period ($m.s^{-1}$) - Maximum and minimum seawater temperature (°C) - Maximum salinity & Standard deviation of salinity values over the period (‰)

(3) Granulometric

Mean of grain-size distribution (mm) - Kurtosis of grain-size distribution (mm) - Trask Index (So) - Organic matter content (%) - Median of the grain-size distribution (mm) - Silt and clay content (%)

(4) Other

Average fetch (km)

ii) Intertidal seagrass beds

(1) Meteorological

Minimum, Mean and Maximum air temperatures (°C) - Mean and Maximum daily range of air temperature (°C) - Cumulative frost duration (minutes) - Cumulative rainfall (mm) - Maximum wind velocity over the period ($m.s^{-1}$) & Standard deviation of the daily maximum wind velocity over the period

(2) Hydrological

Minimum current velocity & Maximum current velocity over the period ($m.s^{-1}$) - Maximum seawater temperature (°C) & Standard deviation of seawater temperatures over the period - Maximum salinity & Standard deviation of salinity values over the period (‰)

(3) Granulometric

Mean of grain-size distribution (mm) - Kurtosis of grain-size distribution (mm) - Trask Index (So) - Organic matter content (%)

(4) Biometric variables

Shoot density (shoot.m^{-2})- Aboveground biomass (g.m^{-2}) - Sheath length (mm) - Ratio above-to-belowground biomass - Belowground biomass (g.m^{-2}) - Number of leaves per shoot - Proportion of broken leaves (%) - Brown algae biomass (g.m^{-2}) - Red algae biomass (g.m^{-2}) - Green algae biomass (g.m^{-2})

(5) Other

Average fetch (km)

iii) Subtidal bare sediment

(1) Hydrological

Maximum & minimum current velocity over the period ($m.s^{-1}$) - Maximum seawater temperature (°C) & Standard deviation of seawater temperatures over the period - Maximum salinity & Standard deviation of salinity values over the period (‰)

(2) Granulometric

Mean of grain-size distribution (mm) - Kurtosis of grain-size distribution (mm) - Trask Index (So) - Organic matter content (%) - Median of the grain-size distribution (mm) - Silt and clay content (%) - Gravel content (%)

(3) Other

Depth (m)

iv) Subtidal maerl beds

(1) Hydrological

Maximum and minimum current velocity over the period ($m.s^{-1}$) - Maximum seawater temperature (°C) & Standard deviation of seawater temperatures over the period - Maximum salinity & Standard deviation of salinity values over the period (‰)

(2) Granulometric

Mean of grain-size distribution (mm) - Kurtosis of grain-size distribution (mm) - Trask Index (So) - Organic matter content (%) - Median of the grain-size distribution (mm) - Silt and clay content (%) - Sand content (%)

(3) Other

Depth (m)

c) Explaining spatial and temporal β diversity patterns

i) Community temporal variability: influence of fetch and depth

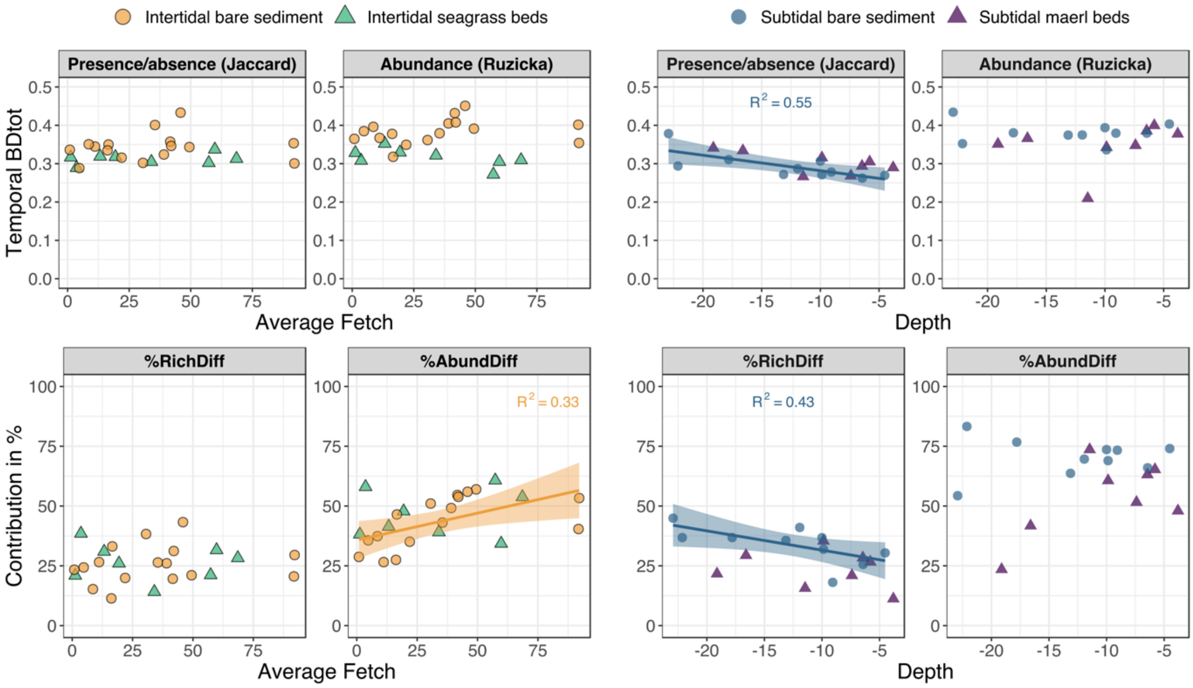

Figure 1. *Relationships between community temporal variabilities and their degree of exposure in the intertidal (estimated using average fetch in kilometers) or their depth (meters) in the subtidal. The overall temporal* $\boldsymbol{\beta}$ *diversity of each site (BDtot) was measured on presence/absence data using Jaccard dissimilarity and on abundance data using its quantitative form, the Ružička difference index. When all years contain a different set of species with no species in common, the maximum value that BDtot can take is 0.5 for the two dissimilarity measures. The overall contributions of richness differences and of total abundance differences to the total temporal* $\boldsymbol{\beta}$ *diversity of the assemblages was assessed by decomposing the Jaccard dissimilarity and the Ružička difference index respectively using Podani-family decompositions as described in Legendre (2014). With this type of decomposition, the amount of richness differences and of species replacement sum to the BDtot calculated on presence/absence data so that* $\boldsymbol{BD_{Total(Jaccard)} = Repl_{Total} + RichDiff_{Total}}$ *. The two components are thus fully complementary and can therefore be expressed as a relative proportion of BDtot so that* $\boldsymbol{Repl_{Prop} = Repl_{Total}/BD_{Total}}$ *and* $\boldsymbol{RichDiff_{Prop} = RichDiff_{Total}/BD_{Total}}$ *and* $\boldsymbol{Repl_{Prop} + RichDiff_{Prop} = 1}$ *(Legendre, 2014). The same applies to abundance differences and balanced abundance variation for abundance data. For this reason, and for simplicity's sake, the contribution of richness differences and of total abundance differences are expressed as a percentage of BDtot and those of species replacement and balanced abundance variation were omitted. Only significant linear relationship at the* $\boldsymbol{\alpha = 0.05}$ *threshold are shown. Model were fitted and tested for each habitat separately.*

ii) Spatial and temporal β diversity: role of habitat structure through *Zostera marina* biometry

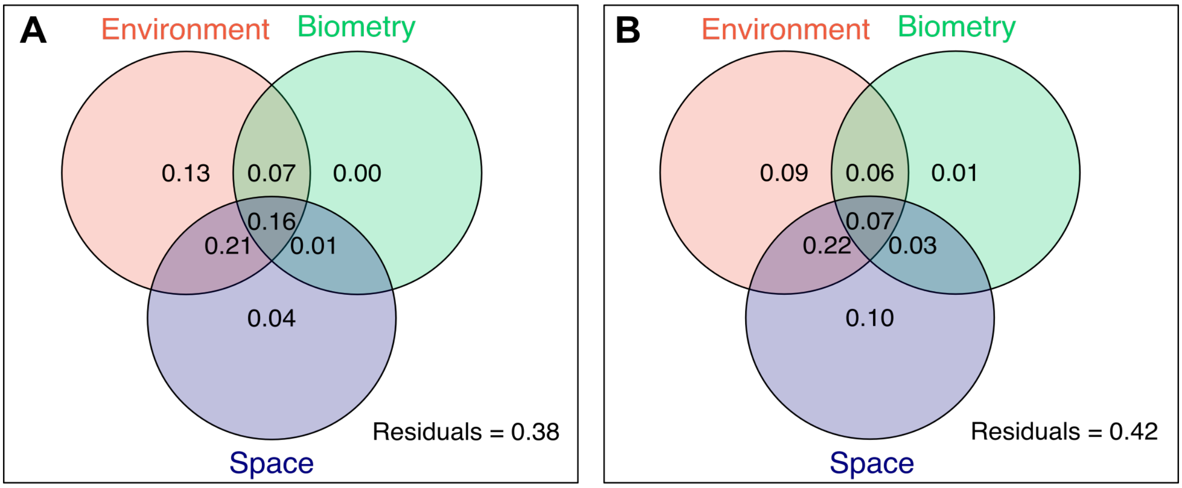

Figure 2. *Spatial and temporal* $\boldsymbol{\beta}$ *diversy of infaunal seagrass communities partitioned into fractions explained by either abiotic variables (Environment), spatial variables (i.e. dbMEM; Space), seagrass characteristics such as shoot density, above- and below-ground Zostera marina biomasses (Biometry) and unexplained variance (Residuals).* ***A.*** *When second-degree polynomials of abiotic variables are included; or* ***B****. when only linear relationships are considered. Temporal signal was non significant and was not included in the final models represented here. Fractions are expressed in terms adjusted* $\boldsymbol{R^2}$*. For details on the variable included, please refer to the Material and Methods section of the article and to section I of the Supplementary material.*

iii) Residual correlations among species in the polynomial models of Figure 4

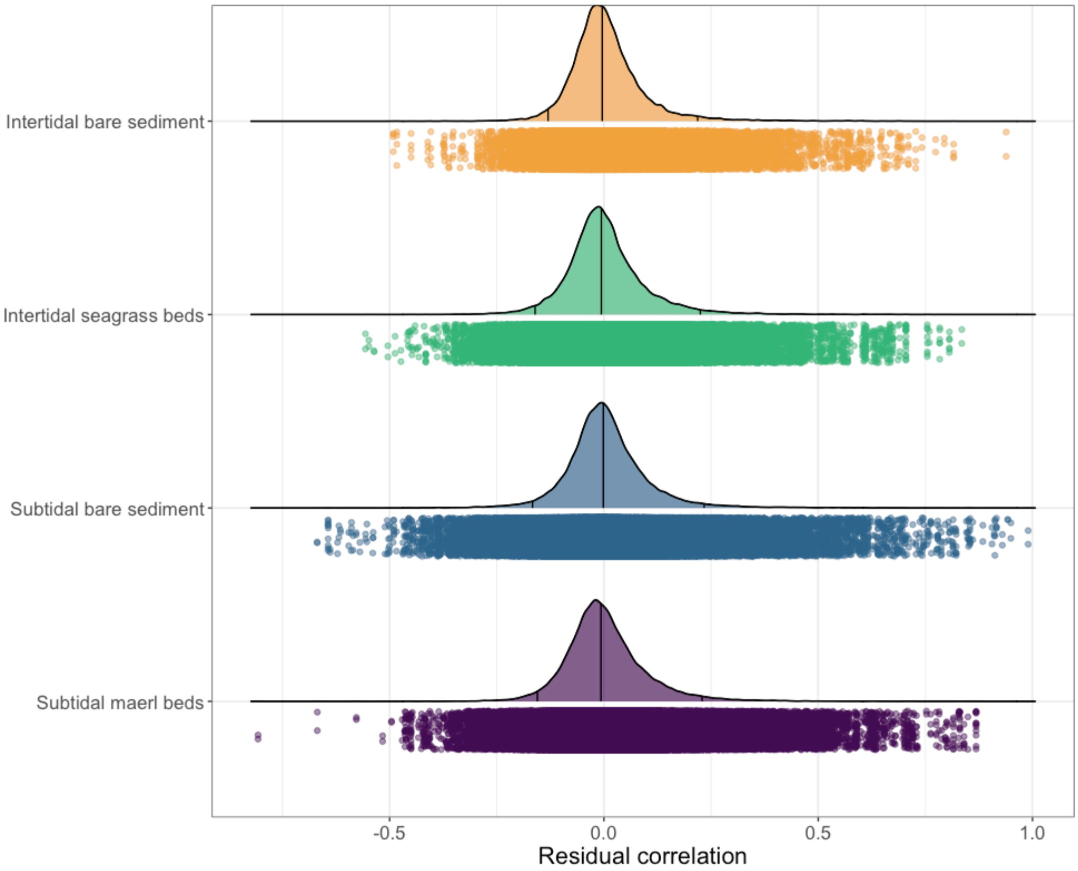

Figure 3. *Residual Kendall correlations among species within each habitat after accounting for the variance explained by the selected polynomial abiotic variables and by the selected spatial variables (dbMEM). The three lines on the distribution indicate the 0.025, 0.5 (median) and 0.975 quartiles. Each point below the density distribution represents a pairwise residual Kendall correlation between species.*

d) Selected variables in the variance partitioning models

All variables are ordered in the same order than they were selected in their respective set

i) Intertidal bare sediment

(1) Spatial variables selected

MEM3 - X (longitude transformed into geodetic coordinates) - MEM15 - MEM 13 - Y (latitude transformed into geodetic coordinates) - MEM1 - MEM2 - MEM14

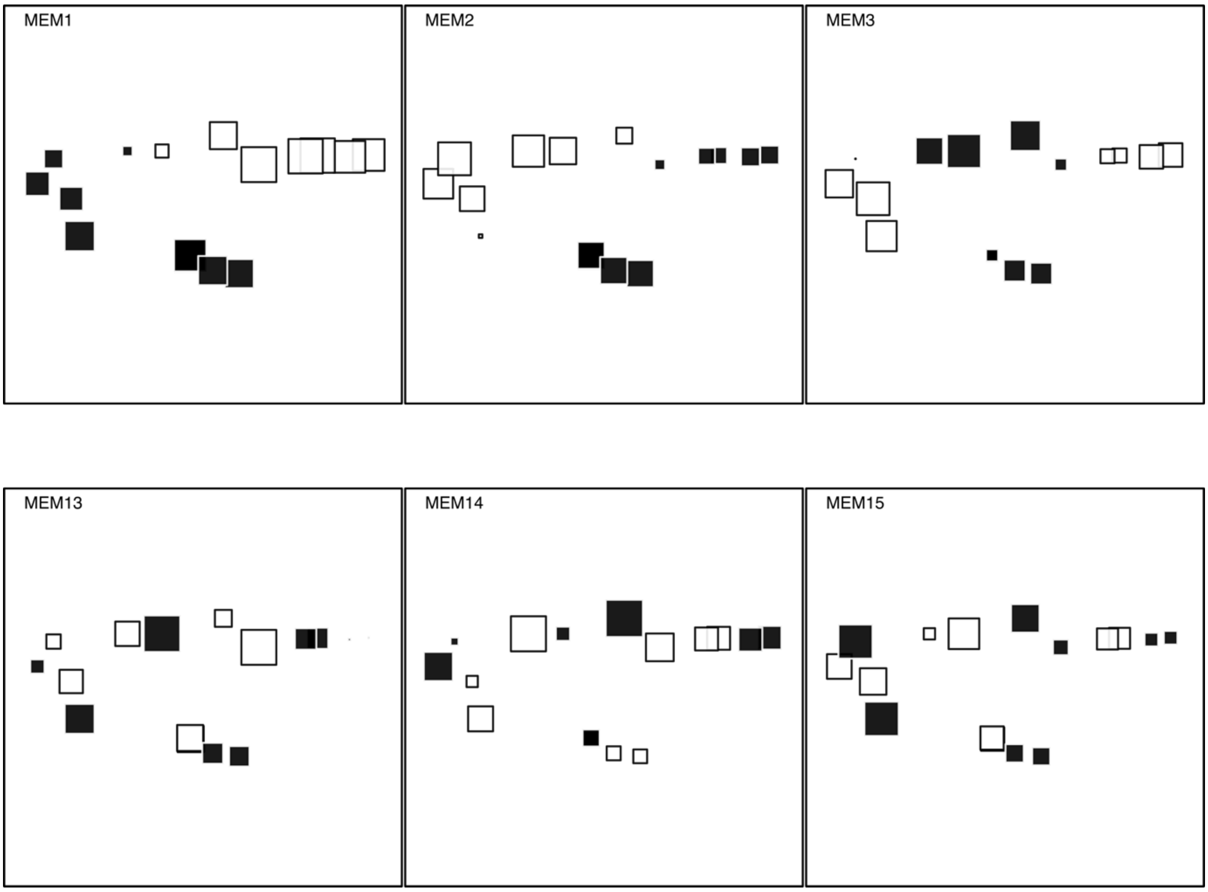

Figure 4. *Selected spatial dbMEM eigenfunctions for the variance partitioning of intertidal bare sediment communities. Black squares correspond to positive values in each eigenvector while white squares correspond to negative values. The position of the squares represent their spatial coordinates along the coast of Brittany while their size is proportional to the absolute value of their position along each eigenvector. Signs may be reverted in the construction of the eigenvectors with no consequence for the analysis; reverted signs would interchange black and white in the figure. See Figure 1 in the main article for details.*

(2) Selected abiotic variables

(a) Raw variables selected

Silt and clay content - Median of the grain-size distribution - Maximum current velocity - Average fetch - Maximum salinity - Seawater salinity standard deviation - Organic matter content - Kurtosis of grain-size distribution - Minimum current velocity - Mean daily range of air temperature - Seawater minimum temperature Seawater maximum temperature - Mean wind velocity - Cumulative rainfall - Mean of the grain-size distribution

(b) Selection with polynomials of 2nd degree

Silt and clay content - Median of the grain-size distribution - Maximum current velocity second degree polynome - Median of the grain-size distribution second degree polynome - Average fetch - Mean daily range of air temperature - Average fetch second degree polynome - Maximum current velocity - Maximum salinity second degree polynome - Maximum salinity - Organic matter content - Minimum current velocity seconde degree polynome - Kurtosis of grain-size distribution - Salinity standard deviation - Seawater minimum temperature - Mud content second degree polynome - Mean wind velocity - Seawater minimum temperature second degree polynome - Mean of the grain-size distribution - Maximum daily range of air temperature - Cumulative rainfall - Mean of the grain-size distribution second degree polynome

ii) Intertidal seagrass beds

(1) Spatial variables selected

X (longitude transformed into geodetic coordinates) - MEM7 - Y (latitude transformed into geodetic coordinates) - MEM2 -MEM1

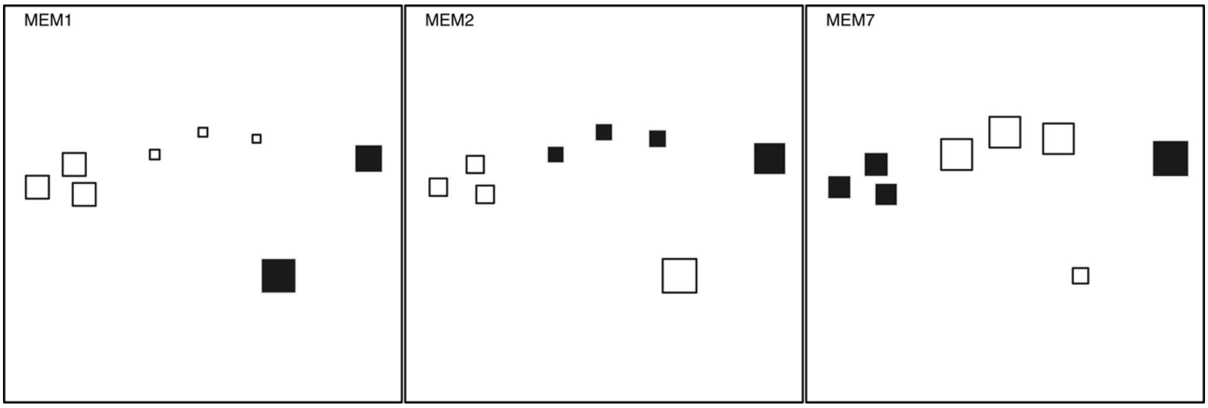

Figure 5. *Selected spatial dbMEM eigenfunctions for the variance partitioning of intertidal seagrass communities. The position of the squares represent their spatial coordinates along the coast of Brittany while their size is proportional to the absolute value of their position along each eigenvector. Black squares correspond to positive values in each eigenvector while white squares correspond to negative values. Signs may be reverted in the construction of the eigenvectors with no consequence for the analysis; reverted signs would interchange black and white in the figure. See Figure 1 in the main article for details.*

(2) Selected abiotic variables

(a) Raw variables selected

Average fetch - Trask Index (So) - Salinity standard deviation -Maximum current velocity - Seawater maximum salinity - Mean daily range of air temperature - Seawater maximum temperature - Seawater temperature standard deviation - Mean air temperature - Organic matter content

(b) Selection with polynomials of 2nd degree

Average fetch - Maximum current velocity second degree polynome - Organic matter content - Salinity standard deviation - Average fetch second degree polynome - Maximum current velocity - Mean daily range of air temperature - Seawater maximum salinity - Maximum wind velocity - Cumulative frost duration second degree polynome - Maximum air temperature - Seawater maximum temperature second degree polynome - Trask Index (So) second degree polynome - Maximum salinity second degree polynome - Trask Index (So) - Mean air temperature second degree polynome - Minimum air temperature second degree polynome

(3) Biometric variables selected

(a) Raw variables selected

Shoot density - Aboveground biomass - Sheath length - Ratio above-to-belowground biomass

(b) Selection with polynomials of 2nd degree

Shoot density - Aboveground biomass - Belowground biomass second degree polynome - Sheath length - Red algae biomass - Shoot density second degree polynome - Aboveground biomass second degree polynome - Number of leaves per shoot second degree polynome

iii) Subtidal bare sediment

(1) Spatial variables selected

Y (latitude transformed into geodetic coordinates) - MEM8 - MEM7 - MEM1 - X (longitude transformed into geodetic coordinates) - MEM9 - MEM2

(2) Selected abiotic variables

(a) Raw variables selected

Maximum current velocity - Silt and clay content – Depth - Standard deviation of salinity - Gravel content - Standard deviation of seawater temperatures - Maximum salinity - Maximum seawater temperature - Organic matter content

(b) Selection with polynomials of 2nd degree

Maximum current velocity - Silt and clay content – Depth - Standard deviation of salinity - Depth second degree polynome - Standard deviation of seawater temperatures - Gravel content - Maximum salinity - Maximum seawater temperature - Standard deviation of salinity second degree polynome - Organic matter content - Kurtosis of grain-size distribution - Median of the grain-size distribution second degree polynome - Gravel content second degree polynome -

Organic matter content second degree polynome - Mean of grain-size distribution second degree polynome - Standard deviation of seawater temperatures second degree polynome

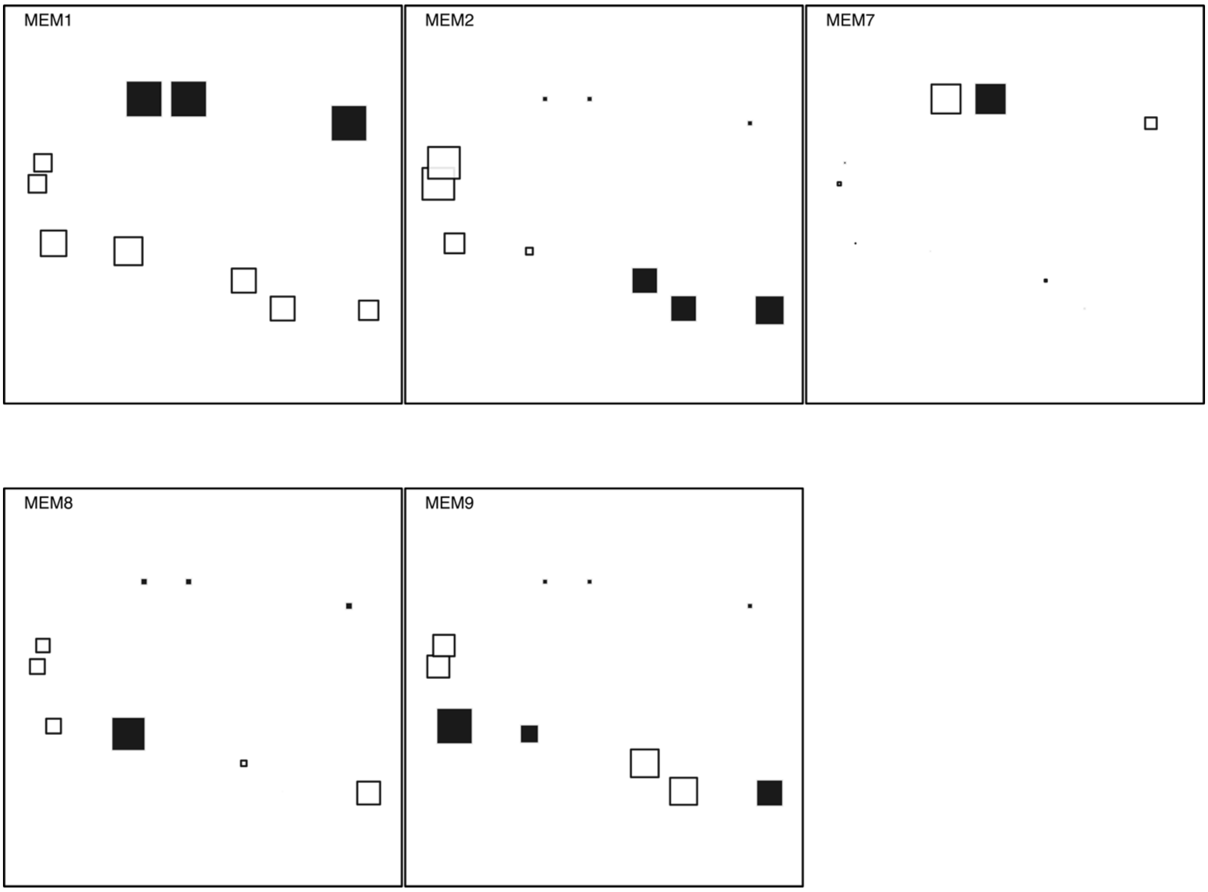

Figure 6. *Selected spatial dbMEM eigenfunctions for the variance partitioning of subtidal bare sediment communities. The position of the squares represent their spatial coordinates along the coast of Brittany while their size is proportional to the absolute value of their position along each eigenvector. Black squares correspond to positive values in each eigenvector while white squares correspond to negative values. Signs may be reverted in the construction of the eigenvectors with no consequence for the analysis; reverted signs would interchange black and white in the figure. See Figure 1 in the main article for details.*

iv) Subtidal maerl beds

(1) Spatial variables selected

MEM1 - Y (latitude transformed into geodetic coordinates) - X (longitude transformed into geodetic coordinates) - MEM7

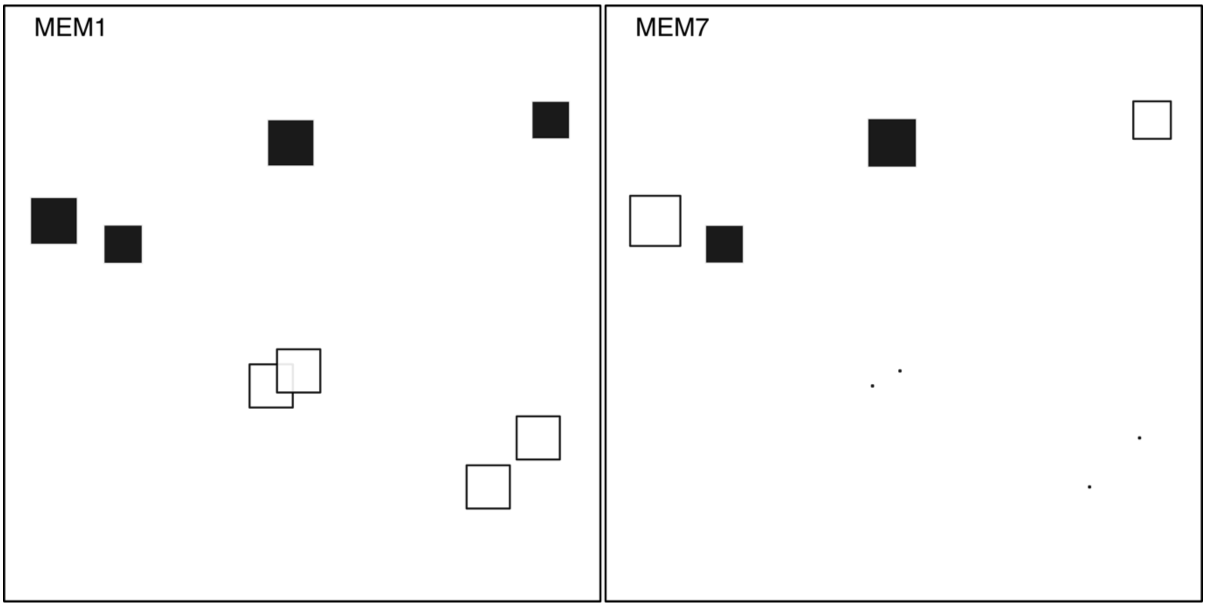

Figure 7. *Selected spatial dbMEM eigenfunctions for the variance partitioning of subtidal maerl communities. The position of the squares represent their spatial coordinates along the coast of Brittany while their size is proportional to the absolute value of their position along each eigenvector. Black squares correspond to positive values in each eigenvector while white squares correspond to negative values. Signs may be reverted in the construction of the eigenvectors with no consequence for the analysis; reverted signs would interchange black and white in the figure. See Figure 1 in the main article for details.*

(2) Selected abiotic variables

(a) Raw variables selected

Depth - Maximum current velocity - Sand content - Mean of grain-size distribution - Standard deviation of seawater temperatures - Maximum salinity - Kurtosis of grain-size distribution - Maximum seawater temperature - Organic matter content - Trask Index (So) - Minimum current velocity

(b) Selection with polynomials of 2nd degree

Depth - Maximum current velocity - Depth second degree polynome - Sand content - Maximum current velocity second degree polynome - Maximum salinity - Silt and clay content - Kurtosis of grain-size distribution - Mean of grain-size distribution - Maximum seawater temperature - Organic matter content - Standard deviation of seawater temperatures - Standard deviation of salinity

e) Appendix

i) Coordinates of the meteorological stations

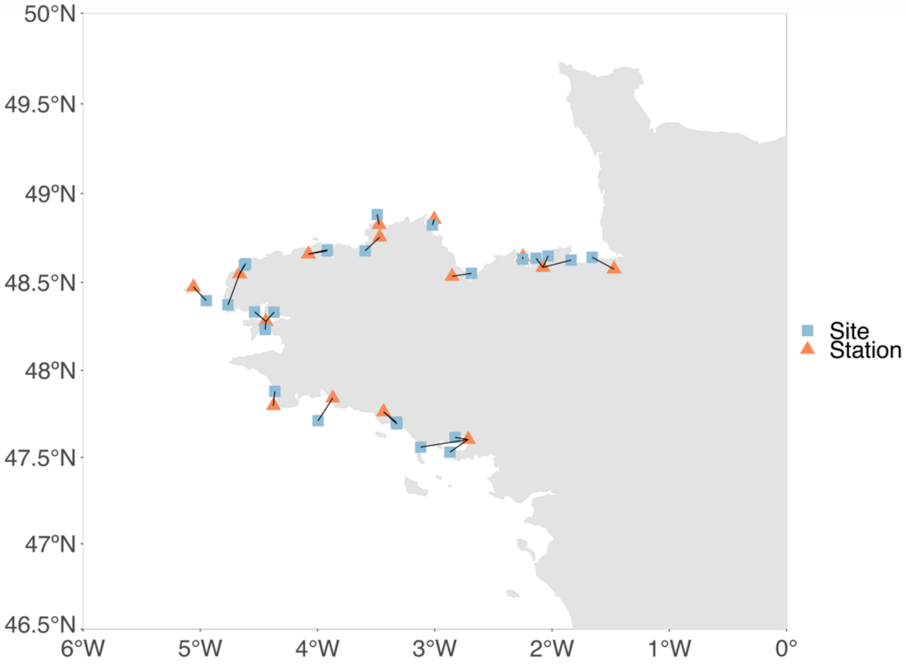

Figure 8. *Coordinates of the Météo France meteorological stations used to retrieved the data for each intertidal site. Monitored sites are represented with blue squares, meteorological stations with orange triangle. Lines link the monitored sites to the meteorological stations used to retrieved the data.*

f) References

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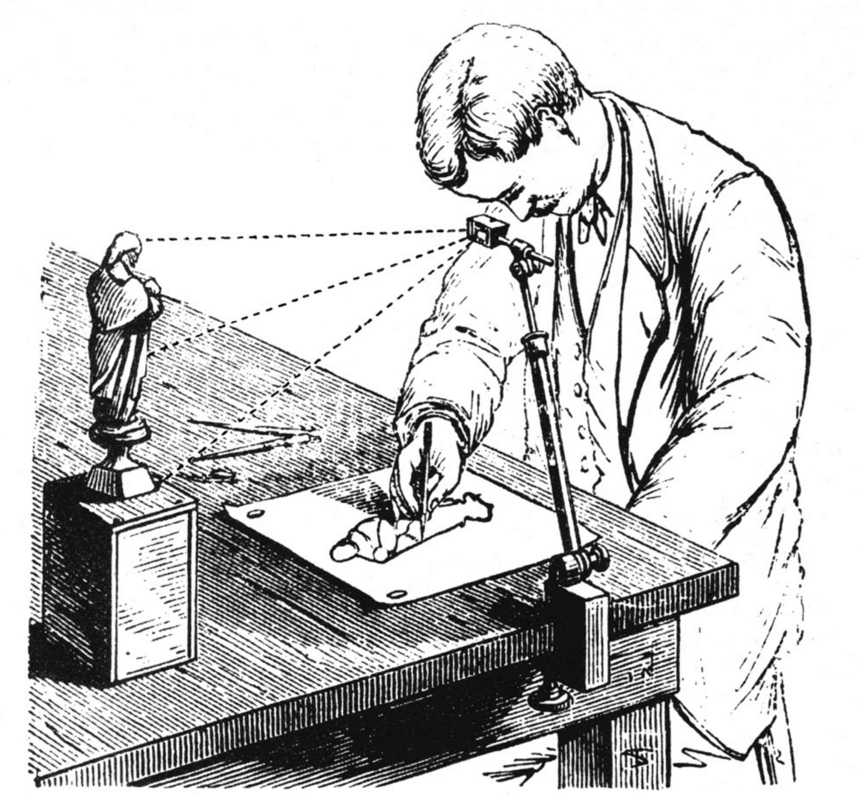

CHAPITRE 4

Broad-scale monitoring: promises, success, and challenges, a first-hand feedback

Long-term monitored sites are *'listening places' – places where we press our ears to the earth and strain to hear its pulse* (Janzen 2009). In his *musings on the future,* Janzen (2009) lauded the value of long-term monitoring data and their capacity to provide a much needed observation window into ecological systems in the face of a rapidly changing world. The fundamental role of long-term data in advancing ecological understanding and informing conservation policies has been repeatedly praised over recent years (Hawkins et al., 2017; Kuebbing et al., 2018; Lindenmayer et al., 2012; Magurran et al., 2010; Sukhotin & Berger, 2013) and undeniably, long-term monitoring programs have been fruitful in both aspects (Hughes et al. 2017). Nonetheless, long-term monitoring approaches are also faced with inherent limitations and challenges such as apprehending the drivers underlying observed changes, or dealing with heterogeneous and missing data (Magurran et al., 2010; Peters, 2010; Yoccoz et al., 2001). While the merits of long term monitoring covering multiple sites, such as the REBENT program on which this thesis has been built, are generally well recognized (Kuebbing et al. 2018), they remain rare commodities, especially in marine ecosystems (Buckley et al., 2018 Preprint). It seems therefore timely to 1) highlight the questions they allow to address and how they can contribute to our understanding of ecosystems and their conservation, 2) identify key leverage points that may hinder their exploitation, 3) delineate the best practices for ensuring their success.

This chapter aims to provide a first-hand feedback on the benefits and challenges associated to the exploitation of broad-scale monitoring data. Through examples from this work and from the literature, this chapter argues that broad-scale monitoring data are key assets for developing a more predictive understanding of natural communities and guiding their conservation, but must be considered alongside other approaches to fully deliver their promises. Importantly, the following discussion is largely based on examples from benthic systems that have been the focus of this work but readers may find that the arguments developed here have a more general scope, reaching beyond the marine environment, and may be transposed to other biological systems.

1. Knowing what is out there

a) How many species are there?

The first and perhaps most obvious benefit of broad-scale monitoring program is to enhance our knowledge of the natural history and taxonomic composition of the surveyed area. Within a context of accelerated biodiversity loss and massive species extinctions at global scale (Barnosky et al. 2011, Pimm et al. 2014, Ceballos et al. 2015), bridging the substantial gaps existing in our knowledge of species diversity is essential (Mora et al., 2011). This lack of taxonomic knowledge is conspicuous in marine systems where, according to the latest estimates, 91% of species in the ocean still await description (Mora et al., 2011). There are also important taxonomic biases in our understanding of diversity and on this aspect, Troudet et al. (2017) identified major shortfalls in our knowledge of key benthic taxonomic groups such as polychaetes, bivalves and malacostracans.

In the context of the REBENT monitoring program, a total of 1,629 species have been inventoried from 2003 to 2017 across the monitored seagrass meadows, maerl beds, and intertidal and subtidal bare sediment sites. More than 2 millions organisms have been collected and identified so far. In terms of habitat, 1,135 species have been observed in maerl beds, 923 in seagrass meadows, 634 in subtidal bare sediment and 608 in intertidal bare sediment. The taxonomic diversity of seagrass beds and subtidal bare sediment at the regional scale is starting to be well estimated (Figure 1). In contrast, for intertidal bare sediment and maerl beds it remains to be fully characterized. This may be explained by the highly dynamic nature of intertidal bare sediment in both space and time (Chapter 3). Indeed, although they may be locally poor, the high β diversity (compositional variation of communities; Whittaker, 1972) of macrofaunal communities in this habitat allows for an unexpectedly high diversity at regional scale, as highlighted for polychaetes in Chapter 2. In addition, these communities exhibit high variability at finer temporal scales than the yearly sampling of the program allows to apprehend (Quillien et al., 2015),

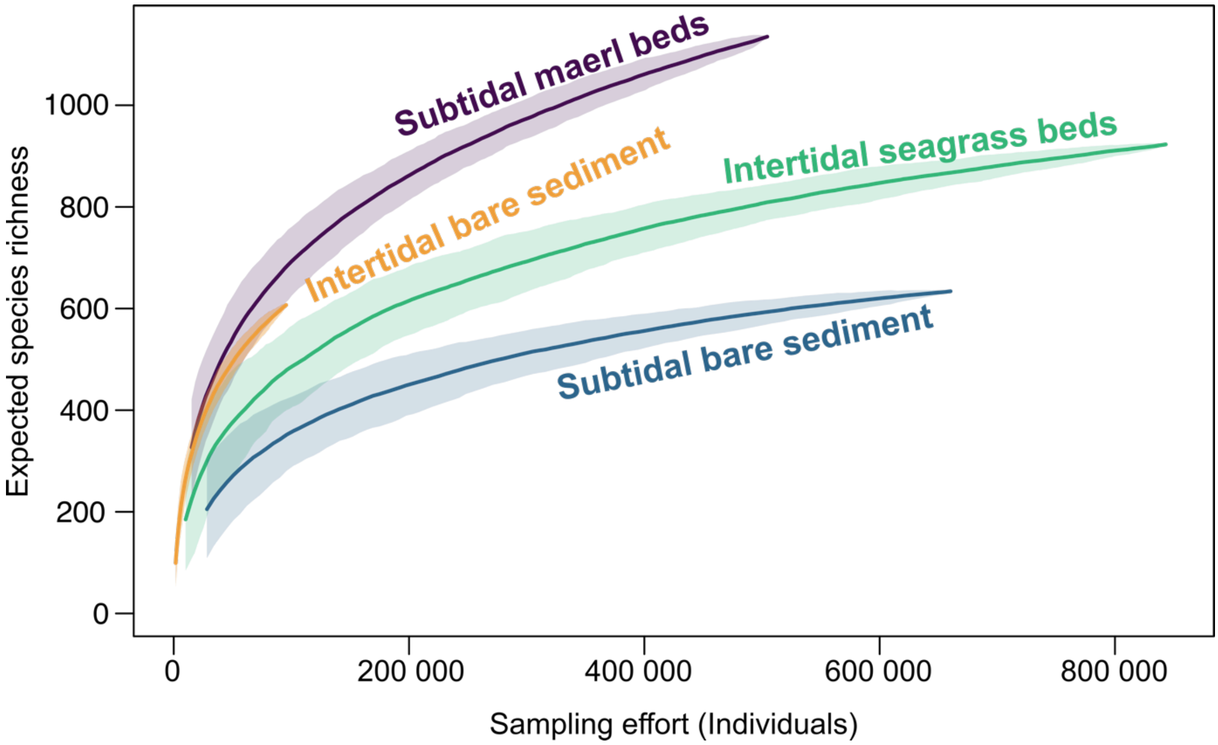

Figure 1. *Sampled-based richness accumulation curve for each of the four habitats studied in this thesis based on all samples collected in the context of the REBENT monitoring program from September, 1th, 2003 to November, 6th, 2017. The unit of sampling effort for computing these accumulation curves are the sampling occasions of a given habitat in a given site at a given season and year (replicate core, grab or dip net samples within each of these sampling occasions were pooled; both spring and autumn season are included; both epifaunal and infaunal samples are included – and pooled – for seagrass habitat). This analysis was performed using the* specaccum *function of the* vegan *package using the random method. To account for difference in total abundances in the different habitats, the x-axis, representing sampling effort, was rescaled by multiplying the number of sampling occasions by the average abundance per sampling occasion in each habitat.*

which may affect our capacity to quantify their overall richness. Maerl beds on the other hand, are highly speciose and may also show important variation of composition in time (Chapter 3), which may explain the absence of conspicuous saturation in the accumulation curve of this habitat. The latter highlights the tremendous richness of maerl beds compared to other habitats and further support the need for protecting this habitat in the region (Grall & Hall-Spencer, 2003).

Overall, these data tend to confirm that Brittany is a hotspot for benthic diversity (Gallon et al. 2017). Lying at the crossroads of two biogeographic zones (see Figure 4 of the Introduction) and comprising a mosaic of environments (Derrien-Courtel et al., 2013), Brittany is therefore of particular interest from a taxonomic point of view. These two factors have also played an important role in terms of the ecological understanding that the REBENT data have brought during this thesis (see below). Undeniably, the diversity of environmental settings encompassed by the REBENT monitoring program is a strength that should be highlighted.

b) Observing rare species to better understand their role and drivers?

The sampling efforts provided by the repeated surveys of multiple sites in time foster, in particular, the probability of observing rare species (Figure 2). In this respect, between 300 and 400 macrofaunal species not seen in Brittany since the 1950-1960's have been re-observed during the REBENT program (J. Grall, personal communications). Since the beginning of the REBENT in 2003, 371 species have been observed only once and 50% of the species were observed less than 7 times over the 855 sampling occasion[5]. Additionally, less than 27 specimens have been collected for 50% of the inventoried species.

Rare species, those found with either low abundance or occurrence in the samples (Gaston 1997)[6], often represent a high proportion of marine communities, especially in benthic systems (Gray et al., 2005; Snell Taylor et al., 2018). Transient species, *i.e.* species with low occurrence, typically account for 20 to 60% of the richness of benthic communities (Snell Taylor et al., 2018; Wlodarska-Kowalczuk et al., 2012). They were found in this thesis to make an important contribution to the diversity of the seagrass meadows of the region (Chapter 1 and 2). Apprehending the determinants of their rarity remains a central question from both a conservation and a theoretical perspective (Violle et al., 2017). However, evaluating the fraction of rare species that is attributable to detection errors (Iknayan et al., 2014) and apprehending whether there are general ecological laws that may explain rarity remain challenging (Sgarbi & Melo 2018). In this context, long-term monitoring may help ameliorate some

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[5] A sampling occasion is here defined as the sampling of one habitat in a given site for a given year and a given season (between the two seasons surveyed in the REBENT)

[6] Rarity comprises many facets and its definition may be highly variable among studies (Violle et al., 2017)

aspects of our understanding of rare species, from their underlying drivers to their potential interactions with other species and ecological roles (e.g. Benedetti-Cecchi et al., 2008; Hewitt et al., 2016). In this thesis for instance, rare species were shown to play different roles in the functional redundancy of communities between seagrass and maerl beds (Chapter 2). Although inherently difficult, the study and understanding of the occurrence, distribution and ecological role of rare species may benefit from broad-scale monitoring programs and the Perspectives section (section I.5.b) below offers some proposals for venturing in this direction.

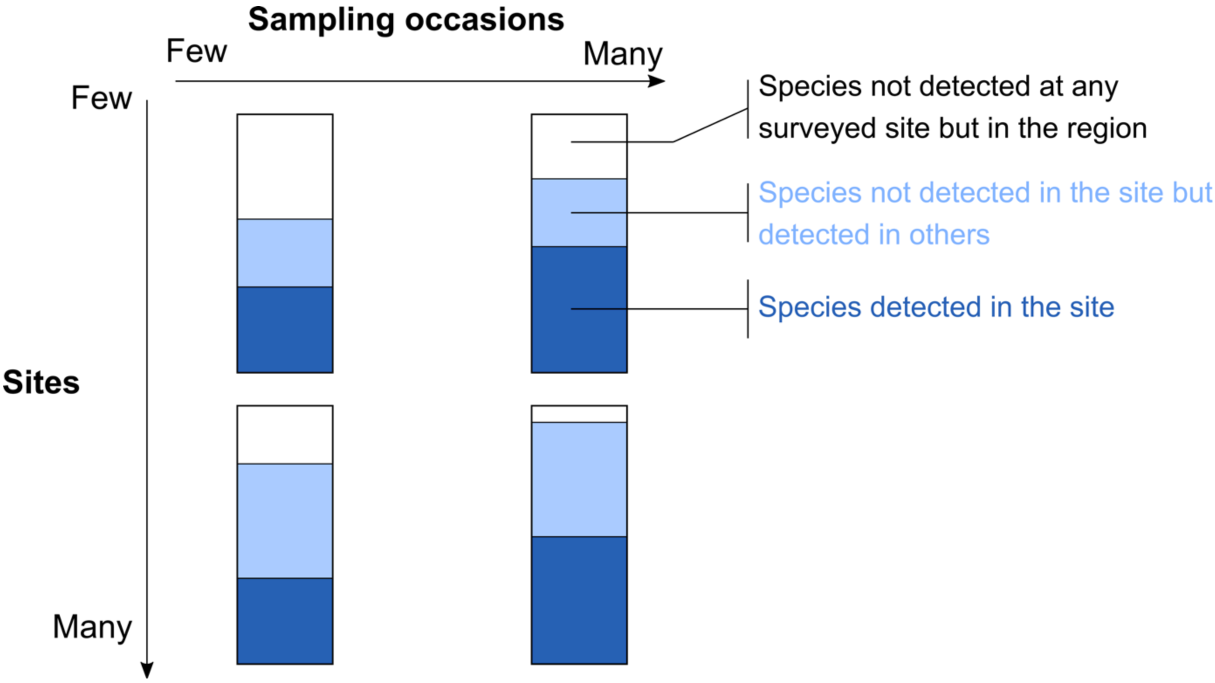


Figure 2. *The pool of species in a metacommunitiy that is represented in a site comprises species that have been detected in the site, those that have not yet been detected at the site but have been detected in other sites, and those that have not yet been detected at this or any site, but occur in the region. (Adapted from Iknayan et al., 2014)*

2. Apprehending community dynamics in space and time

a) Regulation of community size and limits of an α-diversity perspective

Precisely estimating the richness of a region, an habitat, or a site is a challenge on its own (Iknayan et al. 2014), and although this provides valuable information for conservation purposes, it is not sufficient to guide conservation policies. Indeed, protected areas should not only capture current diversity, but also ensure its maintenance in space and time in the face of potential future biodiversity changes (Chiarucci et al., 2011). This requires apprehending the temporal dynamic of biodiversity and the drivers underlying changes in community compositions. It is increasingly clear that measures of α diversity (the local diversity of communities; Whittaker, 1960) is not an appropriate currency for this purpose because important biodiversity changes may remain concealed when looking through the sole lens of species richness for example (Hillebrand et al., 2017; McGill et al., 2015). Indeed, examples of substantial community changes that were accompanied by constant or inconsistent variation of community richness have blossomed over recent years (Dornelas et al., 2014; Magurran et al., 2015, 2018).

From an ecological perspective, there is increasing evidence that in the absence of major environmental perturbations, the total richness and abundance of communities are generally regulated over time (Gotelli et al. 2017). In agreement, Chapter 3 showed that the temporal β diversity of benthic communities was generally dominated by species replacement with variation of the total richness of communities only contributing to around 25% of the temporal variability of communities on average. The extent of such regulation may be variable and was found, for example, to be affected by the presence of maerl beds. This highlights that ecological processes, such as the facilitation provided by foundation species, may affect the regulation of community size in terms of both richness and abundance. However, the high contribution of species replacement to the temporal β diversity of these benthic communities was consistent across habitats. Additionally, it was also found to dominate the spatial β diversity of seagrass communities in Chapter 1. Such a high contribution of species replacement to the spatial β diversity of communities was also retrieved from other benthic systems (e.g. Victorero et al., 2018) and seems to be a general feature in many aquatic and terrestrial ecosystems (Soininen et al., 2018). Although the extent to which β diversity is driven by species replacement varies according to the environment, scales of study and type of organisms (Soininen et al., 2018), it is intriguing to see such constancy even in highly variable environments such as the intertidal (see Chapter 3). Gotelli et al. (2017) found in particular that the total abundance of communities, but not the richness, was more regulated in marine environments than in terrestrial ecosystems. In this work however, there was no conspicuous regulation of abundances in intertidal, while in the subtidal only maerl beds displayed some level of abundance regulation (Chapter 3).

Regulation of community size in terms of both abundance and richness, as well as their potential underlying ecological processes, remain to be more fully apprehended in a range of ecosystems. Nonetheless, the results above reinforce the notion that biodiversity measures that do not account for species identities and community structure may be relatively insensitive to biodiversity changes in the absence of major perturbation (Magurran & Henderson, 2010) and that fully apprehending the dynamics of communities and detecting potential early signs of biodiversity alterations requires addressing additional facets of biodiversity.

b) β diversity and the need to consider space and time together

The importance of accounting for the composition of communities and their spatial variation (spatial β diversity) for protecting biodiversity at broad spatial scales is now widely recognized (Bush et al., 2016; Socolar et al., 2016a). However, incorporation of spatial β diversity in conservation designs remains hampered by the important gaps remaining in our knowledge of species distribution and community variability (McGill et al., 2015; Socolar et al., 2016b; Whittaker et al., 2005). Because of these gaps, important efforts have been directed at using biodiversity surrogates that can be easily mapped, using satellite and aerial remote sensing for instance, and be used to predict biodiversity distribution through statistical models (Buhl-Mortensen et al., 2014; Edgar et al., 2016). In benthic systems for example, mapping the distribution of biogenic habitats has been an important component of conservation planning but the efficiency of these habitat classification schemes in adequately reflecting biodiversity spatial structures has proved to be highly variable (Shokri & Gladstone 2013).

The main underlying rationale behind the mapping of benthic habitats for biodiversity conservation is that within-habitat variability should not affect the appreciation of diversity at broad spatial scale (Fraschetti et al., 2008). Chapter 1 showed that important variation in space and time can exist within biogenic habitats (here seagrass) at a regional scale. In particular, epifaunal and endofaunal communities associated to these seagrass meadows did not exhibit similar spatial and temporal variation, which highlights the difficulty to find appropriate proxies for the whole diversity of these habitats. Chapter 3 presented these variations in a multi-habitat context for the endofaunal compartment and showed that while among-habitat β diversity was indeed higher than within-habitat variations (a necessary conditions for their use as biodiversity surrogates), the extent of among-habitat variation was highly variable across locations. Overall, the three chapters of this thesis have highlighted in different ways that the effect of foundation species on their associated communities was variable in space and time. Therefore, the effects of biogenic habitats cannot be apprehended based on their spatial extent or density alone (Crotty et al. 2018) and broad-scale monitoring data are pivotal to inform on their associated β diversity and guide conservation actions.

In particular, broad-scale monitoring data are needed to apprehend the temporal variability of community spatial structures. Such a joint consideration of space and time is essential because the variability of communities in these two dimensions is intricately related (Collins et al. 2018). Indeed, biodiversity is governed at multiple scales (Levin 2000) so that the composition of a community and its variability result from the integrated effects of both local (e.g. biotic interactions, local environmental conditions) and broad-scale factors (e.g. climatic constraints, dispersal; Leibold & Chase, 2017). The response of communities to environmental changes may be magnified or dampened depending on their composition and structure, the local context, and how global and local drivers interact (Brook et al., 2008). This means that communities in different locations may react differently to the same broad-scale drivers (Starko et al. 2018). Apprehending whether communities exhibit similar temporal dynamics across space is a key indicator of the scales at which they are governed and is essential to guide conservation actions towards allocating efforts on broad scale measures or on site-specific actions (see Chapter 1 for example). For this purpose, broad-scale monitoring data can provide a picture of which changes are local or specific to a few locations and which reflect more general and widespread changes (Verheyen et al. 2017). Additionally, understanding how the spatial β diversity of communities varies in time provides critical information on the stability of the ecosystem (see Chapter 2; Wang & Loreau, 2014) and is increasingly recognized as a key early-warning indicator for potential regime shifts (Fisher et al. 2015, Collins et al. 2018).

c) Statistical challenges associated to missing data and latest developments to overcome these limitations

Apprehending how the spatial structure of biodiversity varies in time (space-time interaction) requires repeated surveys with consistent methodological approach, which can be logistically and financially demanding over broad spatial extent, especially in the marine realm. As a result, most of the existing broad scale data on benthic community variations are from “snap shot” surveys (Boström et al., 2011) whereas, conversely, long-term series are often restricted in their spatial extent (Buckley et al. 2018). However, although examples remain scarce in benthic systems (Zajac et al., 2013), studies jointly considering space and time over various spatial and temporal extent are nonetheless increasingly emerging in terrestrial and aquatic ecosystems (Collins et al. 2018). Statistical tools to characterize and quantify β diversity in both space and time are also becoming increasingly available. Although these methods have been reviewed elsewhere (Buckley et al., 2018; D’Amen et al., 2017; Legendre & Gauthier, 2014), it seems important here to address one specific constraint associated with the exploitation of broad scale monitoring data and largely eluded in existing reviews: the ubiquity of missing data. Indeed, while the problem linked to the usual lack of replicates in long-term monitoring series, and originally preventing the test for the existence of a space-time interaction, has been elegantly solved (Legendre et al., 2010), long term series remain plagued by missing observations. This can result in highly unbalanced sampling designs, which prevent the use of many of the approaches classicaly used to test for space-time interaction in community data.

Surprisingly, despite the inherent difficulty of sustaining complete monitoring across multiple sites and over long time period, especially in environments with limited accessibility such as benthic systems (McArthur et al. 2010), the challenges posed by missing data are rarely evoked when addressing the sampling issues existing in the context of biodiversity monitoring (Magurran et al., 2010; Yoccoz et al., 2001). This thesis has highlighted different possible strategies for coping with unbalanced datasets and missing observations. A first option is to discard whole years or sites with missing observations to retrieve balanced datasets. This approach was adopted in Chapter 1 and 2 and allows for the use of the latest developed approaches to quantify and characterize space-time interaction (Legendre et al. 2010, Legendre & Gauthier 2014, Legendre 2018). However, given the cost of acquiring long-term data over broad spatial extent, this solution may seem sub-optimal.

Recent developments in the form of LCdBD (Local Contributions to dynamic Beta Diversity; see Chapter 3) and measures of distances among community trajectories using *directed segment path dissimilarity* (D_{DSP}; De Cáceres et al., submitted), allow for accommodating for missing observations. Indeed, measures of trajectory distances among communities were here found to be robust to missing observations in a small simulation study presented in Figure 3. Although not explicitly tested and quantified, the notion of a space-time interaction is implicit in this approach as it addresses the extent to which communities have exhibited distinct variation in time compared to the regional mean. These techniques for trajectory analysis could therefore offer a way to deal with slightly unbalanced datasets and provide new perspectives for the analysis of monitoring data. For instance, measures of D_{DSP} could potentially be used to apprehend the drivers governing to what extent different communities exhibit similar or different temporal trajectories (see the perspectives in section I.5.b).

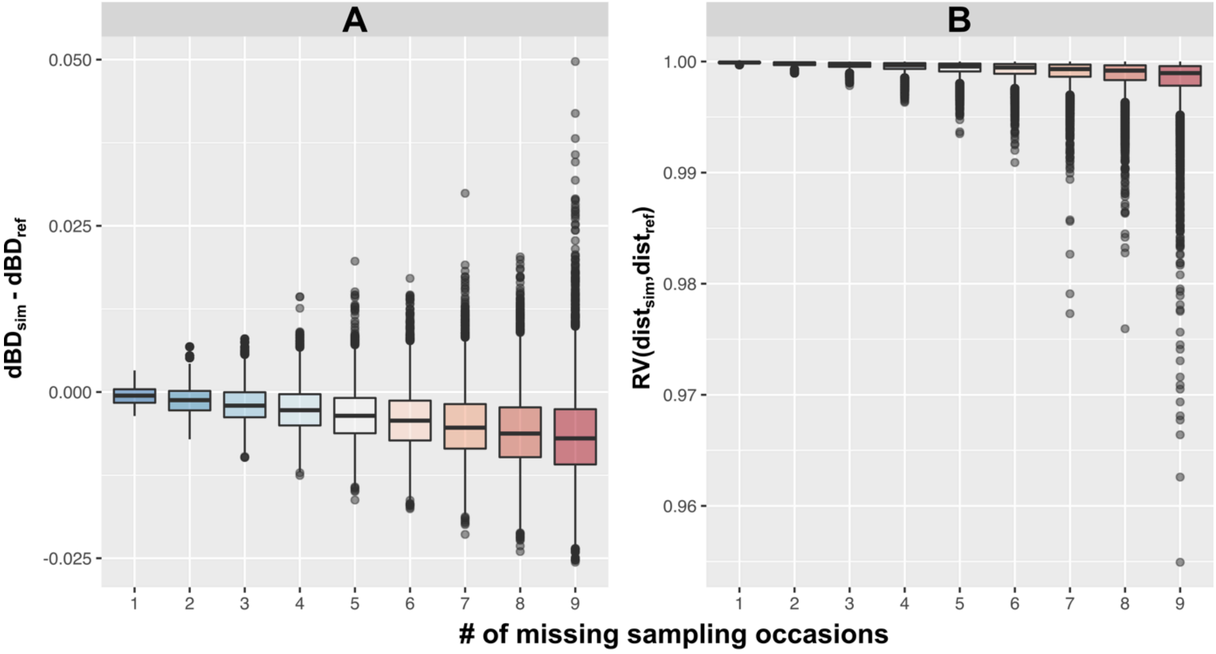


Figure 3. *Assessment of the impact of missing sampling occasions and unbalanced sampling on the estimations of trajectory distances. The simulation was performed using the complete and balanced data set collected in spring for the endofauna of three seagrass meadows and for which all core samples were available from 2006 to 2015. The nine sediment cores sampled at each site for each year were aggregated to estimate abundances at the site level. One such set of 9 cores therefore represents a sampling occasion. To simulate unbalanced datasets, we randomly removed between 1 and 9 sampling occasions across the three sites (over 30 possible). 10,000 simulations were performed for each number of sampling occasions removed and at least 2 sampling occasions were kept for each site to calculate the trajectory distances (see Chapter 3 for calculation method of trajectory distances).* ***A.*** *The analysis was based on centered trajectories. The estimation of the trajectory distances among sites was based on the total dynamic Beta Diversity (dBD), which represents the total variance of the trajectory among the 3 sites. Simulated values were compared to the reference value computed on the complete dataset (without missing sampling occasions) by subtracting the reference value* (dBD_{ref}) *from simulated dBD* (dBD_{sim})*. Positive values indicate that total dynamic Beta Diversity was overestimated with the incomplete dataset and conversely, negative values indicate an underestimation with the incomplete dataset.* dBD_{ref} *was equal to 0.166 so that a value equal to 0.05 represents an overestimation of around 30% while values around -0.025 represent an underestimation of around 15%.* ***B.*** *RV coefficients were also used to assess the conformity between simulated and reference trajectory distances. RV coefficients were computed based on Principal Coordinates Analyses (PCoA) of the simulated and reference trajectory distances using the two first axes of the PCoA. RV values were all greater then 0.96 indicating that simulated distances with unbalanced datasets closely matched with reference ones, even with potentially highly unbalanced datasets (30% of missing observations with 9 sampling occasions removed over the 30 available ones).*

Information provided by LCdBD may also help allocating monitoring efforts towards sites representative of the regional trend or on the contrary towards sites with unusual dynamics. This may allow, once the trajectories of communities have been apprehended over a certain duration, to alleviate the need to monitor all sites across all time periods. For instance, among the sites exhibiting similar trajectories, some could be only monitored every two or three years instead of yearly, while reference/sentinel sites would continue to be monitored yearly to inform on finer scale dynamics (Hewitt & Thrush, 2007). Efforts could even be re-allocated to increase time replication in sentinel sites or in those with unusual dynamics while alleviating the efforts in other sites. Note however, that while this would allow for adequately monitoring biodiversity trends at the regional scale, it may, as stated above, represent a challenge for statistical analysis if the purpose of the monitoring is to model and understand the spatial and temporal β diversity of communities.

3. The "ecology of the long"

As exemplified in Chapter 3, LCdBD have great potential to yield substantial ecological insights in the future, especially if applied over long time series and across multiple sites. For instance, they revealed that despite their highly dynamic nature, intertidal communities preserved similar spatial structure across 9 years. Overall, results from Chapter 3 have uncovered the imprints of strong historical legacies in the contemporary structure of communities at regional scale for both intertidal and subtidal compartments. This highlights one of the key virtues of long-term time series. Indeed, only an "ecology of the long" (Peters 2010) can assess the rate and direction of changes and distinguish directional trends from short-term variability (Lindenmayer et al. 2012, Hawkins et al. 2017). Baselines against which evaluate the temporal variability of communities are highly dependent upon the observation windows (Figure 4) and Chapter 3 emphasized the need for long-term series to adequately define the envelop in which community variation may be defined as "normal". In this respect, with 15 years of data for the oldest series contained in the monitoring program, the REBENT has already fulfilled one of its initial

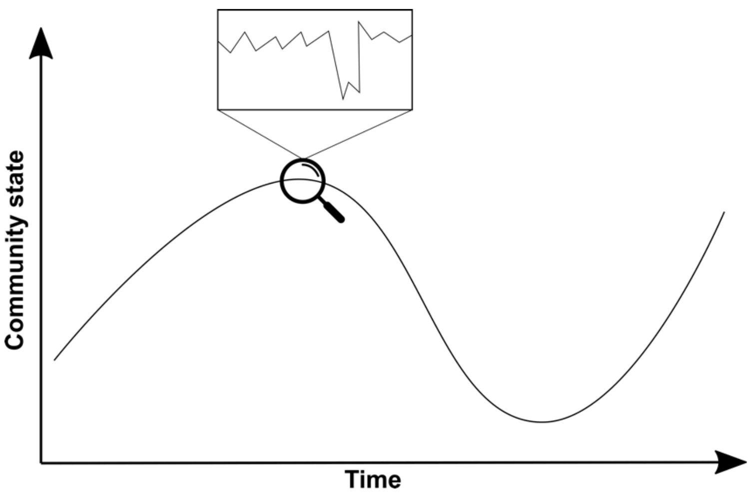
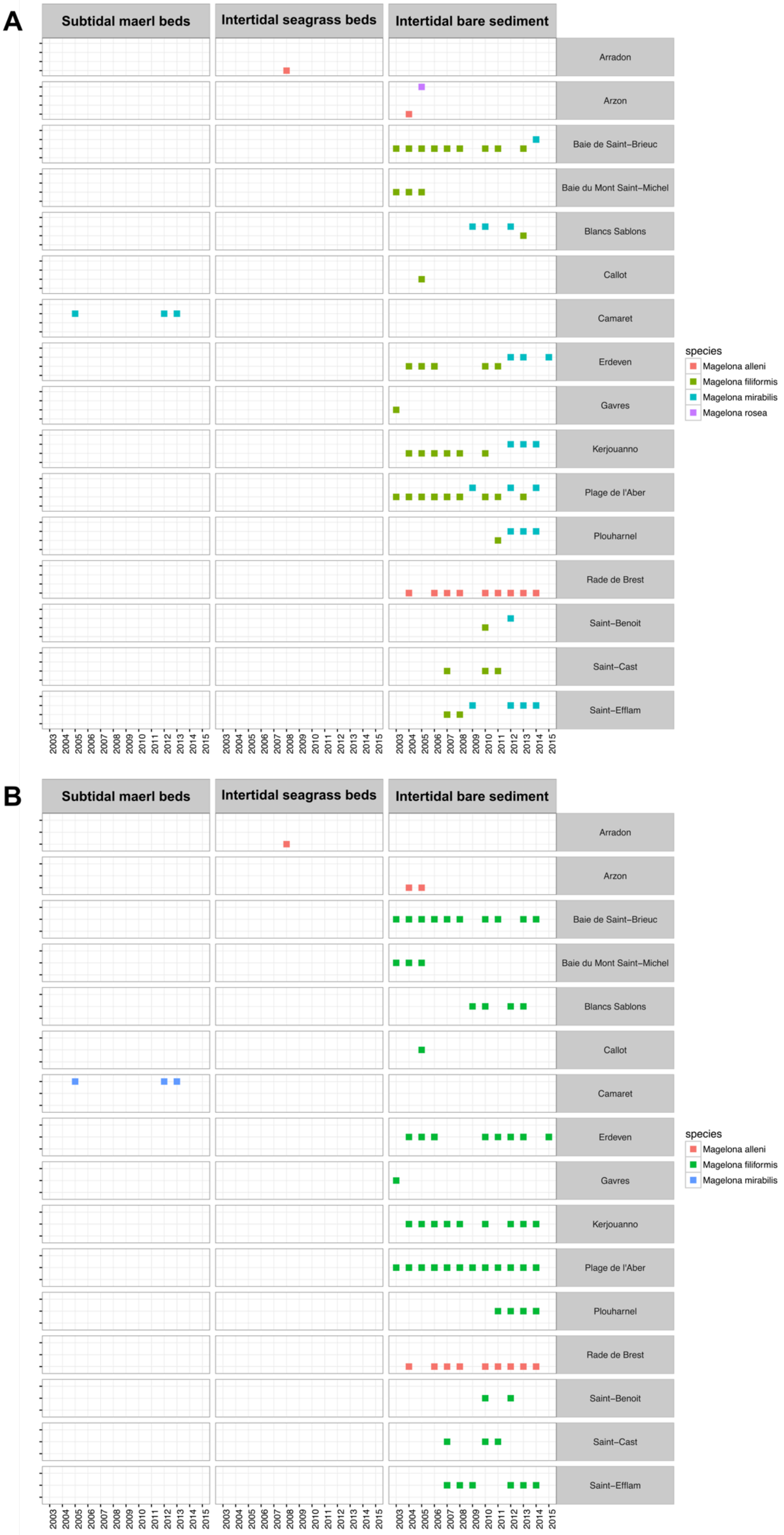


Figure 4. Influence of the time scale of observation in assessing the full extent of biodiversity change. Although one might observe an abrupt change at a given scale (e.g. months), knowing the long-term dynamic of the system is necessary for allowing a full evaluation of the extent of these changes.

objectives, which was to provide baseline data for the diversity of the Brittany region following the Erica oil spill (Bajjouk et al. 2015).

Another key challenge for the exploitation of long-term data that should be noted here is the potential inconsistencies of the data in time due to changes of taxonomic expertise during the monitoring, variation in the sampling protocol (Ellingsen et al., 2017; Magurran et al., 2010), or evolution in the taxonomic knowledge of the targeted taxa (Costello et al., 2018). The REBENT monitoring program has maintained consistent protocols since 2005, after an initial calibration phase. However, despite a constant scientific supervision of the monitoring programme by J. Grall, several field and laboratory personnel were involved in data acquisition over the years. Additionally, changes in the taxonomy of benthic species and training of the laboratory personnel through, for instance, inter-calibration exercises performed in the context of the RESOMAR network (http://resomar.cnrs.fr/Atelier-taxonomique-Benthos-2014) were found in this thesis to impact the taxonomic resolution of the data across the years. To deal with these inconsistencies, taxonomic experts were gathered to scrutinize the distribution of each taxon in space and time and homogenize the taxonomy of the database (Figure 5; see the Material and Methods section of Chapter 1 for details). This labour-intensive work based on expert's knowledge

Figure 5. *Illustration of the need for taxonomic homogenization on long-term time series. Presence of species belonging to the* Magelona *genus across all sites and habitats in which they were recorded. A. Distribution before homogenization. B. Distribution after taxonomic homogenization. A shift occurred in 2012 between* Magelona filiformis *and* Magelona mirabilis, *which coincided with changes in taxonomic expertise in the REBENT program. Homogenization removed this shift that could have contributed to temporal β otherwise. Homogenization thus allowed for controlling for a potential observer effect on our assessment of β diversity.*


A
Subtidal maerl beds
Intertidal seagrass beds
Intertidal bare sediment
Arradon
Arzon
Baie de Saint–Brieuc
Baie du Mont Saint–Michel
Blancs Sablons
Callot
Camaret
Erdeven
Gavres
Kerjouanno
Plage de l'Aber
Plouharnel
Rade de Brest
Saint–Benoit
Saint–Cast
Saint–Efflam
2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015
species
Magelona alleni
Magelona filiformis
Magelona mirabilis
Magelona rosea
B
Subtidal maerl beds
Intertidal seagrass beds
Intertidal bare sediment
Arradon
Arzon
Baie de Saint–Brieuc
Baie du Mont Saint–Michel
Blancs Sablons
Callot
Camaret
Erdeven
Gavres
Kerjouanno
Plage de l'Aber
Plouharnel
Rade de Brest
Saint–Benoit
Saint–Cast
Saint–Efflam
2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015
species
Magelona alleni
Magelona filiformis
Magelona mirabilis

should be compared to more automatic procedure for dealing with temporal inconsistencies in long-term series such as those proposed by Ellingsen et al. (2017), in order to assess the *cost-effectiveness* of this approach. Nonetheless, this work stresses out the critical importance of this step in the exploitation of broad scale monitoring data.

Irrespective of these methodological consideration, long-term data are critical to determine the effects of extreme events and time lags in responses (Peters 2010, Lindenmayer et al. 2012), document and apprehend "ecological surprises" (Cloern et al., 2016; Paine et al., 1998) and help unmask chronic and/or cumulative impacts before critical thresholds are reached (Kuussaari et al. 2009, Dunic et al. 2017). In particular, some changes in ecosystems are not perceptible when observed over short time scales and long-term perspectives are needed to reveal this "invisible present" (Magnuson 1990). Long-term monitoring series are essential tools to identify when communities may be approaching a tipping points at which a sudden shift to an alternate state may occur (Hewitt & Thrush, 2010; Scheffer & Carpenter, 2003). In this respect, Chapter 3 highlighted the potential of LCdBD in providing key information that may serve as early detection signs of on-going changes.

For instance, some communities displayed distinct trajectories from the regional mean trend, but did not exhibit particular differences in their modern community structure. This could be a consequence of any of the three following scenarios: 1) the communities of these sites are converging with those of the other sites of the region but were different at the beginning of the study, *i.e.* signs of potential on-going homogenization or return to a more normal state after a local perturbation; or on the contrary 2) the communities of these sites are diverging from those of the other sites of the region while they were similar at the beginning of the study; and lastly 3) the communities of these sites simply show unusual variability around their mean state. These three cases have different implications for the resilience of these communities and their response to future changes. Therefore, better understanding the distinct trajectories of these communities and their underlying drivers will be essential to assess their vulnerability and evaluate whether, and to what extent, these dynamics may lead to potential state changes, either gradual or potentially sudden. Nonetheless, this illustrates the potential of LCdBD in guiding research efforts towards sites with unusual dynamic that warrant further consideration.

4. Linking changes to their underlying drivers: the key challenge

One of the major challenges associated with the exploitation of broad scale monitoring data is to link observed variation of communities to their underlying drivers (Wagner & Fortin 2005). This thesis has adopted two different statistical modeling approaches to gain a mechanistic understanding of the broad scale β diversity structures observed. Indeed, both a species-based and taxonomic approach (Chapter 3) and a trait-based and functional approach (Chapter 2) have been used in this general context. These approaches reflect the two main streams existing nowadays in macroecology for understanding the drivers of community variation (Kraft et al. 2015, D'Amen et al. 2017) and the following sections discuss the challenges associated with each approach, emphasize the achievements of each chapter as well as propose ways to ameliorate the developed approaches.

a) Deciphering the role of abiotic and biotic drivers: statistical tools and necessary data

Long-term monitoring data are generally acknowledged to have a limited power to bring causative explanation to observed variations because of the correlative nature of the relationships they highlight, and because more than one process can create the same pattern (Peters 2010). Nonetheless, observational studies can often explore wider range of variation in ecological drivers under natural conditions than can typically be tested in field or lab experiments (Witman et al., 2015). As such, they can yield additional insights compared to more controlled or replicated measurements performed over a more limited range of conditions (Figure 6; Kreyling et al., 2018). In particular, broad-scale monitoring data, when spanning broad environmental gradients, increase the likelihood of driver orthogonality through the repeated surveys in time of multiple sites (Verheyen et al. 2017). In turn, this orthogonality of drivers may allow deciphering their relative importance through a range of statistical approaches.

i) The variance partitioning approach: achievements and potential limits

Although the purpose of Chapter 3 was not to untangle the relative influence of different environmental drivers, the variance partitioning approach used in this work may serve this purpose. For instance, it can be used to disentangle the role of anthropogenic from natural abiotic and biotic drivers (Serna-Chavez et al., 2018). Here, it was used to assess the overall role of abiotic constraints in comparison to biotic and stochastic drivers, which has been one of the major utilization of variance partitioning over recent years (Cottenie 2005, Soininen 2014). Through this approach, abiotic filtering generally emerges as an important factor governing the spatial variation of communities (Cottenie 2005) but its extent is variable among organisms and environments and, generally, an important part of community variation is left unexplained (Soininen 2014), as observed in this work.

Soininen (2014) found that the variation explained by abiotic variables was in general higher in marine environments than in terrestrial and freshwater ones, although data for benthic systems still remained scarce. Ysebaert & Herman (2002) found that environmental variables accounted for 30% of the spatial and temporal variation of bare sediment communities at a landscape-scale over 6 years, 27% of this signal being spatially structured. These results are in line with the estimates found in the present work. However, Yamada et al. (2014) found that the predictability of community variation with abiotic variables differed among functional groups in seagrass, explaining from around 10% for the sessile endofauna to around 40% for sessile epifauna. These results confirm the conclusions made from Chapter 1 that epifaunal and endofaunal communities would respond differently to abiotic conditions within seagrass meadows. They also highlight the need to reiterate the approach led in Chapter 3 across different spatial and temporal scales to gain a better understanding of the role of abiotic constraints on benthic communities.

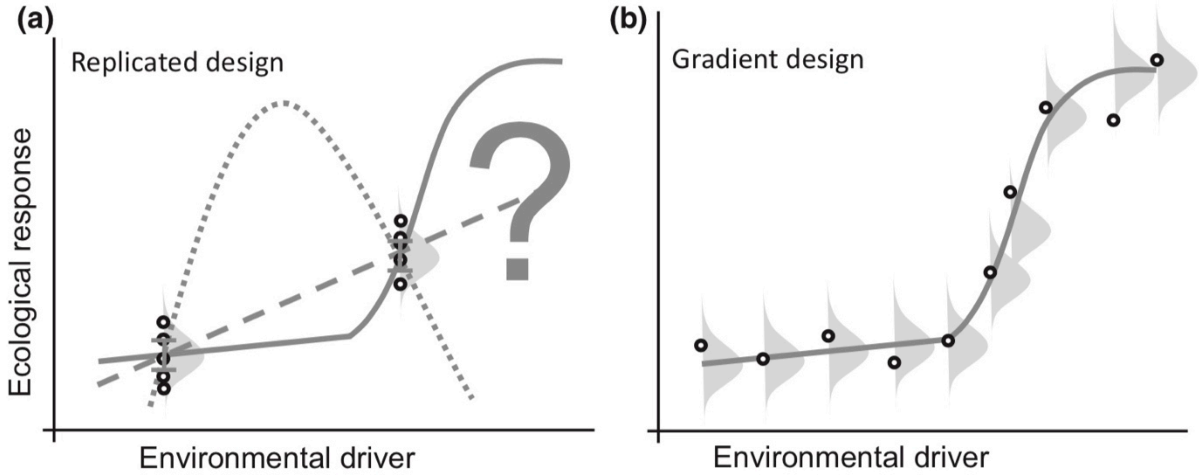


Figure 6. ***A.*** *Replicated experiments offer high confidence and precision in the estimates of the local response of communities through high replication but offer such a precision vision for a limited number of conditions only.* ***B.*** *Gradient studies on the other hand, offer lower precision for the estimates of the effects of each condition due to the absence of replication, but offer estimates across a wider range of conditions. As such they may be better suited for characterizing non-linear responses for instance (from Kreyling et al., 2018).*

ii) Retrieving environmental data: a potential challenge for coastal research

The first essential step in this approach is to retrieve adequate environmental data. Although this may seem trivial, the availability of accurate environmental data can be extremely limiting in some environments. In the context of broad scale monitoring such as the REBENT, it is not possible to directly measure *in situ* all relevant variables to model community dynamics due to logistical constraints. Therefore, there is often a need to retrieve *a posteriori* data matching with the temporal and spatial extent of the monitoring data. Open-access databases allowing for retrieving historical environmental data over broad spatial extent are increasingly available. For the marine environment for instance, the National Oceanic and Atmospheric Administration NOAA (https://www.noaa.gov), the European Copernicus program (http://copernicus.eu), and the Bio-ORACLE database (Tyberghein et al., 2012) provide important resources for this purpose. However, these data often have low resolution (between 10 to 50 km^2) which limits their use in coastal ecosystems at regional or finer spatial scales because of missing data or poor estimations resulting from edge effects of the models at the sea-land interface (Doney 1999). Additionaly, while data for the surficial layers of the ocean are often more readily available, they do not represent the proximate environment of benthic species so that environmental variables near the seafloor and ideally reflecting limiting factors causally linked to the species of interest should be preferred for the modelling of benthic species (Reiss et al., 2011).

In this work, we benefited from the availability of a hydrological model (MARS3D; PREVIMER) developed specifically for the region under study and providing high-resolution data (2.5 km grain) across several depth levels. Despite this resolution, we had to deal with missing data and edge effects for intertidal sites by adapting the coordinates of extraction points (see Supplementary material of Chapter 3). Using data from existing long-term environmental monitoring programs in the region and instrumenting some of the monitored sites allowed us to calibrate the hydrological model output to obtain accurate environmental data near the seafloor, even for sites such as Arradon located in a spatially complex inner bay for which appropriate model data are generally hard to retrieve (Figure 7). This shows 1) the value and the need for regionally built models with high resolution in transition zones such as coastal ecosystems; and 2) the need to couple biodiversity and environmental monitoring. This point can be achieved by instrumenting the monitored sites. *In situ* sensors and autonomous devices have been increasingly developed recently for monitoring the marine environment but their cost, operational lifetimes and their *in situ* reliability in harsh environments such as intertidal areas may hamper their generalization across multiple sites in monitoring programs such as the REBENT (Mills & Fones 2012).

In this context, building gateways between existing programs monitoring different aspect of environmental and biodiversity changes in a same region is essential (Muller-Karger et al. 2018). To date, long-term environmental monitoring programs have been more developed than biological ones, especially in Europe (Benedetti-Cecchi et al., 2018). As such, the development of future biodiversity monitoring may aim to match with existing environmental monitoring structure to take advantage of existing environmental series. For instance, Chapter 3 has shown the capacity of meteorological data to predict community variation in intertidal communities because the tidal regime of the region exposes benthic organisms to aerial conditions (Finke et al., 2007). Therefore, in addition to the necessity of sharing data so that each program may fuel each other, there is also a need to coordinate monitoring efforts (Muller-Karger et al. 2018). This need is already recognized at the European scale through initiatives such as the Joint European Research Infrastructure network for Coastal Observatory (see http://www.jerico-ri.eu/).

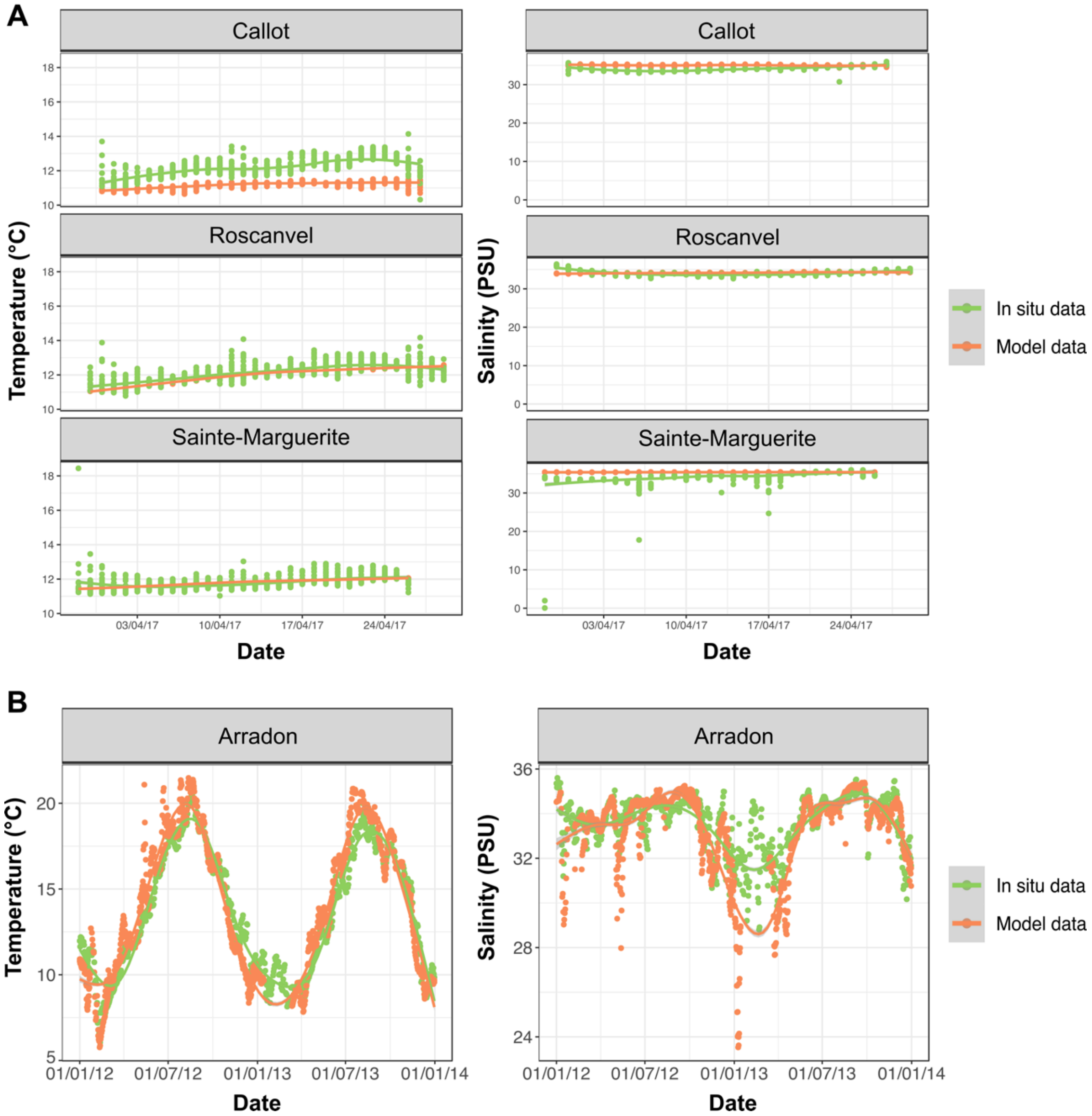


Figure 7. *Adequacy between the environmental data used in this thesis (retrieved from the MARS3D hydrological model provided by PREVIMER) and data measured in situ.* ***A.*** *Temperature and salinity probes were deployed in three intertidal seagrass sites for nearly a month in April 2017 and were used to calibrate the spatial coordinates for extracting data from the hydrological model (the meadows being intertidal, coordinates needed to be shifted to avoid edge effects).* ***B.*** *The seagrass meadow of Arradon lies in an inner bay and the accuracy of the hydrological model needed to tested and calibrated to avoid edge effects. This was done using environmental data provided by the RESCO - Réseau d'observations Conchylicoles* (Fleury et al. 2018).

iii) Ways forward for the statistical modelling of communities

An important question when environmental data have been retrieved is how to summarize them and under which form they should be incorporated in analyses such as variance partitioning. In this respect, Chapter 3 showed that while benthic communities had similar predictable variation across habitats, better accounting for extreme events was needed to more accurately account for the effect of abiotic conditions on these communities. Measures of how many times abiotic variables such as temperature exceeded a certain threshold (see Jurgens & Gaylord, 2017) could be a useful addition to the models of Chapter 3. These included mean, minimum, maximum or standard deviation of the variables over the months preceding each sampling occasion, but they to fully characterize the variability of intertidal environments for example. Including the frequency of extreme events could enhance the predictive power of these models but this first requires defining what an "extreme event" is for the benthic communities under studies, knowledge that is currently lacking. As a first approache, extreme events could be defined as values above or below 2 standard deviations from the mean for instance. Alternatively, *changepoint* analysis could be performed on the environmental time series to identify extreme events (Killick & Eckley 2014). In any case, characterizing not only the mean environmental conditions but also their variability is essential, as well as accounting for non-linear relationships through, for example, the use of polynomials (Chapter 3).

Recent advances in multivariate statistical analysis may also help refine estimates from Chapter 3 and achieve in the future a better understanding of the role of biotic interactions. For example, the role of biotic factors have often been related to the fraction of variance that was spatially or temporally structured but unrelated to abiotic variables in the variance partitioning approach (Cottenie 2005). Recent development now allow to better estimate this fraction using spatially-constrained null model (Clappe et al., 2018). It is now also possible to test for the significance of the shared fraction between spatial and abiotic variables (Bauman et al., 2018) as well as to decompose the relationship between communities and abiotic conditions across multiple spatial scales (Guénard & Legendre 2018).

In the specific context of this thesis aiming to evaluate the role of biogenic habitats on the diversity of benthic communities, it would also be important to disentangle the multiple direct and indirect effects through which alteration of biogenic habitats may affect communities (Liu et al. 2018). Effects of environmental changes mediated by species interaction may be more important than their direct effects for certain taxa (Ockendon et al. 2014). These mediations of environmental effects through the response of the foundation species has only been superficially addressed in Chapter 3 and could be more thoroughly explored through Structural Equation Modeling (SEM; Lefcheck, 2016; Shipley, 2009) using insights provided by this thesis to build and test models of hypothesized causal relationships (see example using trajectory distances in the Perspective section I.5.b)). As an example of application, Miller et al. (2018) showed using SEM that most of the effects of the giant kelp *Macrocystis pyrifera* on its associated communities were indirect and mainly mediated by alteration of light rather than food availability. Interestingly, while SEM have mostly been developed and applied in ecological studies on univariate data, limiting its use on community data to summary statistics such as species diversity or LCBD indices (Legendre & De Cáceres 2013), this approach could potentially be adapted to multivariate community data through the use of SEM in redundancy analysis framework (Lovaglio & Vittadini 2014).

Lastly, in order to better apprehend the role of biotic interactions in generating the observed diversity of benthic communities, one may go a step further from the exploration of the residual correlations among species performed in Chapter 3 by incorporating latent correlations among species through Latent Variable Models (LVM; Letten et al., 2015; Warton et al., 2015), or by using Hierarchical Modelling of Species Communities (HMSC; Ovaskainen et al., 2017). Due to computational limitations, these tools were previously limited to communities with a small number of taxa (Warton et al. 2015). However, new advances now allow these approaches to be applied to richer communities (Ovaskainen et al. 2017). These methods apprehend species interaction through their co-occurrences. Species that co-occur more or less than expected by chance have positive or negative associations. Analysis of such species association networks has, for instance, highlighted different effects of biotic homogenization of plant communities than when viewed through the lens of species composition (Li et al., 2018). It could therefore be an appropriate extension to the methods used in this study to better characterize the potential effects of seafloor alteration and benthic homogenization. As shown in rocky intertidal communities, species co-occurences may in some instances fail to fully reflect species interactions but these approaches nonetheless provide important additional insights into community assembly (Freilich et al., 2018). Therefore, it would be interesting to test these approaches in seagrass meadows for which Chapter 2 suggested an important role of mass effects (hence, an absence of strong species interactions) in comparison to maerl beds where niche based processes where hypothesized to be stronger. In particular, additional insights may arise from an analysis such as HMSC as it allows including trait data in the analysis of how species responses to environmental gradients co-vary and of their residual correlations.

b) Trait-based approach to bridge ecological knowledge across scales

Chapter 2 showed that complementing broad-scale monitoring data on species abundances with information on their biological traits can yield a better mechanistic understanding of community variation. In particular, the variance partitioning approach of Chapter 3 did not outline major differences between seagrass and intertidal bare sediment and could not explain the intriguing β diversity patterns observed within seagrass in Chapter 1, nor the different temporal variation observed between seagrass and intertidal bare sediment in Chapter 3. Conversely, the trait-based approach led in Chapter 2 allowed to formulate hypotheses regarding the mechanisms governing the diversity of each habitat and revealed key differences between biogenic and bare habitats. As such, Chapter 2 exemplifies the capacity of trait-based approaches to upscale insights derived from theory and fine-scale experiments to the mechanisms governing communities on broader spatial and temporal scales, thereby allowing to better apprehend the drivers of biodiversity at scales relevant for its conservation (Hirt et al., 2018; Violle et al., 2014).

i) Trait-based approach: a new perspective on old data for better apprehending the resilience and functioning of communities

As highlighted in Chapter 2, generating trait distributions at the community level by combining species spatial and temporal distributions to trait data available from the literature and from databases can provide essential information on the resilience of communities by bringing a better understanding of the mechanisms governing species coexistence and their variability across space and time (Kuczynski & Grenouillet, 2018; Violle et al., 2014). In turn, this enhances our predictive abilities regarding the potential responses of communities in the face of future environmental changes (Cadotte et al., 2015). In particular, this approach is appealing for the retrospective analysis of historical data and allows for instance to gain insights into how the relative importance of abiotic and biotic drivers may have changed over the past decades, even in the absence of environmental data (e.g. Kuczynski & Grenouillet, 2018). It therefore provides an interesting window into the mechanisms through which global changes have affected communities over recent decades (Abonyi et al., 2018; Floury et al., 2018). Notably, trait-based approaches allow for addressing two key mechanisms in the functioning and conservation of ecosystems at broad scale in the face of environmental changes, which are: 1) the functional complementarity of communities; and, 2) functional compensations among species allowing for the maintenance of ecological functions despite variation of species (Chapter 2; Burley et al., 2016).

ii) Trait-based approach and monitoring data: a happy marriage?

One of the major assets of this approach for broad-scale monitoring is that traits provide a "*common currency across biological organizational levels and taxonomic groups*" (Violle et al., 2014), and therefore open-up novel comparative possibilities to outline general ecological rules across different ecological systems and over broad spatial extent (Webb, 2012). This was highlighted in Chapter 2 in maerl beds for example, with different beds harboring different communities across the region while exhibiting similar functional composition and structure. This finding echoes results from studies performed across different biogeographic regions in reef, mangrove and seagrass systems and showing the maintenance of similar functional structure of fish and benthic macrofauna across geographically and taxonomically distant communities (Barnes & Hendy, 2015; Hemingson & Bellwood, 2017). Therefore, while taxonomy may primarily reflect biogeographic and evolutionary history at broad spatial scales, trait-based approaches transcend taxonomy and may better reflect ecological constraints (Bremner et al., 2003). Such robustness across biogeographically distinct regions provides an important scope for using traits as a standardized tool to monitor and understand biodiversity changes at global scale (Jackson et al., 2016), provided the development of a sound ecological understanding of species traits and of their responses to environmental changes. As a result, species traits are increasingly heralded as an essential component to monitor, an *essential biodiversity variable* (Pereira et al. 2013), for reporting global biodiversity changes and provide better guidance to conservation policies (Pereira et al. 2013, Kissling et al. 2018). However, the incorporation of trait-based approaches at broad spatial and temporal scales as well as their potential operationalization in monitoring programs is hampered by major challenges (Kissling et al., 2018; Violle et al., 2014).

iii) Trait-based approaches at broad scales: challenges ahead

(I) Accounting for within-species variability

The scales at which direct measurements of traits are possible are inherently limited, except perhaps for some specific taxa and traits such as organismal size (Kiørboe et al., 2018). As a result, most broad-scale endeavors based on biological traits use the approach developed in Chapter 2, which consists in generating trait distribution *a posteriori* from species distributions and available knowledge on their traits (Degen et al. 2018, Kiørboe et al. 2018). However, it has been shown in terrestrial plants that the accuracy of trait values retrieved from databases was variable and that their use may lead to different results than *in situ* measurements (Cordlandwehr et al. 2013). A major caveat of this approach is that it only provides crude estimates of within-species variability that may yet play an important role in the functioning and dynamics of ecosystems (Bolnick et al., 2011; Raffard et al., 2018).

As a practical example of this, measuring seafloor ecosystem functions, such as productivity, or nutrient fluxes, is inherently difficult at broad scale (Snelgrove et al., 2014). Reconstructing community trait composition using species distribution and trait databases allows better predict macrofaunal secondary production than a species-centric approach (Bolam & Eggleton 2014). However, within-species phenotypic variability is known to be substantial in benthic communities (Riera 2009, Sanford & Kelly 2011). For instance, bioturbation activity of benthic species can be population dependent (Wohlgemuth et al., 2017), and their activity may be altered following environmental stress (Murray et al., 2017). This may alter nutrient fluxes and production in ways that trait composition reconstructed *a posteriori* can hardly predict (Godbold et al., 2011). Comparison of this *a posteriori* approach to *in situ* measurements across several scales and environments, as performed in terrestrial ecosystem (Cordlandwehr et al. 2013), will be an important step to estimate the accuracy of the current *modus operandi*. Apprehending within-species plasticity is key for better understanding species coexistence (Turcotte & Levine 2016) as well as their vulnerability to environmental changes (Forsman & Wennersten 2016). Notably, understanding its drivers and consequences is a major argument in favor of a trait-based perspective instead of species-centric approaches (Violle et al., 2012). Its incorporation within broad-scale approaches is inherently challenging and overall, the estimation error made by *a posteriori* reconstructions of community trait composition is potentially less problematic at broad scale than when studying ecological processes at fine spatial and temporal scale (Albert et al., 2011; Cordlandwehr et al., 2013). However, these caveats should be beared in mind when interpreting broad-scale trait distributions. This section aims to stress out the need to carefully consider when and how intraspecific variability should be incorporated in trait-based approach, beyond terrestrial systems (Albert et al. 2011). This should be an important area of development for trait-based approach in particular in benthic systems in years to come.

(2) Achieving better taxonomic and geographic coverage of trait information through collaborations

Shortfalls in the knowledge of many benthic taxa (Troudet et al., 2017) restrict the availability of trait data, which remain a limiting factor for the integration of trait-based approaches in macroecology (Tyler et al. 2012). Although the marine biodiversity of the study area for this thesis is among the most documented in the world (Costello et al., 2010), these limits were conspicuous throughout the present work. For this reason and given the extensive work required for collating trait data for many species, Chapter 2 was restricted to polychaete species for which abundant resources are available (Faulwetter et al., 2014; Giangrande, 1997; Jumars et al., 2015). Polychaetes often represent an important fraction of benthic community diversity, abundance and biomass (Hutchings 1998). For instance, in this work they represented on average 45% of the total abundance of the communities and contributed up to 91% in some communities. Additionally, polychaetes are highly diverse in their ecological strategies, which make them better indicators of the functioning of the communities compared to other groups such as sponges for example. While such a taxonomic focus has rarely been used in benthic trait-based studies since these approaches were introduced in marine ecology (Beauchard et al., 2017; Bremner et al., 2003), trait-based studies in other systems are predominantly higher level taxa-specific This state of affairs is largely attributable to the difficulty of findings traits appropriate to describe species niches across highly different taxonomic groups (Salguero-Gómez, Violle et al., 2018). However, other taxonomic groups may respond differently than polychaetes (Dauvin et al., 2016) and an obvious follow-up to this work would be to assess to what extent the conclusions of Chapter 2 hold when the trait-based approach is used on the complete community or other high level taxonomic groups.

Ensuring the robustness of statistical analysis to trait data representativeness (Borgy et al. 2017) and assessing possible ways of dealing with missing data have recently been important areas of development in trait-based ecology (Kim et al., 2018; Pakeman, 2014). Nonetheless, achieving a better taxonomic and geographic coverage will be essential to provide more accurate estimations of functional diversity and to better account for key facets of biodiversity such as functional rarity (Mouillot et al., 2014; Violle et al., 2017). Collating trait data is extremely labour intensive and collective efforts and data sharing will be pivotal to achieve a better taxonomic and geographic coverage of trait information, and thereby fully harness the potential of trait-based approach for monitoring and understanding community responses to environmental changes (Kissling et al. 2018).

In this perspective, the traits selected in Chapter 2 are the result of a consensus between the participants of the workshop on functional traits organized in Brest in April 2017 with the aim of coordinating the collection of traits between the different French research institutes working along the Atlantic coast and in the English Channel. Such collective endeavors are be essential to collate data for the many species identified in the REBENT database (see section I.1.a) and should not only be based on harnessing existing databases but also on measuring *in situ* the traits expressed by the local populations of the region. Only through such collaborative work at broad scale can we hope to unleash the full potential of trait-based approaches.

(3) Incorporation of trait-based approach in monitoring programs

Monitoring traits at the community level is far from being a simple task – drawing towards impracticability – and how trait information can be incorporated in monitoring programs deserves careful consideration, especially in marine benthic environments (Kissling et al. 2018). Monitored sites could be priority for gathering *in situ* trait data and for conducting experimental or fine-scale observational trait-based approach. The monitoring of trait variation of selected species should also be considered. This is currently done in the context of the REBENT for the foundation species *Zostera marina*, but should also be applied to some macrofaunal species. For example, species with potential key roles in the ecosystem due to their bioturbation activities or high abundance/biomass could be targeted in a first evaluation of this approach. Monitoring the traits of newly detected non-indigenous species is also worth considering (Cardeccia et al. 2018). The perspective section offers some proposals regarding rare species in this general context.

Overall, the study of species traits provides a common ground across diverse disciplines and therefore offers an opportunity to achieve an exciting but extremely challenging synthesis of knowledge spanning physiology, population biology, evolutionary biology, community ecology and ecosystem ecology (Enquist et al. 2015). As such, trait-based approaches provide a key framework to bridge ecological theory and empirical knowledge across spatial and temporal scales (Webb et al., 2010) and integrate experimental knowledge to broad scale data (Hirt et al. 2018), such as those provided by monitoring program. This may greatly contribute to achieve mechanistic insight across scales that are relevant to those at which human societies impact, manage and benefit from nature (Isbell et al. 2017).

5. Conclusions and perspectives

a) *Broad-scale monitoring as research platforms for upscaling ecological knowledge to scales relevant for conservation*

Achieving a better understanding of the functioning of natural ecosystems requires *in situ* observations and experiments to confront results and hypotheses obtained from "*model systems*" to the complexity, heterogeneity and variability of the "*real world*" (Snelgrove et al., 2014). However, the spatial and temporal domain of empirical observations remain, to date, largely restricted, providing only a limited window into the multiple scales at which natural ecosystems are governed (Estes et al. 2018). In marine benthic ecosystems in particular, *in situ* observational studies or manipulative experiments suffer from strong logistical constraints, which limit their spatial and temporal replicability and the extent over which they can be implemented (Jenkins & Uyà, 2016; Witman, et al. 2015). For instance, Witman and collaborators (2015) found that among 311 *in situ* experiments performed in rocky and biogenic habitats between 1961 and 2014, 65.3 % were conducted within one location only. Similarly, across 352 studies adressing the response and recovery of benthic communities after experimentally induced or natural disturbance, Jenkins and Uyà (2016) found that only 12 % lasted more than 3 years, the median duration being 10 months. These two benthic examples illustrate that the scales of current ecological understanding is not in adequacy with the broad scales at which society manages and benefits from nature (Isbell et al., 2017; Snelgrove et al., 2014). This mismatch is likely one of the most important factor impeding the successful transitioning of current ecological knowledge into applied solutions for the management of ecosystems (Cadotte et al., 2017).

Broad-scale monitoring programs provide an intermediate perspective between the tools used to guide conservation and those able to provide a mechanistic understanding of biodiversity and ecosystem functioning (Figure 8). This chapter has shown through examples from this thesis the potential of broad sale monitoring to upscale knowledge at relevant scale for conservation and bridge process and pattern studies. Different approaches can be used for this purpose, each being associated with specific strengths and challenges. In particular, broad-scale monitoring only provides a window into the effects of currently observable conditions (Isbell et al.

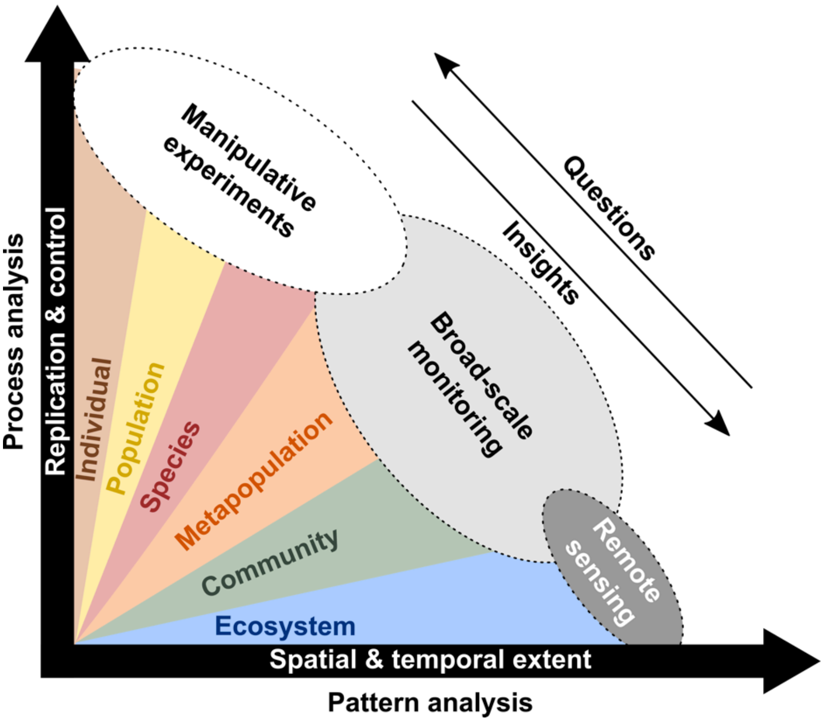


Figure 8. *The scaling of data collection in ecology along two key constraints: the degree of control and the scale of the studies. These two axes trade off and allow addressing either ecological processes, thereby providing mechanistic insights into the functioning of ecosystems and the drivers of species and communities for a limited number of controlled conditions, or patterns, thereby providing insights into the natural variability of species, communities and ecosystems while embracing their full complexity. Process studies (e.g. manipulative experiments) fuel the interpretation of observations made at broader scale while observations made in natural ecosystems give rise to hypotheses, which can then be explored by process studies. This cycle is needed to apprehend biodiversity across space and time and, in this process, broad-scale monitoring provide a key link between manipulative experiments and techniques such as remote sensing that are used to guide conservation. Inspired from Mouquet et al. 2015, Janzen 2009 and Lepetz et al. 2009*

2017) and although some sites may provide spatial analogues to future conditions (Carter et al. 2007), other complementary approaches are needed to gain a more comprehensive and predictive understanding of community responses. For example, correlative studies can only approximate, although sometimes with good accuracy, the fundamental niche of species that can only be fully defined with manipulative experiments (Boulangeat et al., 2012).

To overcome these limitations, monitoring programs need to be thought in concert with other approaches. Process studies (e.g. manipulative experiments) can fuel the interpretation of observations made at broader scale while observations made in natural ecosystems give rise to hypotheses, which can then be explored experimentally (Figure 8; Janzen, 2009; Peters, 2010). In this respect, this thesis has built upon existing empirical and theoretical knowledge to gain a deeper understanding of benthic systems using the broad-scale data of the REBENT monitoring. In doing so, it has raised new questions and hypotheses to be tested experimentally. This cycle is needed to apprehend biodiversity across space and time and can be better achieved if *in situ* manipulative experiments or fine-scale observational studies are embedded within the context of broad-scale monitoring programs (Witman et al. 2015). Coordinated experiments that integrate experimental approaches with natural biodiversity and environmental gradients can yield important mechanistic insights by incorporating more realistic variations in terms of community composition, structure, and abiotic conditions (Duffy et al. 2015, Edgar et al. 2016). Brittany provides, through its mosaic of environments and its position at the crossroads of two biogeographic zones, an ideal playground for experimenting across biodiversity and environmental gradients. In this context, data acquired in the REBENT program can be used to choose ideal and contrasted sites for experimental purposes and to interpret the results of such manipulative experiments in the light of available long-term knowledge. In conclusion, I feel that the REBENT monitoring provides an ideal platform to bridge distinct interests, disciplines, and approaches around a common and dazzlingly heterogeneous and rich system, about which we still have much to discover.

b) Perspectives

Several perspectives have been discussed during this chapter. Most were concerned by a methodological perspective, and addressed with the aim of ameliorating the exploitation of broad-scale monitoring data. Moreover, several ecological questions and hypotheses that have been raised during this thesis are worth testing and developing in future research and are further discussed below.

i) Linking diversity with ecosystem functioning

Firstly, while Chapter 2 provided important insights into the functioning of benthic communities by addressing how and why the ecological roles of polychaete species varied across space and time at the regional scale, important questions remain regarding how these variation observed in terms of trait composition translate in terms of ecosystem functioning. Indeed, characterizing the variation of the ecological roles of species does not account for the variation in the performance of species in achieving these roles. Yet, this seems to be a key driver of ecosystem functioning in marine systems (Strong et al. 2015). One may then wonder whether the similar trait compositions found in different maerl beds, despite variations of their associated communities, may or may not entail similar functioning of these communities. Likewise, it remains unclear how community variations within-seagrass meadows that are potentially dominated by transient species affect their functioning?

To answer these questions, a first approach that could be conducted would be to perform *in situ* measurements of nutrient fluxes and/or measures of respiration and primary production using benthic chambers in some of the sites monitored by the REBENT program. For instance, an approach such as the one conducted by Martin et al. (2005) that compared the metabolism of two habitats in a single site, could be repeated across three or four contrasted sites (contrasted in terms of environments and biodiversity) and for two years of survey of the REBENT program. These measures and their variability could then be related to the taxonomic and trait-based composition and structure of the observed communities. Sites harboring more than one habitat should be prioritized in such an endeavor in order to achieve a sampling design capable of differentiating the habitat effect from the effect of the local conditions. Specifically, this could be performed in spring and late summer/autumn in three sites: one exposed intertidal site harboring a seagrass meadow and bare sediment (e.g. Sainte-Marguerite, Arcouest, Molène), one subtidal site harboring a maerl bed and bare sediment (e.g. Trévignon that have displayed great temporal stability in the results of this thesis), and one site such as the Bay of Brest or Bay of Morlaix, where all four habitats can be found. Depending on available resources, additional sites could be included to enhance the ability to disentangle the relative role of habitat and location.

Additionally, one of the surveys of the REBENT program could be complemented for selected sites by a trophic analysis of the communities using stable isotopes or fatty acids. This approach would ideally be conducted at the same times as the proposed experiment described above, and would focus on evaluating the spatial variability of the food web structures of communities across different sites and habitats. This was performed in the specific context of green tides in some of the bare sediment monitored in the REBENT program (Quillien et al., 2016) and the effects of seagrass meadows and maerl beds on trophic pathways have also been assessed separately elsewhere (Grall et al., 2006; Van der Zee et al., 2016). However, using a standardized methodology for comparing food webs from different habitats in different abiotic conditions should help to untangle the effect of foundation species from that of abiotic constraints, To the best of my knowledge such a study has not been performed yet, and the REBENT offers an ideal setting to initiate it. Furthermore, this analysis would benefit from the long-term knowledge acquired on these sites to fuel the interpretations regarding the functioning of the studied communities.

ii) Gaining insights on rare species and their drivers

Secondly, this thesis has evidenced an important role of rare and transient species in the diversity of benthic communities, especially in seagrass systems. However, important interrogations remain regarding their ecological role and the extent to which the scale of observation of this study has influenced this finding. Several approaches articulated around the monitoring program could bring some answers to these questions.

In the first instance, complementing the sampling protocol of the REBENT program with sampling conducted at finer spatial and temporal scales could help apprehend to what extent the probability of species detection of the monitoring is affected by its spatial and temporal design. For this purpose, I suggest to use the seagrass meadow of Sainte-Marguerite for the following reasons: this meadow is relatively exposed so that transient species may have an important contribution to its diversity; this site is also accessible, which allows for an intensive sampling; and specific work on its associated communities and trait compositions has been already performed during this thesis with the internship of Anna Le Joncour. Sampling could be performed across several tides before and after the sampling conducted in the context of the REBENT monitoring program. In a first instance, this could be done only for epifauna as the sampling method is less invasive than the one for infauna. Additionally, a sampling with greater spatial coverage of the meadows could be performed simultaneously to the one used for the REBENT program and, depending on available resources, adjacent habitats could be sampled to evaluate the potential role of mass effects in explaining the epifaunal diversity of the meadows.

While the design of this fine-scale sampling needs to be discussed and adapted to available resources, using data from such an extensive sampling concomitant to the one conducted for the REBENT program would allow a first assessment of the extent to which rare species (from the perspective of the monitoring) arise from methodological biases, as well as characterize species potentially present through mass effect from other habitats (see for instance the approach of Sgarbi & Melo, 2018). Species detectability could then be compared across several spatial and temporal scales using data from these intensive sampling sessions and from the overall REBENT database. Relationships between species detectability at these different scales and their traits could also be evaluated *a posteriori* using trait data available from the literature and from databases.

Importantly, the "intensive sampling sessions" could serve to measure traits from species we know are not often found in the REBENT. In this perspective, a "red list" of species known to be rare, *i.e.* rarely observed since the beginning of REBENT program, could be constructed so that when specimens of rare species are retrieved in any sample during the monitoring program, all possible measurements are made to characterize their traits, such as their size, their reproductive state whenever possible, morphological characteristics for polychaetes such as buccal appendix[7], or their overall morphological state (e.g. damaged or not). Although they may bring little information on their own, these measures may on the long-term provide critical insights into the functional facet of their rarity (Violle et al., 2017). This would also help fill missing data from the literature and databases for future trait-based approaches. Importantly, all specimens of these rare species should be kept for potential future analysis[8] and for morphological comparisons. As an example, shells of rare bivalve specimen could be examined using schlerochronology.

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[7] Morphological characteristics of polychaetes are closely related to their functional role and can be easily translated into biological traits more usually used in trait-based approaches such as feeding mode, or mobility (Otegui et al., 2016)

[8] Genetic tools could be used if organisms have not been preserved in formalin for instance.

iii) Explaining the differences of community trajectories

Thirdly, understanding what drives different communities to exhibit more or less similar trajectories in time is a key ecological question. Indeed, asynchrony among communities is an important factor governing the stability of ecosystem functioning (Wilcox 2017). In the face of environmental changes that tends to favor the synchrony of phenological events among distinct populations (Koenig & Liebhold 2016) and homogenize the composition of communities in space (Olden et al., 2018), understanding the mechanisms maintaining the spatial and temporal heterogeneity is therefore essential. From a more practical perspective, understanding under which circumstances communities may evolve similarly or not can provide important insights to allocate monitoring efforts (Hewitt & Thrush, 2007). For this purpose, Structural Equation Modeling (SEM; a statistical approach allowing to untangle direct and indirect relationships among variables, see for instance Lefcheck, 2016) could be used with Chapter 3 data in order to assess the direct and indirect relationships existing between the environmental trajectories of the sites and the trajectory of their communities using D_{DSP}. Figure 9 proposes a SEM model for this purpose. However, although conceptually appealing, assessing linear relationships between trajectory distances may suffer from similar caveats as those highlighted for community analysis between taxonomic and geographic distances (Legendre et al., 2015). Therefore, a simulation study ensuring that linear relationships among trajectory distances are meaningful should be performed beforehand.

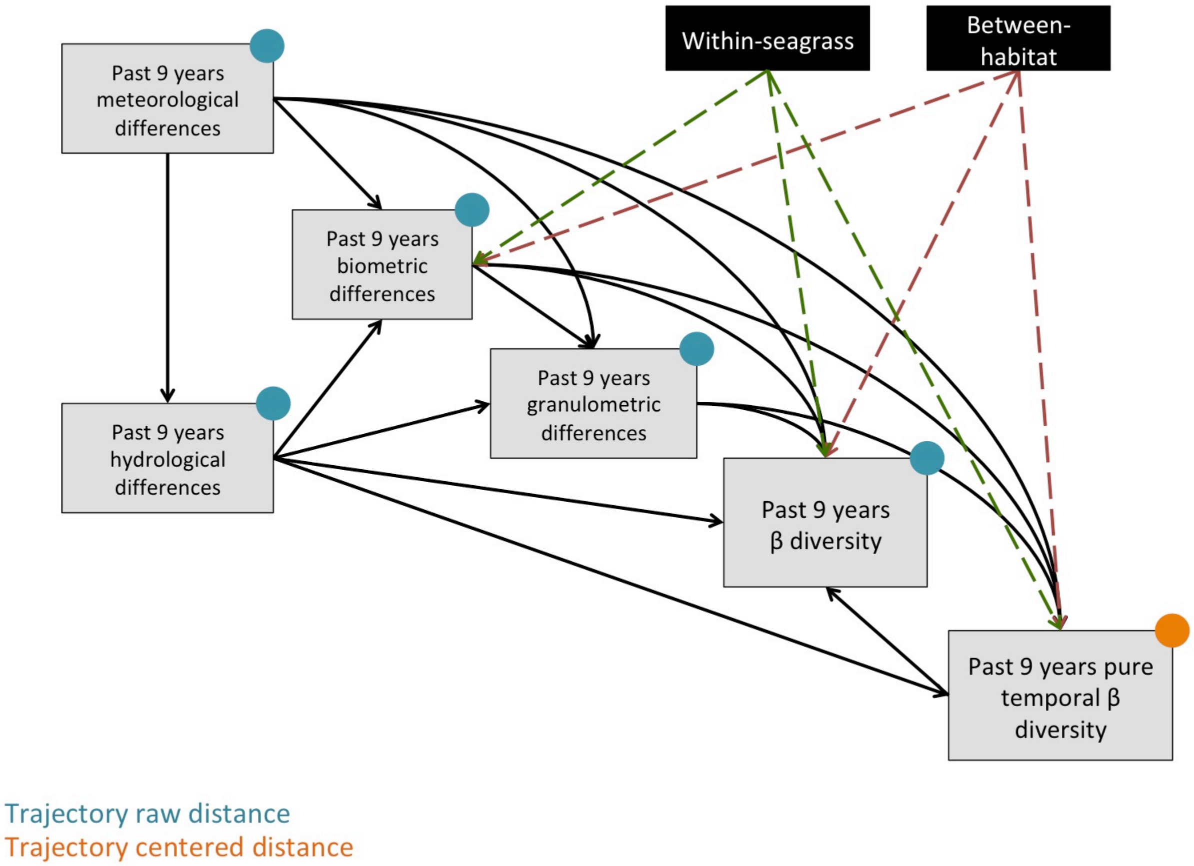

***Figure 9.** Conceptual model for determining the direct and indirect drivers of the differences of benthic community temporal trajectories through Structural Equation Modeling. Here trajectories would be computed on data from Chapter 3 over 9 years and the example focuses on intertidal communities and on the effects of seagrass meadows. The distances between the raw trajectory of two communities (Past 9 years β diversity) comprises both spatial and temporal variation while these distances in term of centered trajectory represent their pure temporal differences over the 9 years. Therefore, this model allows apprehending the main factors determining their persistent spatial differences as well as the factors that have led to their different temporal trajectories over the 9 years. Regarding the explicative variables, only raw trajectories are used to account for both the initial positions (spatial differences) and the temporal dynamics of the sites. The differences between two sites in terms of the meteorological conditions they have experienced over the past 9 years could directly influence their differences in terms of community over this period or indirectly through their effects on hydrological conditions and on their effects on the characteristics of the foundation species (biometric variables on* Zostera marina*). Similarly, hydrological differences could affect directly the communities or indirectly through the foundation species or through changes in sediment nature. The role of the habitat would be taken into account in two ways: 1) through the distances between the trajectories of the meadows in terms of the plant characteristics (all bare sediment would be at 0 for these variables across all time period) and 2) through a factor coding for the habitat and assessing whether trajectory distances within-seagrass beds and among seagrass and bare sediment are greater or lower than within-bare sediment.*

DISCUSSION

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CONCLUSION

Les fonds marins sont affectés depuis plusieurs décennies par de profonds changements. Parmi ceux-ci, la dégradation des habitats biogéniques observée à l'échelle mondiale apparait comme l'une des menaces les plus importantes pesant sur la biodiversité côtière (Hoegh-Guldberg & Bruno 2010, McCauley et al. 2015). Ces habitats sont des clés de voute de nombreux processus écologiques en milieux côtiers (Bouma et al., 2009) et jouent en particulier un rôle facilitateur pour les espèces benthiques, ce qui promeut la diversité locale des sédiments (Sunday et al., 2017) et pourrait jouer un rôle prépondérant dans la réponse des communautés benthiques face aux changements environnementaux en cours (Bulleri et al., 2018; Bulleri, et al., 2015).

Le constat initial de cette thèse était cependant que notre compréhension de l'influence de ces habitats sur le fonctionnement et la diversité des communautés benthiques se limitait en grande majorité à des échelles spatiales et temporelles restreintes, ce qui ne permettait pas d'évaluer pleinement leur rôle dans le devenir des communautés benthiques (Airoldi et al., 2008). De ce fait, il apparaissait essentiel de complémenter ce savoir par des connaissances acquises à de plus grandes échelles afin, notamment, de mieux appréhender la complexité et la variabilité naturelle de ces écosystèmes benthiques (Witman et al., 2015). L'un des enjeux majeurs de l'intégration des connaissances existantes à des échelles supérieures étant de fournir une meilleure compréhension de ces écosystèmes à des échelles qui soit plus en adéquations avec celles auxquelles la société gère et bénéficie de ces ressources naturelles (Isbell et al. 2017) et auxquelles les politiques de conservation s'intéressent (Cadotte et al., 2017).

Dans ce contexte, trois contributions majeures de ce travail de thèse peuvent être soulignées. La première a été de documenter les patrons de diversité β des communautés à grandes échelles spatiales et temporelles, et d'identifier les rôles relatifs des habitats biogéniques et des facteurs locaux, tels que l'environnement abiotique, dans les variations des communautés. Cet aspect est en premier lieu essentiel dans un contexte spatial car si la cartographie des habitats benthiques au travers d'outils télémétriques joue un rôle prépondérant dans la détermination des stratégies de conservations, l'efficacité de ces approches à représenter pleinement les patrons de diversité reste à déterminer (Edgar et al. 2016). Le chapitre 1 a ainsi mis en évidence d'importantes variations des communautés au sein des herbiers à une échelle régionale, mettant en exergue le besoin de complémenter ces approches télémétriques par une caractérisation des variations spatiales des communautés au sein des habitats. En outre, le chapitre 3 a mis en évidence que si les variations inter-habitats des communautés d'endofaune sont en effet généralement plus importantes que celles intra-habitat à une échelle régionale (condition essentielle pour l'utilisation des approches télémétriques dans les politiques de gestion de la diversité), l'importance de ces différences inter-habitats pouvait grandement varier selon les conditions locales. À cela il convient d'ajouter que les variations spatiales des communautés d'endofaune peuvent être grandement découplées de celles des communautés d'épifaune comme le chapitre 1 l'a montré. Ces résultats mettent ainsi en exergue la nécessité de pleinement caractériser la diversité β des communautés afin d'assurer une priorisation adéquate des actions de conservation (Socolar et al., 2016a).

L'intérêt des suivis à grandes échelles spatiales et temporelles comme le REBENT est double dans ce contexte. En effet, ces suivis permettent d'une part de caractériser plus finement les structures spatiales des communautés, et d'autre part, d'appréhender leur stabilité dans le temps. Ainsi, les chapitres 1 et 3 ont montré que les variations temporelles des communautés différaient selon les sites, une interaction espace-temps pouvant d'ailleurs s'exprimer différemment pour les communautés d'épifaune et d'endofaune (chapitre 1). Cette hétérogénéité spatiale des dynamiques et des trajectoires temporelles des communautés est un défi majeur pour la gestion des écosystèmes. En outre, celui-ci est voué à s'accentuer dans le future de part l'hétérogénéité spatiale des changements environnementaux et des impacts anthropiques (Burrows et al. 2011, Halpern et al. 2015). Pour faire face à ce défi, le chapitre 4 propose, en s'inspirant de l'approche menée dans le chapitre 3 et autour des opportunités que représentent les suivis à grandes échelles spatiales et temporelles, des approches analytiques pour mieux comprendre et potentiellement prédire ces dynamiques des communautés.

Dans ce contexte, le chapitre 3 a aussi mis en évidence l'importance de la fenêtre temporelle des observations pour établir l'étendue d'un changement observé. Sur près d'une décennie, et malgré des variations dans le temps des communautés et l'occurrence d'évènements extrêmes tels que les tempêtes de 2008 et de 2014 (Fichaut & Suanez 2011, Masselink et al. 2016), les structures spatiales des communautés à l'échelle régionale sont apparues remarquablement stables, mettant en évidence une forte empreinte historique dans la structure spatiale régionale actuelle des communautés benthiques. Cela met en exergue le rôle des suivis à long-terme pour fournir un état de référence des communautés qui ne soit pas simplement une image statique, à partir de laquelle il peut être difficile de juger l'importance d'un écart observé, mais une enveloppe de possibilités que l'on pourrait juger « normales » et à laquelle peuvent être comparés des changements observés (Hawkins et al. 2017)

La deuxième contribution majeure de cette thèse a été d'identifier les mécanismes régissant la diversité des communautés et de permettre ainsi de mieux envisager la vulnérabilité des communautés benthiques et leurs potentielles réponses face à de futurs changements des fonds marins. Les chapitres 2 et 3 ont ainsi confirmé la capacité des habitats biogéniques à amenuiser l'influence des contraintes abiotiques sur les communautés qu'ils abritent (Bulleri et al. 2015). Cet effet s'effectue principalement au travers d'une réduction de l'impact des évènements extrêmes sur les communautés mais ne semble pas s'opérer sur les variations des conditions abiotiques moyennes (chapitre 3). Cependant, il semble que les principaux effets néfastes des changements globaux sur les communautés soient d'avantage associés à l'accentuation des épisodes extrêmes qu'aux variations des conditions moyennes dans lesquels vivent les espèces (Vasseur et al. 2014). Ainsi, le chapitre 3 a montré sur une période de 9 ans que la présence d'herbiers permettait en zone intertidal le maintien d'une structure régionale plus stable des communautés que dans le sédiment nu. Collectivement, les résultats des chapitres 2 et 3 confirment le rôle fondamental que jouera la présence de ces habitats biogéniques dans la réponse future des communautés benthiques aux changements environnementaux (Bulleri et al. 2018).

Cependant, les résultats des chapitres 2 et 3 ont aussi mis en avant que différentes espèces fondatrices affectaient les communautés benthiques par le biais de différents processus écologiques. Cela confirme que l'identité des espèces fondatrices et les processus écologiques auxquelles ces espèces sont associées doivent être clarifiés et pris en compte pour mieux envisager le futur des communautés benthiques (Pessarrodona et al., 2018). Ainsi, le chapitre 2 a montré que si les herbiers et les bancs de maërl favorisaient tous deux la diversité taxinomique et fonctionnelle des communautés benthiques, les différents processus sous-tendant ces effets positifs menaient à différentes vulnérabilités des communautés associées. La diversité des herbiers semble ainsi reposer en grande partie sur la présence d'espèces rares, et est donc associée à une redondance fonctionnelle moindre que celle des bancs de maërl (chapitre 2). Cela montre que, contrairement à ce qui est généralement admis, tous les systèmes diversifiés ne sont pas obligatoirement associés à une forte redondance fonctionnelle (Mouillot et al. 2013). Caractériser les liens entre diversité taxinomique et diversité fonctionnelle est donc essentiel pour guider les actions de conservation et assurer 1) le maintien de l'ensemble des facettes de la biodiversité et 2) la résilience des communautés benthiques sur le long-terme (Pollock et al., 2017; Thrush & Dayton, 2010)

À ce titre, la troisième contribution majeure de ce travail a été d'approfondir notre compréhension du rôle des habitats biogéniques et de l'hétérogénéité des fonds marins dans le fonctionnement et la résilience des communautés benthiques. Face à une homogénéisation croissante des fonds marins côtiers (Airoldi & Beck 2007, Airoldi et al. 2008), les résultats du chapitre 3 mettent ainsi l'accent sur la nécessité de préserver la diversité β des fonds marins en préservant d'une part les structures biogéniques et d'autre part l'hétérogénéité existant au sein des sédiments nus, afin d'assurer un maintien des fonctions écologiques auxquelles contribuent les espèces de macrofaune benthique. En particulier, la préservation des populations d'espèces fondatrices paraît cruciale pour assurer le maintien de ces fonctions écologiques sur le long terme (chapitre 2 et 3). En outre, ce travail de thèse n'a considéré que les effets indirects des espèces fondatrices sur le fonctionnement des écosystèmes via leurs effets sur les communautés d'endofaune. Il est important de remettre ces résultats en perspective en rappelant l'apport additionnel de ces habitats sur la diversité via les communautés d'épifaune (chapitre 1) ainsi que le rôle directe que ces espèces fondatrices jouent dans le fonctionnement des écosystèmes (Alsterberg et al. 2017, Liu et al. 2018).

En conclusion, ce travail de thèse a permis d'approfondir notre compréhension des déterminants de la diversité des communautés benthiques et de fournir des éléments essentiels permettant de mieux prédire leur devenir face aux changements environnementaux à venir. Les résultats de ce travail ont mis en évidence la nécessité de préserver l'hétérogénéité des fonds marins et réaffirmé le rôle de l'homogénéisation biotique des communautés comme l'une des menaces les plus importantes pesant sur la biodiversité côtière et le fonctionnement de ces écosystèmes (Olden et al., 2018). Le maintien des populations d'espèces fondatrices est apparu à cet égard comme une priorité absolue pour préserver la biodiversité des fonds marins côtiers. Ce travail de thèse a aussi permis d'affirmer l'apport incontestable des suivis à grandes échelles spatiales et temporelles dans notre compréhension des communautés naturelles. Ces outils fournissent un complément essentiel aux approches expérimentales et théoriques et sont de précieux atouts afin de mieux prédire, et donc gérer, le devenir des communautés naturelles.

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UNIVERSITE BRETAGNE LOIRE / SCIENCES DE LA MER ET DU LITTORAL

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Titre : Diversité taxinomique et fonctionnelle des habitats benthiques dans l'espace et dans le temps : une perspective régionale et décennale

Mots clés : Suivis biologiques | Écologie numérique | Habitats biogéniques | Diversité β | Traits biologiques | Trajectoire des communautés | Échelles d'observation | Homogénéisation biotique | Conservation | REBENT

Résumé : Ce travail de thèse s'appuie sur les données d'un suivi à long-terme mené à une échelle régionale pour mieux appréhender les facteurs gouvernant la diversité des fonds marins côtiers. En considérant de multiples échelles spatiales et temporelles ainsi que différentes facettes de la diversité de ces communautés, l'objectif principal a été de fournir des connaissances permettant de mieux prédire les potentielles réponses des communautés benthiques face aux changements environnementaux à venir. Cette thèse s'inscrit en particulier dans un contexte de la menace de l'homogénéisation des fonds marins et de la disparition à large échelle des habitats biogéniques, réservoirs de biodiversité formés par des *espèces fondatrices*. La comparaison de deux de ces habitats, les herbiers de Zostères intertidaux et les bancs de mäerl subtidaux, à des sédiments dépourvus d'espèces fondatrices a mis en évidence le rôle fondamental de ces habitats biogéniques dans le maintien de la diversité et du fonctionnement des fonds marins à long-terme. Ils contrôlent profondément les dynamiques temporelles des communautés et leurs capacités de réponse aux variations des conditions environnementales, assurent une plus grande stabilité des structures spatiales des communautés à une échelle régionale. Ils semblent par-là essentiels au maintien à long-terme des fonctions écologiques auxquelles contribuent les espèces benthiques. Cependant, ce travail montre que ces espèces fondatrices opèrent selon des mécanismes différents et que les implications en terme de vulnérabilité des communautés sont donc aussi différentes. Cette étude montre enfin qu'au sein d'un habitat donné, la richesse locale des communautés est relativement stable dans l'espace et le temps et met en évidence le besoin de caractériser les variations de compositions de communautés pour guider les actions de conservations à larges échelles. À ce titre, et à l'échelle régionale, les variations de composition contribuent à une richesse taxinomique et fonctionnelle dans les sédiments dépourvus d'espèces fondatrices aussi importante que dans les habitats biogéniques. Ce résultat impose de réévaluer la valeur de conservation qui pourrait leur être attribué de part leur richesse locale limitée. Les suivis à grandes échelles spatiales et temporelles sont dans ce contexte essentiels pour fournir un lien entre les connaissances empiriques et théoriques existantes à des échelles locales, et les échelles supérieures auxquelles s'intéressent les politiques de conservation.

Title: Taxonomic and functional diversity of benthic habitats: variability and drivers from a regional and decadal perspective

Keywords: Monitoring | Numerical ecology | Biogenic habitats | β diversity | Trait-based approach | Community trajectory | Scales | Biotic homogenization | Conservation | REBENT

Abstract: This thesis takes advantage of long-term monitoring data covering a regional scale to better apprehend the main drivers of the diversity of coastal seafloors. Through consideration of multiple spatial and temporal scales and different facets of community diversity, the main objective of this work was to provide a better predictive understanding of the responses of benthic communities to environmental changes. In particular, this thesis addressed the potential consequences of the on-going homogenisation of the seafloor and the global loss of biogenic habitats, havens of diversity made by *foundation species*. Through comparison of two such habitats, intertidal seagrass meadows and subtidal maerl beds, with bare sediment devoid of foundation species, this thesis has highlighted the key role of biogenic structures for long-term maintenance of the diversity and functioning of benthic communities. Indeed, these habitats mediate the dynamics and responses of benthic communities to environmental conditions, ensure a greater stability of their spatial structures at regional scale, and appeared essential for the long-term maintenance of the ecological functions benthic invertebrates are associated with. This work also highlighted that foundation species may affect benthic communities through different mechanisms, and that has implications on the structure and vulnerability of these communities. Lastly, this thesis emphasized a strong spatial and temporal stability of community richness despite important underlying changes in composition and thereby stressed the need to better characterise these compositional variations to guide conservation. These variations contributed, for instance, to an unexpectedly high taxonomic and functional richness of bare sediment at regional scale, similar to those of biogenic habitats, despite being locally depauperate. Overall, broad-scale monitoring programs are fundamental assets to bridge local empirical and theoretical ecological knowledge to the broader scales at which society manage and benefits from natural ecosystems.