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THESE

Pour obtenir le grade de

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Spécialité : OCEANOLOGIE BIOLOGIE

Régis Gallon

Diversité, structure et fonctions des communautés à Rhodophytes en Bretagne.

Réponses aux forçages environnementaux dans le contexte du changement global

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Sous la direction de **: Monsieur Feunteun, Eric, Professeur**

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Diversité, structure et fonction des communautés à Rhodophytes en Bretagne

Réponses aux forçages environnementaux dans le contexte des changements globaux

Régis GALLON

Sous la direction du Prof. Eric FEUNTEUN

Thèse réalisée au :
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À mes grands-pères,

INTRODUCTION GENERALE

Les zones côtières

Situées à l'interface atmosphère/continent/océan, les zones côtières sont reconnues pour faire partie des zones les plus productives (Mann 1992, Gattuso *et al.* 1998) et les plus diversifiées (Burke et al. 2001) de la planète. Elles regroupent des écosystèmes[1] complexes évoluant en interaction avec de multiples interactions physiques, chimiques et biologiques qui fluctuent à différentes échelles spatio-temporelles. Cette grande variété de facteurs abiotiques est à l'origine d'une grande diversité d'habitats accueillant une importante diversité d'organismes dont des producteurs primaires (Figure 1). Ces derniers sont essentiels au fonctionnement des zones côtières et participent à l'enrichissement de l'écosystème par l'apport de nutriments ou de matière végétale consommée par les organismes herbivores, filtreurs ou détritivores (Lefeuvre et al. 2004, Lefeuvre et Feunteun et al. 2007). Ces formations végétales sont à la base des réseaux trophiques complexes et diversifiés composés d'espèces résidentes ou à mobilité plus ou moins forte (poissons, céphalopodes, crustacés, oiseaux, mammifères). De nombreuses études se sont intéressées aux herbiers à phanérogames marins tels les zostères ou les posidonies en zone tempérée (i.e. Duarte et Cebrian 1996, Ouisse et al. 2010) ou les marais salés (Lefeuvre et Feunteun et al. 2007). Les algues rouges, en strate herbacées, forment d'importantes prairies sous les forêts de laminaires dont elles peuvent être également épiphytes. Elles s'étendent, en formation prairiales, vers les milieux plus profonds du circalittoral côtier. Les biomasses de ces formations, bien que moins renseignées dans la littérature, sont également importantes (Copertino et al. 2005). Ainsi, les milieux côtiers sont composés d'une mosaïque d'habitat[2] composée de nombreux habitats littoraux, subtidaux benthiques (Christian et Mazzilli 2007). Bien qu'ils ne représentent moins de 15% de la surface totale des océans, ils renferment 40% des biomasses marines et assurent 25% de la production primaire mondiale, 80% de la production globale carbonatée, 50% de la dénitrification globale et 90% de la minéralisation sédimentaire globale (EEA 2006). Par conséquent, de nombreux cycles biogéochimiques sont régulés par ces zones côtières.

[1] « Unité fonctionnelle qui se perpétue de façon autonome au travers du flux de l'énergie et du cycle de la matière entre ses différentes composantes inertes et vivantes lesquelles sont en constante intéraction » (Ramade 1993)

[2] « Lieu où vit l'espèce et à son environnement immédiat à la fois abiotique et biotique » (Ramade 1993)

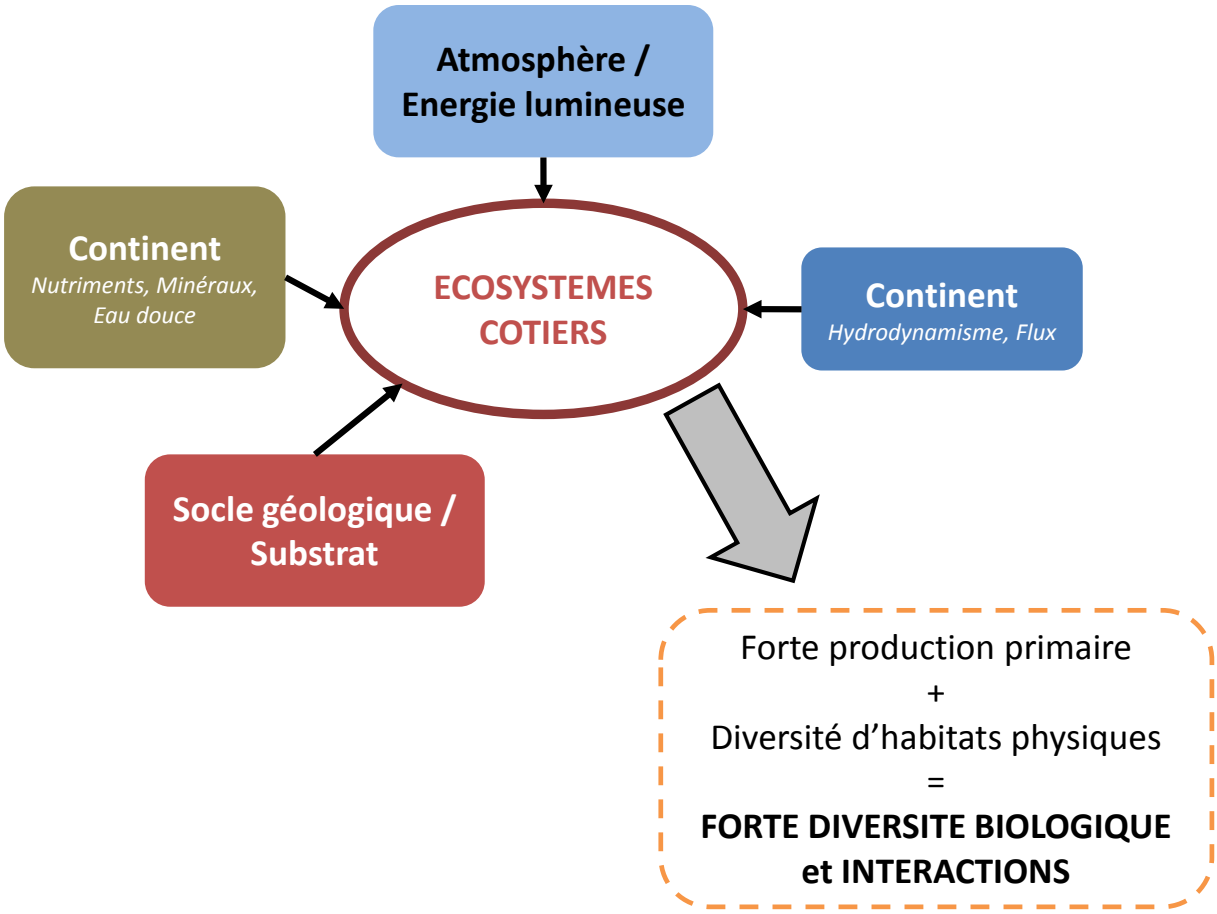

Figure 1 : Schémas expliquant les forçages environnements influençant les écosystèmes côtiers.

Ces zones sont soumises localement à de fortes contraintes anthropiques qui peuvent avoir de multiples conséquences telles que :

- La modification, la fragmentation et la destruction d'habitat qui sont considérées comme les menaces les plus sérieuses pour la biodiversité (Sih et al. 2000). Il apparait que les zones côtières sont les plus durement touchées par la destruction d'habitat.
- Les rejets urbains, industriels induisent une dégradation de la qualité des eaux et des phénomènes d'eutrophisation. Cela induit une augmentation de la production primaire qui a pour conséquence une augmentation des flux de matière organique vers le compartiment benthique microbien et une diminution de la disponibilité en oxygène à proximité du fond.
- La modification des caractéristiques des communautés bentho-pélagiques par la surexploitation des ressources et l'introduction d'espèces exotiques. Cette dernière

peut avoir divers effets sur les communautés : d'un côté, elle peut participer à l'augmentation locale de la diversité dans un écosystème oligospecifique, si une espèce introduite s'installe dans une niche écologique laissée vacante et si les ressources sont suffisamment abondantes ; de l'autre, cette nouvelle espèce peut modifier profondément la structure d'une communauté par compétition (exclusion) ou par modification intrinsèque de l'habitat (modification de la structure et des réseaux trophiques).

À une plus grande échelle, les changements globaux (réchauffement climatique, acidification des océans, modifications des régimes de courants et houles) interfèrent avec les zones côtières. En effet, depuis les 50 dernières années, la température de surface des masses d'eau a augmenté de 0.65°C. Associés à cette augmentation d'autres facteurs ont évolués au cours du temps : 1) augmentation du niveau global des océans, entre 1993 et 2009 les données satellite ont montré une augmentation de 3.3±0.4 mm par an (Pachaury 2007) ; 2) modification de la composition et de la structure des couches atmosphériques entrainant une intensification des tempêtes et cyclones (Bromirski *et al.*, 2003) ; 3) diminution du pH océanique de 0.1 unité depuis le début de l'ère industrielle.

Quelles réponses face à ces impacts ?

En réponses aux impacts précédemment cités, les organismes expriment des comportements biologiques complexes qui se répercutent directement ou indirectement sur la structure et le fonctionnement des écosystèmes. À titre d'exemple, des changements rapides de température peuvent altérer la fitness des organismes en affectant leur physiologie et leur phénologie et par conséquent modifier la distribution et l'abondance des espèces (Hughes *et al.*, 2000; Bellard *et al.*, 2012). Les organismes ont trois réponses possibles aux pressions environnementales : 1) l'adaptation (court terme), l'acclimatation (long terme) ; 2) la migration vers des conditions plus favorables ; 3) l'extinction. Ces différentes réponses peuvent affecter à plus ou moins à plus grande échelle la structure et le fonctionnement des écosystèmes (Kraufvelin 2010).

Dans le contexte de perte de biodiversité, depuis la dernière décennie, de nombreuses recherches se sont intéressées aux relations entre la diversité biologique et les fonctions d'un écosystème (Loreau *et al.* 2001). A l'heure actuelle, bien que mal connues (Naeem & Wright, 2003), cette question peut être abordée par le filtre de quatre hypothèses (Johnson et al. 1996) (Figure 2) :

1- Hypothèse de la « *diversité-stabilité* » (Mc Arthur 1955) : l'efficacité énergétique d'un système et sa stabilité augmentent linéairement avec le nombre d'espèce.
2- Hypothèse des « *rivets pops* » (Ehrlich et Ehrlich 1981) : chaque espèce joue un rôle mais le fonctionnement du système est altéré brutalement à partir d'un certain seuil de disparition.
3- Hypothèse de la « *redondance* » (Walker 1992) : Les espèces aux analogues fonctionnels se remplacent si elles appartiennent au même groupe fonctionnel.
4- Hypothèse de « *l'idiosyncrasie* » (Lawton 1994) : il n'y pas de relation entre richesse spécifique et processus fonctionnel.

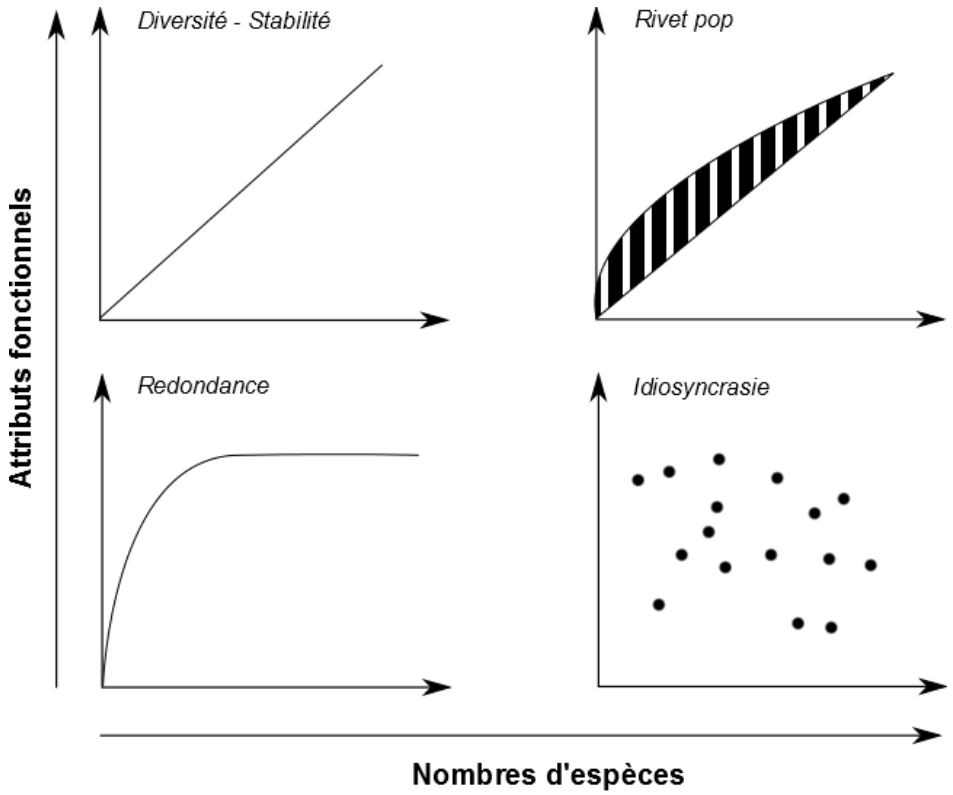

Figure 2 : Hypothèses sur les relations biodiversité et rôle fonctionnel des espèces dans un écosystème.

Actuellement la définition d'un groupe fonctionnel et l'attribution d'une fonction à une ou plusieurs espèces font encore débat, principalement sur le nombre de traits biologiques nécessaires pour définir un groupe (Wright et al 2006).

Les substrats rocheux subtidaux : définition et fonctions

Quelques études, en général réalisées en scaphandre autonome (Van Rein 2009) montrent que les systèmes rocheux subtidaux sont parmi les plus diversifiés et les plus productifs des zones côtières (Wahl 2009) et leur proximité à la côte fait qu'ils sont fortement soumis aux différentes pressions anthropiques (Clynick et al. 2009).

Pour définir les habitats rocheux, on peut s'appuyer sur la typologie Natura 2000 des habitats récifaux (1170) issue de la directive Habitat (92/43/CEE) :

« *Habitats d'origine biogène ou géogène sur fond meuble ou dur, leurs substrats sont rigides et compacts. Ils se situent sur le fond marin dans la zone subtidale et intertidale. Les roches recouvertes de sédiments sont inclues dans ce type d'habitat si les espèces associées sont tributaires du substrat dur et non du substrat meuble.* »

La grande diversité de tailles, de formes, de textures et de rugosité de ces substrats est propice à création d'une mosaïque d'habitats permettant la colonisation par une d'espèces marines riches et diversifiés (Barnes et al. 2001). Parmi ces organismes, les communautés de macroalgues se développent sur l'infralittoral et le circalittoral côtier, à des profondeurs variables allant jusqu'à plusieurs dizaines de mètres et variant suivant la turbidité des écosystèmes. En raison de la forte productivité les assemblages de macroalgues des substrats rocheux subtidaux sont reconnus pour avoir une importance vitale dans le fonctionnement des écosystèmes côtiers adjacents (Wienche & Bischof 2012). On peut reconnaitre à ces phytocénoses trois fonctions importantes :

- Fonction de « *production* » : *D*epuis les recherche de Mann en 1973, les forêts à laminaires ont été reconnues comme faisant partie des écosystèmes les plus productifs de la planètes (Mann, 1973). Leur production a été estimée entre 500 $gC.m^{-2}.an^{-1}$ (Kérambrun, 1984) et 1,8-2 $kgC.m^{-2}.an^{-1}$ (Abdullah & Fredriksen, 2004; Wienche & Bischof, 2012). La production associée aux communautés à rhodophytes peut varier quant à elle de 474 à 1058 $gC.m^{-2}.an^{-1}$ (Copertino et al., 2005).

- Fonction d' « *habitat* » : Les macroalgues sont considérées comme des espèces ingénieures car elles structurent des habitats abritant de nombreux organismes (Christie et al., 2009). La structure physique de ces habitats, elles même dépendant de la diversité, la composition et l'abondance des assemblages conditionnent la valeur

de refuge pour les espèces mobiles et sessiles (Martin-Smith, 1993). Associée à la structure intrinsèque des habitats, la complexité structurelle des macroalgues est tout aussi importante pour la valeur de refuge. Christie et al. (2009) montra que les rhodophytes ayant des structures simples (e.g. *Palmaria palmata*) abritaient moins d'espèces d'invertébrés que celles ayant une structure plus complexe (présence de nervures primaires et/ou secondaires, de protubérances sur le thalle…) telles que *Phycodrys rubens* et *Rhodomela sp*.

- Fonction « trophique » : Dans le cas des macroalgues, 10% de la production nette est consommée directement par les brouteurs alors que 90% est intégré par voie détritique dans les réseaux trophiques sous forme de matière organique particulaire (MOP) ou de matière organique dissoute (MOD) (Pomeroy, 1980; Mann, 1982). Les modalités d'intégration dans les réseaux trophiques de la matière organique produite par les formations à algues rouges restent relativement mal connues. Cela peut surprendre quand on connait la valeur nutritive de nombreuses espèces d'algues rouges, telles que *Porphyra* spp., *Palmaria palmata*, utilisées dans l'aquaculture et dans l'industrie agroalimentaire (Fleurence 1999, Mc Artain 2007).

Les prairies à Rhodophytes : un modèle d'étude très diversifié

Les rhodophytes sont des organismes eucaryotes qui vivent en grande majorité en milieu marin. Les algues rouges se distinguent des autres lignées eucaryotes par des composants biochimiques et ultrastructuraux bien spécifiques. Alors que les algues vertes et les plantes supérieures stockent la matière organique dans les chloroplastes, les réserves en polysaccharides se situent dans le cytoplasme pour les algues rouges. La chlorophylle a est le seul pigment chlorophyllien, elles sont principalement constituées d'un pigment photosynthétique rouge, la phycoérythrine, et accessoirement d'un pigment bleu, la phycocynanine. La présence de ces pigments explique pourquoi ces algues peuvent vivre à très grande profondeur (cent mètres et plus) là où la lumière n'est plus représentée que par des ondes bleues ou violettes, lesquelles ne sont pas absorbées par les chlorophylles, mais bien encore par ces phycobilines, lesquelles après avoir absorbé l'énergie lumineuse, la transmette à la chlorophylle a.

Depuis le début du 20ème siècle jusqu'à maintenant, en se fondant sur des critères morpho-anatomiques et des traits d'histoires de vie, les algues rouges sont divisées en deux

grands groupes, les *Bangiophyceae* et les *Florideophyceae* (Dixon 1973). Les rhodophytes sont caractérisées soit par un cycle digénétique, le gamétophyte haploïde libère des gamètes mâles ou femelles et le sporophyte diploïde dissémine des spores méiotiques, soit par un cycle trigénétique, trois générations se succèdent car la phase diploïde se déroule en deux périodes distinctes : la première (carposporophyte) est issue du zygote et se développe en parasite sur le gamétophyte femelle, elle disséminera des carpospores (spores mitotiques diploïdes) donnant la deuxième génération diploïde : le tétrasporophyte.

Le long du littoral breton, les algues rouges occupent le substrat rocheux depuis la zone infralittorale inférieure jusqu'au circalittoral proche (<60m) (**Figure 3**); le facteur limitant la distribution bathymétrique étant l'accès à la lumière, cette limite varie selon la turbidité des eaux. Au total, plus de 600 espèces ont été inventoriés depuis le début du 20ème siècle (Le Gall, com. pers.).

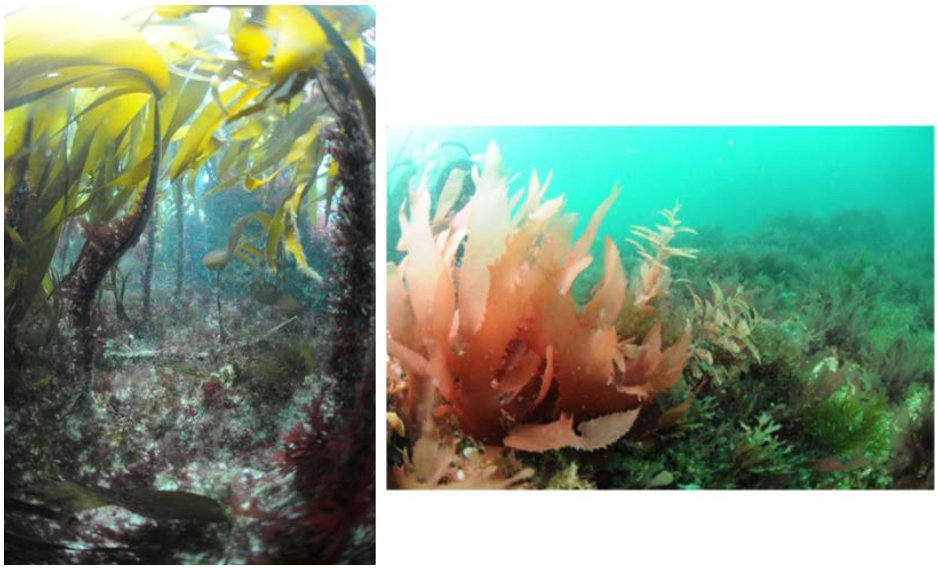

Figure 3 : Prairie de rhodophytes en sous-strate de laminaires (*Laminaria hyperborea)* et dans la zone circalittorale proche.

La Bretagne : carrefour biogéographique

La Bretagne représente une zone d'étude privilégiée pour comprendre la structuration des communautés à rhodophytes face à des contraintes environnementales car elle constitue une zone de transition biogéographique délimitée au sud par les masses d'eau tempérées chaudes de la province Lusitanienne et au nord par les masses tempérées froides de la province Boréale (Figure 4). De récentes études phylogénétiques se basant sur des invertébrés benthiques vivant dans le substrat meuble (Jolly et al. 2006, Ayata et al. 2010) ainsi que sur

des macroalgues (Couceiro et al. 2013), ont permis de localiser la frontière biogéographique au niveau de la Mer d'Iroise. La ségrégation entre le nord et le sud de la Bretagne est fortement influencée par des phénomènes hydrodynamiques (Ayata et al. 2010). L'existence de fronts halins et thermiques localisés entre le sud de la Bretagne et la Cornouaille (Le Boyer et al. 2009 ; Pingree et al. 1975) limite le transport larvaire et donc la connectivité entre le Golfe de Gascogne et la Manche, notamment pour les espèces à cycle benthodémersal.

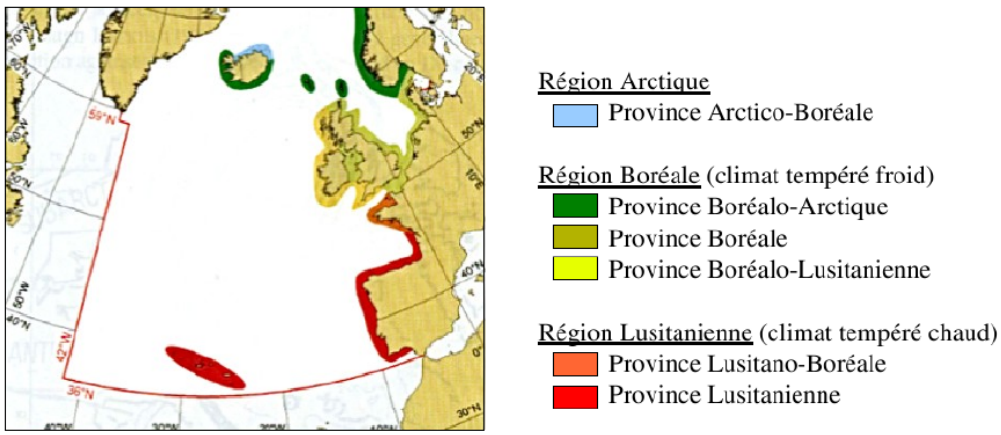

Figure 4 : Biogéographie dans l'Atlantique Nord-Est, d'après Dinter (2001)

De plus, il existe à l'intérieur du golfe de Gascogne de nombreuses structures hydrodynamiques (plumes d'estuaires, lentilles d'eaux dessalées, up et downwelling) susceptibles de favoriser soit la rétention locale soit le transport vers le sud ou l'export vers le nord. Les eaux de la Manche occidentale se caractérisent quant à elles, par un fort brassage de la colonne d'eau à la faveur du fort hydrodynamisme généré par les courants de marées et par de faibles apports d'eau douce (Pingree et al. 1982). La marée est également responsable d'une circulation résiduelle orientée du sud-ouest vers le nord-est avec des vitesses de courants résiduels comprises entre 1 et 5cm.s^{-1} (Salomon et Breton 1993) (Figure 5). La présence d'irrégularités topographiques (îles, plateaux rocheux…) est à l'origine de la formation de structures tourbillonnaires particulièrement bien développées dans le golfe Normand-Breton. L'orientation du courant est indiquée par des flèches blanches. Les vitesses de courants résiduels sont indiquées en m.s^{-1} (d'après Salomon et Breton 1993).

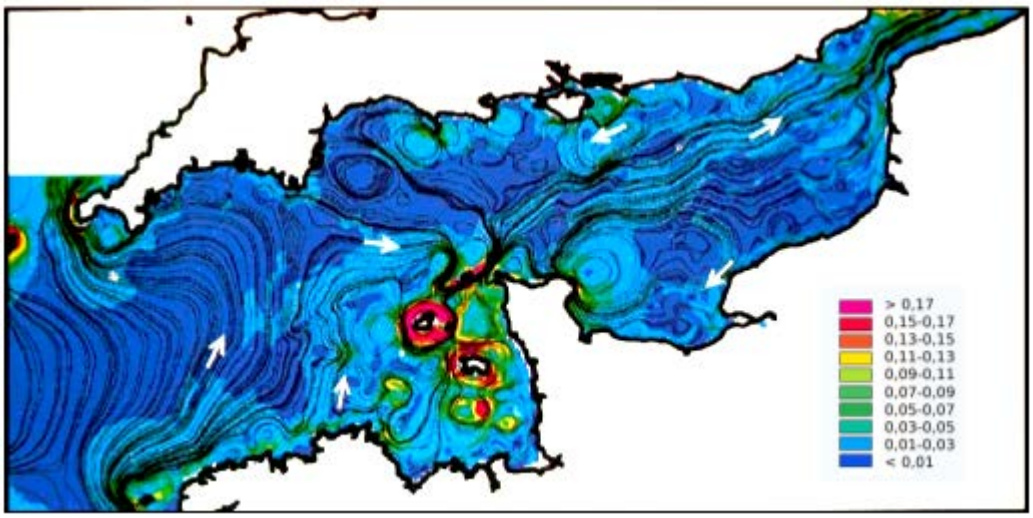

Figure 5: Circulation résiduelle en Manche en condition de marée moyenne et sans vent.

Le golfe Normand-Breton et ses spécificités environnementales

Le golfe Normand-Breton couvre une superficie totale de 14 000 km². Situé en Manche occidentale, il est délimité par une ligne joignant au nord le Cap de la Hague et la fosse des Casquets puis à l'ouest jusqu'au Héaux de Bréhat (Figure 6). Il contient de nombreuses îles (Guernesey, Jersey, Serq, Aurigny, Chausey) et plusieurs grands plateaux rocheux (les Minquiers, les Ecrehoux, les Roches Douvres). A l'intérieur du golfe, la bathymétrie n'excède pas 60 m de profondeur avec une profondeur augmentant progressivement en direction du nord-ouest. La circulation résiduelle dans le golfe est fortement marquée par la présence de tourbillons cycloniques et anticycloniques (Orbi 1986, Salomon et Breton 1991) (Figure 6). Les principaux tourbillons cycloniques sont localisés autour des îles de Guernesey et de Jersey ainsi qu'autour du plateau des Minquiers. Les tourbillons anticycloniques sont quant à eux plus petits et localisés au nord et à l'ouest de Jersey, au nord de Saint-Brieuc et à l'entrée du Mont-Saint-Michel. Ces tourbillons peuvent participer à la rétention des particules en zones côtières en augmentant le temps de résidence des masses d'eau (Largier 2003). Ainsi ces structures tourbillonnaires pourraient expliquer l'isolement des eaux du golfe Normand-Breton par rapport aux eaux d'origine atlantique de la Manche (Bailly et Guéguéniat 1999). Plus récemment, Ménesguen et Gohin (2006) ont suggéré l'existence de deux types de tourbillons dans le golfe : (1) des tourbillons induits par des effets de caps qui agissent comme des zones d'accumulation et (2) des tourbillons qui se développent autour des îles et se comportent comme des zones accumulation plus faibles autour de Jersey ou, à l'inverse, comme des zones de dissémination autour de Guernesey.

La température de surface suit un gradient côte-large allant du nord-ouest vers le sud-est et qui fluctue en fonction des saisons. Par ailleurs, Pingree et al. (1974) a décrit la présence d'un front thermique persistant (SO –NE) entre les îles de Jersey et Guernesey. Ce front est associé à une zone d'accumulation d'organismes planctoniques. Un front similaire a également été décrit au nord-Ouest de Guernesey. Ces fronts thermiques peuvent être des facteurs essentiels pour expliquer la distribution spatiale des espèces benthiques.

Les concentrations en chlorophylle-a se distribuent également le long d'un gradient spatial (Ménesguen et al. 2007). Les plus fortes valeurs (>2 µg/l) sont observées le long de la côte ouest Cotentin alors que les plus faibles valeurs (<0.75 µg/l) sont localisées à l'ouest de Jersey, mais également dans le fond de la baie du Mont Saint Michel en raison de sa forte turbidité. Ces valeurs apparaissent cependant relativement plus faibles en moyenne que sur de nombreux sites du Nord-Ouest et du Sud de la Bretagne.

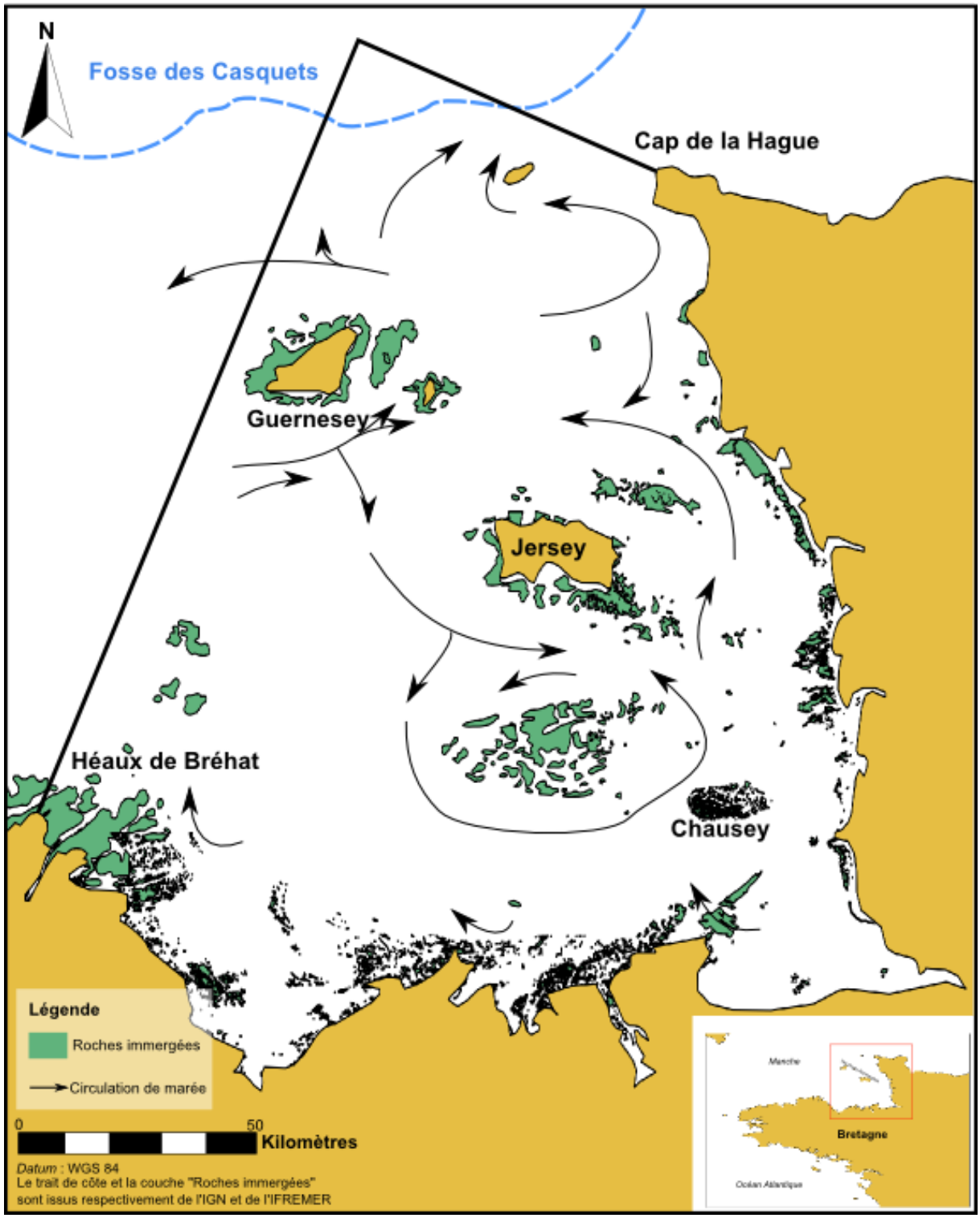

Figure 6 : Localisation, description et circulation de marée à l'intérieur du golfe Normand-Breton d'après Orbi (1986).

Les roches de Penmarc’h

Les roches de Penmarc’h constitue un secteur Natura 2000 d’une surface de 455.78 km² (dont 40% de surface rocheuse) et se situe à l’interface entre la mer d’Iroise à fort hydrodynamisme et le golfe de Gascogne au marnage et à l’hydrodynamisme moins important (Figure 7). Ces deux entités sont séparées par un ensemble de pointes et de récifs ayant des pentes très abruptes notamment à proximité de l’isobathe -50m. Ces massifs rocheux sont fortement exposés à la houle du large et aux vents dominants. Les apports terrigènes sont limités sur ce secteur et favorisent donc des eaux claires (Doré 2012).

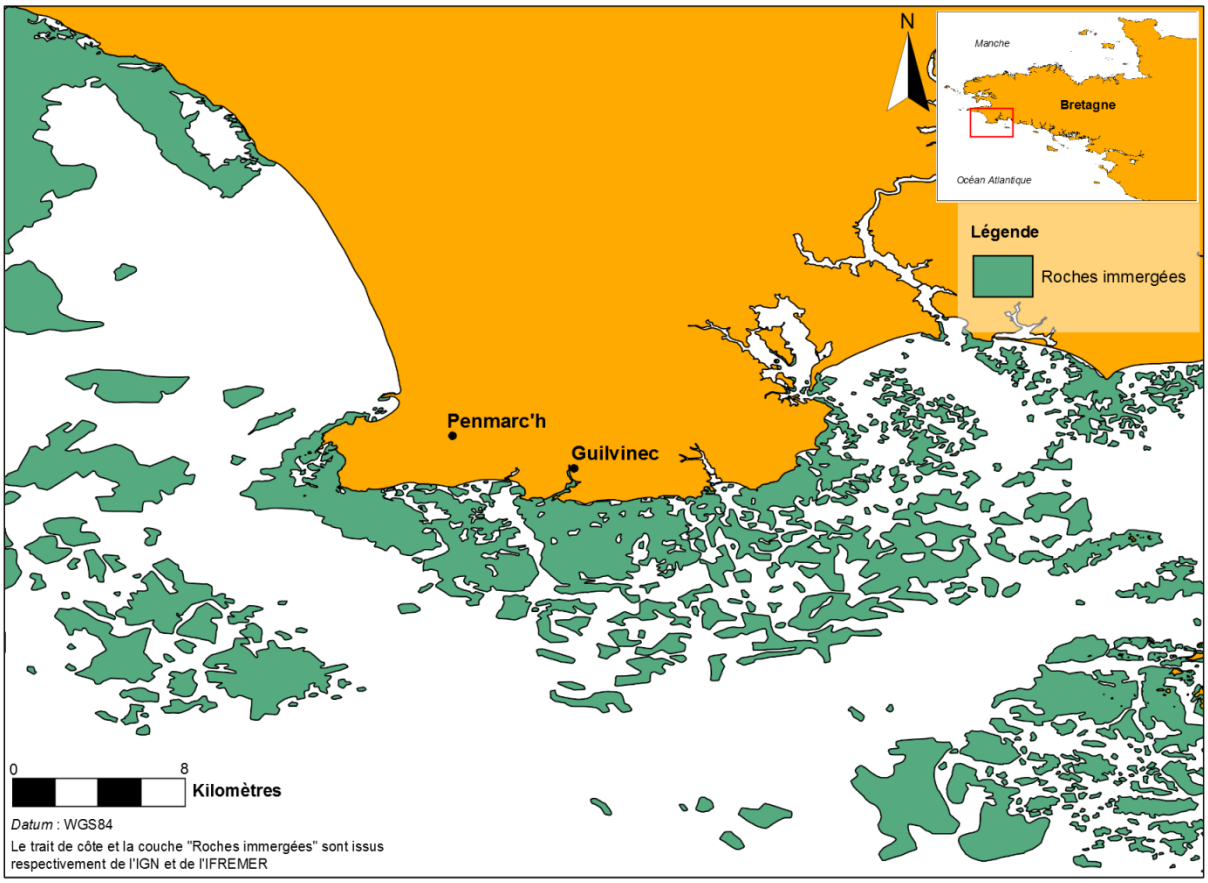

Figure 7 : Localisation et description du secteur des roches de Penmarc’h

Objectifs scientifiques et plan de la thèse

Bien que les formations à rhodophycées soient extrêmement étendues, leurs rôles au sein des écosystèmes restent encore bien méconnus. Elles se développement non seulement sur les substrats rocheux mais également en plaquage sur les substrats meubles peu remaniés, depuis la surface (au-dessus du 0 des cartes) jusqu'à des profondeurs de plusieurs dizaines de mètres. Leurs biomasses sont fortes et elles contribuent recyclage du carbone inorganique dissous en carbone organique assimilable pour les systèmes adjacents. Contrairement aux habitats à Laminaires où l'intégration de la matière organique repose sur le paradigme de « l'outwelling » développé par Odum (1968) - c'est-à-dire que les laminaires produisent plus de matière que les organismes ne peuvent en consommer sur place - l'intégration de la matière organique issue rhodophycées reste encore insuffisamment comprise bien que la production associée à ces habitats soit probablement équivalente à celle des phanérogames marines plus largement étudiées.

L'objectif de la thèse est de mettre en évidence les liens existant entre la diversité, la structuration des assemblages à rhodophytes et les attributs fonctionnels de ces assemblages au sein des écosystèmes côtiers. Ce travail s'articule autour de trois parties :

Au préalable , un protocole d'échantillonnage a été développé et appliqué dans le cadre de cette thèse pour optimiser la prise d'information afin de décrire et suivre la structuration des assemblages vivant sur les substrats rocheux face à des contraintes environnementales.

(1) Comment les habitats à rhodophytes sont-ils structurés face à des forçages environnementaux dans un contexte de changements globaux? La quantité de matière organique produite est-elle aussi influencée par ces forçages environnementaux et dépend elle de la composition des assemblages ?

Cette première partie, dans un premier temps, décrit l'évolution de la distribution des communautés algales autour de la Bretagne entre 1992 et 2012. Pour cela, deux méthodes d'analyses complémentaires (multivariées et modèles de distribution) ont été employées pour suivre la distribution de ces assemblages. Dans un second temps, une campagne échantillonnage *in situ* réalisée sur deux façades océaniques a permis d'analyser et de modéliser la structure des assemblages en fonction des conditions abiotiques contrastées et le lien existant entre cette structure et la quantité de matière produite.

(2) Comment évoluent la biomasse et la productivité des assemblages au cours d'un processus de colonisation ? Est-ce-que la biomasse et la productivité sont contrôlées par la composition (diversité et abondance relative) des assemblages ? ou au contraire est ce qu'il existe une redondance fonctionnelle entre les espèces qui conduirait à un maintien de la biomasse et de la productivité quelle que soit la structure et/ou la biomasse des assemblages ?

Cette seconde partie décrit le processus de colonisation au sein d'un habitat à rhodophytes à la suite d'une perturbation simulée par l'utilisation de plaques de granit posées à même la roche, au sein d'habitats colonisés par les rhodophytes, pour suivre à la fois l'évolution de la production et de la productivité au cours de la colonisation. Les résultats seront analysés de manière à identifier un potentiel lien entre diversité, production et productivité

(3) Quel est le devenir de la matière organique issue des habitats à rhodophytes dans le réseau trophique ?

Cette dernière partie est la plus exploratoire du manuscrit, étant donné que les analyses chimiques ont été réalisées durant l'été 2013. Elle se compose de deux études préliminaires ayant recours à deux traceurs, les acides gras et les marqueurs isotopiques, permettant de rechercher des voies d'intégrations de la matière organique produite par les algues rouges dans les réseaux trophiques formés par les espèces caractéristiques des habitats à rhodophycées.

PARTIE 1 :
MÉTHODOLOGIE

I-1 Article 1: « Optimization of an "*in situ*" subtidal rocky-shore sampling strategy for monitoring purposes. »

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Optimization of an "*in situ*" subtidal rocky-shore sampling strategy for monitoring purposes

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ABSTRACT

This study compared 2 standardized protocols to monitor subtidal rocky shores. We tested 2 sampling methods (temporal unit and quadrat) to assess the efficiency of extracting biota parameters (diversity, abundance, and biomass) of macroalgae, Mollusca, and Porifera with respect to time–cost and the number of sampling units. Species richness and occurrence of rocky subtidal habitats were better described by visual censuses than by quadrats. The same estimated richness was provided by the 2 methods. The association of a visual census and a quadrat was the most efficient way for responding to the requirements. A minimum of 5 sampling units per discrete area is recommended for accurately describing habitats. Then, we tested the sensitivity of the proposed protocol on the Bizeux Islet to study the variations of community structures according to depth and station. Based on the results, recommendations for monitoring purposes have been proposed according to European directives.

1. Introduction

After the ratification of the Bern Convention on the conservation of European wildlife and natural habitats, European states implemented regulations to protect, conserve, and restore threatened habitats. The habitat directive (HD, 92/43/EEC) was first voted to maintain and/or restore biodiversity in Europe by listing habitats and species of common interest according to their status (i.e., potentially rare, endangered, vulnerable, endemic). This directive was very useful in defining protected areas in which 1 or several listed habitats or species occurred and for designing management plans for their conservation. To fix management limits, the notion of "good ecological status" was introduced in the Water Framework Directive (WFD, 2000/60/EC) and based on a set of indices, including biological. More recently, it has been suggested that an ecosystem-based approach represents one of the most important requirements for sustainable environmental management (Van Hoey et al., 2010). The Marine Strategy Framework Directive (MFSD, 2008/56/EC) has deeply integrated this approach in defining the "good environmental status" (GES) of marine habitats from the coastal baseline to 200 nautical miles offshore. Eleven descriptors have been created to monitor all compartments of marine habitats (see in Lyons et al., 2010). These descriptors are split into 2 categories: ecosystem state and environmental pressures. Among descriptors for ecosystem state, descriptor 1 concerns the biodiversity of all marine habitats, descriptor 2 aims to limit the invasion of alien biological species, descriptor 4 is to conserve all the elements of the ecosystem's biodiversity to enable it to function efficiently, and descriptor 6 focuses on maintaining sea-floor integrity. Marine ecosystems have been separated into functional compartments including benthic habitats. For benthic habitats, the extent of their distribution and conditions are the main criteria for GES. Conditions should be described through species composition; community structure, defined by occurrence and the relative abundance of species; and biomass compared with physical, hydrological, chemical, and various pressure parameters. Besides the aim to maintain biodiversity, condition indicators should also reflect food-web structure, impacts of non-indigenous species, and sea-floor integrity (notably, versus physical pressures).

As a consequence, there is an increasing need for surveys in order to obtain reliable data on biological diversity and, more specifically, to detect the occurrence of rare species (for HD purposes); determine the relative abundance of species to calculate qualitative indicators of good ecological status for WFD; and compile quantitative information on community structure and habitat diversity for MSFD. It must be stressed, however, that there is a lack of effort to coordinate surveys and propose methods that simultaneously satisfy several objectives.

Despite their commonness and the importance of their roles in the ecological functions of coastal systems, the rocky subtidal habitats remain rarely studied, mainly because they are difficult to sample (Van Rein et al., 2009). Indeed, it is practically impossible

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to use corers, nets, and more general devices that are manipulated from the surface; therefore, there are only 2 common ways by which to describe the communities. First, remotely operated vehicles (ROVs) or cameras that operate from the surface provide representations that are accurate enough to differentiate main habitats (Akçali and Cirik, 2007; Meinesz, 2007) and measure habitat area (Yamamuro et al., 2000). A few samples might be taken by some types of ROVs, but, globally, surface coverage remains low and more accurate habitat characteristics (for example EUNIS 4 or 5 levels) cannot be described. The only way to provide accurate descriptions of communities in circalittoral region (e.g., a depth from 10 to 40 m) is by sampling performed using scuba-diving equipment (Guidetti et al., 2004). Using scuba-diving equipment requires technical skills and presents a number of limitations. In particular, the dive time and depth is limited by security constraints (Joiner, 2001); therefore, far more than for terrestrial environments, scuba-diving sampling requires design methods that optimize efficiency and reduce time. A number of methods are used to characterize rocky shore communities. Quadrats are among the quantitative methods most used to describe species richness and abundance in subtidal rocky habitats in all European countries (Murray, 2001; Pagola-Carte and Saiz-Salinas, 2000; Taylor, 1998; Terlizzi et al., 2003) and are helpful for monitoring specific characteristics such as seagrass cover (Duarte and Kirkman, 2001), seaweed distribution and structure (Pehlke and Bartsch, 2008), and invertebrate distribution (Detwiler et al., 2002). It must be stressed, however, that quadrats generally address only a small sampling surface and there is obviously a need for adequate small- and large-scale spatial replication to efficiently assess the diversity of benthic organisms (Murray, 2001). The so-called "underwater visual census" (UVC) method, used to survey reef fishes, is done on a large scale. UVC benthic surveys are typically done by laying out rope or lines on the sea bottom, after which a diver follows the lead lines and counts the species. Such rope transects are slow to deploy and retrieve, limiting the number of transects that can be completed within a specific time period. Several methods for carrying out UVC surveys without using transect lines have been developed to increase the efficiency of sampling. For example, timed swims, manta-tows, flow meters, and underwater transect video recording. To our knowledge, no published studies have attempted to compare the efficiency of a quadrat method with UVC methods for European coastal areas.

The aim of this paper is to compare the efficiency of sampling in terms of time and the efficiency of the sampling unit for an innovative standardized visual search method (large area investigated) and a classical quadrat (definite small area) in order to describe the community of red algae biocenosis in the infralittoral and circalittoral rocky habitats of Northern Brittany (Western France). We focused on 4 major taxa: Rhodophyta, Heterokontophyta, Mollusca, and Porifera. Macroalgae and Porifera are considered engineer species that are important as habitats for complex and diversified biocenoses (Bell, 2008). In addition, these clades belong to different trophic levels – primary producers (macroalgae), suspensivorous feeders (Porifera), and grazers–omnivore-deposit feeders (Mollusca) – and their diversity and abundance could reflect the complexity of subtidal biocenoses; therefore, we presume that these taxa constitute good surrogates for evaluating benthic subtidal rocky shore biodiversity.

The methods are developed to address to the issues of HD, WFD, and MFSD as they enable us to describe the community structure by providing the following:

(i) Specific composition and species occurrence.
(ii) Species relative frequencies.
(iii) Species abundance (density and biomass).

We first tested the efficiency of each method to sample species diversity, occurrence, and abundance by modeling the relationship between sampling effort and community structure. We have discussed and illustrated the tradeoff between sampling effort and the quality of the information obtained through each method and combination of methods to characterize the community, especially in terms of species richness and structure under 2 contrasting conditions. The discussion will provide arguments for choosing methods according to environmental objectives issued, for example, by different European directives.

2. Materials and methods

2.1. Study area

The subtidal area – Bizeux Islet (48°36.677 N/2°01.602 W – WGS84) – is a granitic islet with an area of approximately 0,025 km^2 and is located at the outlet of the Rance River, in the bay of Saint-Malo (south of English Channel). It is protected against dominant wind and waves (Fig. 1) and is part of a turbid system with strong bidirectional marine tidal currents enforced by the tidal hydropower dam of the Rance Estuary. The tidal maximal amplitude is 13 m during spring tides and current velocity can be as much as 10 knots.

2.2. Sampling methods

We sampled 2 stations characterized by contrasting environmental conditions: (i) station 1, a rocky plateau, with a gentle slope ranging from −2 to −8 m Cartes Marine (CM; i.e., corrected to the lowest astronomical tide level) in the north, was protected from the Rance dam's tidal currents; and (ii) station 2, in the south, was directly exposed to the dam's tidal currents and the subtidal area was characterized by 10-m-high subtidal cliffs (−2 to −13 m CM) with rock boulders at the bottom. At each station a transect line was placed on the steeper slope to cross all algal belts over a limited distance: (i) a kelp belt extending from a depth of 0 m to depths with kelp density <5 ind m^{-2}, (ii) red seaweed belts from the lower limit of the kelp belt to depths with red seaweeds density <5 ind m^{-2}, and (iii) belts without seaweed.

Two sampling methods were used in the successive algal belts:

Underwater visual census (*UVC*): Visual census was composed of 4 observation sequences of 5 min each: (i) From 0 to 5 min, divers moved at 50 cm above the bottom and listed all the species observed. (ii) From 5 to 10 min, divers stopped and listed all species within an area of 1.0 m^2. (iii) From 10 to 15 min, diver activities were identical to those of the first sequence. (iv) From 15 to 20 min, diver activities were identical to those of the second sequence. When in doubt during subtidal identification, the species were collected and identified at the laboratory.

Quadrat sampling (*QS*): We used a 0.25 m^2 rectangular quadrat adapted to sampling macroorganisms from 1 to 30 mm, as suggested by Murray (2001). In each algal belt, a minimum of 5 quadrats were randomly set at each side of the transect line. All divers scratched off macroalgae, Mollusca and Porifera phyla in each quadrat with a trowel, and then species were placed on labeled bag and frozen at −20 °C.

Ten scuba divers collected samples from February through April 2010. Access to the sampling sites was conditioned by the hydroelectric production of the Rance dam. The dives took place during slack water and were limited to 60 min. For the 2 methods, each collected species was placed into labeled plastic bags during the dive. Sampling effort for each method is given in Table 1. A minimum of 5 sampling units were made according to a sampling design decided before diving. According to the area investigated,

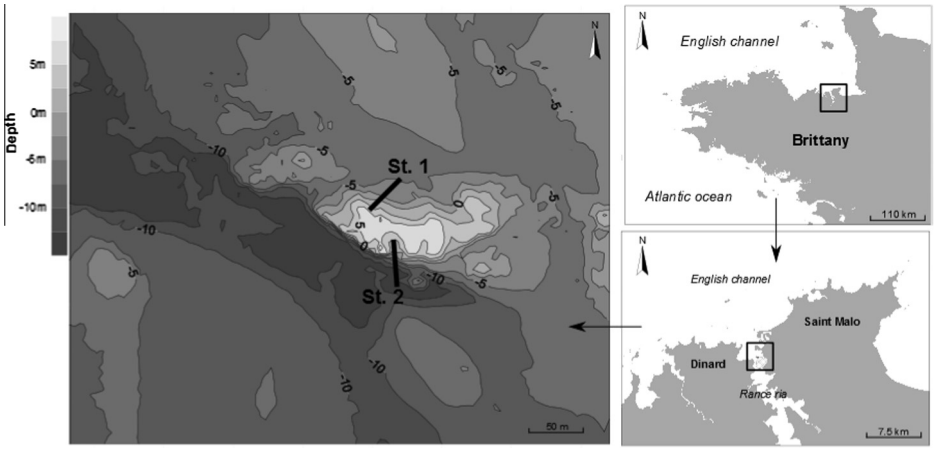

Fig. 1. Multi-beam map (resolution: x and y = 0.5 m; z = 0.01 m) of the study area in the mouth of the Rance.

Table 1
Sampling effort for each method between the 2 stations, below the total time in parenthesis is expressed in minutes. 15′ are necessary for one quadrat and 20′ for one UVC. S1: Station 1 (North); S2: Station 2 (South). C1: brown seaweed belts; C2: red seaweed belts; C3: aphytal belts.

	Station 1			Station 2			TOTAL
	C1	C2	C3	C1	C2	C3	
UVC	6 (120′)	6 (120′)	5 (100′)	6 (120′)	6 (120′)	5 (100′)	34 (680′)
QS	8 (120′)	7 (105′)	9 (135′)	6 (90′)	10 (150′)	8 (120′)	48 (620′)

the visual census required 20 min (estimated area of 10 m^2 surveyed) and the quadrat method required 15 min (0.25 m^2).

2.3. Species identification

All samples were filtered on a 1-mm mesh sieve and residues were stored in a freezer at −20 °C. All organisms were identified to species level using the following identification field keys: macroalgae (Cabioc'h et al., 2006; Hiscock, 1986), Mollusca (Alastair Graham, 1988; Hayward and Ryland, 1995; Poppe and Goto, 1991), and Porifera (Ackers et al., 1992; Doré et al., 2008). All species names were verified and updated from the European Register of Marine Species database (Costello et al., 2008) and Algaebase (Guiry and Guiry, 2013).

2.4. Biomass measurements

All individuals collected were dried in a stove for 48 h at 80 °C to obtain the dry weight.

2.5. Abiotic data

Water depth (corrected to the lowest astronomical tide level) was calculated from bathymetric data derived from a digital terrain model. Hydrodynamic data were extracted from a hydro-sedimentary model (SOGREAH, 2001).

2.6. Data analyses

The objectives of the statistical analyses were to (1) determine the link between sampling effort and robustness of each method; (2) determine the link between sampling effort and a reliable description of assemblage frequency of occurrence and abundance; (3) examine the ability of the sampling design and methods to detect assemblage variations according to environmental parameters (namely, depth and currents).

2.6.1. Relationship between sampling effort and efficiency

The entire dataset was pooled to analyze the efficiency of each method to estimate species richness. Total richness, mean richness per unit, and diversity estimators (Chao2 and ICE) were used to describe the diversity listed by both methods. The completeness index (CI) calculated was the ratio between the richness observed and the richness estimated by Chao2 (Chao, 1984). CI was assessed using the method developed by Soberón et al. (2007) and was calculated for each method using the estimated richness calculated for all methods combined for all phyla. We also tested the capture rate (i.e., the ratio between richness and the sampling effort or the number of species per minute of sampling effort). Accumulation curves were computed to test relationships between sampling effort and assemblage richness for each method. Each combination of samples was drawn randomly to evaluate the richness observed (Coleman et al., 1982). We calculated the theoretical species richness for each method and clade combination using Chao's method (Chao, 1984). The accumulation curves were then expressed as a percentage of the maximal theoretical species richness. The number of sampling units where half the maximum richness is achieved was determined using a model for describing species–area and species–sample relationships (Dengler, 2009). Species–sample relationships necessarily reach a maximum of richness value asymptotically (Dengler, 2008; Gotelli and Colwell, 2001). According to this postulate, we chose the Lomolino function (Lomolino, 2001; Tjørve, 2003)

$$S = \frac{asympt}{\left(1 + slope^{\log\left(\frac{xmid}{A}\right)}\right)} \quad (1)$$

where S is species richness, A is area (samples), *slope* is the maximum slope of increase of richness, *asympt* is the asymptotic maximum number of species (we forced the model to choose the Chao estimator as asymptote), and *xmid* is the number of sampling units where half the maximum richness is achieved.

2.6.2. Relationship between species occurrence and abundance rank correlations and sampling effort

Both visual census and quadrat were used to describe diversity and occurrence frequencies. Relative abundance and biomass parameters were calculated from only the quadrat samples. The assemblage structure was expressed using 2 metrics: occurrence frequency and species relative abundance. In terms of occurrences, we defined rare and common species according to Gaston (1994). The cutoff point was calculated using the first quartile of frequency distribution of species occurrence (i.e., 25% of species with the lowest occurrence). The species occurrence frequency was calculated by incrementing sample by sample from a minimum of 2 samples to the total samples for each method and it was compared with a reference sample. The reference sample was composed by total samples for each method. For relative abundance, we calculated the ratio of the number of individuals for each species to the total number of individuals for all species. The same procedure as above was carried out. A training dataset was extracted from the total dataset using a bootstrap procedure (100 repetitions). Occurrence frequencies and relative abundance were calculated for each method ($n = 2$) and for each phylum ($n = 3$).

Similarity between the reference and samples was calculated using spearman's correlations. The average spearman correlations were then plotted against sampling effort expressed as a time and number of samples.

2.6.3. Ability of the sampling design and methods to detect assemblage variations according to environmental parameters

Finally, we separated the dataset according to stations and to belts to test the performance of the 2 methods combined (UVC + QS) in detecting variation of assemblages between the 2 stations along a bathymetric gradient. Hierarchical clustering analyses using the Jaccard distance and boxplots associated to Kruskal–Wallis tests were performed to verify and assess the performance of the combined method to discriminate different assemblages.

All analyses were performed using the R software (R-Team, 2010) and the vegan (Oksanen et al., 2010) and ade4 (Chessel et al., 2004) packages.

3. Results

3.1. Comparison of sampling efficiency

3.1.1. Species richness

After 34 dives totaling approximately 22 h of observation, 125 species were identified comprising 41 macroalgae (38 *Rhodophyta* and 3 *Heterokontophyta)*, 32 Porifera, and 52 Mollusca. The 2 methods provided complementary information on species richness; neither method, taken individually, enabled us to sample total species richness. If specific richness is higher for macroalgae and Porifera with UVC than with QS, specific richness remains unexpectedly similar for Mollusca using both methods (Table 2).

Each method listed more than 45% exclusive species (i.e., species listed by only 1 method). According to our rarity cut-off point, only rare species (occurrence <2) were exclusively collected by 1 method. There was not significant difference in listing common species (occurrence >2) by both methods (Kruskal–Wallis test, $df = 2$, p-value <0.01) (Fig. 2). This clearly indicated that common species were listed by both methods regardless of total sampling time (Table 3).

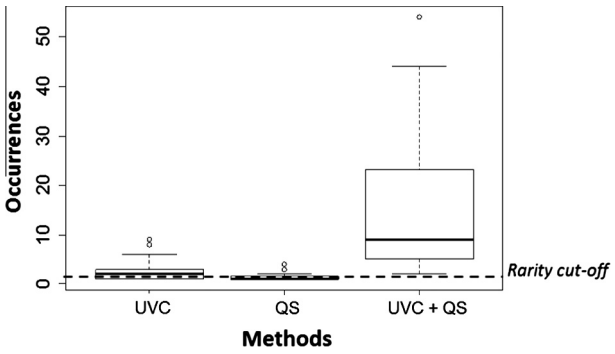

Fig. 2. Boxplots of species occurrences. Bold line: median; quartiles from the bottom upwards: 12.5–25–75–97.5 quartiles. UVC = exclusive species listed by UVC ($n = 38$); QS = exclusive species listed by QS ($n = 22$); UVC + QS = species listed by both methods ($n = 65$).

Although the completeness indices were generally low, both Chao and ICE estimators gave the highest values of estimated richness for macroalgae and Porifera with UVC. In contrast, estimated richness given by the Chao estimator was higher with QS for Mollusca.

For each taxa, UVC listed, on average, more species per sampling unit than quadrats (U-Test, $df = 1$, p-value <0.05 for each taxa) and the capture rates by QS were generally lower than for UVC (U-Test, $df = 1$, p-value <0.05 respectively, for macroalgae, Porifera, and Mollusca). Referring to the difference in the surface area investigated and the difference in overall underwater sampling time between the 2 methods, UVC was expected to be a more efficient way by which to describe the diversity of the target phyla. For Mollusca, despite the fact that capture rates and the average number of species per quadrat were low, QS allowed a better detection of new Mollusca species per sampling unit.

For all clades, UVC reached the asymptote quicker than quadrats. The asymptote was reached for UVC in macroalgae and Porifera (Fig. 3). The visual census reached half of the total estimated richness within approximately one half the sampling effort than was needed for QS. Lomolino's slopes were similar among methods, and comprised between 1.98 and 2.11 sp mn^{-1} according to methods and taxa. The xmid point was always higher with quadrats 23.21–32.51 according to taxa versus 10.29–20.71 for

Table 3
Number of species listed only by each method (UVC and QS), listed by both methods (UVC + QS), and the Jaccard similarity based on presence/absence of data provided by temporal unit (UVC) and quadrats (QS). Values in parenthesis refer to percentage of species listed only by each method relative to the total richness of the phylum considered.

Phyla	UVC	QS	UVC + QS	Jaccard similarity
Macroalgae	13 (31%)	5 (13%)	23	0.56
Porifera	12 (36%)	7 (21%)	14	0.43
Mollusca	13 (25%)	11 (21%)	28	0.54

Table 2
Species richness collected for each sampling method and estimation of total richness of assemblages using the Chao-2 estimator (Chao, 1984) and the incidence-based coverage estimator (ICE) (Lee and Chao, 1994); the completeness index is the ratio between observed and estimated richness. Catch: capture rate (nb species/mn); UVC: temporal unit; QS: quadrat sampling; N: number of sampling units; S: species richness; IC: completeness index; $S_{mean} \pm SD$: mean number of species captured per sampling unit with standard deviation.

	Time per sample	Macroalgae							Porifera							Mollusca						
		N	*S*	$S_{mean} \pm SD$	*Chao*	*ICE*	*CI*	*Catch.*	*N*	*S*	$S_{mean} \pm SD$	*Chao*	*ICE*	*CI*	*Catch.*	*N*	*S*	$S_{mean} \pm SD$	*Chao*	*ICE*	*CI*	*Catch.*
UVC	20	34	36	6.6 ± 4.7	42	39	0.67	1.09	34	26	5.9 ± 2.8	27	27	0.68	0.79	34	41	5.9 ± 3.8	67	47	0.57	1.37
QS	15	48	28	2.7 ± 3	34	31	0.53	0.97	48	21	2.5 ± 2.5	30	26	0.55	0.72	48	39	3.8 ± 3.6	72	47	0.54	1.00
Total richness			41		53	49				33		38	38				52		72	58		

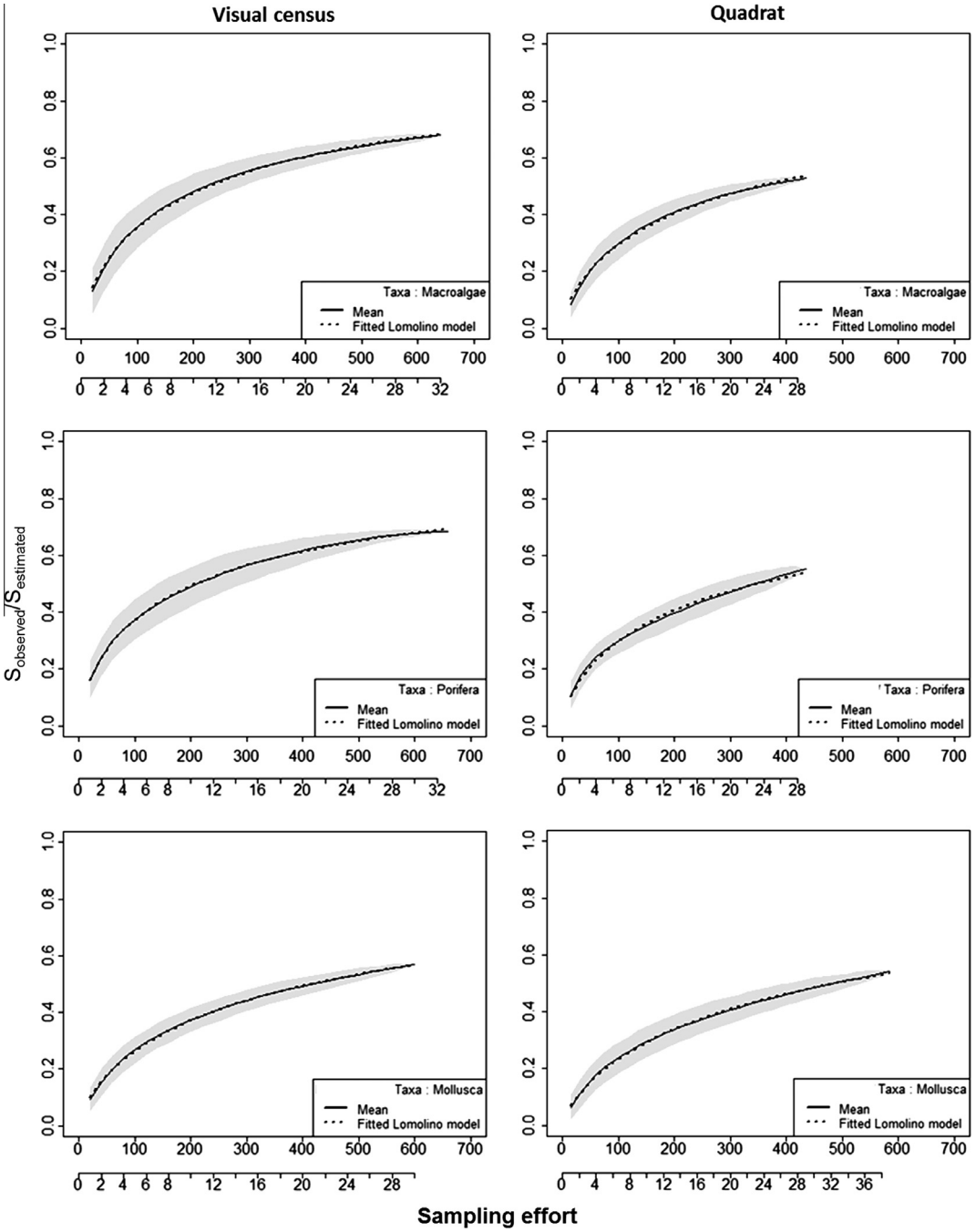

Fig. 3. Variation of the completeness of the sampling (expressed as the percentage of total estimated richness, Sobs/Spred) according to the sampling effort in minutes (upper abscissa) and in sampling units (lower abscissa). The mean (plain line) and standard deviation (gray) are calculated after 100 permutations.

UVC. The xmid values were significantly higher for Mollusca than for the 2 other taxa (Table 4). This was also related to the higher number of unique species and duplicates found among Mollusca.

Table 4
Parameters predicted by the Lomolino model on the accumulative curves. S: estimated species richness, slope: maximum species increase per sampling unit, xmid: number of samples needed to obtain half the estimated richness. Temporal unit (UVC), quadrat sampling (QS).

		Lomolino model parameters		
Taxa	Methods	S	Xmid	slope
Macroalgae	UVC	53	11.23	2.08
	QS	53	23.40	1.99
Porifera	UVC	38	10.39	2.0
	QS	38	23.21	1.98
Mollusca	UVC	72	20.71	2.05
	QS	72	32.51	2.11

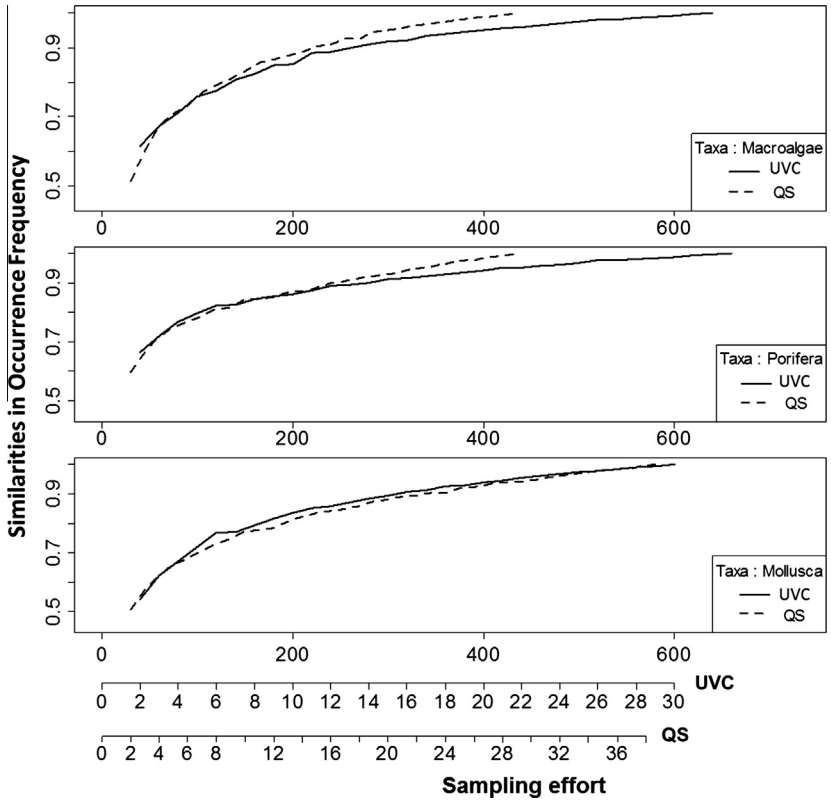

Fig. 4. Relations between species occurrence rank correlations (Rho Spearman coefficient) and sampling effort of assemblages. The spearman coefficient (Rho) was calculated using the "leave-one-out" bootstrap (100 repetitions) on the "presence only" dataset. Top abscissa: sampling effort in minutes; bottom abscissa: sampling effort in sampling units. Plain line: visual census – dash line: quadrats.

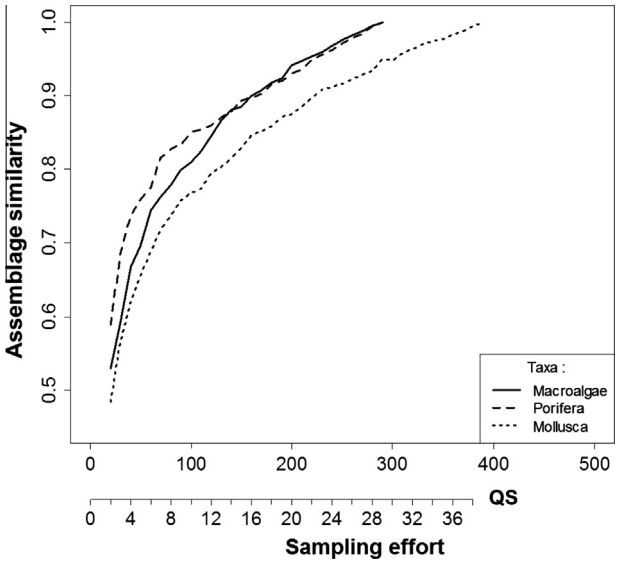

Fig. 5. Relationship between species abundance rank correlation and sampling effort in communities of A, macroalgae; B, Porifera; C, Mollusca. The spearman coefficient (Rho) was calculated using the "leave-one-out" bootstrap on the abundance dataset (wet weight g/m^2 for seaweeds/Porifera and density in dm^2 for Mollusca). Top abscissa: sampling effort in minutes; bottom abscissa: sampling effort in sampling units.

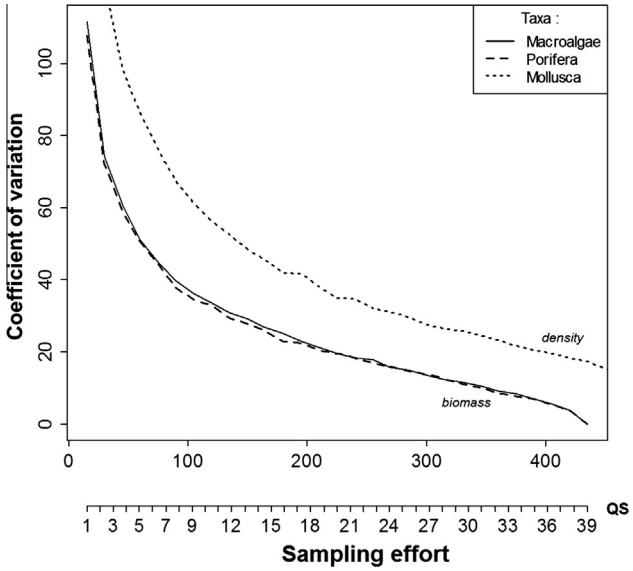

Fig. 6. Relationship between sampling effort and abundance/biomass (coefficient of variation). Biomass was used for macroalgae and Porifera, density for Mollusca. The longer abscissa represents the sampling effort expressed in minutes; the shorter abscissa represents the sampling effort expressed in units.

3.1.2. Occurrence comparison

Similarities of 0.80 were obtained after 5–8 sampling units both in quadrats and UVCs. Quadrats enabled us to obtain species rank correlations of 0.9 between the observed and reference community after 250 min for macroalgae and Porifera, while it took 400 min for UVCs (Fig. 4). In Mollusca, maximum correlations of 0.9 were obtained after 28 and 38 sampling units, respectively, for UVCs and quadrats.

3.1.3. Relative abundance

Descriptions of the relative abundance (i.e., biomass rank of species in the community) were obtained using quadrats. The

Table 5
Link between the sampling effort of the random combination UVC + QS and: (i) the percentage of the estimated richness (Chao 2); (ii) the similarity of occurrence frequencies calculated using the "leave-one-out" bootstrap; (iii) the coefficient of variation of the biomass (mean/SD) for macroalgae, Porifera, and Mollusca. The coefficient of variation of biomass and density are calculated using quadrats only.

Sampling effort	Macroalgae			Porifera			Mollusca		
	Richness UVC + QS	Occurrence frequencies similarity	Biomass (CV)	Richness UVC + QS	Occurrence frequencies similarity	Biomass (CV)	Richness UVC + QS	Occurrence frequencies similarity	Density (CV)
2UVC + 2QS	0.45 ± 0.065	0.6 ± 0.004	109.56	0.53 ± 0.084	0.64 ± 0.003	107.77	0.38 ± 0.089	0.55 ± 0.002	182.64
3UVC + 3QS	0.54 ± 0.068	0.67 ± 0.003	74.31	0.59 ± 0.082	0.7 ± 0.003	73.36	0.45 ± 0.073	0.63 ± 0.002	125.8
4UVC + 4QS	0.56 ± 0.078	0.72 ± 0.004	58.3	0.58 ± 0.09	0.75 ± 0.002	58.86	0.52 ± 0.059	0.68 ± 0.002	100.27
5UVC + 5QS	0.6 ± 0.079	0.76 ± 0.003	51.09	0.57 ± 0.104	0.78 ± 0.002	51.12	0.53 ± 0.078	0.72 ± 0.003	88.5
6UVC + 6QS	0.61 ± 0.08	0.79 ± 0.002	44.86	0.62 ± 0.08	0.8 ± 0.002	43.25	0.6 ± 0.047	0.75 ± 0.001	76.04
7UVC + 7QS	0.65 ± 0.082	0.82 ± 0.002	38.98	0.64 ± 0.057	0.82 ± 0.001	39.5	0.62 ± 0.08	0.78 ± 0.001	69.66
8UVC + 8QS	0.65 ± 0.042	0.84 ± 0.003	36.61	0.65 ± 0.068	0.84 ± 0.001	34.28	0.63 ± 0.055	0.8 ± 0	58.85
9UVC + 9QS	0.67 ± 0.029	0.86 ± 0.002	33.82	0.66 ± 0.047	0.85 ± 0.001	32.28	0.63 ± 0.072	0.82 ± 0.001	57.29
10UVC + 10QS	0.67 ± 0.043	0.87 ± 0.001	30.86	0.66 ± 0.072	0.87 ± 0.001	29.64	0.64 ± 0.072	0.83 ± 0.001	51.58
11UVC + 11QS	0.69 ± 0.033	0.88 ± 0.001	27.37	0.67 ± 0.058	0.88 ± 0.001	28.02	0.63 ± 0.082	0.85 ± 0.001	49.42
12UVC + 12QS	0.71 ± 0.046	0.9 ± 0.002	26.58	0.68 ± 0.052	0.89 ± 0.001	25.81	0.64 ± 0.07	0.86 ± 0.001	46.81
13UVC + 13QS	0.71 ± 0.035	0.91 ± 0.001	23.94	0.66 ± 0.078	0.9 ± 0.001	23.39	0.65 ± 0.056	0.87 ± 0.001	41.52
14UVC + 14QS	0.75 ± 0.033	0.92 ± 0.001	22.32	0.64 ± 0.066	0.91 ± 0.001	21.49	0.66 ± 0.053	0.89 ± 0.001	40.9
15UVC + 15QS	0.75 ± 0.034	0.93 ± 0.001	20.89	0.66 ± 0.068	0.92 ± 0.001	20.91	0.65 ± 0.058	0.89 ± 0.001	37.49
16UVC + 15QS	0.77 ± 0.033	0.93 ± 0.001	20.1	0.65 ± 0.066	0.93 ± 0.001	19.89	0.66 ± 0.064	0.9 ± 0.001	36.35
17UVC + 17QS	0.77 ± 0.028	0.94 ± 0	18.35	0.68 ± 0.059	0.94 ± 0.001	18.04	0.67 ± 0.054	0.91 ± 0.001	33.28
18UVC + 18QS	0.79 ± 0.025	0.95 ± 0.001	17	0.7 ± 0.053	0.94 ± 0.001	17.17	0.66 ± 0.041	0.92 ± 0.001	32.33
19UVC + 19QS	0.8 ± 0.031	0.95 ± 0.001	15.94	0.73 ± 0.029	0.95 ± 0.001	15.62	0.67 ± 0.038	0.93 ± 0.001	31.27
20UVC + 20QS	0.81 ± 0.024	0.96 ± 0	14.77	0.74 ± 0.031	0.95 ± 0.001	14.84	0.68 ± 0.042	0.94 ± 0.001	29.67
21UVC + 21QS	0.82 ± 0.029	0.97 ± 0.001	13.58	0.76 ± 0.03	0.96 ± 0	13.98	0.68 ± 0.042	0.95 ± 0.001	27.82
22UVC + 22QS	0.83 ± 0.02	0.97 ± 0	12.84	0.79 ± 0.047	0.97 ± 0.001	13.06	0.69 ± 0.034	0.95 ± 0	26.9
23UVC + 23QS	0.84 ± 0.022	0.98 ± 0	11.83	0.81 ± 0.041	0.97 ± 0.001	11.04	0.68 ± 0.041	0.96 ± 0.001	25.58
24UVC + 24QS	0.84 ± 0.013	0.98 ± 0	10.21	0.84 ± 0.032	0.98 ± 0	9.74	0.66 ± 0.049	0.97 ± 0.001	23.39
25UVC + 25QS	0.83 ± 0.023	0.98 ± 0	9.49	0.86 ± 0.026	0.98 ± 0	9.15	0.66 ± 0.03	0.97 ± 0	22.3
26UVC + 26QS	0.82 ± 0.019	0.99 ± 0	8.29	0.89 ± 0.019	0.99 ± 0	8.3	0.65 ± 0.043	0.98 ± 0	22.03
27UVC + 27 QS	0.82 ± 0.02	0.99 ± 0	6.7	0.9 ± 0.018	0.99 ± 0	6.82	0.62 ± 0.027	0.98 ± 0	20.71
28UVC + 28 QS	0.82 ± 0.017	1 ± 0	5.29	0.92 ± 0.017	1 ± 0	5.3	0.59 ± 0.032	0.99 ± 0	20.24
29UVC + 29QS	0.82 ± 0	1 ± 0	3.54	0.94 ± 0	1 ± 0	3.97	0.56 ± 0.03	0.99 ± 0	18.3

bootstrap procedure was applied to analyze the relationship between sampling effort and species biomass rank correlations between observed and reference communities. To obtain a similarity of 0.8 in Porifera, macroalgae, and Mollusca, respectively, 6, 6, and 14 quadrats were necessary (Fig. 5).

3.1.4. Biomass

The variability coefficient of the abundance decreased rapidly with sampling effort from 100, 100, and 130 in macroalgae, Porifera, and Mollusca, respectively, for 2 quadrats to 0, 0, and 20, respectively, in macroalgae, Porifera, and Mollusca, respectively, for 39 quadrats. This showed an aggregative distribution of the macrobenthic communities (Fig. 6).

3.1.5. The efficiency of the combination: temporal unit and quadrat

To test the capacity of our sampling design to discriminate discrete habitats of rocky shores, we resampled our dataset to produce 29 different combinations of sampling units. Each combination was composed of an equal number of UVCs and quadrats (Table 5). We calculated the variation of species richness, species occurrence rank correlations, and abundance variation coefficients according to sampling effort. This enabled us to choose the sampling effort to apply according to the objectives of the study. For example, if the objectives were to describe a reliable community structure, it was necessary to obtain species occurrence rank correlation (Rho) greater than 0.75 between the sample and reference community. In our case, this required a minimum of 5, 4, and 6 sampling units for macroalgae, Porifera, and Mollusca, respectively. Seventy-five percent of the estimated richness was obtained using 14 sampling units for macroalgae and 21 replicates for Porifera. For Mollusca, the maximum effort did not enable to sample 75% of the total diversity. In terms of abundance, for both macroalgae and Porifera, 14 sampling units were enough to obtain 25% variability of biomass; more than 23 replicates were needed for Mollusca.

3.1.6. Application to the Bizeux Islet communities

To describe Bizeux Islet communities, we tested the combination of visual censuses and of 5 quadrats per belt because it provided a tradeoff between a good description of communities' structure and the immersed working time.

Using a bootstrap procedure, we extracted 100 repetitions of 5 visual censuses and 5 quadrats per belt. Each extraction enabled us to detect similar spatial patterns within the study site and this standardized reduced sampled procedure clearly showed different patterns of community structure according to stations and belts.

First, in term of presence–absence, the bootstrap procedure revealed that for each phylum and each station, the specific composition strongly varied according to depth; however, macroalgal species assemblages were strongly similar in the brown seaweed belt (C1) of the 2 stations (Fig. 7), while Porifera and Mollusca showed marked intra-station and inter-station differences in their specific composition from the first belt. In the deeper belt, no difference was detected in species composition of Porifera between the 2 stations (Jaccard dissimilarity = 0.1), while differences in macroalgae species composition between the 2 stations appeared in C2 and C3. Species assemblages of Mollusca exhibited the highest differences between belts and stations (Jaccard dissimilarity from 0.55 to 0.65).

Second, in terms of biomass analysis, the bootstrap procedure also revealed intra- and inter-substantial differences between stations. Although the 2 stations shared the same macroalgae assemblages in C1, the algal biomass was different between the two stations.

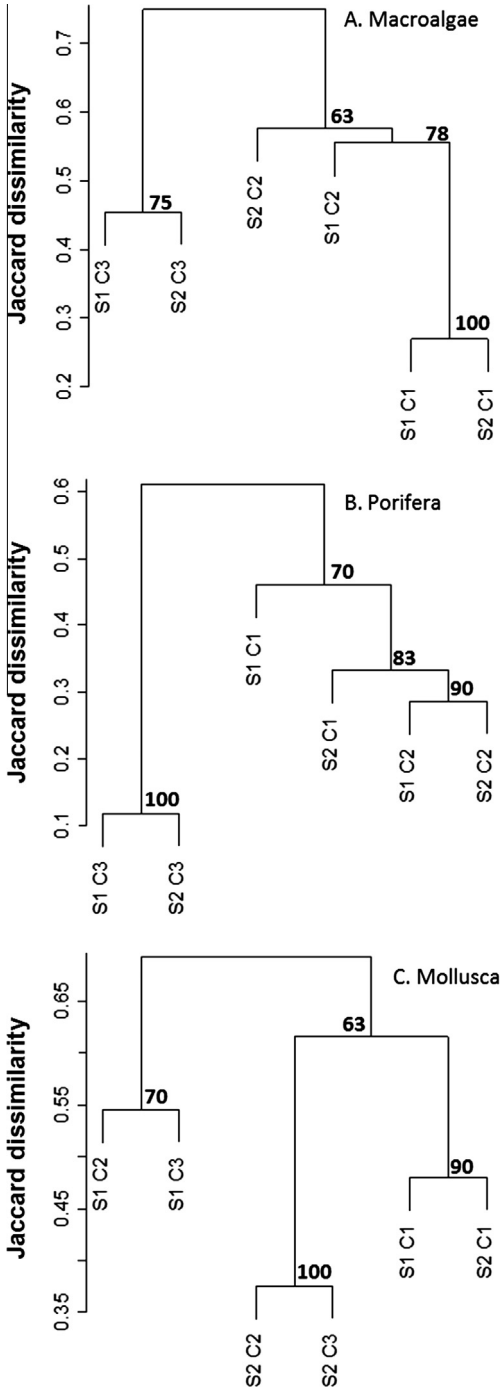

Fig. 7. Hierarchical clustering analysis using Jaccard dissimilarity of assemblages of macroalgae (A), Porifera (B), and Mollusca (C). This analysis is based on the dissimilarity (presence–absence) of species assemblages sampled using a combination of 5 quadrats and 5 visual censuses. S1: Station 1 (north); S2: Station2 (south); C1: brown seaweed belt; C2: red seaweed belt; C3: aphytal belt. Numbers indicate the result of bootstrap (n = 100).

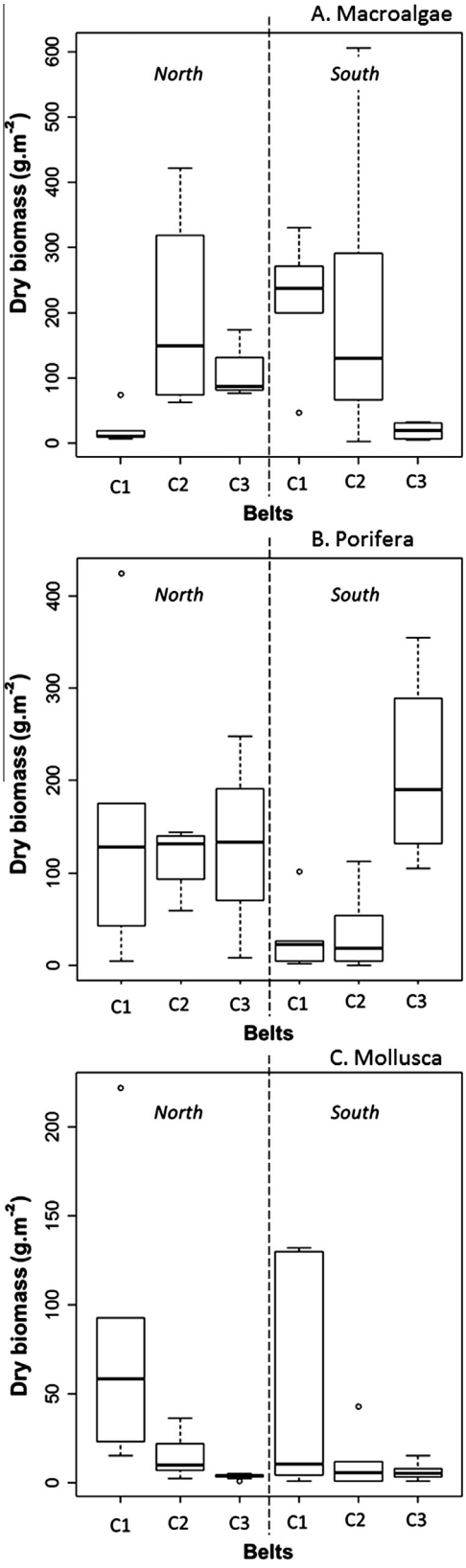

Fig. 8. Distribution of dry biomass (g m^{-2}) of macroalgae (A) and Porifera (B) and density (ind m^{-2}) for Mollusca (C). C1: brown seaweed belt; C2: red seaweed belt; C3: aphytal belt.

Overall, the algal biomass structure varied according to station and depth (Kruskal–Wallis test, df = 2, p-value <0.001). Furthermore, overall, the mean biomass of macroalgae communities was higher in the south (158.2 ± 90 g m^{-2}) than in the north (93.5 ± 65 g m^{-2}) (Fig. 8). The upper belt (C1 + C2) communities of the south station were principally characterized by *Sargassum muticum* (301.5 ± 60.21 g m^{-2}), *Undaria pinnatifida* (247.1 ± 63.51 g m^{-2}), *Phyllophora crispa* (152.2 ± 12.27 g m^{-2}), *Osmundea osmunda* (86.12 ± 20.2 g m^{-2}), *Calliblepharis jubata* (126.25 ± 51.2 g m^{-2}), *Bornetia secundiflora* (114.38 ± 14.59 g m^{-2}), and *Plocamium cartilagineum* (184.68 ± 47.2 g m^{-2}). The upper belts of the north station were dominated by *C. jubata* (78.6 ± 12.56 g m^{-2}), *Chondracanthus*

acicularis (57.4 ± 23.24 g m^{-2}), *Heterosiphonia japonica* (98.78 ± 25.2 g m^{-2}), and *P. cartilagineum* (167 ± 84.1 g m^{-2}). *S. muticum* (301.5 ± 60.21 g m^{-2}), *U. pinnatifida* (247.1 ± 63.51 g m^{-2}) were present in the north station but their biomass is lower (respectively 98.6 ± 45 g m^{-2} and 56 ± 21.3 g m^{-2}). The biomass of the lower belt (C3) for the 2 stations depended on 1 species, *Sphaerococcus coronopifolius*, which was abundant in the north station and less abundant in the south station.

For Porifera, a higher biomass occurred in the deeper belt (Fig. 8). In the south station, biomass was clearly higher in C3 with 1338.25 ± 170 g m^{-2}; but only 50 ± 27 g m^{-2} in C1 and 254 ± 90 g m^{-2} in C2 (Kruskal–Wallis test, $df = 2$, p-value < 0.01). Although the C3 belt of the 2 stations shared the same species, because of the environmental conditions, we observed a substitution in dominant species: *Dysidea fragilis* and *Hemimycale columella*. These 2 species were dominant in the north station (45.24 ± 16.22 g m^{-2} and 27.45 ± 20.86 g m^{-2}, respectively) and their biomass was less in the south (9.32 ± 7.48 g m^{-2} and 0.61 ± 0.84 g m^{-2}, respectively), in favor of *Amphilectus fucorum* and *Haliclona simulans* (30.35 ± 30.68 g m^{-2} and 35.42 ± 49.19 g m^{-2}, respectively).

For specific composition, Mollusca exhibited large differences in terms of composition according to station and depth. *Haliotis tuberculata*, *Acmaea virginea*, *Crisilla semistriata*, and *Anomia ephippium* were present in the south. In contrast, in the north station, the dominant species were *Cerithiopsis barleei*, *Diodora graeca*, and *Elysia viridis*. Density was clearly structured according to depth. The C1 belts for the 2 stations (shallow) were characterized by a high density of *Rissoa parva* (804 ± 248 ind m^{-2}), *Tricolia pullus* (888 ± 365 ind m^{-2}), and *Modiolarca subpicta* (264 ± 120 ind m^{-2}). In the C2 and C3 belts, the density of these species was significantly lower than in C1.

These results clearly showed that the choice of these specific combinations of sampling unit allows us to highlight substantial substitution of species dominance or specific composition of assemblages.

4. Discussion

It is generally accepted that designing sampling strategies for ecosystem studies often must consider the tradeoff between increasing accuracy of the measurements and reducing the costs of the study. Studying benthic communities of subtidal rocky habitats requires scuba-diving approaches that are costly and involve highly trained staff. The most important constraint is that access to sampling sites and sampling time is limited to approximately 1 h per dive and 2 dives per day to comply with security conditions; therefore, more so than in more accessible terrestrial environments, it is necessary to design sampling plans specifically to increase sampling efficiency.

This paper compared the efficiency of 2 different methods that are commonly used to study benthic communities of rocky habitats: quadrats and visual censuses.

Our study clearly showed that, for a given sampling effort, species richness and occurrence of rocky subtidal habitats were better described by visual censuses than by quadrats. First, the sampling rate of species was nearly 1.4 times greater on using visual censuses. This is most likely because of the surface area covered by sampling, which is much higher in visual censuses (approximately 25 m^2) than in quadrats (0.25 m^2). This increases the probability of contact with less-abundant species. Second, the Lomolino's xmid point showed that it took approximately one-half the time less time to sample half of the estimated species richness using UVCs than using quadrats. Ten to 20 UVCs were necessary to reach one-half the diversity, which requires considerable sampling effort; therefore, we suggest using another parameter: the inflexion point of accumulation curve. These curves are typically asymptotic with a rapid increase of species richness until an inflexion point, after which the curves tend to an asymptote. Beyond the inflexion point, the most common species are sampled, and the probability to catch rare species requires increasing sampling effort. For a visual census, this inflexion point was reached after 5–8 UVCs and Qs, which represented from 50% to 65% of the total richness, according to targeted taxa.

Third, similarities of 0.8 between sample and reference communities according to phyla were obtained after 4–5 visual censuses and 7–8 quadrats. It took about twice as long to reach similarities of 0.9.

Visual censuses are structurally discarded to provide quantitative information: relative abundance metrics of the community are obtainable only by using quadrats. The relative abundance of species appeared to be better and more rapidly described for Porifera and macroalgae than for Mollusca. The similarity between sampled and reference community structure increased more rapidly. A species abundance rank correlation of 0.8 was obtained after 70–90 min (6–8 samples) with quadrats. This suggests that a community's relative abundance was correctly described for such a sampling effort.

This sampling effort also enabled us to provide average biomass or densities that were associated with high variances (variation coefficients of 50%) most likely resulting from the aggregative distribution of benthic communities. It would be necessary to sample 15–20 quadrats to reduce the variation coefficient to 15%.

The sampling protocols designed for the Water Framework Directive usually recommend applying a minimum of 3 quadrats of 1.0 m^2 per belt to produce good indicators of the environmental status of rocky shores. In our study, we show that such an effort leads to similarities <0.65 regardless of phyla. Such results appear to be too low to obtain a reliable description of community structure in a given habitat. In turn, this is likely to lead to misinterpretations of the derived indicators. In our case, we decided to apply an effort that enabled us to obtain similarities of 0.75 between sampled and reference communities. From this value we assumed that we could describe communities to EUNIS level 5 because we provided information of dominant and engineer species. For species frequency of occurrence, this 0.75 similarity target was obtained with 3 UVCs for red algae and Porifera, and 4.5 for Mollusca (Fig. 4). For the relative abundance of species, this 0.75 target was achieved after 3, 3, and 5 quadrats for red algae, Porifera, and Mollusca, respectively.

Consequently, if the objectives of studies are to characterize habitat (detecting dominant species) at the Eunis-4 level, 3 UVCs are needed; however, to describe correctly the diversity at the Eunis-5 level at a similarity of 0.75 or 0.8), we recommend securing 5–6 UVCs per discrete area. For the Habitat and Marine Strategy Directives, which need to add abundance to the diversity to understand the functionality of ecosystems, we showed that in our sampling site, 5–8 quadrats were sufficient to obtain accurate information on abundance (biomass or density) with variation coefficients of 50%.

In our study, we decided to test combined methods (UVCs + QS) that enabled us to get a good representation of specific diversity and abundance, which are key factors to studying the influence of environmental pressures on community structure.

Our sampling plan, combining 15 sampling units per station distributed in 3 distinct belts, enabled us to detect significant variations in diversity and community structure relative to environmental factors (depth, hydrodynamics). In this study, the distribution of macroalgae appeared sensitive to hydrodynamics and depth. This is consistent with previous studies that show that water motion is a key determinant of community structure (Hurd,

2001) because of shear stress (removes macroalgae and some herbivores), the influence on the feeding rates of herbivores, and the effect on sediment movement (Airoldi and Cinelli, 1996; Blanchette, 1996; Kawamata, 1998; Kiirikki, 1996; Viejo et al., 1995).

The combination of methods (UVCs + QS) tested for this paper needs to explore protocols to reduce the time of a UVC or to adjust the size of the quadrat according to the study. For, mollusks, we must increase the effort to get a good representation of the communities. The size of mollusks ranged from 1 mm to 5 cm; consequently, during the UVC study, the probability of missing small specimens was high. Most often, small gastropods are algae dwellers; therefore, it is important to collect algae to increase small-species capture probability. For small and cryptic species, the scale of UVCs and quadrats must be adapted to be able to sample their habitats. The proposed protocol is useful for the macrobenthos (more than 10 mm); for macroalgae and Porifera, we managed to describe dominant assemblages with the precision of the Eunis-5 and Eunis-6 levels. This combination brings 2 complementary views of habitats, although quadrats bring a lot of information (quantitative and qualitative) on their structure. The visual census gives a vision of the landscape rarely analyzed in the sublittoral temperate rocky shore but it contributes to a better understanding of scale-dependent patterns and processes in physical and biological variables (Dungan et al., 2002). It is also recommended that sampling should be performed along with obtaining *in situ* photographs to eventually numerically evaluate the cover (Beuchel et al., 2010) and maintain backup data on the campaign.

5. Conclusion

The combination of UVC and quadrat is useful for analyzing the modification of communities on fine and large scales. A sampling effort can be composed of 10 min of UVCs and 1 quadrat; it mixes both qualitative and quantitative parameters that are very useful in describing an ecosystem or defining a habitat (Eunis-5 and Eunis-6 levels). A minimum of 5 sampling units (UVCs + Qs) per discrete area are necessary to respond to the requirements of the habitat directive to detect habitats of EU community importance. For the Water Framework Directive, the parameters extracted give reliable information on the community structures and the information can be integrated into quality indicators. Finally, our protocol is adapted for the Marine Strategy Framework Strategy because it enables us to detect variations of diversity and community structure (D1: biodiversity), invasive species (D2: non-indigenous species), sea-floor integrity (D6: sea-floor integrity), and the functional structure of communities thanks to the quantitative approach (D4: marine food webs). Although our conclusions are inferred from 2 stations, we make the assumption that because of the contrasting environmental conditions, the benthic assemblage structure of the area investigated is representative of the majority of the subtidal area of the western Atlantic's north coast.

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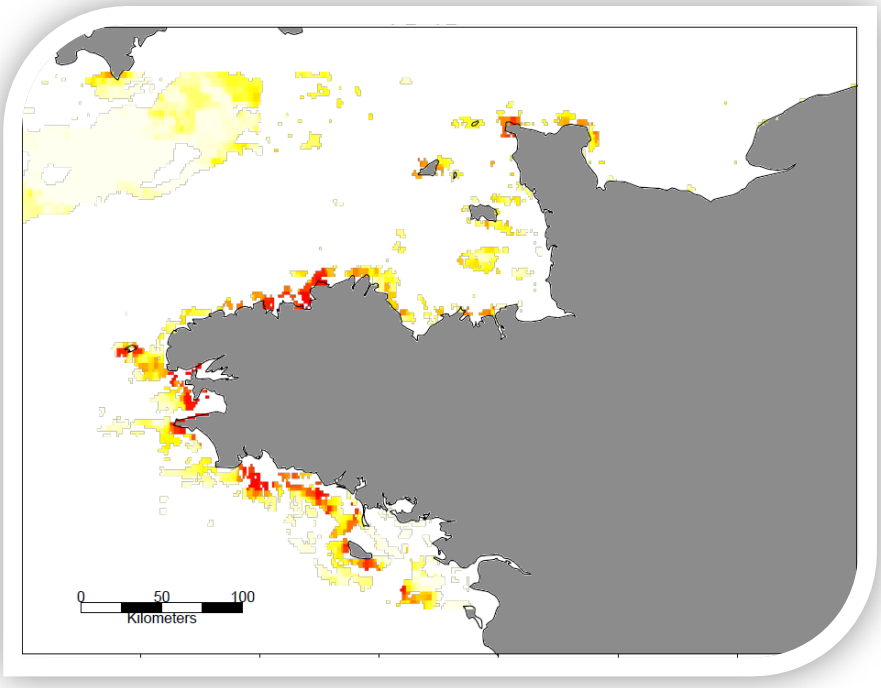
PARTIE 2 :

DISTRIBUTION BIOGEOGRAPHIQUE ET STUCTURATION DES COMMUNAUTES A RHODOPHYTES



II-1 Contexte de l'étude

La structure des communautés d'algues est influencée par de nombreux facteurs environnementaux ; la température influence la distribution spatiale des communautés, la pénétration de la lumière ainsi que la sédimentation interagissent pour maintenir l'hétérogénéité des habitats (Irving & Connell, 2002), l'abondance en nutriments et la source de nutriments influent sur la richesse algale (Gordillo, 2012), l'hydrodynamisme est un facteur majeur dans la structuration des habitats (Wernberg & Connell, 2008). Dans le contexte des changements globaux, la dimension temporelle s'ajoute à la dimension spatiale ce qui rend d'autant plus complexe la compréhension des patrons d'organisation des assemblages et de leurs évolutions en réponses aux forçages (Figure I-1).

Dans ce premier chapitre, les effets des changements globaux seront étudiés à l'échelle de la Bretagne pour évaluer l'impact sur la distribution des communautés à rhodophytes. Puis dans un deuxième chapitre, la structure de ces communautés (richesse, la diversité et abondance relative) et la quantité de matière organique qu'elles produisent seront étudiées à l'échelle du golfe Normand Breton pour comprendre et modéliser les relations entre les paramètres physico-chimiques des habitats, la structure et la fonction de production des assemblages.

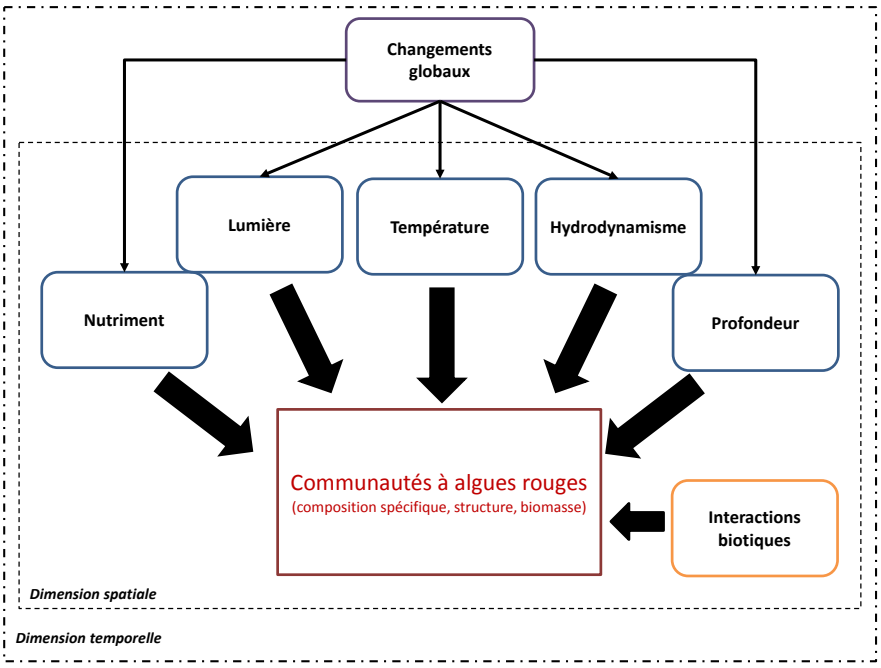


Figure I-1 : Facteurs influençant le fonctionnement et la structuration des communautés à algues rouges.

II-2 Article 2: « Twenty years of observed and predicted changes in subtidal red seaweed assemblages along a biogeographical transition zone: inferring potential causes from environmental data »

En révision dans Journal of Biogeography

Régis Gallon, Marine Robuchon, Boris Leroy, Line Le Gall, Myriam Valero and Eric Feunteun

Régis Gallon, Marine Robuchon : Prélèvements *in situ* (2010-2012), analyses, rédaction

Boris Leroy : Analyses (modélisation)

Line Le Gall, Eric Feunteun : Prélèvements *in situ* (2010-2012), amélioration du manuscrit

Myriam Valero : Amélioration du manuscrit

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ABSTRACT

Aim To assess the environmental changes within a marine biogeographical transition zone and how these changes have affected seaweed assemblages and distributions over the past two decades.

Location Brittany (Western France) is a biogeographical transition zone between the cold-temperate and warm-temperate regions.

Methods We assessed spatio-temporal variations of three environmental parameters (sea surface temperature [SST], suspended inorganic matter [SPIM], and chlorophyll-*a*) over the past 20 years in five adjoining regions by using generalised linear models (GLMs). Then, we used two complementary approaches to investigate changes in the assemblages and distributional patterns of red seaweeds based on sampling surveys conducted during two separate periods (1992–1998 and 2010–2012) over the past 20 years, namely, multivariate data analysis and species distribution models (SDMs) with a set of modelling procedures.

Results The coastal water temperature in Brittany has increased by 0.7 °C on average over the past two decades. At a finer scale, changes in SST showed that Brittany constitutes a mosaic of contrasting conditions, with the West and North-Western Brittany regions being colder and affected lesser by climate change compared to the other three regions. Increasing SST primarily caused a significant change in subtidal red seaweed assemblages over the 20-year period, whereas SST amplitude acted as the main driver of species distribution. Between the two periods, SDMs predicted significant species shifts for seven out of 10 representative species and reductions in the distribution ranges of most species.

Main conclusions Our study confirmed important differences across the different regions of the studied biogeographical transition zone. Changes in abiotic parameters and red seaweed assemblages are expected to occur at varying extremes across these regions, with the west and north-western Brittany representing the most stable zones that might constitute a potential refuge for certain species when responding to global changes.

Keywords

Assemblages/Biogeographical transition zone/Brittany/Global change/North Atlantic/Sea surface temperature/Species distribution modelling/Subtidal red seaweeds

INTRODUCTION

The fourth report of the Intergovernmental Panel on Climate Change (IPCC) indicated that global sea surface temperature (SST) has increased by an average of 0.13 °C per decade over the last 50 years (Pachauri, 2007). These rapid shifts in temperature are expected to alter the survival of organisms, by affecting their physiology and phenology (for reviews, see Hughes *et al.*, 2000; Bellard *et al.*, 2012), leading to three non-exclusives responses: (i) acclimatisation (at short timescales) or adaptation (at long timescales), (ii) migration towards places exhibiting suitable temperature ranges, and (iii) extinction. Shifts in species geographical ranges towards polar latitudes, higher altitudes, or deeper waters are the most documented responses for various species in almost all natural systems worldwide (for review, see Parmesan, 2006).

Within this context of shifting species ranges, biogeographical transition regions constitute an important focus area. In these regions, the response of species located at either the southern or northern range limits of a given species may be compared. Lima *et al.* (2007) investigated this by evaluating the direction and intensity of distribution changes of intertidal macroalgae located along the Portuguese coastline (North-East Atlantic). The temperature in the North-Eastern Atlantic region represents the main abiotic factor limiting seaweed growth and reproduction; thus, temperature directly controls the geographic boundaries of this group of organisms (reviewed by Eggert, 2012). In contrast to the expected general poleward shift, Lima *et al.* (2007) reported marked differences in the responses of cold-water and warm-water species. For instance, while the range of warm-water seaweeds has extended northwards, no significant change was observed for cold-water species. They demonstrated that single-species responses may be highly variable and that generalisations about poleward shifts, due to increasing temperature, should be made with caution.

There is increasing empirical evidence supporting northward shifts and/or changes in seaweed assemblages along European coasts. For instance, the brown seaweeds *Bifurcaria bifurcata* and *Cystoseira tamariscifolia* are extending northwards along the British and Irish coasts (Hiscock *et al*., 2004; Mieszkowska *et al*., 2005). Diez *et al*. (2012) detected substantial changes in the seaweed communities of the Cantabrian Sea (i.e. the Bay of Biscay, extending along the west coast of France to the Spanish border) during 1991– 2008. These observed changes were confirmed by recent insights obtained from species distribution models (SDMs), which, with the development and the accessibility of recent and future environmental data, have been widely used to evaluate the potential impact of climate change on biodiversity and species distribution (e.g. Thuiller, 2004; Bellard *et al*., 2012). To the best of our knowledge, studies involving SDMs have used single models, such as generalised additive models or maximum entropy (MaxEnt) models to date. SDMs have been applied to seaweeds, particularly the polar and cold-temperate communities of the North-Eastern Atlantic (Müller *et al*., 2009), intertidal brown seaweeds (Martinez *et al*., 2012; Jueterbock *et al*., 2013) and kelps (Bekkby &Moy, 2011; Raybaud *et al*., 2013). These studies have generally predicted changes in species composition and abundance in response to temperature increases.

SDMs of seaweeds have traditionally used mean, minimum, or maximum seawater temperature as predictors; however, various non-climatic factors might also act as the limiting factor in seaweed distribution, especially at local scales. For example, nutrient concentration and water turbidity may alter seaweed metabolism and hence affect their performance and survival. Recently, seaweed SDMs that combine temperature variables with other environmental factors and focus on intertidal brown seaweeds have been developed (Martinez *et al*., 2012; Jueterbock *et al*., 2013; Raybaud *et al*., 2013). These studies confirmed the predominant role of temperature in driving species distributions for some

species, especially extreme temperature values, rather than mean values. However, these studies also showed that, for some other species, non-climatic variables served as better predictors of distribution, thus highlighting the difficulty of making general predictions about seaweed distributions based on temperature parameters alone. While this difficulty in obtaining reliable predictions has been clarified for intertidal habitats exposed to extreme environmental conditions, it might not hold true for subtidal habitats, where the amplitude of abiotic variables is less drastic (Helmuth *et al.*, 2002). However, information about subtidal communities inhabiting hard substrata remains scarce (Juanes *et al.*, 2008). Moreover, subtidal seaweed assemblages are mainly composed of red seaweeds, which have a higher species richness than brown seaweeds (Guiry & Guiry, 2013), offering the possibility of assessing a large range of species-specific responses.

This study aimed to assess the environmental changes within a marine biogeographical transition zone (Brittany, France), and their impact on subtidal red seaweed assemblages and distributions over the last two decades. Brittany is a hotspot for seaweed species biodiversity (Kerswell, 2006; Santelices *et al.*, 2009) and a biogeographical transition zone between the Celtic Sea and the South European Atlantic Shelf" ecoregions and also between the Northern European Seas and Lusitanian provinces within the realm "temperate Northern Atlantic" (Spalding *et al.*, 2007). Furthermore, the coastline of Brittany is heterogeneous, both in terms of environmental conditions and marine species communities (Dauvin, 1997), and it serves as a refuge zone for numerous species (reviewed by Provan, 2013). Therefore, Brittany represents a highly relevant zone for studying the species range shifts of seaweeds. Here, we first assessed the environmental changes (SST, concentration of suspended inorganic matter [SPIM], and chlorophyll-*a*) that occurred over the last two decades. Second, we compared red seaweed assemblages that occur within kelp forests between two survey periods (1992–1998 and 2010–2012) along the Brittany coastline, to detect potential changes in assemblage

composition in relation to changing environmental conditions at global and regional scales. We implemented species distribution models based on a combination of approaches, including both climatic and non-climatic predictors, to elucidate how red seaweed species have responded to environmental changes over the last two decades. By using both multivariate data analysis of actual data and the most up-to-date SDMs, we sought to better explain the observed and predicted changes in red seaweeds, induced by global change in the Brittany transition zone.

MATERIALS AND METHODS

Study area

The study area encompassed Brittany and a portion of Normandy (France, North-Eastern Atlantic; Fig. 1a). The sampled area extended from 49°N to 47°N and encompassed approximately 600 km of coastline. Within this study area, we delineated five regions *a priori*: Normandy, North Eastern Brittany, North Western Brittany, West Brittany, and South Brittany (Fig. 1a). All these sites are located in the upper subtidal zone and are characterised by rocky substratum, which, at these depths, host (i) kelp assemblages dominated by the two kelp species *Laminaria digitata* (Hudson) J.V. Lamouroux and *Laminaria hyperborea* (Gunnerus) Foslie and (ii) red seaweed assemblages located beneath the kelp canopy.

Environmental data

Six environmental parameters were used to assess and model the distribution of red seaweeds assemblages, including the mean and amplitude of SST, SPIM and chlorophyll-*a*. SST and SPIM and chlorophyll-*a* raw data were extracted from the CERSAT database (Appendix S1). SST and SPIM and chlorophyll-*a* concentrations were measured at 12.00 h. SST data were extracted from datasets collected between 1992 and 2012; however, data for chlorophyll a

and SPIM were not available before 1998 and were only extracted from 1998 to 2012. Annual means and monthly averaged annual minima and maxima were calculated for each variable. We calculated 'amplitude' as the difference between monthly averaged annual minima and maxima.

Red seaweed data

Sampling surveys

Data about red seaweeds were collected during three distinct diving surveys in the five previously defined regions. The first survey was conducted by divers from the 'Association pour la Découverte du Monde Sous-marin' (ADMS), who explored the entire Brittany coast during 1992–1998 (Castric-Fey, 2001). During this first survey, 163 sites were explored. The second survey targeted 39 sites, which were sampled during August 2010–September 2011 and were also spread along the entire Brittany coastline. At each site, seaweeds were collected from three to six 1/10 m^2 plots. Furthermore, additional samples were collected from 22 sites during a 10-min visual census, according to Gallon *et al*. (2013). Each specimen was identified using morphological criteria. Most specimens were identified to the species level, while the remaining were identified to the lowest taxonomic level possible (genus or family level). The third survey was performed within the framework of the CARTHAM project of the French Marine Protected Areas Agency. Twenty sites were sampled along the Brittany and Normandy coasts during July 2011–August 2012.

In all three surveys, the dives did not exceed a depth of 40 m. Only the first two surveys (from south Brittany to North Eastern Brittany) were used for multivariate data analyses, while all three surveys (from south Brittany to Normandy) were used for SDMs. To improve the performance of the models, we included species records from the OBIS database (http://www.iobis.org/).

Red seaweed classification

To link changing patterns with species ecological characteristics, we classified the species according to their affinity to cold or warm waters. We defined cold-water species as species that have a northern latitudinal limit strictly over 60° and warm-water species as species that have a northern latitudinal limit equal to or below 60°.

Data analyses

Evolution of abiotic variables

To map variations in SST, SPIM concentration, and chlorophyll-*a* concentration along the Brittany coastline, values were extracted for each cell located at 10 km from the coastline. Among the five defined regions, generalised linear models were computed to visualise trends between 1992 and 2012 for SST and between 1998 and 2012 for SPIM concentration and chlorophyll-*a* concentration.

Pre-treatment of databases

Some modifications were made to the original data to synchronise datasets. The substratum type at each site was checked, and sites that were not on rocky substratum were removed from the analyses. Specimens were identified to the species level, except for some genera where such identification was problematic (Appendix S2). The identification level varied between the first two surveys; therefore, some specimens were pooled into a single group named after the genera (Appendix S1). As the sampling techniques used were not appropriate for collecting the encrusting algae, the group was removed from all datasets. Singleton species (i.e. species only recorded once) were eliminated from the databases.

Evolution of biological data

We studied variation in red seaweed assemblages in relation to time and space using several methods. Firstly, we verified that there was no sampler effect between 2010 and 2012 by a permutational multivariate analysis of variance (PERMANOVA, df = 1, pseudo F = 1.152, p-value = 0.076). Then, we tested three hypotheses with a PERMANOVA: (i) assemblages differed from one sampling period to the other, (ii) assemblages differed from one region to another, and (iii) assemblages differed from one pair 'sampling period/region' to another. Secondly, when differences were observed, we identified the species contributing to most of these differences by using the Similarity Percentage Analysis (SIMPER) routine. Thirdly, we performed constrained canonical analysis (CCA) to highlight relationships between changes in red seaweed assemblages and changes in the mean and amplitude of SST and SPIM and chlorophyll-*a* concentrations. All analyses were based on a Bray–Curtis dissimilarity matrix, with presence/absence data being calculated using the vegan package (Oksanen *et al*., 2013) in R-software (R-team, 2013).

Species distribution modelling

Environmental predictor variables

The predictors used for SDMs were derived from the raw data of SST, SPIM and chlorophyll-*a* (Appendix S1). The annual mean, the amplitude, and the monthly averaged annual minimum and maximum for the two periods, 1992–1998 and 2010–2011, were extracted. We also calculated mean, minimum, maximum, and amplitude for these three parameters during the period of seaweed growth (March–September), obtaining 24 predictors. The distribution model was based on hard substratum only.

Modelled species

We modelled the distributions of selected species based on two criteria: (i) species must be present during the two survey periods and (ii) at least 30 records per species are necessary for model training and evaluation (Wisz *et al*., 2008). Ten species were selected: *Ahnfeltiopsis devoniensis* (n = 111), *Calliblepharis ciliata* (n = 630), *Calliblepharis jubata* (n = 261), *Ceramium* spp. (n = 1480), *Drachiella spectabilis* (n = 218), *Gastroclonium ovatum* (n = 384), *Kallymenia reniformis* (n = 540), *Phyllophora pseudoceranoides* (n = 507), *Plocamium* spp. (n = 1770), and *Sphaerococcus coronopifolius* (n = 115).

Modelling process

Species records were aggregated into 0.02° cells, which corresponded to the lower resolution of the abiotic variables. We selected a set of variables that were not intercorrelated (Pearson's rho < 0.70) and best predicted the distribution for all 10 species (for detailed protocol, see the Supplementary Information in Leroy *et al*., 2013). We modelled the distribution of the 10 selected species by an ensemble modelling approach (Araújo & New, 2007; Thuiller *et al*., 2009) using seven niche-based modelling techniques: (1) Generalised Linear Models (GLMs), (2) Generalised Additive Models (GAMs), (3) Generalised Boosted Models (GBMs), (4) Classification Tree Analysis (CTA), (5) Multivariate Adaptive Regression Splines (MARSs), (6) Random Forests (RFs), and (7) MaxEnt. As the chosen models required data for both species presence and the available environmental conditions, we generated five sets of 1000 randomly selected pseudo-absences with equal weighting for presence and absence (Barbet-Massin *et al*., 2012). We calibrated the models for 1992–1998 and 2010–2012 to integrate the entire range of environmental conditions available for the selected species. Models were calibrated with 70% of data selected at random and then the predictive performance of each model was evaluated based on the remaining 30% (Guisan &

Thuiller, 2005) by using the True Skill Statistic criterion (TSS; Allouche, 2006). This process was repeated five times to obtain an average value of model performances, and the final models were calibrated using all data. TSS scores were interpreted using the same classification as Landis & Koch (1997). Models with TSS evaluations below 0.6 were removed. We computed response curves for each model based on the 'evaluation strip' method described by Elith *et al*. (2005). Background variables were fixed at the average value for the presence points of the species. Consensus distributions were obtained using the weighted average consensus (WAC) method (Thuiller *et al*., 2009), which involves averaging model distributions with weights proportional to their TSS score. The final maps were obtained by averaging a composite model from the 10 pseudo-absence runs.

RESULTS

Spatiotemporal changes in abiotic conditions

Abiotic variables (means and amplitudes) have significantly changed over the last 20 years (Table 1a); however, different patterns were observed among the five study regions (Figs. 1b–d, Table 1b).

The mean SST has globally risen by 0.7 °C; however, while this rise averaged 0.040 °C·y^{-1} for Normandy and North Eastern Brittany, it averaged 0.025 °C·y^{-1} for North Western, West, and South Brittany (Table 1b). SST amplitude has risen for Normandy and South Brittany, but remained stable for North Eastern, North Western, and West Brittany. Rather than a latitudinal gradient, changes in SST mean and amplitude revealed a mosaic of contrasting conditions, with a cold, resilient water body in North-Western and West Brittany.

SPIM concentration was generally low and remained relatively stable along the entire coastline, except for two areas, the boundary of Normandy with North-Eastern Brittany and in the southern part of South Brittany, where a significant increase in SPIM concentration has

been documented since 2006 (Fig. 1c). Average annual amplitude has increased in all regions;

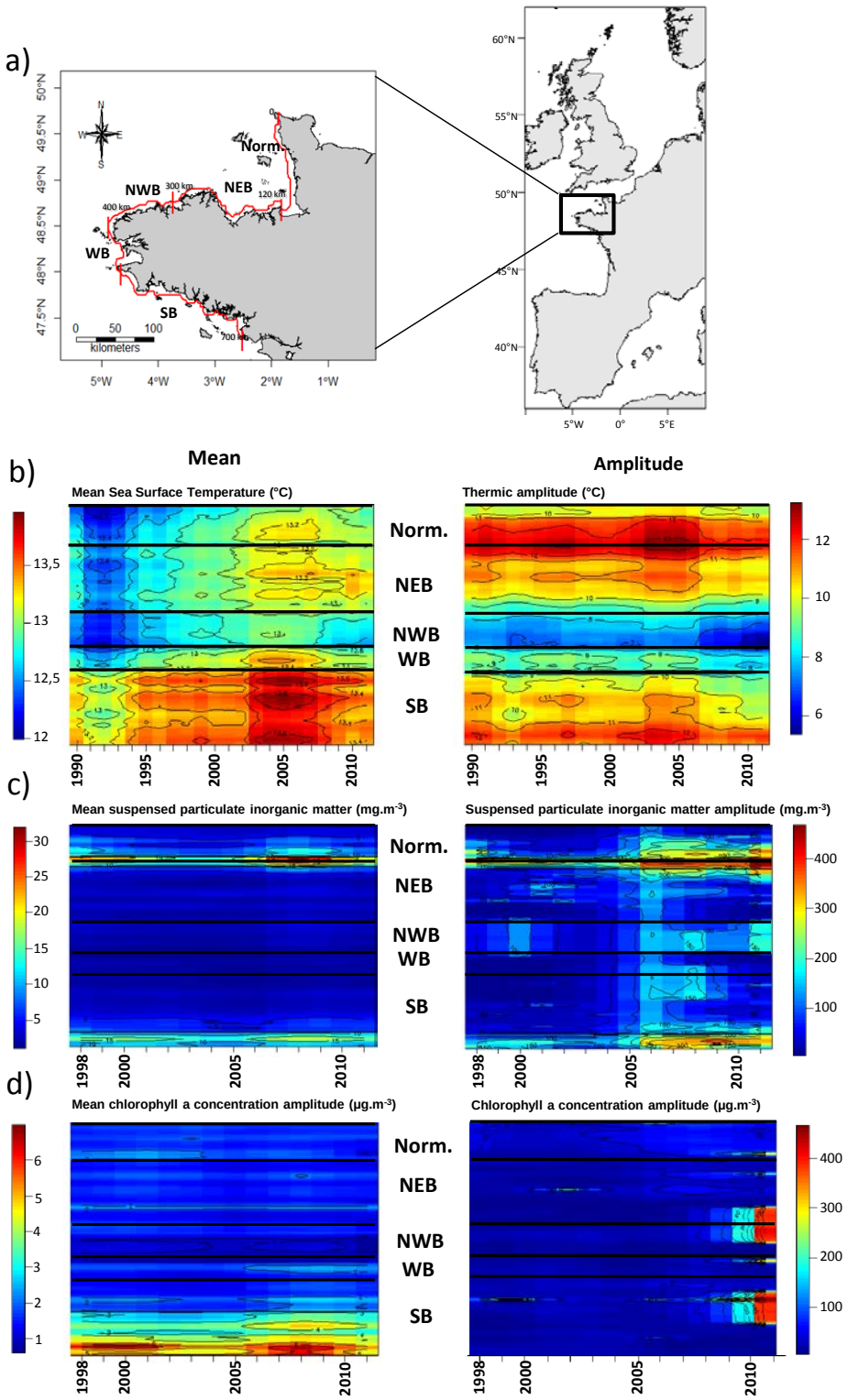

Fig. 1 Localisation of the study area (a) and temporal evolution along the Brittany coastline for (b) Sea Surface Temperature (SST), (c) concentration of Suspended Particulate Inorganic

matter (SPIM), and (d) concentration of Chlorophyll a (CHLa). ‘Average’ corresponds to the annual means, while annual ‘amplitude’ corresponds to the difference between the average annual minima and maxima. Time range: 1990–2012 for SST and 1998–2012 for SPIM and CHLa. (Regions: Norm., Normandy; NEB, North Eastern Brittany; NWB, North Western Brittany; WB, West Brittany; and SB, South Brittany).

Table 2 Summary of the PERMANOVA results testing the factors 'period' and 'region'. The factor 'period' corresponds to two periods of the survey (T1: 1992–1998 and T2: 2010–2012). The factor 'region' corresponds to the different regions that were surveyed (see Fig. 1). Both the global test (a) and the pairwise tests of the factor 'period' within each level of the factor 'region' (b) are presented. Regions: NEB, North Eastern Brittany; NWB, North Western Brittany; WB, West Brittany; and SB, South Brittany.

	Degree(s) of freedom	**F-model**	**Part of variance explained**	**p-value**
(a)				
Period	1	71.1	0.231	<0.001
Region	3	8.8	0.086	<0.001
*Period*Region*	3	5.3	0.051	<0.001
Residuals	194		0.631	
(b)				
Region NEB				
- *Period*	1	28.1	0.342	< 0.001
- *Residuals*	54		0.658	
Region NWB				
- *Period*	1	12.2	0.367	< 0.001
- *Residuals*	21		0.633	
Region WB				
- *Period*	1	13.2	0.159	< 0.001
- *Residuals*	70		0.841	
Region SB				
- *Period*	1	36.0	0.424	< 0.001
- *Residuals*	49		0.576	

specifically, mean values have increased in Normandy, North Eastern Brittany, and North Western Brittany, whereas the mean values have remained stable in West and South Brittany (Fig. 1c; Table 2b).

Over the two decades, higher chlorophyll-*a* concentrations were recorded in South Brittany (~3–6 $\mu g \cdot m^{-3}$, with peaks in 1998–2001 and 2006–2009; Fig. 1d) compared to the other four regions (~1–3 $\mu g \cdot m^{-3}$). Over the two decades, chlorophyll-*a* concentrations increased in West Brittany and South Brittany, but slightly decreased in the other three regions (Fig. 1d; Table 2b).

Overall, West Brittany was the least impacted region by changes in all the measured abiotic variables over the last 20 years.

Spatiotemporal changes in red algal assemblages along the Brittany coastline

The PERMANOVA results highlighted significant differences between the two study periods and the five study regions (Table 2a); however, the part of the variance explained by the factor 'period' (23.1%) was more than two times higher than the part of the variance explained by the factor 'region' (8.6%). The interaction between period and region was also significant; hence, we analysed the differences within each region. Differences between sampling periods appeared significant in all the Brittany regions (Table 2b). However, the magnitude of differences varied among regions. The magnitude was minimal for West Brittany, intermediate for both North Eastern and North Western Brittany, and maximal for South Brittany. The species that contributed the most towards discriminating between the two periods, as detected by SIMPER procedures, are presented in Appendix S2. A summary of changes in the occurrence frequencies of species between the two periods is presented in Table 3.

Globally, different patterns emerged among the species that contributed the most to the differences between the two periods. Firstly, the frequency of some species homogeneously decreased across the four Brittany regions between 1992–1998 and 2010–2012 (e.g. *Ceramium* spp., *Gastroclonium ovatum*, and *Heterosiphonia japonica*). Secondly, some species present in the 1992–1998 period were absent in the 2010–2012 period (e.g. *Gracilaria gracilis, Seirospora seirosperma*, and *Kallymenia requienii*). Thirdly, the frequency of several species (e.g. *Cryptopleura ramosa, Phyllophora crispa, Corallina* spp., *Plocamium* spp., and *Heterosiphonia plumosa*) homogeneously increased across regions between the two periods. Fourthly, one species was absent during the first sampling period and appeared in the four regions during the second sampling period (*Dilsea carnosa*). We observed a marked increase in cold-water species compared to warm-water species and a greater decrease in warm-water species compared to cold-water species (Table 3), indicating that assemblages gained cold-water species and lost warm-water species.

Relationship between abiotic and biotic changes

The CCA presented in Figure 2 displays both the spatiotemporal variations of red seaweed assemblages and the evolution of abiotic parameters between 1992–1998 and 2010–2012. The CCA results were consistent with the PERMANOVA results, as they highlighted clear differences in biotic assemblages between the two study periods. Moreover, it appeared that between the two study periods, the evolution of red seaweed assemblages was mainly driven by the increase in mean SST. Across regions, assemblages appeared to be distributed along a north–south gradient in 1992–1998, but not in 2010–2012, where the assemblages of North Eastern Brittany appeared to have become isolated from the other regions.

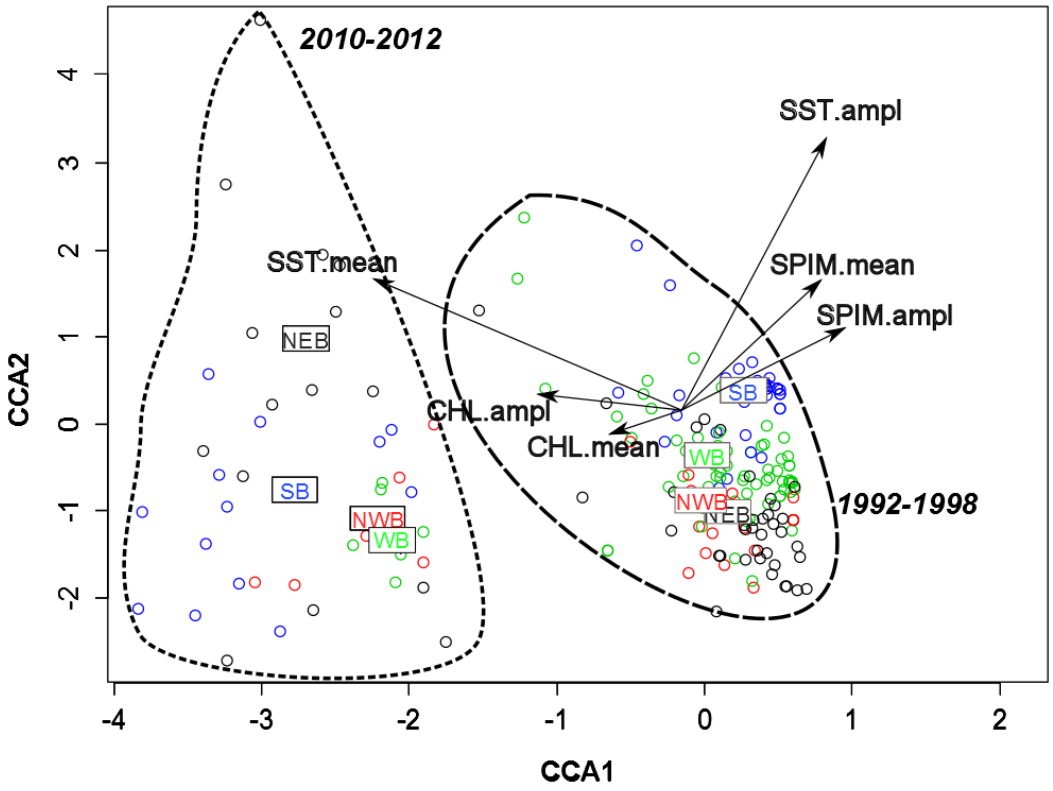

Fig. 2 Canonical correspondence analysis of red seaweed assemblages that were sampled during the periods 1992–1998 and 2010–2012 constrained by mean SST (SST.mean), SST amplitude (SST.ampl), mean chlorophyll a concentration (CHL.mean), amplitude of chlorophyll a concentration (CHL.ampl), mean SPIM (SPIM.mean), and SPIM amplitude (SPIM.ampl). The six environmental parameters contributed significantly towards explaining the observed pattern. Regions: NEB, North Eastern Brittany; NWB, North Western Brittany; WB, West Brittany; and SB, South Brittany.

Table 3 Reported distribution ranges and summary of changes in the occurrence frequencies between the two study periods, both over all Brittany regions and within each region, for species contributing to more than 1% of global dissimilarity between the two periods according to the SIMPER procedure. Regions: NEB, North Eastern Brittany; NWB, North Western Brittany; WB, West Brittany; and SB, South Brittany.

Species	**Distribution**	**Thermal water affinity**	**Changes in the occurrence frequencies between 1992–1998 and 2010–2012**				
			Brittany	**NEB**	**NWB**	**WB**	**SB**
Gracilaria gracilis	60/30 (30) + MS	warm	↓	↓	↓	↓	↓
Cryptopleura ramosa	60/30 (30) + MS	warm	↑	↑	↑	↑	↑
Phyllophora crispa	70/35 (35) + MS	warm	↑	↑	↑	↑	↑
Ceramium spp.	N/A	N/A	↓	↓	↓	↓	↓
Corallina spp.	N/A	N/A	↑	↑	↑	↑	↑
Gastroclonium ovatum	60/30 (30) + MS	warm	↓	↓	↓	↓	↓
Heterosiphonia japonica	60/40 (20) Introduced	warm	↓	↓	↓	↓	↓
Plocamium spp.	N/A	N/A	↑	↑	↑	↑	×
Heterosiphonia plumosa	60/30 (30)	cold	↑	↑	↑	↑	↑
Dilsea carnosa	80/35 (45) + NWA	cold	↑	↑	↑	↑	↑
Callophyllis laciniata	65/35 (30)	cold	↑	↑	↑	↑	↑
Seirospora seirosperma	60/30 (30)	cold	↓	↓	↓	↓	↓
Kallymenia reniformis	60/30 (30)	cold	↑	↓	↑	↑	↑

Kallymenia requienii	35/30 (5) + MS	warm	↓	↓	↓	↓	↓
Phyllophora sicula	55/35 (20) + MS	warm	↓	↓	↓	×	×
Calliblepharis ciliata	60/30 (30)	cold	≈	↑	↑	×	×
Gelidium corneum	55/30 (25)	cold	↓	↓	↓	↑	↓
Callithamnion tetragonum	65/30 (35) + NWA	cold	↓	↓	↑	↑	↓
Phyllophora pseudoceranoides	70/40 (30) + NWA	cold	↓	↑	↓	↑	↓
Phycodrys rubens	80/35 (45) + NWA	cold	↑	↑	×	×	↑
Meredithia microphylla	60/30 (30) + MS	warm	↑	↑	×	×	×
Cystoclonium purpureum	70/40 (30) + NWA	cold	↓	↓	×	↓	↓
Delesseria sanguinea	70/40 (30)	cold	↑	×	↑	↑	≈
Palmaria palmata	70/30 (30) + NWA	cold	↑	↑	↑	×	×
Chondrus crispus	70/35 (35) + NWA	cold	↑	×	↑	↑	×
Lomentaria articulata	65/30 (35) + MS + NWA	warm	↑	×	↑	↑	↓
Sphaerococcus coronopifolius	60/30 (30) + MS	warm	↑	↑	↑	×	↓
Polyneura bonnemaisonii	55/40 (5)	cold	↑	↑	×	↑	×
Aglaothamnion hookeri	70/30 (40) + NWA	cold	↓	×	×	↓	↓

Halurus equisetifolius	55/30 (25) + MS	warm	↑	×	≈	↑	↑
Rhodymenia holmesii	55/30 (25)	cold	↑	↑	↑	×	×
Calliblepharis jubata	55/35 (20) + MS	warm	↓	↓	↑	×	×
Porphyra spp.	N/A	N/A	≈	×	×	×	×

Distribution is provided in degrees as the highest latitude/lowest latitude (latitude range); MS means that the species is also present in the Mediterranean Sea; NWA means that the species is also present in the North Western Atlantic.

Species distribution modelling

Model performance

All calibrated models exhibited good prediction performances, with average TSS scores ranging from 0.695 for the GLM to 0.972 for the RF analyses, with an overall average value of 0.847 (see Appendix S3).

Species responses

A specific combination of variables was chosen to model the distribution of each seaweed species (Table 5). Although the number and order of variables significantly explaining the distribution varied among species, the amplitude of SST (either globally or during the growth period) appeared to be the best predictor for the 10 modelled species.

The 10 modelled species expressed similar response patterns to SST variables (Figs. 3a, b). All the species exhibited a peak in their probability of presence for an SST amplitude of around 1 °C, with these probabilities collapsing to a minimum of 0–0.25 when the SST amplitude reached 2 °C (Fig. 3a). The values for all species remained low for their probability of presence beyond an SST amplitude of 2 °C, except for *Calliblepharis ciliata*, which exhibited a probability of presence beyond 0.50 at an SST amplitude of 6 °C. During the growth period (Fig. 3b), the effect of an increase in SST amplitude was also negative for all species, but was less important.

The probability of species presence consistently varied for species sensitive to annual average concentrations of chlorophyll-*a* and decreased until chlorophyll-*a* concentration reached 2.5 $\mu g \cdot m^{-3}$ and remained constant beyond this value (Fig. 3c). Conversely, responses to chlorophyll-*a* concentrations during the growth period were highly variable among species (Fig. 3d).

The modelled species were more sensitive to high SPIM concentrations during the growth period than during the entire year (Figs. 3e, f). Increasing SPIM concentrations greatly reduced the probability of presence for all modelled species (Fig. 3f).

Latitudinal and coastline distributions

The models predicted a northward latitudinal shift for most species, with the notable exception of *Kallymenia reniformis*, *Phyllophora pseudoceranoides*, and *Plocamium* spp. (Fig. 4a; Appendix S3). Furthermore, they predicted a considerable range contraction for most species, except *Plocamium* spp., the range of which was predicted to remain stable, and *Sphaerococcus coronopifolius*, the range of which was predicted to increase in size. The 2010–2012 coastline distribution projections were characterised by (i) reduction in the potential distribution area for most species, especially *Ahnfeltiopsis devoniensis*, *Drachiella spectabilis*, and *Calliblepharis ciliata*, and (ii) a shift towards North-Eastern Brittany for seven of 10 species (Fig. 4b; Appendix S3). The predicted shifts and range contractions were not related to the ecological characteristics of the species (Appendix S3).

Table 4 Observed and predicted changes in relation to the thermal affinity of the species. The species that were considered contributed to more than 1% of the global dissimilarity between the assemblages of 1992–1998 and 2010–2012.

	Observed rise in occurrence frequency	**Observed reduction in occurrence frequency**	**Predicted northward shift**	**Predicted range contraction**
Warm-water species				
	50 %	50 %	100 %	80 %
($N_{observed}$ = 17 and $N_{predicted}$ = 5)				
Cold-water species				
	62.5 %	37.5 %	33 %	100 %
($N_{observed}$ = 12 and $N_{predicted}$ = 3)				

N is the number of species in each category.

Warm-water species: species occurring in the Mediterranean Sea

Cold-water species: species not recorded in the Mediterranean Sea

Table 5 Environmental variables selected for the species distribution modelling of each species. Numbers correspond to the order of importance in the consensus model. G stands for the growth period.

	SST								SPIM					Chlorophyll a						
	Ampl	Ampl G	Max	Max G	Mean	Mean G	Min	Min G	Ampl	Ampl G	Max G	Min	Min G	Ampl	Ampl G	Max	Mean	Mean G	Min	Min G
Ahnfeltiopsis devoniensis		1			2			9	8	6					3	5	4	7		
Calliblepharis ciliata	1	2			3			9	10	7				4		8	5	6		
Calliblepharis jubata	2	1					3	8	6	5						9	4	7		
***Ceramium* spp.**	1	2					3	8	10	9				5	4		6	7		
Drachiella spectabilis	1	2				7	5		8	3						9	4	6		
Gastroclonium ovatum	1	2					3	9	10	7				5		4	6	8		
Kallymenia reniformis	2	1	3					8	10	5				6	4			9	7	
Phyllophora pseudoceranoides	1	2					3	9	10	7				5	4		6	8		
***Plocamium* spp.**	2	1	3	4							5	9		8		10		6	7	
Sphaerococcus coronopifolius	1	2	4					7				10	8	5		3	6			9

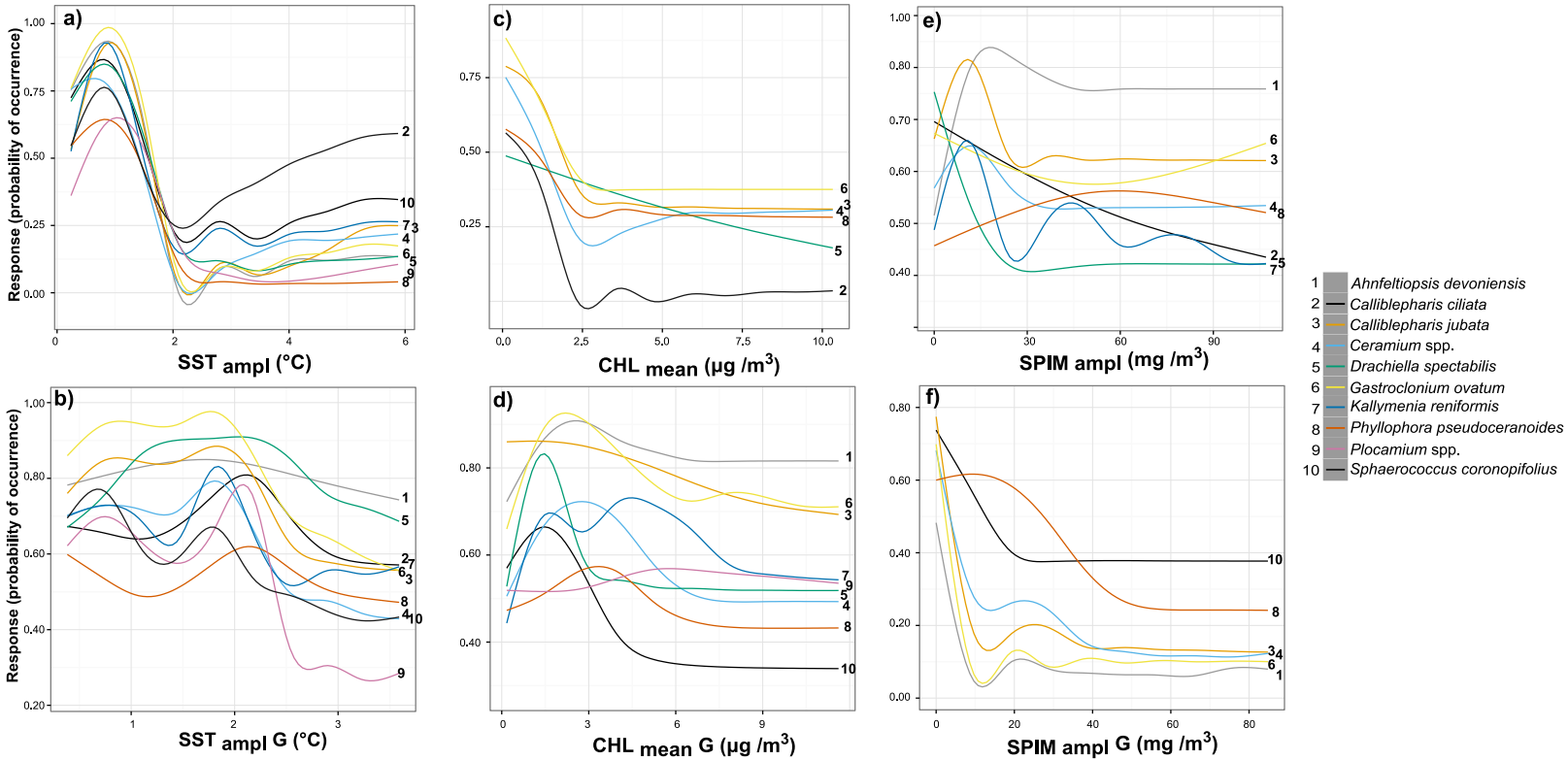

Fig. 3 Response curves of all species that were modelled. Plain line: average predicted values for all models; grey bands: 95% confidence intervals. Only the important variables are shown: (a) Annual amplitude SST; (b) Growth SST amplitude; (c) Annual $CHLa_{mean}$; (d) Growth $CHLa_{mean}$; (e) SPIM amplitude; and (f) Growth SPIM amplitude. SST: Sea Surface Temperature; CHLa: concentration in Chlorophyll a; and SPIM: concentration in suspended particulate inorganic matter.

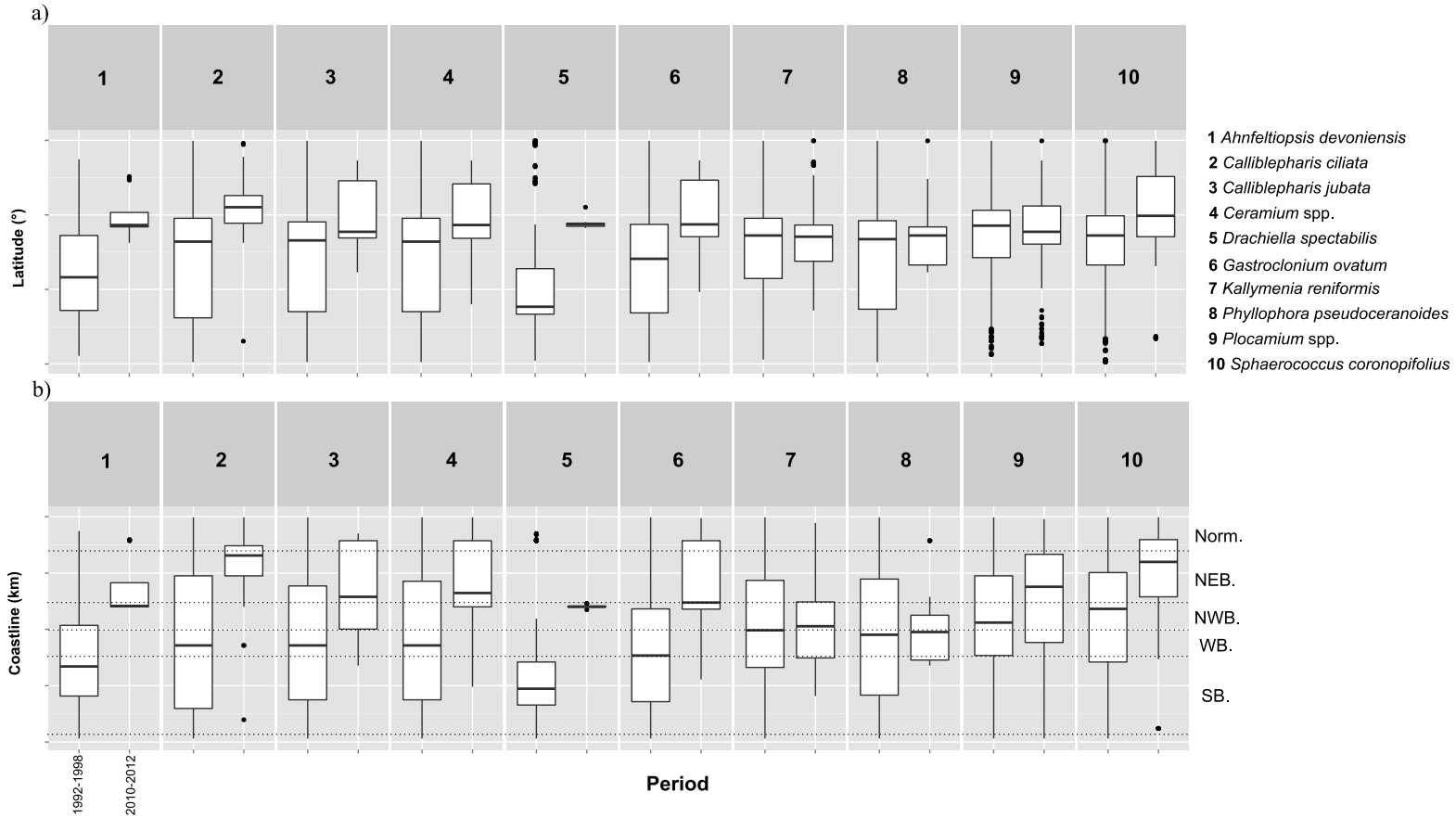

Fig. 4 Latitudinal distribution (a) and distribution along the coastline (b) for the 10 species that were modelled between the two study periods (1992–1998 and 2010–2012). Values were extracted from the two projections (1992–1998 and 2010–2012).

DISCUSSION

SST has globally increased by 0.7 °C along the Brittany coastline of France over the last two decades, whereas SPIM concentrations have remained relatively stable and chlorophyll-*a* concentrations have slightly increased during this period. Nevertheless, this global trend has concealed more complex environmental patterns, with the evolution of various abiotic parameters being highly varied at a local scale. Assuming that these rapid environmental changes have affected the ecology of red seaweeds, we investigated changes in assemblages using multivariate analyses and changes in potential species distributions using SDMs over the past 20 years. Our results revealed strong changes in the distributions of both species and assemblages of red seaweeds during 1992–1998 and 2010–2012. Red seaweeds appear to be strongly dependent on SST, specifically, mean temperature, when considering assemblages, and temperature amplitude, when regarding singles species responses. Therefore, we assumed that temperature has been the main driver of the observed changes, supporting the findings of previous studies (Bartsch *et al*., 2012, and references therein).

Recorded changes in abiotic conditions

The SST warming rate calculated in this study for Brittany (0.7 °C over the last two decades, i.e. 0.35 °C per decade) was slightly higher than but generally consistent with values estimated by Lima & Wethey in 2011 for the Eastern Atlantic coast (0.27 ± 0.13 °C per decade). At a finer scale, within Brittany, the average SST and the amplitude of SST together indicated that, over the last 20 years, North Western and West Brittany represent the regions least impacted by SST variations, whereas North Eastern and South Brittany represent the regions most impacted by increasing SST and SST amplitude, respectively.

Changes in the other abiotic parameters were detected at a further local scale. SPIM amplitude has increased in two areas since 2006; specifically, at the boundary of Normandy with North-

Eastern Brittany and in the southern part of South Brittany. These two areas are known to carry a large amount of terrigenous material from drainage basins. The amplitude of chlorophyll-*a* concentration has increased in two areas, specifically at the boundary between North-Eastern and North-Western Brittany and in South Brittany. These local increases correspond to zones where green tides (i.e. algal blooms) have been observed. Variations in SST and SPIM and chlorophyll-*a* concentrations in Brittany were the least altered in West Brittany over the past 20 years, which corroborates current knowledge about the hydrodynamic features of this region (Le Boyer *et al*., 2009).

Observed changes in red seaweed assemblages

Our findings showed varying patterns to the changes in red seaweed assemblages across the four Brittany regions over the last two decades. The observed changes were strongly correlated to changes in environmental conditions, particularly mean temperature. The strongest changes in assemblages occurred in the region most impacted by temperature rise (South Brittany). Conversely, the smallest changes in assemblages occurred in West Brittany, the least impacted region.

Specifically, we documented increases in the occurrence of several species (*Corallina* spp., *Cryptopleura ramosa*, *Dilsea carnosa*, *Heterosiphonia plumosa*, *Plocamium* spp., and *Phyllophora crispa*). Interestingly, some studies about recent changes in European seaweed communities obtained similar results for most of these species. For instance, Diez *et al*. (2012) did not find *P. crispa* in their 1991 survey, but found some specimens in their 2008 survey, with an increase in the frequencies of *C. ramosa*, *Corallina* spp., and *Plocamium* spp. between the two surveys. In contrast, Husa *et al*. (2008) described an increase in the frequency of *P. crispa* between their 1994 and 2008 surveys. These findings might indicate that these four species have benefitted from recent environmental changes. These

observations seem to be in accordance with previous studies for *Corallina* spp., which have shown that an increase in temperature could be beneficial for the calcification and growth of coralline seaweeds (e.g. Jian-Zhang *et al*., 2010).

We also recorded strong decreases in the frequency of *Ceramium* spp., *Gastroclonium ovatum*, and *Heterosiphonia japonica* during 1992–1998 and 2010–2012. *Heterosiphonia japonica* is an invasive species from the Western Pacific, with other studies reporting an increase in its frequency during 1991–2008 on the Basque coast (Spain, Diez *et al*., 2012), 1994–2003 in Norway (Husa *et al*., 2008) and 1998–2011 in Brittany (Derrien-Courtel *et al*., 2013). *Heterosiphonia japonica* has been frequently observed in Brittany (pers. obs.); hence, the observed decrease in its occurrence frequency in the present work was probably related to it primarily occurring epiphytically, rather than epilithically, while our sampling effort only focused on the latter habitat type.

We observed the disappearance of several species during 1992–1998 and 2010–2012. *Gracilaria gracilis* was not recorded in the 2010–2012 survey, whereas it was present at every site in the 1992–1998 survey. Similar to *H. japonica*, *G. gracilis* has been observed throughout Brittany, but not in our sampling sites (which were limited to epilithic species), indicating that these species no longer occur under the kelp canopy. *Kallymenia requienii* and *Seirospora seirosperma* were also not recorded in the 2010–2012 survey. The former is a warm-water species that has not been previously recorded in Brittany. To our knowledge, the latter species has not been observed in Brittany in recent years (Guiry & Guiry, 2013), but was observed in Norway in 2003 (Husa *et al*., 2008) and was observed at low frequencies in Spain during 2008 (Diez *et al*., 2012).

Modelled changes in red seaweed distributions

For the 10 modelled species, the best predictor of distribution was SST amplitude, either for the whole year or just during the growth period, re-affirming the crucial role of temperature in shaping the patterns of seaweed distribution, as highlighted by previous studies (Jueterbock *et al*., 2013; Raybaud *et al*., 2013). The current results indicate that the distribution of red seaweeds seems to be limited by the temperature range they can cope with, rather than the mean annual temperature.

The models developed here predicted both a northward shift and a contraction of the predicted suitable range for most species over the last two decades, based on the major observed increase in SST. Our models predicted a northward shift in the distribution ranges of seven of 10 species, with the distributions of the remaining three species either contracting or remaining stable. The lack of predicted northward range expansion might indicate that new environmental conditions further north of Brittany are not adequate for these species. Indeed, North-Eastern Brittany is warmer and has been warming at a faster rate than the other Brittany regions over the last two decades, which might have resulted in North-Western and West Brittany becoming isolated, where changes in temperature conditions have been less drastic. This isolated status might be considered to serve as a refuge for many species.

Synthesis

We observed a correlation between the changes in environmental conditions over the last two decades and the documented changes in red seaweed communities. Similarly, when using the same environmental variables, strong changes were predicted from the species distribution models of a restricted species set. Three of the modelled species were among the most discriminant species between the 1992–1998 and 2010–2012 surveys. *Plocamium* spp. was the only taxon that was not predicted to be subjected to range contraction. This prediction

may be corroborated by the observed increase in the occurrence frequency of this species between the 1992–1998 and 2010–2012 surveys. *Ceramium* spp. and *Gastroclonium ovatum* were predicted to be subjected to strong range contraction. These predictions were corroborated by the observed decrease in their occurrence frequency between the two survey periods. Therefore, our predictions that environmental changes have had a strong impact on red seaweeds were strengthened on combining the two different approaches. We initially used multivariate analysis based on real but discrete data, which enabled detection of changes in whole species assemblages. These results were then combined with SDMs, which enabled prediction of the entire distribution for a reduced number of modelled species.

However, we did not observe the expected increase in warm-water species, and shifts were not predicted for all species. Therefore, we hypothesised that this complex pattern of responses to environmental changes might have two origins. Firstly, species might track changes in environmental conditions, but not fast enough, resulting in a time lag between abiotic changes and the resulting changes in biotic assemblages. This pattern type has already been observed for several taxa in the terrestrial realm (Devictor *et al.*, 2012). Secondly, environmental changes occur heterogeneously at very small spatial scales, resulting in complex global variations when species track these changes. These types of local changes are highly likely, given the mosaic of different environments recorded along the Brittany coastline in the current study. Similar outcomes have been documented for recent trends in the range shifts of marine taxa in North America; it has been suggested that marine species shift at different rates and in different directions because they closely track the complex mosaic of local climate velocities (Pinsky *et al.*, 2013).

Study limitations

Here, we compared red seaweed assemblages that were sampled at an interval of 20 years. While important changes in red seaweed assemblages were revealed over this timeframe, several disadvantages were noted. Firstly, the sampling scheme was not identical between the two periods; hence, we had to remove the details of or simplify the results of the most recent study to allow comparison with the sampling data of the first study.

Secondly, the presence of some taxa (i.e. *Ceramium* spp., *Corallina* spp., and *Plocamium* spp.) was evaluated at the generic level; hence, our results for these genera might not reflect the responses of individual species, as responses to climatic stress might differ within a genus (Harley, 2006). Furthermore, the data used in this study are based on morphological identification, whereas global taxonomic knowledge has evolved since the 1990s, highlighting many cases of cryptic diversity, such as in the genera *Corallina* (Walker *et al*., 2009; Hind & Saunders, 2013) and *Plocamium* (Saunders *et al*., 2005). Hence, the use of molecular systematics, such as DNA-barcoding, for red seaweed identification (e.g. Saunders & McDevit, 2012) could be used to unravel genuine species distributions and enhance our understanding of species-specific responses to environmental changes in the future.

Thirdly, if marine species track highly local environmental changes, as suggested by Pinsky *et al*. (2013), they might migrate not only along a latitudinal gradient but also along a depth gradient. In the present study, we did not have access to information about the depth at which the samples were collected; therefore, we could not test this hypothesis. Collecting pertinent local information about abiotic conditions, including the depth, to cover the entire ecological range of a species would contribute towards further accurately predicting species responses to global changes (Owen *et al*., 2013).

Concluding remarks

The impact of environmental changes on red seaweeds in Brittany over the last two decades was determined using a combination of two different approaches. Changes in both biotic and abiotic conditions in this biogeographical transition zone were contrasted across adjoining regions. Changes in temperature conditions did not follow a latitudinal gradient. These changes were much milder in North-Western and Western Brittany, which potentially represent a refuge zone for red seaweeds. In contrast, further drastic temperature changes were recorded in North-Eastern Brittany, which potentially represents a thermal barrier to the northward migration of red seaweeds. In conclusion, we recommend both (i) extending the scope of observations to other parts of the European coastline and (ii) collecting data at a very fine scale, to better understand how red seaweeds track environmental changes, and therefore, improve our understanding of the dynamics of marine biogeographical transition zones within the context of global change.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Information about abiotic and biotic data used in the study.

Appendix S2 Occurrence frequencies and contribution to overall dissimilarity of the species in the two periods

Appendix S3 Detailed information about results of species distribution modeling

Appendix S1 Information about abiotic and biotic data used in the study

(a) Description of the six environmental variables

Variable	Description	Resolution in models	URL link	Period
Depth	Height of the water column (m)	2.2km x 2.2km	emodnet-hydrography.eu	
Seafloor substrate	Only hard substrate are kept		IFREMER-JNCC	
Sea surface temperature	Measure of sea surface temperature in °C	2.2km x 2.2km	/ifremer/cersat/products/gridded/sst-l4hr-AVHRR-fnd/V2/cdf	1990-2012
Suspensed inorganic matter	Measure of suspended inorganic matter concentration (10^{-2} g m^{-3})	2.2km x 2.2km	/ifremer/cersat/products/gridded/ocean-color/atlantic/EUR-L4-SPIM-ATL-v01	1998-2012
Chlorophyll a	Measure of chlorophyll a concentration (10^{-2} mg m^{-3})	2.2km x 2.2km	/ifremer/cersat/products/gridded/ocean-color/atlantic/EUR-L4-CHL-ATL-v01	1998-2012

(b) List of species detected in Brittany during the sampling period of 1992-1998 and the one of 2010-2012. A cross indicates the presence of the species.

Species name	**1992-1998**	**2010-2012**
Acrochaetium bonnemaisoniae	x	
Aglaothamnion bipinnatum	x	
Aglaothamnion diaphanum	x	
Aglaothamnion feldmanniae	x	
Aglaothamnion gallicum	x	
Aglaothamnion hookeri	x	
Aglaothamnion pseudobyssoides	x	
Aglaothamnion tenuissimum	x	
Aglaothamnion tripinnatum	x	
Ahnfeltia plicata	x	x
Ahnfeltiopsis devoniensis	x	
Ahnfeltiopsis sp.		x
Anotrichium furcellatum	x	
Antithamnion cruciatum	x	
Antithamnion densum	x	
Antithamnion sarniensis	x	
Antithamnionella spirographidis	x	
Antithamnionella ternifolia	x	
Apoglossum ruscifolium	x	x
Asparagopsis armata	x	x
Bonnemaisonia asparagoides	x	x

Bonnemaisonia clavata	x	
Bornetia secundiflora	x	x
Brongniartella byssoides	x	
Calliblepharis ciliata	x	x
Calliblepharis jubata	x	x
Callithamnion granulatum	x	
Callithamnion tetragonum	x	x
Callithamnion tetricum	x	
Callophyllis laciniata	x	x
Ceramium spp.	x	x
Champia parvula	x	
Chondracanthus teedei	x	
Chondria coerulescens	x	
Chondria dasyphylla	x	
Chondria scintillans	x	
Chondrus crispus	x	x
Chylocladia verticillata	x	x
Compsothamnion decompositum	x	
Compsothamnion gracillimum	x	
Compsothamnion thuyoides	x	
Corallina spp.	x	x
Cordylecladia erecta	x	
Cruoria pellita	x	
Cryptopleura ramosa	x	x
Cystoclonium purpureum	x	x

Dasya arbuscula	x	
Dasya ocellata	x	
Delesseria sanguinea	x	x
Dilsea carnosa		x
Drachiella heterocarpa	x	
Drachiella spectabilis	x	
Dudresnaya verticillata	x	
Erythroglossum laciniatum	x	x
Furcellaria lumbricalis	x	x
Gastroclonium ovatum	x	x
Gelidium corneum	x	x
Gelidium spinosum	x	x
Gelidium spp.	x	x
Gigartina pistillata	x	x
Gonimophyllum buffhamii	x	
Goniotrichum elegans	x	
Gracilaria compressa	x	
Gracilaria gracilis	x	
Gracilaria multipartita	x	
Gracilaria sp.		x
Gracilariopsis longissima	x	
Griffithsia corallinoides	x	x
Gymnogongrus crenulatus	x	x
Gymnogongrus griffithsiae	x	
Halarachnion ligulatum	x	

Halopithys incurva	x	x
Halurus equisetifolius	x	x
Halymenia latifolia	x	
Haraldiophyllum bonnemaisonii	x	
Heterosiphonia japonica	x	x
Heterosiphonia plumosa	x	x
Heterosiphonia sp.		x
Hypnea musciformis	x	
Hypoglossum hypoglossoides		x
Jania rubens	x	
Kallymenia reniformis	x	x
Kallymenia requienii	x	
Liagora viscida	x	
Lomentaria articulata	x	x
Lomentaria clavellosa	x	x
Lomentaria orcadensis	x	
Mastocarpus stellatus	x	x
Membranoptera alata	x	x
Meredithia microphylla	x	x
Microcladia glandulosa	x	
Monosporus pedicellatus	x	
Myriogramme minuta	x	
Myriogramme sp.		x
Naccaria wiggii	x	
Nemalion helminthoides	x	

Neosiphonia harveyi	x	
Nitophyllum punctatum	x	x
Osmundea pinnatifida	x	x
Palmaria palmata	x	x
Petalonia fascia		x
Phycodrys rubens	x	x
Phyllophora crispa	x	x
Phyllophora pseudoceranoides	x	x
Phyllophora sicula	x	x
Phyllophora spp.		x
Plocamium spp.	x	x
Plumaria plumosa	x	x
Polyides rotundus		x
Polyneura bonnemaisonii	x	x
Polyneura spp.		x
Polysiphonia elongata	x	x
Polysiphonia spp.	x	x
Porphyra spp.	x	x
Pterosiphonia spp.	x	x
Pterothamnion crispum	x	
Pterothamnion plumula	x	
Ptilothamnion pluma	x	
Radicilingua thysanorhizans	x	
Rhodomela confervoides	x	
Rhodophyllis divaricata	x	

Rhodymenia coespitosella	x	
Rhodymenia deliticulata		x
Rhodymenia holmesii	x	x
Rhodymenia pseudopalmata		x
Rhodymenia sp.		x
Schizymenia dubyi	x	
Schottera nicaeensis	x	x
Scinaia furcellata	x	
Scinaia turgida	x	
Seirospora seirosperma	x	
Solieria chordalis	x	x
Spermothamnion mesocarpum	x	
Spermothamnion repens	x	
Spermothamnion strictum	x	
Sphaerococcus coronopifolius	x	x
Stenogramma interrupta	x	
Stypocaulon scoparium		x

Appendix S2: Occurrence frequencies of the species in 1992-1998 and 2010-2012 and contribution of each species to overall dissimilarity between the two surveys according to the SIMPER routine. The taxa listed have a contribution of over 1% of the total dissimilarity. The results are presented globally (a) and for the four Brittany regions (b-e).

(a) Globally	**Occurrence frequency in 1992-1998**	**Occurrence frequency in 2010-2012**	**Contribution to overall dissimilarity**	**Cumulative contribution to overall dissimilarity**
Gracilaria gracilis	1.000	0.000	0.037	0.037
Cryptopleura ramosa	0.012	0.795	0.028	0.064
Phyllophora crispa	0.049	0.795	0.026	0.090
Ceramium spp.	0.945	0.308	0.026	0.116
Corallina spp.	0.049	0.744	0.025	0.141
Gastroclonium ovatum	0.779	0.179	0.024	0.165
Heterosiphonia japonica	0.755	0.179	0.022	0.187
Plocamium spp.	0.209	0.744	0.022	0.209
Heterosiphonia plumosa	0.061	0.641	0.021	0.230

Dilsea carnosa	0.000	0.564	0.021	0.251
Callophyllis laciniata	0.018	0.615	0.020	0.271
Seirospora seirosperma	0.656	0.000	0.020	0.291
Kallymenia reniformis	0.325	0.513	0.018	0.310
Kallymenia requienii	0.613	0.000	0.018	0.328
Phyllophora sicula	0.479	0.077	0.016	0.344
Calliblepharis ciliata	0.344	0.385	0.016	0.361
Gelidium corneum	0.485	0.231	0.016	0.377
Callithamnion tetragonum	0.509	0.256	0.016	0.393
Phyllophora pseudoceranoides	0.442	0.385	0.016	0.409
Phycodrys rubens	0.025	0.410	0.015	0.424
Meredithia microphylla	0.055	0.410	0.014	0.438
Cystoclonium purpureum	0.466	0.026	0.014	0.452
Delesseria sanguinea	0.160	0.385	0.014	0.466
Palmaria palmata	0.018	0.385	0.013	0.479
Chondrus crispus	0.172	0.410	0.013	0.492

Lomentaria articulata	0.160	0.385	0.012	0.504
Sphaerococcus coronopifolius	0.184	0.256	0.012	0.516
Polyneura bonnemaisonii	0.080	0.333	0.012	0.528
Aglaothamnion hookeri	0.399	0.000	0.011	0.539
Halurus equisetifolius	0.123	0.282	0.011	0.549
Rhodymenia holmesii	0.012	0.333	0.010	0.559
Calliblepharis jubata	0.239	0.179	0.010	0.569
Porphyra spp.	0.166	0.179	0.010	0.579

(b) North-Eastern Brittany	**Occurrence frequency in 1992-1998**	**Occurrence frequency in 2010-2012**	**Contribution to overall dissimilarity**	**Cumulative contribution to overall dissimilarity**
Gracilaria gracilis	1.000	0.000	0.040	0.040
Phyllophora crispa	0.071	1.000	0.038	0.079
Plocamium spp.	0.167	0.929	0.033	0.112
Corallina spp.	0.071	0.786	0.032	0.144
Ceramium spp.	0.952	0.214	0.031	0.175
Phyllophora sicula	0.857	0.143	0.028	0.204
Gastroclonium ovatum	0.738	0.000	0.027	0.231
Meredithia microphylla	0.048	0.714	0.026	0.257
Cryptopleura ramosa	0.000	0.643	0.024	0.281
Gelidium corneum	0.595	0.000	0.022	0.303
Phyllophora pseudoceranoides	0.357	0.643	0.021	0.324
Kallymenia requienii	0.595	0.000	0.021	0.345

Heterosiphonia japonica	0.810	0.500	0.021	0.366
Calliblepharis ciliata	0.167	0.571	0.021	0.386
Kallymenia reniformis	0.571	0.286	0.020	0.407
Callophyllis laciniata	0.048	0.429	0.019	0.426
Seirospora seirosperma	0.524	0.000	0.017	0.443
Polyneura bonnemaisonii	0.095	0.357	0.017	0.460
Dilsea carnosa	0.000	0.429	0.016	0.476
Sphaerococcus coronopifolius	0.167	0.357	0.015	0.491
Callithamnion tetragonum	0.429	0.000	0.014	0.506
Palmaria palmata	0.024	0.357	0.014	0.520
Rhodymenia holmesii	0.000	0.429	0.014	0.533
Calliblepharis jubata	0.357	0.143	0.013	0.547
Heterosiphonia plumosa	0.024	0.357	0.013	0.560
Phycodrys rubens	0.000	0.357	0.012	0.572

Antithamnion sarniensis	0.333	0.000	0.011	0.583
Bornetia secundiflora	0.143	0.214	0.010	0.593
Cystoclonium purpureum	0.310	0.000	0.010	0.603

(c) North-Western Brittany	**Occurrence frequency in 1992-1998**	**Occurrence frequency in 2010-2012**	**Contribution to overall dissimilarity**	**Cumulative contribution to overall dissimilarity**
Callophyllis laciniata	0.000	1.000	0.030	0.030
Gracilaria gracilis	1.000	0.000	0.030	0.061
Chondrus crispus	0.059	1.000	0.029	0.090
Heterosiphonia plumosa	0.059	1.000	0.029	0.119
Corallina spp.	0.118	1.000	0.028	0.147
Cryptopleura ramosa	0.118	1.000	0.027	0.174
Lomentaria articulata	0.000	0.833	0.026	0.200
Heterosiphonia japonica	0.824	0.000	0.022	0.222
Phyllophora crispa	0.176	0.833	0.021	0.243
Calliblepharis jubata	0.235	0.833	0.021	0.265
Dilsea carnosa	0.000	0.667	0.021	0.286
Seirospora seirosperma	0.765	0.000	0.021	0.307

Rhodymenia holmesii	0.000	0.667	0.020	0.327
Ahnfeltiopsis devoniensis	0.765	0.000	0.020	0.347
Mastocarpus stellatus	0.059	0.667	0.020	0.367
Kallymenia reniformis	0.412	1.000	0.020	0.387
Plocamium spp.	0.412	1.000	0.020	0.407
Osmundea pinnatifida	0.118	0.667	0.019	0.426
Ceramium spp.	0.882	0.333	0.018	0.444
Callithamnion tetragonum	0.353	0.667	0.018	0.462
Delesseria sanguinea	0.000	0.500	0.015	0.477
Palmaria palmata	0.000	0.500	0.015	0.493
Gelidium corneum	0.765	0.500	0.015	0.508
Gastroclonium ovatum	0.824	0.500	0.015	0.523
Halurus equisetifolius	0.412	0.500	0.015	0.538
Sphaerococcus coronopifolius	0.118	0.500	0.015	0.553

Phyllophora sicula	0.529	0.000	0.014	0.567
Kallymenia requienii	0.471	0.000	0.012	0.580
Phyllophora pseudoceranoides	0.412	0.167	0.012	0.592
Apoglossum ruscifolium	0.059	0.333	0.011	0.603
Calliblepharis ciliata	0.176	0.333	0.011	0.613
Gigartina pistillata	0.118	0.333	0.010	0.624
Hypoglossum hypoglossoides	0.000	0.333	0.010	0.634
Gymnogongrus crenulatus	0.118	0.333	0.010	0.644

(d) West Brittany	**Occurrence frequency in 1992-1998**	**Occurrence frequency in 2010-2012**	**Contribution to overall dissimilarity**	**Cumulative contribution to overall dissimilarity**
Cryptopleura ramosa	0.000	1.000	0.032	0.032
Gracilaria gracilis	1.000	0.000	0.032	0.064
Rhodymenia pseudopalmata	0.000	1.000	0.032	0.097
Callophyllis laciniata	0.015	1.000	0.032	0.129
Corallina spp.	0.015	1.000	0.032	0.161
Lomentaria articulata	0.000	0.833	0.027	0.188
Phyllophora crispa	0.015	0.833	0.027	0.215
Chondrus crispus	0.212	1.000	0.027	0.241
Membranoptera alata	0.045	0.833	0.026	0.267
Plocamium spp.	0.303	1.000	0.023	0.290
Halurus equisetifolius	0.076	0.667	0.021	0.311
Kallymenia reniformis	0.227	0.667	0.021	0.331

Gymnogongrus crenulatus	0.015	0.667	0.020	0.351
Heterosiphonia plumosa	0.106	0.667	0.019	0.371
Gastroclonium ovatum	0.742	0.333	0.019	0.389
Heterosiphonia japonica	0.606	0.000	0.017	0.407
Dilsea carnosa	0.000	0.500	0.017	0.423
Callithamnion tetragonum	0.485	0.667	0.017	0.440
Gelidium corneum	0.303	0.500	0.016	0.456
Seirospora seirosperma	0.561	0.000	0.016	0.473
Phyllophora pseudoceranoides	0.288	0.500	0.016	0.489
Apoglossum ruscifolium	0.030	0.500	0.015	0.504
Chylocladia verticillata	0.000	0.500	0.015	0.519
Polyneura bonnemaisonii	0.076	0.500	0.015	0.534
Osmundea pinnatifida	0.000	0.500	0.014	0.548
Kallymenia requienii	0.515	0.000	0.014	0.562

Ceramium spp.	0.924	0.667	0.013	0.575
Cystoclonium purpureum	0.394	0.000	0.012	0.587
Aglaothamnion hookeri	0.409	0.000	0.012	0.598
Hypoglossum hypoglossoides	0.000	0.333	0.011	0.610
Delesseria sanguinea	0.076	0.333	0.011	0.621

(e) South Brittany	**Occurrence frequency in 1992-1998**	**Occurrence frequency in 2010-2012**	**Contribution to overall dissimilarity**	**Cumulative contribution to overall dissimilarity**
Gracilaria gracilis	1.000	0.000	0.027	0.027
Heterosiphonia japonica	0.921	0.000	0.025	0.052
Seirospora seirosperma	0.921	0.000	0.023	0.075
Ceramium spp.	1.000	0.231	0.022	0.097
Kallymenia requienii	0.868	0.000	0.021	0.118
Cryptopleura ramosa	0.000	0.769	0.021	0.139
Gastroclonium ovatum	0.868	0.154	0.020	0.159
Heterosiphonia plumosa	0.026	0.769	0.020	0.178
Cystoclonium purpureum	0.842	0.077	0.019	0.198
Lomentaria clavellosa	0.789	0.000	0.019	0.217
Dilsea carnosa	0.000	0.692	0.019	0.235
Phycodrys rubens	0.000	0.692	0.018	0.254

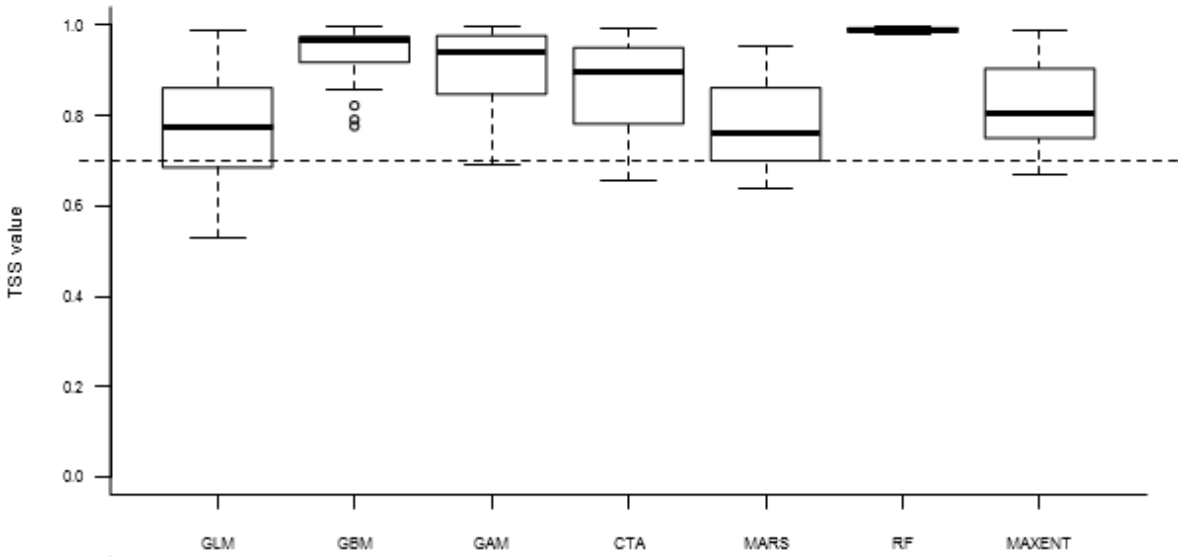
Phyllophora pseudoceranoides	0.816	0.154	0.018	0.272
Liagora viscida	0.763	0.000	0.018	0.289
Jania rubens	0.684	0.000	0.017	0.306
Microcladia glandulosa	0.737	0.000	0.017	0.323
Spermothamnion repens	0.737	0.000	0.017	0.340
Aglaothamnion hookeri	0.737	0.000	0.017	0.357
Gracilaria compressa	0.711	0.000	0.017	0.373
Callithamnion tetragonum	0.711	0.154	0.016	0.389
Aglaothamnion tenuissimum	0.711	0.000	0.016	0.405
Pterosiphonia spp.	0.711	0.000	0.016	0.421
Stenogramma interrupta	0.684	0.000	0.016	0.437
Bonnemaisonia clavata	0.684	0.000	0.016	0.453
Drachiella spectabilis	0.684	0.000	0.016	0.469
Gelidium spinosum	0.684	0.000	0.016	0.484

Goniotrichum elegans	0.684	0.000	0.016	0.500
Gracilariopsis longissima	0.684	0.000	0.016	0.515
Spermothamnion mesocarpum	0.684	0.000	0.016	0.531
Gelidium corneum	0.553	0.231	0.015	0.546
Scinaia furcellata	0.632	0.000	0.015	0.561
Gelidium spp.	0.684	0.154	0.015	0.576
Lomentaria articulata	0.684	0.154	0.015	0.591
Calliblepharis ciliata	0.711	0.385	0.014	0.605
Delesseria sanguinea	0.500	0.538	0.013	0.619
Kallymenia reniformis	0.184	0.462	0.013	0.632
Sphaerococcus coronopifolius	0.395	0.154	0.013	0.645
Phyllophora crispa	0.026	0.538	0.013	0.658
Porphyra spp.	0.184	0.462	0.012	0.670
Corallina spp.	0.053	0.462	0.012	0.682

Callophyllis laciniata	0.000	0.462	0.011	0.692
Radicilingua thysanorhizans	0.500	0.000	0.010	0.703
Ahnfeltia plicata	0.500	0.000	0.010	0.713

Appendix S3 Detailed information about results of species distribution modeling

(a) TSS evaluations of the seven models used for the ensemble forecasting



(b) Results of the Student-test assessing the differences between the periods 1992–1998 and 2010–2012 regarding the latitudinal distributions (b1) and the distributions along the coastline (b2). Latitudinal values are expressed as decimal degrees.

(b1)	**T-test**	**df**	**p-value**
Ahnfeltiopsis devoniensis	-9.43	19.64	< 0.01
Calliblepharis ciliata	-18.91	305.61	< 0.01
Calliblepharis jubata	-9.37	84.53	< 0.01
Ceramium spp.	-14.97	531.39	< 0.01
Drachiella spectabilis	-26.11	154.12	< 0.01
Gastroclonium ovatum	-16.21	525.22	< 0.01
Kallymenia reniformis	-2.10	393.69	0.04
Phyllophora pseudoceranoides	-2.91	26.20	0.01
Plocamium spp.	1.51	403.31	0.13
Sphaerococcus coronopifolius	-11.06	609.93	< 0.01

(b2)	**T-test**	**df**	**p-value**
Ahnfeltiopsis devoniensis	-9.75	17.81	< 0.01
Calliblepharis ciliata	-26.33	372.68	< 0.01
Calliblepharis jubata	-8.55	75.80	< 0.01
Ceramium spp.	-18.23	470.92	< 0.01
Drachiella spectabilis	-43.20	507.54	< 0.01
Gastroclonium ovatum	-18.22	403.37	< 0.01
Kallymenia reniformis	-2.19	350.28	0.03
Phyllophora pseudoceranoides	-1.56	26.03	0.13
Plocamium spp.	-3.59	351.96	< 0.01
Sphaerococcus coronopifolius	-12.17	640.36	< 0.01

II-3 Article 3: « From diversity to functionality of red seaweed communities: a scale-dependent relationship »

Soumis à Journal of Phycology

Régis Gallon and Eric Feunteun

Régis Gallon : Prélèvement *in situ*, analyses, rédaction

Eric Feunteun : Prélèvement *in situ*, amélioration du manuscrit

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ABSTRACT

The coastal areas are known to be among the most productive of the biosphere. In the context of biodiversity loss, most studies investigate the relationship between biodiversity and biomass. Our study focussed on red seaweed assemblages. Initially, we investigated the relationship between biomass (as a consequence of the production function) and (i) the species richness and (ii) the structure of communities. We then examined the organization of red seaweed communities between two contrasting oceanic coasts: the Normand-Breton Gulf and Penmarc'h. Our results showed that at the assemblage scale there was a strongly positive relationship between species richness and biomass; however, for a given richness, biomass was not correlated with the structure of biomass, which highlighted the functional redundancy of some species. At a large scale, communities differed between the two oceanic coasts; due to the hydrodynamic and bathymetric characteristics of the Normand Breton Gulf, the biomass of assemblages was higher than for Penmarc'h. Temperature and turbidity also seemed to drive the organization of red seaweed assemblages.

Key-words: ecological niche / redundancy / production / community structure / biodiversity.

INTRODUCTION

Coastal areas are known to be among the most productive in the biosphere (Gattuso et al., 1998). They contribute significantly to carbon cycles and to the enrichment of adjacent marine areas. Since the emergence of the concept of functional redundancy (Lawton and Brown 1993), an understanding of community structure and the function of species in communities has been necessary to evaluate the stability and robustness of ecosystems when subjected to short-term (brief disruptions) and mid- to long-term (global change) shifts (Hooper et al. 2005, Bracken et al. 2008). Due to biodiversity loss, the topic of biodiversity and ecosystem functioning (BEF) has been widely studied over the last decade (Loreau et al. 2001). Biodiversity changes cause unexpected and variable responses, both in terms of biocenose structure and the functioning of ecosystems (Kraufvelin 2009). In marine ecosystems, biodiversity patterns and assemblage structure are strongly governed by abiotic factors such as light (Häder and Figueroa 1997), temperature (Eggert 2012), water motion (Hurd 2001), nutrient availability (Kraufvelin et al. 2009), and type and surface of substratum (Downes et al. 2000) together with biotic factors (such as competition and predation). In turn, these factors directly rule ecosystem functioning but can be attenuated by the functional redundancy of species (Walker 1992). Indeed, an erosion of specific richness can alter the ecosystem functioning and related services when functional groups disappear (i.e. top predators or macrophytic primary producers). On the other hand, if a single species of a functional group persists, the function may be preserved (i.e. primary production or food web control).

Because of their high productivity, macrophytes are considered to be essential components of marine ecosystems (Wienche and Bischof 2012) (Table 1). Consolidating the concept of outwelling developed by Odum in 1968 (i.e. marine phanerogams produce more organic matter than consumers can assimilate in situ), 10% of the net production of macroalgae is

consumed directly by grazers whereas 90% is integrated into trophic webs, via detritic pathways, as particulate organic matter (POM) or dissolved organic matter (DOM) (Pomeroy 1980, Mann 1982, Wada 2008). The relationship between biodiversity and production is controversial; Naeem et al. (1994) and Tilman (1996) have demonstrated that primary production is positively related to biodiversity, whereas recent experiments have shown that species composition and the number of functional groups have a more substantial influence than species richness (Bruno et al. 2005, 2006; O'Connor and Crowe 2005).

This study focussed on subtidal red seaweed communities that extend, mostly on rocky substrata, as algal meadows from lower infralittoral (sub-strata of kelps) to upper circalittoral zones. These habitats are still poorly understood despite their functional role as primary producers (Miller 2009) and habitat providers (Marx 1985), probably because they are located at depths where their sampling requires scuba diving. We measured macroalgal diversity, species composition, and biomass in two coastal areas of Brittany (France): the north of the Bay of Biscay and the south-west Channel. As the nutrient availability and habitat diversity are thought to decrease with the distance from the coastline and the accessibility to light decreases with depth, we hypothesized that diversity and biomass would decrease along a coastal–offshore gradient and with depth. The first objective was thus to understand the relationship between species richness, community structure, and the production of red seaweeds communities in two contrasting marine ecosystems of the north of the Bay of Biscay and the south-west Channel. The second objective was to evaluate how abiotic factors (temperature, light, nutrients, and depth) influenced this relationship.

Table 1: Primary production described in recent articles of macroalgae and seagrass

Biological model	Production estimated	References
Kelp	500 g $C.m^{-2}.y^{-1}$ to 2 kg C $m^{-2}.y^{-1}$	Kérambrun 1984, Abdullah and Frederiksen 2004, Wienche and Bischof 2012
Seagrass	500 g $C.m^{-2}.y^{-1}$ to 1.2 kg C $m^{-2}.y^{-1}$	Hillman 1995, Duarte 1999, Ouisse 2010
Seaweeds	470 g $C.m^{-2}.y^{-1}$ to 1 kg C $m^{-2}.y^{-1}$	Copertino *et al.* 2005, Miller *et al.* 2009

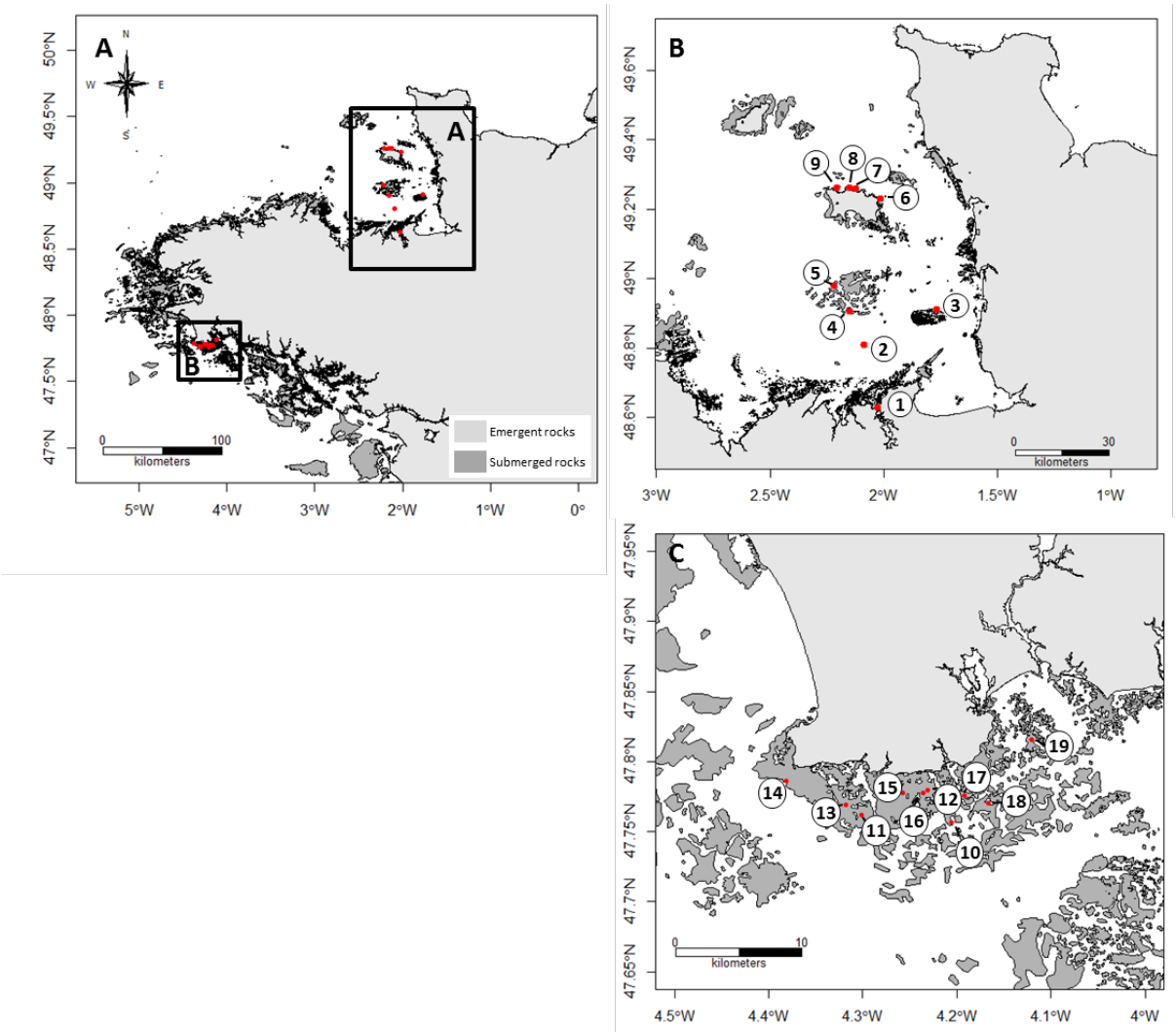

Fig 1: Locations of 19 stations sampled along the Brittany coast. Box B: stations 1–9 sampled in the Normand-Breton Gulf; Box C: stations 10–19 sampled in Penmarc'h. Stations are described in Table 2.

Material and methods

Study area

This study was conducted along Brittany in two oceanic systems (Fig. 1 A). The first, the Normand-Breton Gulf (NBG), situated in the south-western English Channel, exhibits a shallow bathymetry that does not exceed 60 m (Fig. 1 B). It is composed of several islands and flat rock shelves that strongly influence the circulation and the direction of the tidal current. The tidal amplitude ranges up to 16 m and the area receives the inputs of a small catchment area with most rivers converging into Mont Saint Michel Bay. The presence of cyclonic and anticyclonic gyres in the gulf (Salomon and Breton 1991) increases the retention time of water in the coastal area (Largier 2003). The second, Penmarc'h, is situated in southern Brittany (Fig. 1 C). This area is composed of several rocky cliffs with steep slopes. Due to the oceanic influence, they are subjected to important swells and terrigenous inputs are more limited than in the Normand-Breton Gulf. A total of 19 sites were sampled, nine sites in the Normand-Breton Gulf and 10 in Penmarc'h (Table 2)

Table 2: Description of sampling stations. Geographical coordinates (WGS84) are expressed in decimal degrees. Depth max, C1, C2 and C3 are expressed in meters corrected to the lowest astronomical tide level. (CHAU: Chausey Archipelago; JERS: Jersey; MINQ: Minquiers Archipelago; PENM: Penmarc'h; SMAL: Saint Malo Bay)

ID	Name	Site	Latitude	Longitude	Date	Number of quadrats and visual census	Depth max	Number of belts
1	Bizeux	SMAL	48.6290	-2.0250	09-2011	5	13.2	3
2	Basse Trouvée	SMAL	48.8081	-2.0883	09-2011	5	21.2	3
3	L'Etat	CHAU	48.9120	-1.7680	06-2011	5	10.5	3
4	Le Four	MINQ	48.9050	-2.1510	06-2011	7	25.1	3
5	La dérée Anglaise	MINQ	48.9800	-2.2170	06-2011	8	9.3	2
6	Coupe Rock	JERS	49.2316	-2.0148	06-2011	5	17.3	3
7	Ronez Point	JERS	49.2624	-2.1524	06-2011	5	21	2
8	Grune de Becquet	JERS	49.2630	-2.2052	06-2011	3	18.3	3
9	Demie Rock	JERS	49.2586	-2.1233	06-2011	5	11	3
10	Basse Devel	PENM	47.7755	-4.1917	09-2010	5	14.2	3
11	Basse Moeur	PENM	47.7622	-4.3014	09-2010	5	15.1	-
12	Fornigou	PENM	47.7795	-4.2313	09-2010	5	8.7	-
13	Basse Salliou	PENM	47.7688	-4.3178	09-2010	5	16.3	-
14	Basse Bouline	PENM	47.7865	-4.3814	05-2011	5	29.8	3
15	Ar c'har	PENM	47.7777	-4.2572	05-2011	5	16.6	2
16	Gromen	PENM	47.7777	-4.2359	05-2011	5	16.2	2
17	Sonar	PENM	47.7566	-4.2062	05-2011	5	18.5	3
18	Karreg Pell	PENM	47.7702	-4.1664	05-2011	5	20.1	3
19	Basse du chenal	PENM	47.8157	-4.1211	05-2011	5	8	1

Sampling methods

Biological data were collected in the summer months between 2010 and 2012. We adopted the sampling protocol of Gallon et al. (2013) to describe red seaweed communities. At each station a transect line was placed on the steeper slope to cross all algal belts over a limited distance: (C1) kelp belt, density >5 ind·m^{-2}; (C2) brown seaweed belt, from the lower limit of the kelp belt to depths with brown seaweed density <5 ind·m^{-2}; and (C3) red seaweed belt, from the lower limit of the brown seaweed belt to depths with red seaweed density <5 ind·m^{-2}. The lower limit of each belt was recorded and corrected to the lowest astronomical tide level. A minimum of five quadrats were set and five underwater visual censuses (UVC) were performed at each station, three quadrats and three UVC in the lower belt (C3) and one quadrat and one UVC in each upper belt (C1 and C2). Divers scraped all organisms in each 0.01-m^2 quadrat using a trowel and a suction sampler. During an underwater visual census, divers sampled all species they saw during 10 min. Samples were then placed in labelled bags and frozen at -20°C.

Species identification

All samples were filtered through a 1-mm mesh sieve and residues were stored in a freezer at -20°C. The study focussed only on red seaweeds, and all organisms were identified using Cabioc'h (2006) and Hiscock (1986). All species names were verified and updated from the World Register of Marine Species database (Costello 2008) and Algaebase (Guiry and Guiry 2013).

Biomass measurements

Biomass was calculated using the protocol of Crisp (1984) adapted for macroalgae. All species collected were dried for 48 h at 80°C and then sent to a high temperature oven for 6 h

at 520°C. Biomass was expressed as ash free dry weight (AFDW), biomass results were converted into $g \cdot m^{-2}$.

Abiotic variables

The abiotic variables used in this study and their characteristics are described in Table 3. Depth, sea surface temperature (SST), suspended inorganic matter (SPIM), and chlorophyll a (CHL) were used to describe the two oceanic systems. Depth and suspended inorganic matter concentration were chosen because they are proxies of energy availability; seaweeds need sufficient energy (light) to satisfy their physiological requirements and to maintain their competitive capacity (Hutchinson 1957). SST was selected because the warming of waters might cause physiological stress to seaweeds that could limit their development and reproduction (Lüning et al. 1990). Chlorophyll a concentration was selected because it constitutes a proxy of chemical potential for primary production. Primary production of coastal systems is closely correlated with nitrate and phosphate concentrations. For SPIM, SST and chlorophyll a, the annual mean, minimum, and maximum between 2007 and 2012 were measured. The same parameters during the growth period (from March to September) were also measured.

Data analysis

Analysis was carried out using the statistical computing program R (R software 2013). In order to investigate how diversity and biomass are distributed in both systems, we performed an analysis of variance (ANOVA) and a Tukey HSD. We tested variations of assemblages among sites sampled using permutational multivariate analysis of variance (PERMANOVA). The SIMPER (Similarity Percentage Analysis) routine was applied to identify the species responsible for the observed differences. Redundancy analysis ordination (RDA) was carried out to establish a link between the observed assemblages and abiotic factors.

Table 3: Variables used to describe stations

Variable	**Description**	Re**solution**	**Source**	**Period**
Sea surface temperature	Measure of sea surface Temperature in °C	0.02 x 0.02	AVHRR	2007-2012
Suspensed inorganic matter	Measure of Suspensed inorganic matter concentration (10^{-2} g/m^3)	0.015 x 0.01	MODIS	2007-2012
Chlorophyll a	Measure of Chlorophyll a concentration (10^{-2} mg/m^3)	0.015 x 0.01	MODIS	2007-2012

Results

Biomass, diversity, and structure relationships

A total of 80 red seaweed species were sampled during the study, 33 species in the south and 48 species in the north. The average species richness was 13 ± 6 sp·m^{-2}, with 17 ± 6 sp·m^{-2} species in the Normand-Breton Gulf and 9 ± 4 sp·m^{-2} in the Bay of Biscay. The average biomass was 134.92 ± 31.36 g·m^{-2} with 163.9 ± 38.4 g·m^{-2} in the Normand-Breton Gulf and 85.27 ± 18.2 g·m^{-2} in the Bay of Biscay. The community was dominated by 29 species that represented 90% of the biomass; however, there was a strong diversity of species richness, biomass, and assemblage structure among sites. In general, the number and the total biomass of red algae species increased with the depth; in C1 the total biomass was 214.2 g·m^{-2} distributed among 18 species, in C2 it was 552.37 g·m^{-2} among 33 species, and in C3 it was 1452.85 g·m^{-2} among 40 species. Nevertheless, the average biomass and the average richness of assemblages did not vary with depth.

The diversity differed significantly among sampled sites (ANOVA, df = 4, F-model = 2.844, p-value = 0.03). The average diversity per unit was highest in Jersey and the Minquiers (7.11 ± 4.13 spp. and 6 ± 3.77 spp., respectively). The diversity of Penmarc'h (4.53 ± 2.74 spp.) differed significantly from Jersey (Tukey HSD, p-value = 0.049) but not from the other sites. The biomass also differed between sampled sites (ANOVA, df = 4, F-model = 5.24, p-value < 0.001) (Fig. 2). Although Chausey and Saint Malo had an intermediate diversity of red algae (respectively 5.2 ± 2.74 sp·m², 5.12 ± 2.33 sp·m².), their biomass was higher than in all other sites (69.96 ± 53.59 g·m² and 75.06 ± 45.99 g·m², respectively). Jersey had intermediate biomass relative to the others sites with 52.67 ± 40.09 g·m². Minquiers and Penmarc'h had the lowest biomasses (27.33 ± 22.59 g·m² and 28.89 ± 23.24 g·m², respectively).

In all sampled sites, the diversity of red seaweeds and the structure of red seaweed assemblages were not correlated with depth. A relationship between depth and total biomass only occurred in Jersey and Minquiers (R^2 = 0.38 and 0.56, respectively), but was not observed elsewhere.

The total biomass was strongly correlated with the biodiversity in all sites ($R^2 > 0.7$) (Table 4). The correlation between total biomass and biodiversity was strongest for the assemblages of Chausey and Minquiers (R^2 = 0.942 and 0.906, respectively). Saint Malo and Chausey exhibited a high productivity and Minquiers appeared to be the least productive among the sampled sites.

The structure of assemblages (expressed as the Pielou index), was not correlated with biomass, except for Minquiers, where the biomass was positively correlated to the evenness of the assemblage (R^2 = 0.363).

Variation of assemblages

The ordination analysis showed clear differences between the two oceanic systems (Fig. 4). The first axis (43% of the total variance) separated Bizeux (Saint Malo) and L'Etat (Chausey) from the other stations. The second axis (23% of the total variance) separated the Normand-Breton Gulf (1 to 9) from Penmarc'h (10 to 19). The PERMANOVA confirmed this pattern (df = 4, perm = 999, F-model = 3.38, p-value = 0.001). Assemblages differed between most sites, except between Chausey and Saint Malo and between Jersey and Saint Malo (Table 4). Species that contributed most to the discrimination between the sampled sites detected by SIMPER procedures are presented in the supplementary material (Appendix 1). Overall, the 10 species contributing most to the differences between sites were *Plocamium* spp., *Phyllophora crispa*, *Cryptopleura ramosa*, *Phyllophora pseudoceranoides* (abundant in the Normand-Breton Gulf, less in Penmarc'h), *Calliblepharis ciliata*, *Corallina* spp., and *Dilsea*

carnosa (abundant in N2000 "Roches de Penmarc'h" and less common in the Normand-Breton Gulf). *Polyides rotundus*, *Heterosiphonia* spp., and *Phyllophora* spp. contributed to the differentiation of Bizeux (Saint Malo) and L'Etat (Chausey) from the other sites.

Only four abiotic variables significantly affected the structure of red seaweed assemblages (Fig. 5). The annual average sea surface temperature (mean SST_{year}), the growth in average sea surface temperature (mean SST_{croiss}), and the average monthly maxima of chlorophyll a concentration (max CHL_{year}) contributed strongly to the differentiation between the Normand-Breton Gulf and 'Roches de Penmarc'h'. Penmarc'h exhibited a higher annual average temperature than in the NBG; however, during the growth period (March to September), the highest temperatures were localized in the NBG (Fig. 6 A), with differences reaching 1°C. Penmarc'h also exhibited high concentrations of chlorophyll a over the year. From March to May, the concentration of chlorophyll a in Penmarc'h was up to four times higher than in the Normand-Breton Gulf (Fig. 6 B). The average monthly minima of suspended particulate inorganic matter (min $SPIM_{year}$) and depth contributed less to the distribution of red seaweed assemblages (Fig. 5). The concentration of SPIM was lower in Penmarc'h and higher in the NBG.

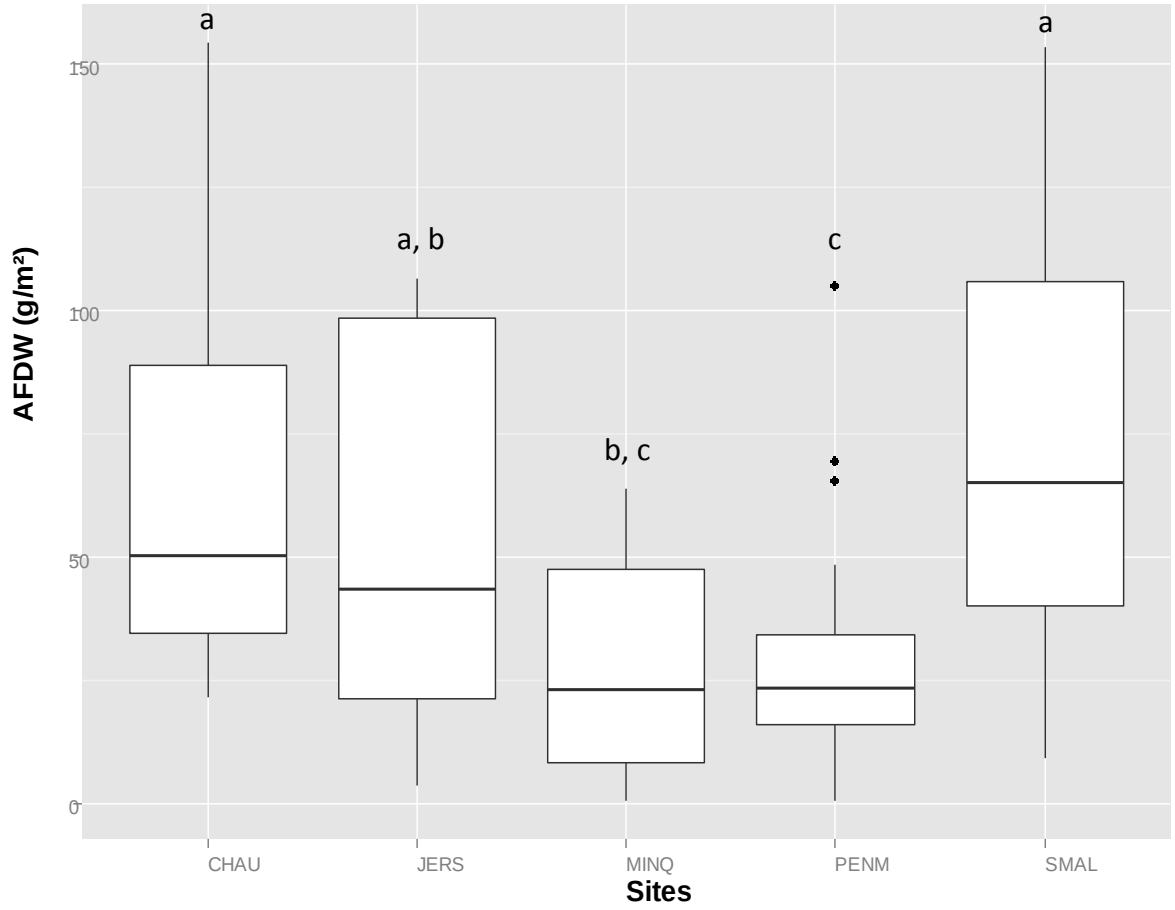

Fig 2: Boxplot of biomass for sites sampled (CHAU: Chausey Archipelago; JERS: Jersey; MINQ: Minquiers Archipelago; PENM: Penmarc'h; SMAL: Saint Malo Bay). Groups were determined by an HSD Tukey test.

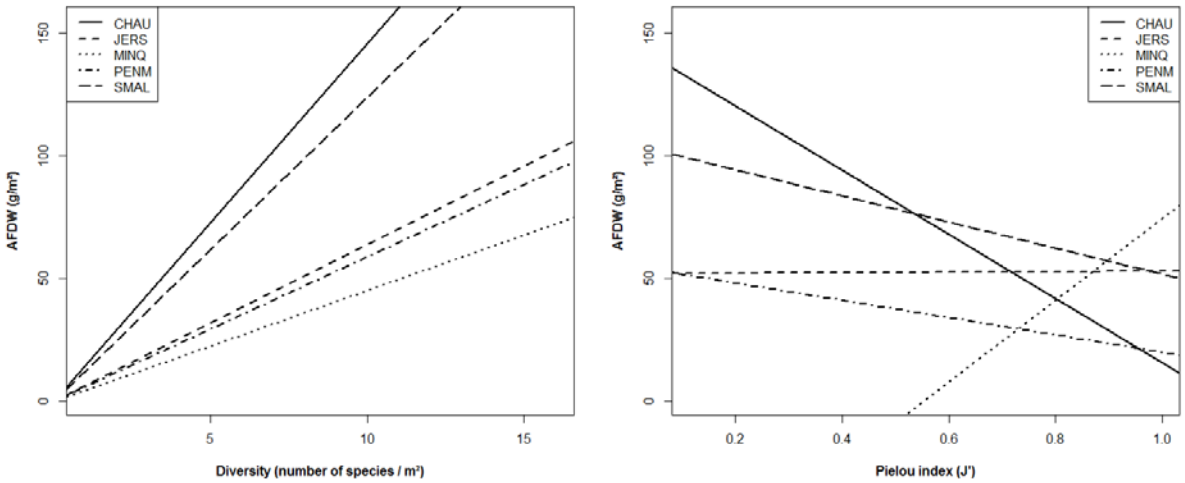

Fig 3: Relationship between ash-free dry weight (AFDW) and (A) the diversity and (B) Pielou index. (CHAU: Chausey Archipelago; JERS: Jersey; MINQ: Minquiers Archipelago; PENM: Penmarc'h; SMAL: Saint Malo Bay). Correlation results are described in Table 3.

Table 4: Result of Pearson correlation between: (i) ash free dry weight (AFWD) and species richness; (ii) ash-free dry weight (AFWD) and Pielou index (J'). (CHAU: Chausey Archipelago; JERS: Jersey; MINQ: Minquiers Archipelago; PENM: Penmarc'h; SMAL: Saint Malo Bay)

	CHAU	JERS	MINQ	PENM	SMAL
AFDW ~ Species richness					
R^2	0.942	0.784	0.906	0.713	0.767
slope	15	6.4	4.5	5.9	12
p-value	**0.0013**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
AFDW ~ J'					
R^2	0.0934	1.93e-05	0.363	0.0999	0.0607
p-value	NS	NS	**0.0293**	NS	NS

Table 5: Results of PERMANOVA pairwise tests (using Bray Curtis distance) to analyze variation of red seaweed assemblages between sites sampled (CHAU: Chausey archipelago; JERS: Jersey; MINQ: Minquiers archipelago; PENM: Penmarc'h; SMAL: Saint Malo bay). p ≤ 0.001 : '***' p ≤ 0.01 : '**' p ≤ 0.05 : '*' p ≤ 0.1 : '-'

Comparison	t-test	p-value
CHAU / JERS	1.5771	0.004**
CHAU / MINQ	1.576	0.004**
CHAU / PENM	1.8916	0.001***
CHAU / SMAL	1.3182	0.097
JERS / MINQ	1.5286	0.004**
JERS / PENM	2.4273	0.001***
JERS / SMAL	1.2269	0.118
MINQ / PENM	2.049	0.001***
MINQ / SMAL	1.6113	0.001***
PENM / SMAL	2.1276	0.001***

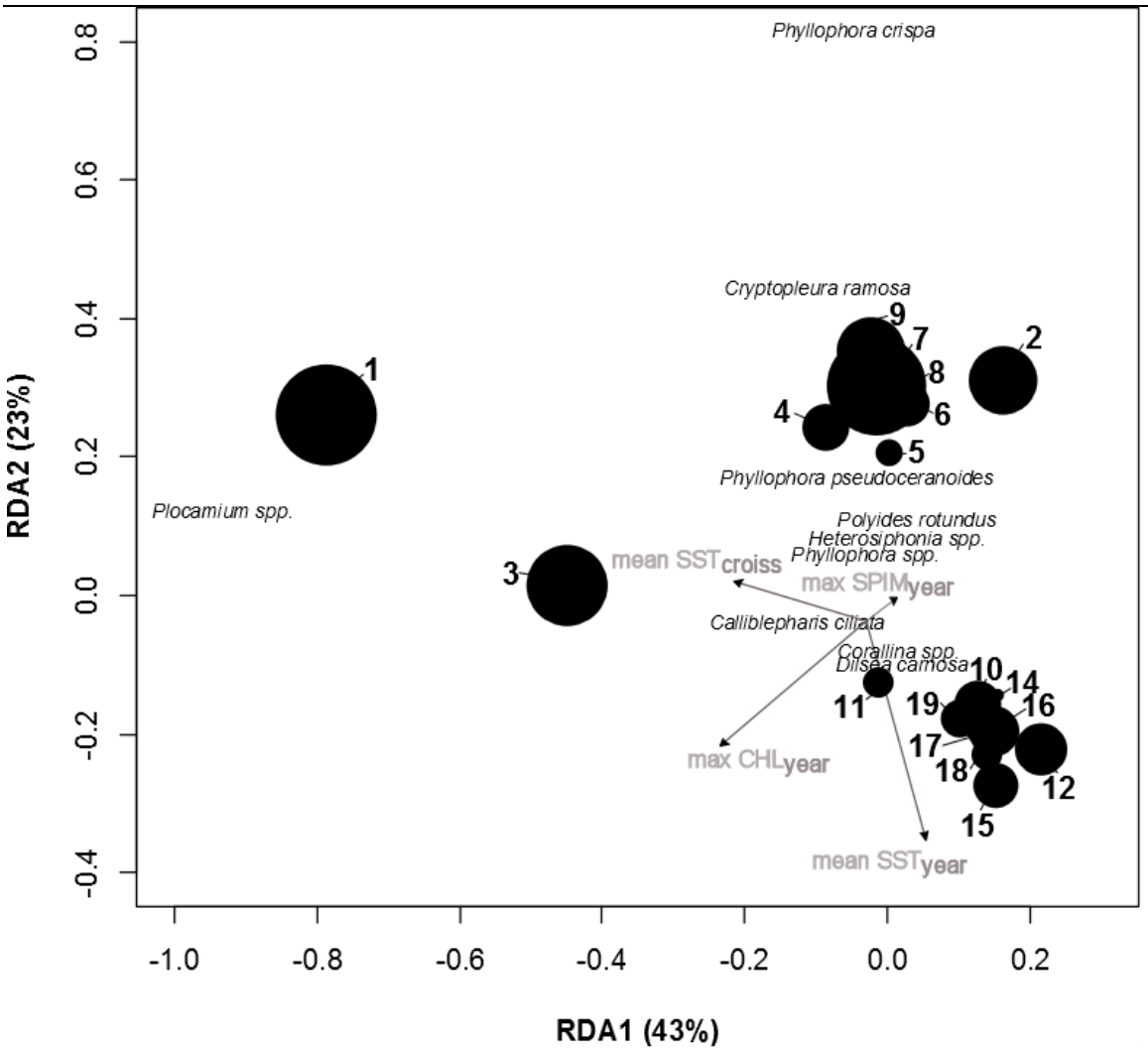

Fig 4: Redundancy analysis ordination of sampled stations based on local environmental variables between 2007 and 2011. All environmental variables were used in the analysis, but only the four most important and significant are shown on the ordination diagram. Station numbers and descriptions are given in Table 1. Length of arrows is proportional to the importance of variables. Bubbles are proportional to the total biomass of red seaweed assemblages.

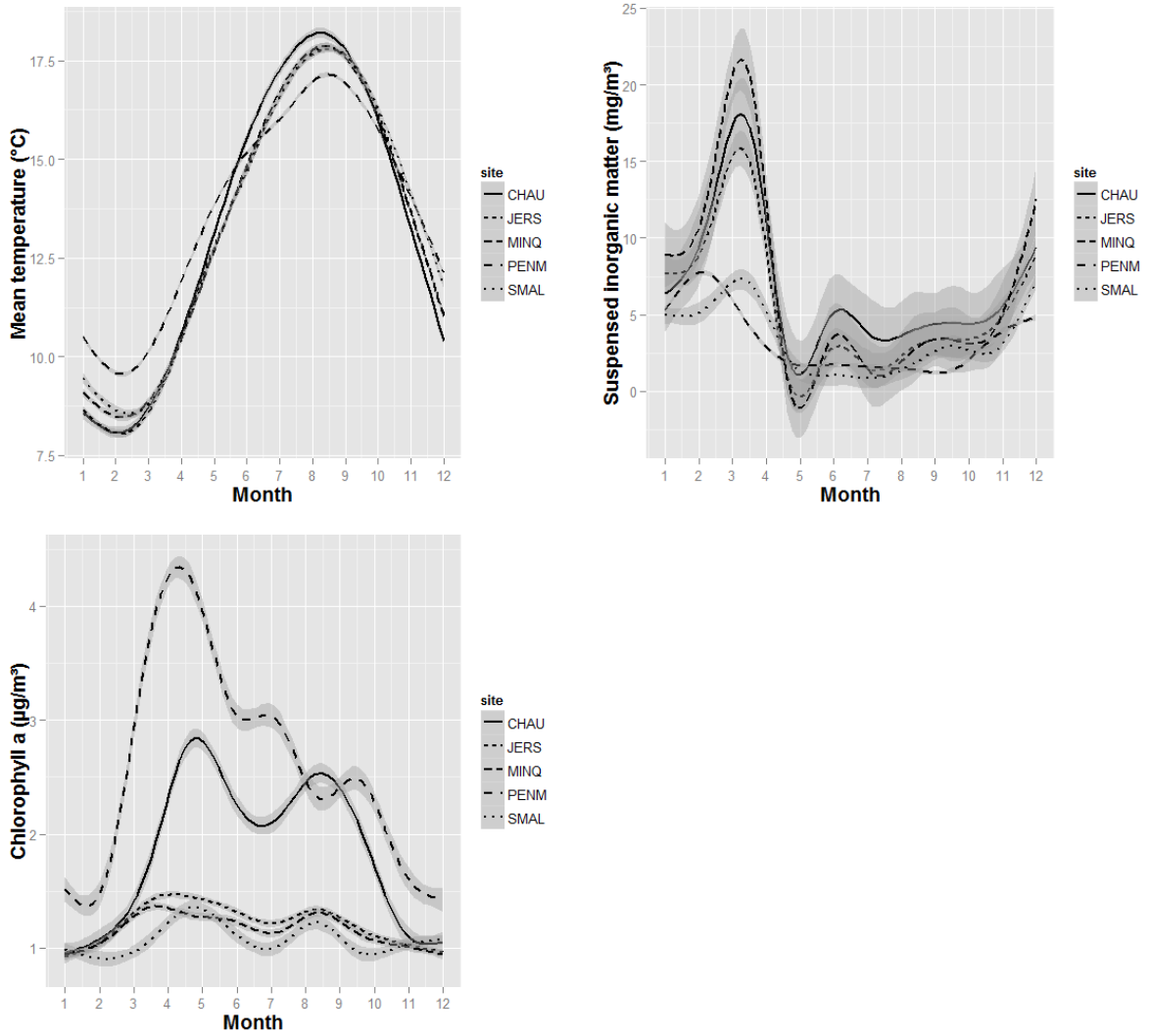

Fig 5: Environmental data from 2007 to 2011 for sites sampled in the Normand-Breton Gulf (CHAU: Chausey Archipelago; JERS: Jersey; MINQ: Minquiers Archipelago; SMAL: Saint Malo Bay) and Penmarc'h (PENM: Penmarc'h). A. Mean temperature expressed in °C; B. Suspended particulate inorganic matter expressed in $mg \cdot m^{-3}$; C. Concentration of chlorophyll a expressed in $\mu g \cdot m^{-3}$.

Discussion

Over the last decade, an increasing number of studies have focussed on the relationship between biodiversity and ecosystem functioning in terrestrial systems. On rocky shores, most research has investigated the role of disturbances on intertidal communities (Kraufvelin et al. 2010, Crowe et al. 2011, 2013) or the role of macroalgal diversity on primary production (Bruno et al. 2005, 2006, Arenas 2009).

The present paper highlights the importance of two environmental factors that govern the structure and composition of macroalgae species assemblages, annual average temperature and average temperature during the growth period, and, to a lesser extent, chlorophyll a concentration, which is considered a good proxy for nutrient concentration. The most expected result was the significant link between species diversity and biomass, but we found no relation between the assemblage structure (characterized by the Pielou index) and biomass except in one site. We also found very strong heterogeneity among sites, which could be explained by complex small-scale patterns in tidal currents, chlorophyll a and suspended matter. Our results suggest an additive relationship between species richness and biomass.

Species richness and biomass relationship

Bruno et al. (2005) demonstrated that the relationship between the number of species of red seaweed and biomass was positive and statistically significant. Worm et al. (2006) noticed general positive effects on ecosystem function. The study of Stachowitz (2008) corroborated the previous studies using short- and long-term experiments and established that seaweed species richness increased with biomass accumulation. The originality of our study was that it consolidates the previous conclusions by a non-experimental approach; we sampled sites in two contrasting oceanic coasts at 19 stations spread over five sites. We found that species richness was positively correlated with biomass in all sites. Theories explaining the positive

correlations between species richness and biomass in terrestrial ecosystems are frequently rooted in the idea of the ecological niche (Leibold 1995). Our results suggest that spatial heterogeneity and niche partitioning (popularized by Tilman et al. 1997) have a positive and additive effect on the relationship between species richness and biomass. Once species settle in a habitat they may find suitable conditions there to grow and reproduce, and when established they will contribute to biomass production. Indeed, this contribution can fluctuate depending on the heterogeneity of abiotic (short and long term disturbances) and biotic factors (competition, grazing, predation, etc.).

The relationship between species richness and biomass also depends on the spatial scale; indeed, the environmental conditions (e.g. temperature, light penetration, and nutrient inputs) affect the development of macroalgal communities. The distinctiveness of Saint Malo and Chausey from the other sites is due to their particular geographic situation. The NBG is characterized by the presence of cyclonic and anticyclonic gyres that increase the residence time of water masses, and therefore the retention time of particles. The Chausey Archipelago is located on the border of two gyres, which favours algal growth by concentrating nutrients; however, the high concentration of suspended particles causes lower species richness. Seaweed assemblages at Saint Malo follow a similar pattern that could be due to the proximity of the Rance estuary, which exports terrigeneous matter and nutrients.

Community structure and biomass relationship

We also investigated the relationship between biomass and community structure (measured by the Pielou index). For most of the sampled sites, the Pielou index values and the biomass did not fluctuate, except at Minquiers ($R^2 = 0.363$); therefore, for a given species richness, the biomass is equivalent regardless of the structure of assemblages. This relationship has been detailed by Walker (1992) and Lawton and Brown (1993). The functional redundancy is

based on the observation that some species perform similar roles in communities, and may therefore be substitutable with little impact. In our study, six species strongly contributed to the production of biomass in red seaweed assemblages: *Plocamium* sp., *Phyllophora pseudoceranoides*, *Phyllophora crispa*, *Cryptopleura ramosa*, *Calliblepharis ciliata*, and *Dilsea carnosa*. When these six species were absent or less abundant in an assemblage, others species contributed more to biomass production.

Distribution of assemblages between two different oceanic coasts

The NBG and Penmarc'h are two contrasting oceanic coasts. The NBG, located in northern Brittany, is characterized by the presence of cyclonic and anticyclonic gyres that influence the transport of particles and the propagation of propagules. Penmarc'h in southern Brittany is influenced directly by offshore inputs. Indeed, Brittany is a biogeographical transition zone between the cold and warm-temperate marine biogeographical regions (Briggs 1995; Spalding et al., 2007). Northern Brittany is influenced by cold water from the North Sea and southern Brittany by warm water from the Bay of Biscay. This transition area could explain the difference in seaweed composition between the two oceanic coasts. Seaweeds are generally kept within their boundaries by the limiting effects of temperature (Hiscock 2004). Northern boundaries are set by lethal low winter temperatures, or by summer temperatures too low for growth and/or reproduction. Southern boundaries are set by lethal high summer temperatures or by winter temperatures too high for the induction of a crucial step in the life cycle. Breeman (1994) further recognized two types of boundaries set by (i) the lethal limits of the hardiest stage in a life history, which may be a cryptic microthallus or perennating structure (where a species is exposed over several years to a lethal temperature), and (ii) growth and reproductive limits, where a species is not exposed every year to a sufficiently high or low temperature for growth and reproduction in the favourable season.

Others factors are probably involved in the distribution of red seaweeds because the 10 species recognized as characteristic of each oceanic coast can survive between 5°C and 20°C and the temperature of sites sampled ranged from 7.5°C to 19°C. According to Breeman (1994), seaweeds are unable to form temperature ecotypes rapidly; if temperature conditions deteriorate in a season, the species will become locally extinct. If temperature conditions improve, a species will extend its geographical range, but some time may elapse before a species meets its potential abundance in relation to the new temperature regime (its 'thermal potential').

In addition to temperature, turbidity and light may influence distribution. Sediment deposition is known to inhibit spore attachment to the substratum and reduce spore survival, and may kill larger plants by scouring or smothering (Devinny and Volse 1978, Norton 1978, Airoldi and Cinelli 1997, Airoldi 1998, Chapman and Fletcher 2002, Connell 2005). A decline in water transparency reduces the total available habitat further. Due to the proximity of Mont Saint Michel Bay, the NGB exhibits a high concentration of inorganic matter exported by the six watersheds (3880 km²). High concentrations appear during storm periods, and sediment deposed on the substratum is resuspended by the swell and currents and the river flows carry out more terrigenous material and nutrient inputs. Thus, the combination of high nutrient concentration and the retention time of the water body due to the gyres favours the production of biomass in the NBG. The biomasses in Penmarc'h are lower despite a high concentration of chlorophyll a (a potential proxy for nutrients); we can hypothesize that there is competition for nutrients between phytoplankton and macroalgae.

To conclude, in red seaweed habitats, biomass is spatial-scale dependent; at the community scale, the biomass does not fluctuate depending on community structure for a given species richness. All seaweeds contribute to the production of biomass and their contribution varies according to biotic and abiotic factors (functional redundancy). At a large scale, the influence

of abiotic factors becomes more important. In our study, temperature and turbidity organized red seaweed assemblages. The hydrodynamic and bathymetric distinctiveness of the Normand-Breton Gulf, in contrast with Penmarc'h, favours the development of four species (*Plocamium* sp., *Phyllophora pseudoceranoides*, *Phyllophora crispa*, and *Cryptopleura ramosa*) that contribute strongly to biomass production.

Acknowledgments

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

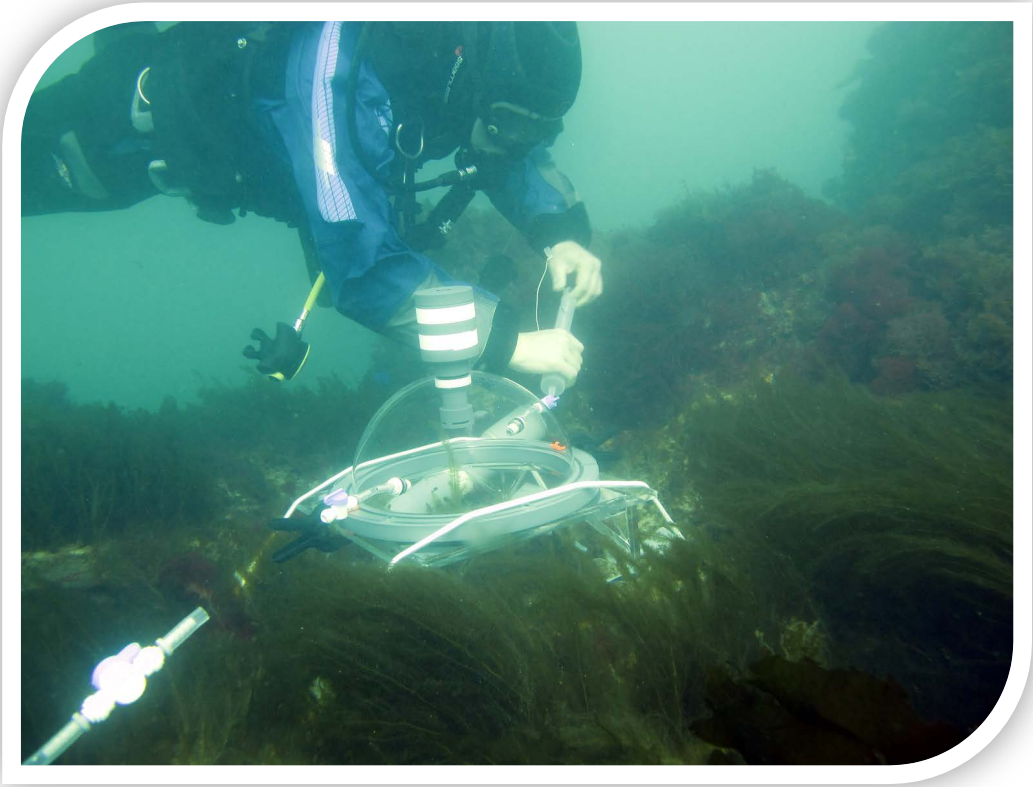
Appendix S1 Contribution of each taxon to overall dissimilarity between sampled sites according to the SIMPER routine. The taxa listed have a contribution of over 1% of the total dissimilarity.

Appendix 1: Contribution of each taxon to overall dissimilarity between sampled sites according to the SIMPER routine. The taxa listed have a contribution of over 1% of the total dissimilarity. (CHAU: Chausey Archipelago; JERS: Jersey; MINQ: Minquiers Archipelago; SMAL: Saint Malo Bay) and Penmarc'h (PENM: Penmarc'h).

	CHAU vs. JERS	**CHAU vs. MINQ**	**CHAU vs. PENM**	**CHAU vs. SMAL**	**JERS vs. MINQ**	**JERS vs. PENM**	**JERS vs. SMAL**	**MINQ vs. PENM**	**MINQ vs. SMAL**	**PENM vs. SMAL**
Plocamium spp.	0,262	0,307	0,316	0,238	0,224	0,216	0,202	0,106	0,206	0,201
Phyllophora crispa	0,173	0,140	0,135	0,151	0,157	0,158	0,163	0,100	0,184	0,177
Cryptopleura ramosa	0,121	0,099	0,086	0,069	0,083	0,080	0,100	0,092	0,084	0,082
Phyllophora spp.	0,069	0,090	0,086	0,066	0,078	0,077	0,073	0,084	0,062	0,063
Dilsea carnosa	0,049	0,059	0,082	0,048	0,042	0,055	0,048	0,084	0,057	0,056
Phyllophora pseudoceranoides	0,017	0,043	0,063	0,036	0,039	0,048	0,029	0,067	0,057	0,055
Heterosiphonia spp.	0,015	0,025	0,042	0,034	0,037	0,043	0,021	0,057	0,032	0,052
Corallina spp.	0,014	0,019	0,035	0,015	0,021	0,031	0,019	0,046	0,031	0,033
Polyides rotundus	0,013	0,017	0,015	0,014	0,020	0,023	0,014	0,045	0,028	0,031
Calliblepharis ciliata	0,013	0,014	0,014	0,013	0,018	0,021	0,014	0,041	0,020	0,027
Myriogramme spp.	0,004	0,013	0,010	0,011	0,017	0,019	0,014	0,034	0,014	0,025
Meredithia microphylla	0,004	0,012	0,007	0,009	0,013	0,019	0,013	0,026	0,012	0,023
Sphaerococcus coronopifolius	0,004	0,003	0,006	0,008	0,009	0,017	0,013	0,020	0,012	0,013
Rhodomela spp.	0,003	0,002	0,006	0,006	0,006	0,010	0,011	0,015	0,009	0,013
Rhodymenia holmesii	0,003	0,002	0,004	0,004	0,005	0,010	0,010	0,011	0,009	0,012
Stypocaulon scoparium	0,002	0,002	0,003	0,004	0,004	0,008	0,006	0,008	0,007	0,010

PARTIE 3 :

SUIVI TEMPOREL DE LA PRODUCTIVITE DES MACROALGUES DURANT LA RECOLONISATION



III-1 Contexte de l'étude

A large échelle, la distribution des communautés à rhodophytes est sensible aux facteurs environnementaux ; parmi les variables testées, la température apparait comme le principal facteur structurant ces communautés (cf. Partie 1 chapitre 1 et 2). A l'échelle des communautés, la redondance fonctionnelle mise en place dans par les cortèges d'espèces assure la stabilité de la production de matière organique qui apparait, de ce fait, peu sensible aux facteurs environnementaux (cf. Partie 1 chapitre 2). A l'échelle individuelle, les variations du métabolisme des organismes qu'ils soient autotrophes ou hétérotrophes sont influencées par la température (Touchette et Burkolder 2000 ; del Gorgio et Williams 2005). Due aux variations de la lumière contrôle de la profondeur et de la turbidité) et de la température (changements saisonniers ou interannuels) à petite échelle de temps, le métabolisme des organismes autotrophes peut subir des changements importants.

Malgré l'émergence de nombreuses méthodes permettant de suivre le métabolisme des communautés benthiques en milieu intertidal ou subtidal, les données concernant les communautés benthiques vivant sur substrat rocheux sont encore limitées. Elles se concentrent essentiellement sur les strates supérieures composées de laminaires. Or en sous-strates de ces laminaires se trouvent des algues rouges et brunes formant des prairies sous-marines qui peuvent s'étendre jusqu'au circalittoral proche et même au-delà.

A partir de mesures *in situ* du métabolisme benthique à l'aide de cloches benthiques, la productivité des communautés à macroalgues sera estimée durant un processus de colonisation s'étalant sur plus d'un an. 37 plaques nues de granite de 50 cm de côté ont été posées sur le substrat rocheux, au sein d'un habitat à rhodophytes, afin de suivre à la fois l'installation des macroalgues mais aussi la biomasse produite et la productivité associée. Ce suivi a permis de tester l'évolution de ces fonctions en réponse à l'évolution de la composition des assemblages d'algues lors du processus de colonisation.

III-2 Article 4: « Productivity of subtidal macroalgal assemblages at different stages of colonization »

En préparation

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Régis Gallon : Prélèvements *in-situ*, analyses en laboratoire, analyses statistiques, rédaction

Aline Migné : Prélèvements *in-situ*, amélioration du manuscrit

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Eric Feunteun : Prélèvements *in-situ*, amélioration du manuscrit

INTRODUCTION

Macroalgae are recognized to be vital in the functioning of marine coastal habitats (Mann 1973, Marsh 1976, Wienche and Bischof 2012). They provide food, dissolved organic matter, shelter and serve as nurseries for many benthic invertebrates and fishes (Mann et al. 1980, Mann 2000). Kelps are the most studied macroalgae because they are among the most productive autotrophs in the world (Mann 2000). Within the kelp canopy, small understory algae are less studied despite being ubiquitous on shallow costal reefs, forming distinct assemblages from the lower intertidal to the upper sublittoral zones. The contribution of these algal assemblages to reef productivity could be substantial (Miller et al 2011).

Understanding the colonization process is fundamental in order to comprehend the life history of benthic organisms. Although species succession during seaweed colonization has long been described (Carliste *et al.* 1964; Turner *et al.* 1969; Foster 1975a, 1975b; Neushul et al. 1976; Davis *et al.* 1982 in Carter et al. 1982), the functions of these assemblages are still poorly known. The relationship between biodiversity and ecosystem functioning (BEF) is very complex and essential to understand the underlying mechanisms and functional consequences of altered community structure (Kraufvelin 2010). A decreased diversity may decrease the recovery potential, the stability and the water quality of marine ecosystems, but a restored biodiversity may multiply the productivity and decrease the variability in the ecosystem (Worm et al. 2006). The diversity effects often change in form and amplitude through time revealing successional dynamics, where the effects can either grow stronger over time (Caldeira et al. 2001, Tilman et al. 2001), grow weaker (Bell et al. 2005, Cardinal et al. 2006) or fluctuate from positive to non-significant if communities reach an equilibrium state (Fox 2004, Hooper and Dukes 2004).
The relationship between species richness- and productivity has long been a subject of interest (e.g., Pianka 1966, Odum 1969) but it is still controversial (Whittaker 2010). Generally, the productivity of macroalgae is assessed indirectly using proxies such as algal cover and biomass accumulation, or directly by determining both the photosynthetic and respiratory rates. Community production and respiration can be estimated by measuring pH and alkalinity to calculate changes in carbon dioxide (Migne et al. 2002) or measuring dissolved oxygen (Miller et al. 2009).

In relation to biomass production , the link with diversity varies qualitatively according to the colonization stage (Cardinal et al. 2004). Species richness has no effect on community

biomass during early stages of colonization because communities are dominated by the most productive species, in which case the production of biomass is regulated by intraspecific mechanisms. In later stages of colonization, inter-specific mechanisms are implemented and regulate the production of biomass of the communities (Cardinal et al. 2004).

The present study aimed to: i) describe the colonization process observed on granite slabs placed in red seaweed-dominated habitats; ii) assess the gross primary production at different stages of the algal colonization and iii) link the gross primary production to the structure of algal assemblages.

MATERIAL AND METHODS

Study sites

Bizeux (48°36.677N/ 2°01.602W – WGS84) is a granitic islet of about 0,025 km² located at the mouth of the Rance river, in the bay of Saint Malo, Southern English Channel (Fig 1). It is protected from dominant wind and waves but submitted to strong bidirectional tidal currents enforced by the tidal hydropower dam of the Rance Estuary. The spring tide maximal amplitude is 13m and current's velocity attains as much as 10 knots. The islet is surrounded by subtidal cliffs from -2 to -13m below ELWS with rock boulders at the bottom on its southern and western sides and by a rocky plateau with a gentle slope (ranging from -2 to -8m) in the east and the north. We sampled 2 stations characterized by contrasting environmental conditions: i) station 1 in the north, was protected from the Rance dam's tidal currents; and ii) station 2, in the south, was directly exposed to the dam's tidal currents.

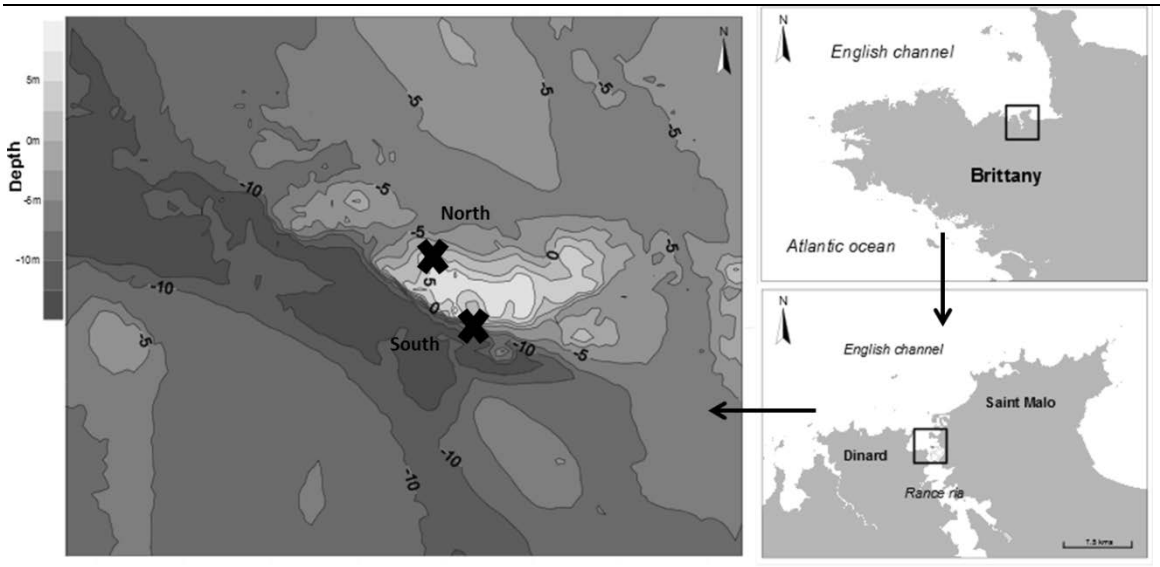

Fig. 1: Location of the two stations studied on the Bizeux islet

Sampling strategy

17 slabs of granite (50cm × 50cm) were positioned by scuba-divers in December 2010 in each station and 4 slabs were positioned in December 2011 in both the North and South stations. Productivity measurements were performed on 3 of them at different occasions corresponding to various stages of colonization (see table 1 for details). For both stations, slabs were laid out at -5m in red seaweed-dominated communities.

In April 2011, a slab that had not been used for productivity measurements was brought up and in September 2011, March 2012, April 2012, the slabs used for productivity measurements were brought up to the laboratory to measure the biomass (ash free dry weight in g/m²) and the number of species and evenness (measured with the Pielou index) of the algal assemblages. A functional group based on the Steneck and Watling (1982) classification was attributed to macroalgae: i) Filamentous: larger algal filaments with little or no cortication; ii) Foliose: thin sheet and tube morphologies; iii) Corticated : morphologically complex, tending to be wiry, tough and ramifying forms, capable of growing erect and filling three-dimensional space. The thalli of these algae are differentiated into an outer layer of small, often thick-walled, cells called a cortex (thus the name "corticated"); iv) Leathery : corticated and morphologically the most complex, with thick-walled cells giving them structural strength sufficient to become very large.

Table 1 : Date of productivity measurements performed on slabs posed in December 2010 and December 2011 in South and North stations

Station	Slabs posed in	Date of measurements	Time of colonization (months)	Slabs number
South	December 2010	2011.04.13	4	16,14,10
		2011.09.22	9	16,14,10
		2012.03.19	15	15,6,9
North	December 2010	2011.04.14	4	1,12,17
		2011.09.23	9	1,12,17
		2012.03.20	15	8,16,9
	December 2011	2012.04.16	4	1,5,16

Dissolved inorganic carbon flux measurements

Three benthic chambers (surface area of 0.09m²), trapping a known volume of water (20L) were installed by scuba-divers on the granite slabs. The trapped water–was mixed by an autonomous stirrer installed in the chambers (Fig. 2).

Benthic net community primary production (NCP) and respiration (CR) were assessed from changes in dissolved inorganic carbon (DIC) concentration through light and dark incubation respectively. Light and dark incubations were performed successively on each measurement date, during slack water and around midday to benefit from the maximum daily irradiance. The benthic chambers were opened between successive incubations to restore ambient conditions. Gross community primary production (GCP) was calculated as:

GCP=NCP+CR

At the beginning and at the end of the 50 min average incubations, 100 ml of seawater contained in the closed chambers were collected by plastic syringe and brought up to the boat to immediately measure pH and temperature (PHC101-15, accuracy ± 0.002, NBS scale) on a subsample. The rest of the sampled water (≈60 ml) was filtered onto a cellulose acetate membrane (0.8 µm) and poisoned with $HgCl_2$ (0.02 %/total sample volume, (Dickson et al., 2007)).For the potentiometric titration of total alkalinity, water samples were stored in 100ml sealed glass bottles. The potentiometric titration was performed on three sub-samples using an automatic titrator (Titroline alpha, Schott SI Analytics, Germany) and by using the Gran method (non-linear least-square fit) applied to pH values from 3.5 to 3.0 (Dickson et al., 2007). The total alkalinity (TA) was expressed in mEq/kg. The dissolved inorganic carbon

concentration was calculated from the pH, TA, temperature and salinity with the R package "SEACARB" (Lavigne & Gattuso, 2012) using the carbonate constant from Millero (2010).

Incident photosynthetically available radiation (PAR in µmol.m^{-2}.s^{-1}) and temperature were measured near the benthic chamber using an ultra-miniature MDS-MKV sensor (Alec ElectronicsTM) and were recorded with a 1 min frequency.

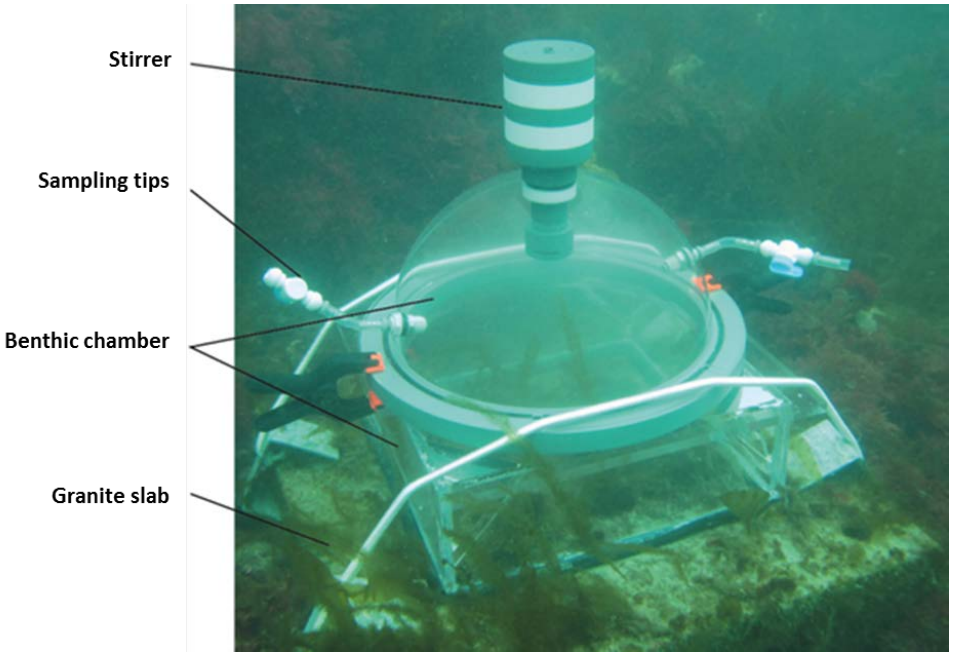

Fig. 2: Closed benthic chamber used for underwater incubation on granite slab in red seaweeds habitat.

Data analysis

First, we analyzed the trends of species richness, evenness and biomass during the colonization process for the slabs set in December 2010. The variations of assemblages between December 2010 and April 2012 were described for both stations. Gross community primary productions (GCP) measured at different stages of colonization could be compared only if they were measured under similar light conditions. Difference in GCP and CR was assessed for i) North slabs after 4 months and 15 months and ii) North slabs set in December 2010 and December 2011 after 4 months.

RESULTS

Temporal variation of algal assemblages

The colonization of slabs appeared highly variable, in term of diversity and assemblage structure between the two stations and inside each station. Whatever the time of colonization there were only two or three species per slab at the north station (Table 3), whereas some slabs at the south station were colonized by more species (P16 and P10 after 9 months ; P15 after 15 months).

In the north station, after 4 months, two small brown algae were dominant on the slabs posed in December 2010: the filamentous *Halopteris filicina* (16.3 $g.m^{-2}$) and the foliose *Desmarescia aculeata* (15.5 $g.m^{-2}$). One leathery brown algae was also present, *Laminaria* spp. (6.7 $g.m^{-2}$). Dominant species were the same on slabs posed in December 2011 and another foliose brown algal species (*Desmarescia ligulata)* was present. After 9 months of colonization, *Halopteris filicina* disappeared, *Desmarescia aculeata* became the only dominant species (400.2±21 $g.m^{-2}$) with a biomass contributing to 82.5% of the total biomass. The two other species *Laminaria latissima* and *Sacchoriza polyschides* contributed together to 21.5% (resp.13.8% and 7.7%) of the total biomass. After 15 months of colonization, *Desmarescia aculeata* remained the dominant species (84.5% of the total biomass) with a slight decrease in biomass (343.3±5.6 $g.m^{-2}$). The biomass of *Laminaria latissima* exhibited a slight increase (55.9±1.56 $g.m^{-2}$) in biomass and in its contribution due to the disappearance of *Sacchoriza polyschides* and low biomass of *Ulva sp*. (Fig. 4).

Slabs set in the South station exhibited a greater variability of colonization. The number of species per slab was very variable. Unlike north slabs after 4 months, those in the south were dominated only by the brown filamentous algae *Halopteris filicina* (12.6 $g.m^{-2}$, 60.3%); the contribution of *Desmarescia aculeata* was 4 times less than in north slabs sampled. The contribution of *Ulva sp.* was relatively high in the earlier stage (30.1%) and decreased in later stages (0.3 and 1.3 %). After 9 and 15 months of colonization, the number of species of south slabs sampled is higher than those of north mainly due to the high diversity on the P16 (9 months, 9 species) and P15 (15 months, 15 species). Nevertheless two brown algae remained dominant for the later stages: i) while *Desmarescia aculeata* was a minority species after 4 months, it later became and remained largely dominant; ii) *Laminaria latissima* appeared after 9 months with a relatively high biomass (60.1±4 $g.m^{-2}$, 22.6%) and its biomass slightly increased after 15 months but not its contribution (73.8±5 $g.m^{-2}$, 20.8%). After 9 months of

colonization 8 new species were settled mainly on slab 16, consisting of 4 brown foliose algae which contributed to 8.8% and 4 red foliose algae which contributed to 0.68% of the biomass (Fig 4). After 15 months, 9 new species, mainly red seaweeds, were sampled and their biomass contribution reached only 4.13%.

Table 2: Number of algal species (S); Evenness (J'); biomass (AFDW, g /m²) on slabs posed at the south and north stations of the Bizeux islet in December 2010 or December 2011 and sampled after 4, 9 or 15 months

Station	Slabs posed in	Time of colonization (month)	Slab	Number of algal species (S)	Evenness (J')	Biomass (AFDW, g /m²)
South	December 2010	4	P5	3	0.81	38.5
		9	P16	9	0.80	362.4
			P14	3	0.84	311.2
			P10	4	0.51	486
		15	P15	15	0.59	500.3
			P6	3	0.80	512.1
			P9	2	0.98	652.3
North	December 2010	4	P8	3	0.94	20.9
		9	P1	3	0.33	762.7
			P12	2	0.76	681.1
			P7	3	0.66	648.8
		15	P8	2	0.59	500.3
			P16	3	0.41	338.9
			P9	3	0.57	407.2
	December 2011	4	P1	3	0.98	52.1
			P5	3	0.65	45.1
			P16	2	0.97	48.9

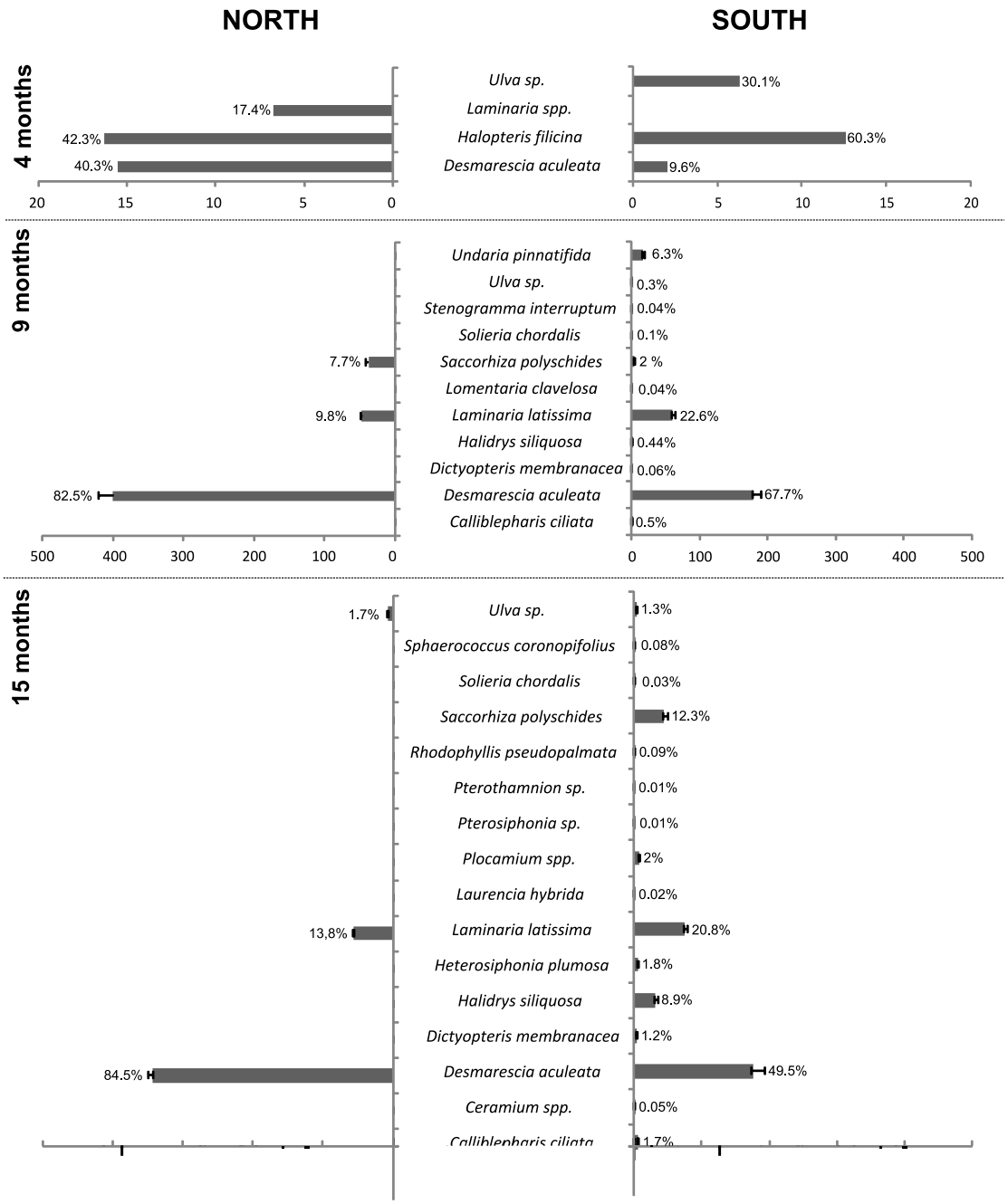

Fig 4: Biomass (mean + SD) of algal species settled on slabs set in December 2010 at the North and South Bizeux stations after 4, 9 and 15 months of colonization.

Temporal variation of algal functional groups.

The distribution of functional groups (Table 3) followed similar patterns in the North and South stations. The contribution of filamentous algae was maximal (from 50% to 65%) for the earlier stage, and this group disappeared or became a minority in the later stages (Fig 5). After 4 months of colonization, the South showed the particularity of a high contribution of foliose algae represented by *Ulva sp.* The last stages of colonization were largely dominated by leathery macrophytes. After 15 months, the 3 other functional groups were present but their contribution didn't exceed 7%.

Table 3 List of species sampled and functional group based on Steneck and Watling (1982) classification.

Species	Phylum	Functional group
Ulva sp.	Chloro.	Foliose
Halopteris filicina	Ochro.	Filamentous
Dyctyopteris membranacea	Ochro.	Foliose
Desmarescia aculeata	Ochro.	Leathery
Halidrys siliquosa	Ochro.	Leathery
Laminaria latissima	Ochro.	Leathery
Laminaria spp.	Ochro.	Leathery
Saccorhiza polyschides	Ochro.	Leathery
Undaria pinnatifida	Ochro.	Leathery
Bornetia secundiflora	Rhodo.	Filamentous
Ceramium spp.	Rhodo.	Filamentous
Heterosiphonia plumosa	Rhodo.	Filamentous
Laurencia hybrida	Rhodo.	Filamentous
Pterosiphonia sp.	Rhodo.	Filamentous
Pterothamnion sp.	Rhodo.	Filamentous
Calliblepharis ciliata	Rhodo.	Foliose
Lomentaria clavelosa	Rhodo.	Foliose
Rhodophyllis pseudopalmata	Rhodo.	Foliose
Stenogramma interruptum	Rhodo.	Foliose
Plocamium cartilagineum	Rhodo.	Corticated
Solieria chordalis	Rhodo.	Corticated
Sphaerococcus coronopifolius	Rhodo.	Corticated

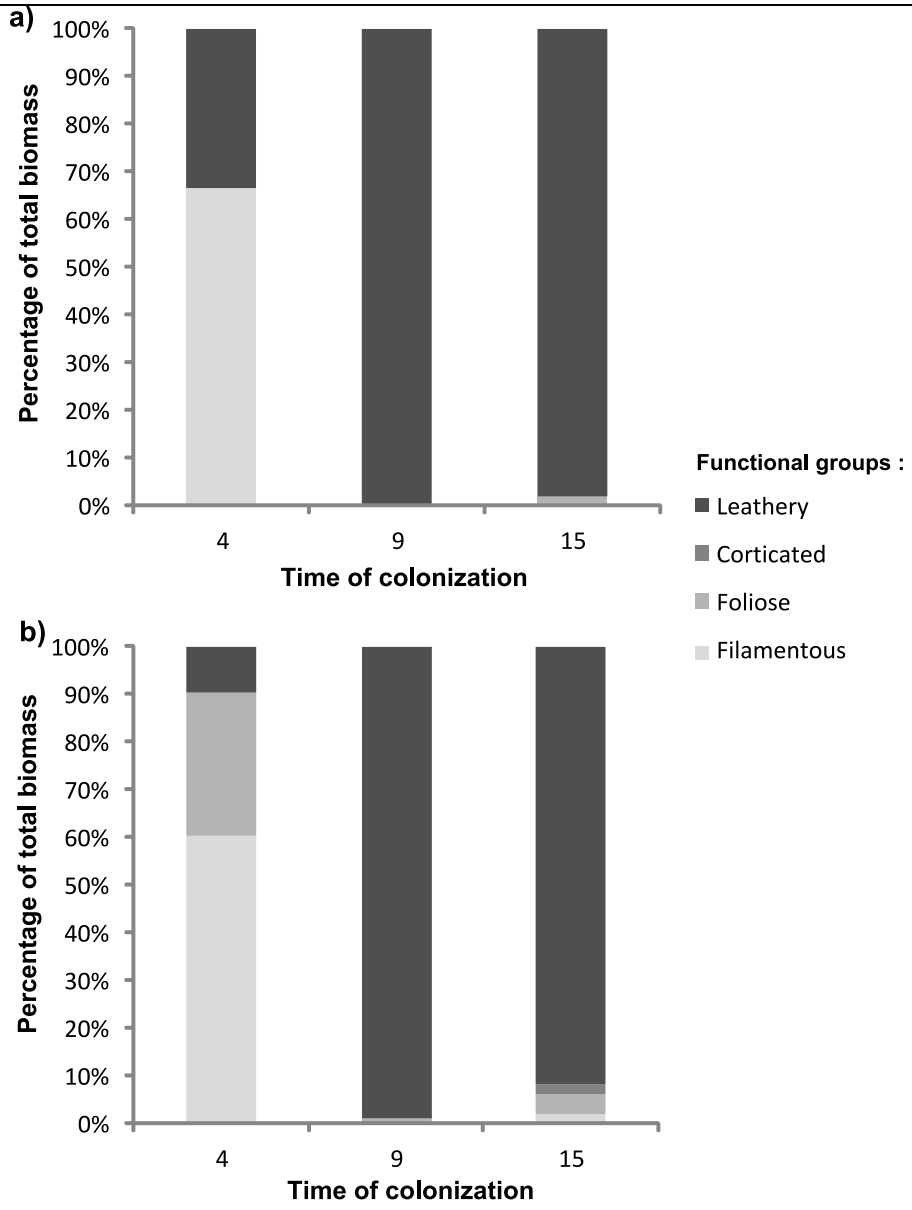

Fig 5: Evolution of the contribution of functional groups after 4, 9 and 15 months on slabs set in December 2010. a) North station, b) South station

Evolution of the productivity of algal assemblages

Concerning the gross primary production, it's difficult to exhibit a trend because incident light was very variable during measurements (Table 4). Only rates measured under similar light conditions were compared. Despite this the mean productivity rate per area of assemblage settled on slabs set in the North of Bizeux was roughly the same after 4 and 15 months (27.51 ± 0.11 and 28.74 ± 3.78 mmolC m^{-2} h^{-1} respectively). The biomass per unit was much higher after 4 months (1.31 ± 0.005 mmolC g^{-1} h^{-1}) than after 15 months (0.07 ± 0.01 mmolC g^{-1} h^{-1}).

The mean productivity of assemblages after 4 months was higher for the slabs set in December 2010 than for the slabs set in December 2011 (14.18 ± 1.76 mmolC m^{-2} h^{-1}).

Table 4: Light (PAR : photosynthetically active radiation in µmol/m²/h) and temperature (T in °C) conditions, both expressed as mean± sd; gross community primary production (GCP in mmolC/m²/h) measured 4, 9 or 15 months after the slabs were posed on the two stations of Bizeux islet.

Station	Slabs posed in	Time of colonization (month)	PAR (µmol/m²/s)	T (°C)	Slab	GCP (mmol/m²/h)
South	December 2010	4	54 ± 24	11.5±0.1	P16	8.62
					P14	6.02
					P10	10.78
		9	80 ± 4	17.1±0.0	P16	6.38
					P14	16.58
					P10	13.08
		15	539 ± 57	9.3±0.0	P15	1.54
					P6	21.3
					P9	23.1
North	December 2010	4	260 ± 53	11.3±0.2	P1	27.39
					P12	27.58
					P7	27.56
		9	37 ± 7	17.3±0.0	P1	5.43
					P12	6.31
					P7	3.89
		15	268 ± 22	9.1±0.0	P8	29.61
					P16	32.02
					P9	24.61
	December 2011	4	307 ± 41	11±0.0	P1	12.14
					P5	15.29
					P16	15.10

DISCUSSION

In general, the colonization observed on the slabs immersed in Bizeux was similar to other colonization processes described in the literature (e.g. Neushul *et al.* 1976, Foster 1975 a; 1975 b, Carter *et al.* 1985),–even if settled communities settled were very variable. This variability can be explained by several factors as shown before : the slope (Somsueb *et al.* 2000) ,the fine-scale hydrodynamics inducing shear stress (Hurd 2000), the light accessibility (Gattuso 2006).–Initial communities were dominated by barnacles and hydroids (*in situ* observations), then the algal colonization began by filamentous algae and continued with foliose and leathery algae., Paul et al. (2006) demonstrated that the filamentous form represents a highly successful growth strategy. In our study, filamentous algae were replaced by leathery brown algae (*Desmarestia aculeata*) and kelps after 9 months of colonization. Red algae appeared as epiphytes of brown algae ~~at~~ after 15 months of colonization~~,~~.

The evolution of gross community primary production (GCP) during the colonization process was prevaricated by the strong variation of light conditions during measurements. Nevertheless for equivalent light conditions the GCP didn't change between 4 and 15 months of colonization. This may result from the substitution of filamentous species such as *Halopteris filicina* which were recognized to have high productivity rates and low abundance (Klumpp and Mc Kinnon 1992) by leathery species with moderate productivity rate and high abundance (*Desmarecia aculeata*). However, in later stages (15 months) the density of the dominant species was so important that it is possible that only the upper part of thalli received enough energy for photosynthesis. Moreover, most of the thalli were colonized by epiphytes which further reduce the area receiving light energy, therefore they must be responsible for the production measured.

In established communities, Miller et al (2009) measured lower production per unit area in filamentous- algae dominated assemblages rather than foliose algae-dominated assemblages. Higher production per unit biomass was observed in filamentous algae dominated assemblages than in foliose algae-dominated assemblages. In the present study, comparable rates per unit area were measured at different stages of the colonization process while greater rates per unit biomass were measured in the early stages of colonization when the assemblages were dominated by filamentous algae.

Perspectives

Our protocol illustrates a new aspect of the colonization process: the establishment of production and productivity functions in benthic assemblages. To further this study, it would be interesting to have autonomous benthic chambers which could measure productivity during one or more circadian cycle in order to follow the variation of productivity with light at different stages of the colonization process.

ACKNOWLEDGMENTS

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PARTIE 4 :

DEVENIR DE LA PRODUCTION DES COMMUNAUTES A RHODOPHYTES DANS LES RESEAUX TROPHIQUES.

IV-1 Contexte de l'étude

La production primaire associée aux milieux rocheux subtidaux est reconnue pour être l'une des plus importante des systèmes côtiers (Dauvin 1997, Wienche et Bischof 2012) et est fortement assujettie aux conditions environnementales (cf. Partie 1 et 2). La matière organique ainsi synthétisée par les producteurs primaires est ensuite consommée localement par des consommateurs primaires ou exportée dans les systèmes adjacents par voie détritique. Concernant les macroalgues, il est généralement admis que 10% de la production nette est consommée directement par les brouteurs alors que 90% entre par voie détritique dans les réseaux trophiques comme matière organique particulaire (MOP) ou comme matière organique dissoute (MOD) (Pomeroy, 1980; Mann, 1982). Néanmoins, ce fonctionnement a surtout été décrit sur les habitats à laminaires (Schaal et al 2008, 2010, Leclerc 2013), la connaissance concernant l'intégration de la matière organique issue des communautés à rhodophytes reste très limitée.

Le suivi du devenir de la matière organique est permis par l'utilisation de marqueurs naturels :

« *Un composé d'origine unique, facilement identifiable, non nocif pour l'organisme, ne subissant aucun processus sélectif lors de l'ingestion ou de l'incorporation, métaboliquement stable et transféré d'un niveau trophique au suivant de manière qualitative et quantitative* » (Dalsgaard et al. 2003).

A l'heure actuelle, il n'existe pas de traceur « idéal », néanmoins l'utilisation combinée des isotopes stables et des acides gras permet d'obtenir une cartographie robuste du réseau trophique.

L'objectif de ce chapitre est, dans un premier temps, d'évaluer la capacité des marqueurs communément utilisés (acides gras et isotopes stables) à distinguer les différents phyla (algues rouges, brunes et vertes) et espèces des communautés à rhodophytes puis de mettre en évidence l'intégration des algues rouges dans les compartiments trophiques supérieurs.

IV-2 Les marqueurs acides gras sont-ils performant pour différencier les compartiments trophiques dans les habitats subtidaux rocheux ?

Les analyses acides gras (AG) sont des outils bien connus pour étudier les interactions trophiques dans les habitats marins. Le concept de marqueurs d'acide gras en tant que marqueurs trophiques a été suggéré lors de deux études de Lovern en 1934 et 1935. Ce concept se base sur le principe de transfert relativement conservatif de certaines molécules vers les niveaux trophiques supérieurs. Il vise à identifier un ou plusieurs acides gras particulier(s), caractéristique(s) d'un producteur primaire et sa (leurs) présence(s) reconnue(s) chez le consommateur (Dalsgaard et al. 2003). Dans les organismes, la production d'acides gras[3] *de novo* ou la transformation des acides gras sont sous la dépendance de l'arsenal enzymatique des organismes avec généralement la formation finale de chaine à 16 carbones (16:0). Les acides gras saturés (AGS) sont à la base de certains acides gras monoinsaturés (AGM) grâce à des processus de désaturation aérobie. Seuls les producteurs primaires sont capables de biosynthétiser des acides gras polyinsaturés *de novo* de type ω3 et ω6 à partir de certains précurseurs. Ces acides gras jouent un rôle essentiel pour les animaux, car, mis à part certaines exceptions (Ito and Simpson, 1996), ces derniers ne possèdent pas les enzymes nécessaires à leur synthèse. Par conséquent, ces acides gras essentiels (AGE) ne peuvent être obtenus par les consommateurs que par l'alimentation (Canual *et al.*, 1995 ; Styrishave and Andersen, 2000 ; Meziane *et al.*, 2003). Les acides gras saturés impairs ainsi que les acides gras ramifiés (AGR) sont spécifiquement produits par des bactéries (Volkman *et al.*, 1980 ; Rajendran *et al.*, 1997). Le transfert trophique peut être suivi sur plusieurs niveaux trophiques par le biais de quelques acides gras (Hall *et al.*, 2006).

Très peu d'études utilisent les acides gras pour analyser les réseaux trophiques associés au milieu rocheux subtidaux (Kelly & Scheibling 2012).

Dans le domaine pélagique, les AG sont largement utilisés pour identifier le phytoplancton et caractériser le régime alimentaire du zooplancton (Dalsgaard *et al.*, 2003). Contrairement au système pélagique où le phytoplancton est le producteur primaire majoritaire, les systèmes benthiques sont caractérisés par une forte diversité de producteurs primaires (macroalgues rouges et brunes, plantes vasculaires, phytoplancton et bactéries) (Kharlamenko et al 2001,

[3] Composé organique à chaine carbonée typiquement paire – Acide carboxylique à chaine aliphatique - Lipides

Dalsgaard *et al.*, 2003). Bien que certains producteurs primaires possèdent une signature AG « caractéristique », la grande diversité de producteurs primaires et de consommateurs rend difficile l'étude de la structuration des réseaux surtout lorsque certains consommateurs sont omnivores et/ou opportunistes (Kharlamenko *et al.* 2001, Alfaro *et al.* 2006). De plus, certains organismes sont capables de modifier la structure de leurs AG, ce qui empêche d'attribuer un régime alimentaire.

L'objectif de cette étude est d'évaluer la capacité des traceurs « acides gras » à discriminer les compartiments principaux structurant les réseaux trophiques en milieu rocheux subtidal et, plus précisément, de montrer l'intégration des algues rouges dans les compartiments trophiques supérieurs.

Matériel et méthode

Site d'étude et échantillonnage

Deux sites rocheux de la baie de Saint Malo ont été échantillonnés : Becfer (48°41.293N / 2°03.040O) et Les Haches des Hébihens (48°38.052N/2°10.968O). L'échantillonnage a été réalisé en plongée par les plongeurs scientifiques du service des stations marines du MNHN. Deux plongées ont été réalisées durant le mois de Septembre 2013. Durant ces plongées, les plongeurs ont récolté la plus grande diversité d'organismes appartenant à des taxa différents. Les plongées se sont concentrées dans la ceinture à dominance de rhodophycées (i.e. la densité en rhodophycées était supérieure à 5 ind/m²). Au laboratoire, les échantillons ont été triés par espèce puis mis dans des sacs plastiques identifiés puis stockés à -20°C.

Assignation des groupes trophiques

Chaque espèce a été assignée à un groupe trophique selon une nomenclature simple. Les macroalgues sont regroupées au sein des producteurs primaires. Parmi ce groupe, une distinction est faite en fonction des phyla : des Rhodophycées (PPr), des Ochrophycées (PPo) et des Chlorophycées (PPc). Au sein des groupes des consommateurs primaires (i.e. les organismes se nourrissant directement de producteurs primaires), deux groupes ont été distingués : les brouteurs (C1Bt) et les filtreurs (C1f). Les prédateurs des consommateurs primaires ont été regroupés dans le groupe des consommateurs secondaires (C2).

Protocole d'extraction des acides gras.

Les échantillons sont lyophilisés à froid et pesés avant analyse. L'extraction des lipides est réalisée sur les individus entiers, selon la méthode de Bligh & Dyer (1959) modifiée par Méziane et al. (2006). Un standard d'AG, le C23[4] (23:0) est mélangé aux échantillons avant l'extraction afin de calculer les concentrations d'acides gras. Les lipides sont extraits par ultrasonication durant 20 minutes avec un mélange d'eau distillée, de méthanol et de chloroforme (1:2:1 ; v:v:v). L'ajout supplémentaire d'eau distillée et de chloroforme (1 :1 ;v :v) permet la formation de deux phases liquides avec une phase aqueuse supérieure et une phase organique en dessous (chloroforme). Les tubes sont centrifugés (5min, 3000rpm) afin d'optimiser le transfert des lipides vers la phase organique. Le chloroforme est ensuite transféré dans un second tube et 2 ml de chloroforme sont ajoutés à la phase aqueuse du premier tube, l'ensemble est de nouveau ultrasoniqué et centrifugé (5min, 3000rpm). La phase organique est transférée ensuite dans le second tube et le chloroforme extrait est évaporé sous flux d'azote pour obtenir l'extrait lipidique brut. Les extraits obtenus sont saponifiés afin de séparer les acides gras des autres composés organiques. La saponification permet l'hydrolyse des extrémités ester de molécules tels que les Tryacylglycérols (TAGs) en milieu basique avec la présence de méthanol (2:1 ; v:v). Les échantillons sont ensuite placés au bain sec (90°C durant 1h30). La réaction est stoppée par l'ajout d'acide chlorhydrique (35%). 1,5ml de chloroforme est ajouté à deux reprises puis les échantillons sont centrifugés (5min, 3000rpm). La totalité du volume de chloroforme est isolée et évaporée sous flux d'azote avant l'ajout d'1 ml de BF3-Méthanol (14% Borontrifluoride – 80% Méthanol) en vue de l'étape de méthylation (10min ; 90°C). Cette réaction consiste à ajouter un groupe méthyl aux AG, produisant ainsi des acides gras méthyl ester (Fatty Acid Methyl Ester ou FAME). Les FAMEs totaux subissent deux rinçages successifs par ajout de chloroforme et d'eau distillée (1:1 ; v:v) suivis d'une centrifugation (5min, 3000rpm). Une fois isolés dans le chloroforme, les échantillons sont stockés à -20°C. L'analyse des extraits est réalisée après évaporation sous flux d'azote et ajout d'hexane. Les acides gras sont séparés et quantifiés par Chromatographie en phase Gazeuse (GC) (Varian CP-3800 ; GC-FID ; gaz vecteur hélium) équipée d'une colonne de type (VF-WAXms à phase stationnement polaire). Les chromatogrammes obtenus présentent une succession de pics aux temps de rétention précis

[4] Acide gras composé de 23 carbones non retrouvé à l'état naturel dans l'environnement.

caractérisant des acides gras précis. L'identification des pics est complétée et confirmée par la lecture de l'échantillon en Chromatographie en phase Gazeuse et Spectroscopie de Masse (GC-MS) (Varian 450-GC 220-Ion Trap MS ; gaz vecteur hélium). Les différents acides gras sont ensuite quantifiés à l'aide d'une méthode d'intégration des pics, la concentration de chaque acide gras est obtenue selon la formule suivante (Schömburg, 1987) :

$$CFA = \frac{AS}{Ais} \times \frac{Cis}{WS}$$

avec CFA : concentration en acides gras ; AS : aire de l'acide gras sélectionné ; Ais : aire du pic du référence (C23) ; Cis : concentration du standard ; WS : poids sec de l'échantillons. Les résultats sont exprimés en % d'acide gras.

Analyses statistiques

Seuls les acides gras ayant une contribution de 0.3% ont été conservés pour les analyses, aucune transformation n'a été réalisée sur les données. Afin d'ordonner les échantillons selon leur degré de similarité, une nMDS (non-metric Multi Dimentional Scaling) a été réalisée sur la matrice de contribution des acides gras (% du total d'acide gras) en utilisant la distance de Bray-Curtis. Une analyse SIMPER (SIMilarity PERcentage) a été faite pour identifier les acides gras qui contribuent le plus à la dissemblance entre les groupes. Les proportions d'acides gras remarquables sont ensuite comparées par un test de Kruskal-Wallis.

RESULTATS

Parmi les organismes prélevés, les consommateurs secondaires présentent la plus grande quantité d'acide gras par unité de tissus extrait (278.44±152.3 $mg.g^{-1}$) et les chlorophycées la plus faible (4.20±12 $mg.g^{-1}$). Au sein du système trophique étudié, 72 AG ont été identifiés, en moyenne 34.22±10.09 AG ont été identifiés dans les consommateurs (C1Bt+C1f+C2) et 30.4±13.38 AG dans les producteurs primaires (PPc+PPr+PPo). Au sein de chaque groupe, il est important de souligner une grande variabilité des quantités d'acides gras ainsi que de la composition des assemblages.

Tableau 1 : Espèces dont les profils acides gras ont été extraits. Pour chaque espèce un classe trophique simplifiée a été attribuée : PPr : Producteur primaire rhodophycée ; PPo : Producteur primaire ochrophycée ; PPc Producteur primaire chlorophycée ; C1f : Consommateur primaire filtreur; C1Bt : Consommateur primaire filtreur ; C2 : Consommateur secondaire.

N°	Espèces	Phyla	Classe trophique détaillée
1	*Torpedo marmorata*	Chordata	C2
2	*Jujubinus sp.*	Mollusca	C2
3	*Heterosiphonia sp.*	Rhodophyta	PPr
4	*Dictyopteris membranacea*	Ochrophyta	PPo
5	*Calliactis parasitica*	Cnidaria	C2
6	*Homarus gammarus*	Arthropoda	C2
7	*Dilsea carnosa*	Rhodophyta	PPr
8	*Calliblepharis ciliata*	Rhodophyta	PPr
9	*Crassostrea gigas*	Mollusca	C1f
10	*Pecten maximus*	Mollusca	C1f
11	*Laminaria hyperborea*	Ochrophyta	PPo
12	*Cliona celata*	Porifera	C1f
13	*Taonia atomaria*	Ochrophyta	PPo
14	*Rissoidae*	Mollusca	C1Bt
15	*Tricolia pullus*	Mollusca	C1Bt
16	*Asterina gibbosa*	Echinodermata	C2
17	*Cancer pagurus*	Arthropoda	C2
18	*Anemonia sulcata*	Cnidaria	C2
19	*Tethya aurantium*	Porifera	C1f
20	*Dictyota dichotoma*	Ochrophyta	PPo
21	*Ulva sp.*	Chlorophyta	PPc
22	*Codium sp.*	Chlorophyta	PPc
23	*Haliclona simulans*	Porifera	C1f
24	*Eunicella verrucosa*	Cnidaria	C1f
25	*Ocenebra erinacea*	Mollusca	C2
26	*Pentapora foliacea*	Bryozoa	C1f
27	*Phorbas plumosus*	Porifera	C1f
28	*Styela clava*	Chordata	C1f
29	*Haliothis tuberculata*	Mollusca	C1Bt
30	*Bispira volutacornis*	Annelida	C1f
31	*Botryllus schlosseri*	Chordata	C1f
32	*Aplidum pallidum*	Chordata	C1f
33	*Ctenolabrus rupestris*	Chordata	C2
34	*Necora puber*	Arthropoda	C2
35	*Dromia personata*	Arthropoda	C2

36	*Inachus sp.*	Arthropoda	C2
37	*Trypterigion delaisi*	Chordata	C1Bt
38	*Venus verrucosa*	Mollusca	C1f
39	*Pecten maximus*	Mollusca	C1f
40	*Calliostoma zizyphinum*	Mollusca	C2
41	*Hyppolyte sp.*	Arthropoda	C2
42	*Pawsonia saxicola*	Echinodermata	C1f
43	*Phtisica marina*	Arthropoda	C2
44	*Liljijborgidae*	Arthropoda	C2
45	*Stolonica socilalis*	Chordata	C1f
46	*Solieria chordalis*	Rhodophyta	PPr

Composition en AG des producteurs primaires.

Au sein des producteurs primaires, la signature AG varie en fonction du groupes taxonomiques (PERMANOVA, df=2, pseudoF= 2.54, p-value=0.006). Le SIMPER réalisé sur le seul groupe des producteurs primaires met en évidence, d'une part que la composition en AG des rhodophytes et des ochrophycées diffère essentiellement par le 18 :4ω3 qui est plus abondant dans les ochrophycées et le 16 :0 plus abondant dans les rhodophycées, d'autre part que la signature des rhodophycées et des ochrophycées se distingue de celle des chlorophycées par 6 AG (Tableau 2). Les chaines saturées telles que 14:0 et 16:0 sont plus abondantes chez les rhodophycées et les ochrophycées que chez les chlorophycées. Les chaines mono-insaturées 17 :1ω9 et 18 :1ω11 sont quant à elles plus abondantes chez les chlorophycées et voire même absentes de certaines rhodophycées. Concernant les chaines polyinsaturées, l'AG 20 :4ω6 est plus abondant chez les rhodophycées et ochrophycées alors que le 18 :3ω3 est plus abondant chez les chlorophycées.

Composition en acide gras des consommateurs.

Parmi les consommateurs, la composition en AG diffère seulement entre les consommateurs secondaires et les consommateurs primaires filtreurs (PERMANOVA ; df=1 ; pseudo-F=2.79 ; p-value=0.023). Leurs différences s'expliquent essentiellement par 2 AG. Les AG 16 :0 et 18 :1ω9, abondants chez les rhodophycées (*Dilsea carnosa*, *Solieria chordalis*, *Calliblepharis ciliata*) et l'ochrophycée (*Dictyota dichotoma*), apparaissent aussi plus abondants dans les consommateurs secondaires (Tableau 3).

Tableau 2 : Résultat de l'analyse SIMPER des acides gras (AG) pour les producteurs primaires. Seuls les acides gras ayant une contribution supérieure à 0.3% ont été conservés dans l'analyse. Les données n'ont pas été transformées.

	AG	Contribution à la dissimilarité (%)	Abondance moyenne (1)	Abondance moyenne (2)
Rhodophycées (1) vs. Ochrophycées (2)	16:0	8,93	38.42	22.57
	18:4ω3	3,72	0.33	7.77
	20:5ω3	3,11	8.49	7.36
	14:0	2,97	10.03	9.91
	18:1ω9	2,79	4.15	7.64
	18:3ω3	2,52	0.15	5.18
	20:4ω6	2,37	9.71	7.86
	18:0	1,97	2.64	5.08
	18:2ω4	1,86	0.71	4.08
	16:1ω7	1,77	4.83	4.40
Rhodophycées (1) vs. Chlorophycées (2)	16:0	13,86	38.42	10.69
	18:3ω3	10,11	0.15	20.37
	20:4ω6	4,36	9.71	1
	18:1ω11	4,12	0	8.23
	14:0	4,03	10.03	1.96
	17:1ω9	3,49	1.45	6.98
	20:5ω3	2,92	8.49	4.95
	18:1ω7	2,22	3.72	4.43
	16:1ω7	2	4.83	2.36
Ochrophycées (1) vs. Chlorophycées (2)	18:3ω3	7,6	5.18	20.37
	16:0	6,83	22.57	10.69
	18:1ω11	4,12	0	8.23
	14:0	3,972	9.91	1.96
	20:4ω6	3,66	7.86	1
	17:1ω9	3,49	0	6.98
	18:1ω9	3,11	7.64	2.83
	18:4ω3	2,81	7.77	3.05
	18:1ω7	2,22	1.47	4.43
	20:5ω3	2,17	7.36	4.95
	18:2ω4	2,05	4.08	3.54

Tableau 3 : Résultat de l'analyse SIMPER des acides gras (AG) entre les consommateurs secondaires et les consommateurs primaires filtreurs. Seuls les acides gras ayant une contribution supérieure à 0.3% ont été conservés dans l'analyse. Les données n'ont pas été transformées. C1f : Consommateur primaire filtreur; C2 : Consommateur secondaire.

	AG	**Contribution à la dissimilarité (%)**	**Abondance moyenne (1)**	**Abondance moyenne (2)**
C2(1) vs. C1f(2)	16:0	5.32	19.99	12.05
	20:5w3	4.37	15.1	15.21
	18:1w9	3.99	9.66	2.64
	22:6w3	3.45	6.87	8.64
	20:4w6	3.09	7	6.77
	16:1w7	2.45	5.04	5.77
	18:0	2.03	6.14	4.82
	18:1w7	1.94	5.19	3.7
	14:0	1.69	1.9	4.04
	22:5w3	1.47	2.71	1.09
	24:1w9	1.24	0	2.49
	18:4w3	1.22	0.43	2.75
	22:4w6	1.16	0.91	1.91
	20:1w9	0.91	1.73	0.55
	20:4w3	0.9	0.18	1.88
	22:2w9	0.85	1.07	1.12

Structure du réseau trophique.

La nMDS (Figure 2) distingue les producteurs primaires et les consommateurs, mais il est difficile de mettre en évidence des sources préférentielles de nourriture. La CAH (figure 3) se basant sur les acides gras caractéristiques des producteurs primaires (Tableau 4) met en évidence quant à elle 4 groupes ; 2 grands groupes s'opposent sur le dendrogramme, le groupe 3 regroupant les producteurs primaires, deux espèces de brouteurs « potentiels » (*Haliothis tuberculata*, *Trypterigion delaisi*) et le groupe 4 qui regroupe essentiellement les consommateurs primaires filtreurs et deux brouteurs *Rissoidae* et *Tricolia pullus*. Le groupe 3 se différencie par une plus forte contribution du 16:0 alors que le groupe 4 présente une signature moyenne plus riche en 16:ω7 et 20:5ω3. Le groupe 3 peut être subdivisé en 4 sous-groupes ; le sous-groupe 3a composé de *Dictyota dichotoma*, *Dilsea carnosa* et *Solieria chordalis* se caractérise par une forte signature en 16:0 (proche de 50% du total d'AG. Les sous-groupes 3b et 3c présentent une signature forte en 18:4ω3 par rapport au sous-groupe 3a. Néanmoins ces deux groupes se distinguent entre eux par une plus forte contribution à la fois du 18:4ω3 et du 18:3ω3 dans le sous-groupe 3c. Au sein du groupe 3, seul le sous-groupe 3b regroupe à la fois des producteurs primaires (*Heterosiphonia sp.* et *Calliblepharis ciliata*) et des consommateurs primaires (*Haliothis tuberculata, Trypterigion delaisi, Jujubinus* sp., *Phtisica marina*, *Liljijiborgidae*, *Bispira volutacornis*), ceci suggère par conséquent une alimentation préférentielle à base de rhodophycées ayant une signature AG similaire.

Une analyse plus précise du ratio 16 :1ω7/16 :0 parmi le groupe 4 révèle que 3 consommateurs primaires filtreurs (*Styela clava*, *Venus verrucosa*, *Pawsonia saxicola*) semblent assimiler préférentiellement les microalgues (ratio >1) (Figure 1).

Tableau 4 : Acides gras utilisés comme marqueurs des producteurs primaires. (* marqueurs mis en évidence dans cette étude)

	Acides Gras		
	Saturés	**Mono insaturés**	**Poly insaturés**
Microalgae		16:1ω7*[1,2,3,4]	16:2ω4[1,2] 16:3ω3[1] 16:4ω1[5] 22:6ω3[5]
Macroalgae			
Chlorophycées			17:1ω9* 18:1ω11* 18:3ω3[5] 18:2ω6[3] 20:4ω3[6]
Rhodophycées	16:0*[5]		20:5ω3*[5]
Ochrophycées			18:1ω9[5] 18:4ω3* 20:4ω6[5]

Références : [1] Dunstan et al. 1994 ;[2] Volkman et al. 1980 ;[3] Richoux and Froneman 2008 ;[4] Jaschinski et al. 2008 ;[5] Kelly and Scheibing 2012 ;[6] Kharlamenko et al. 2001

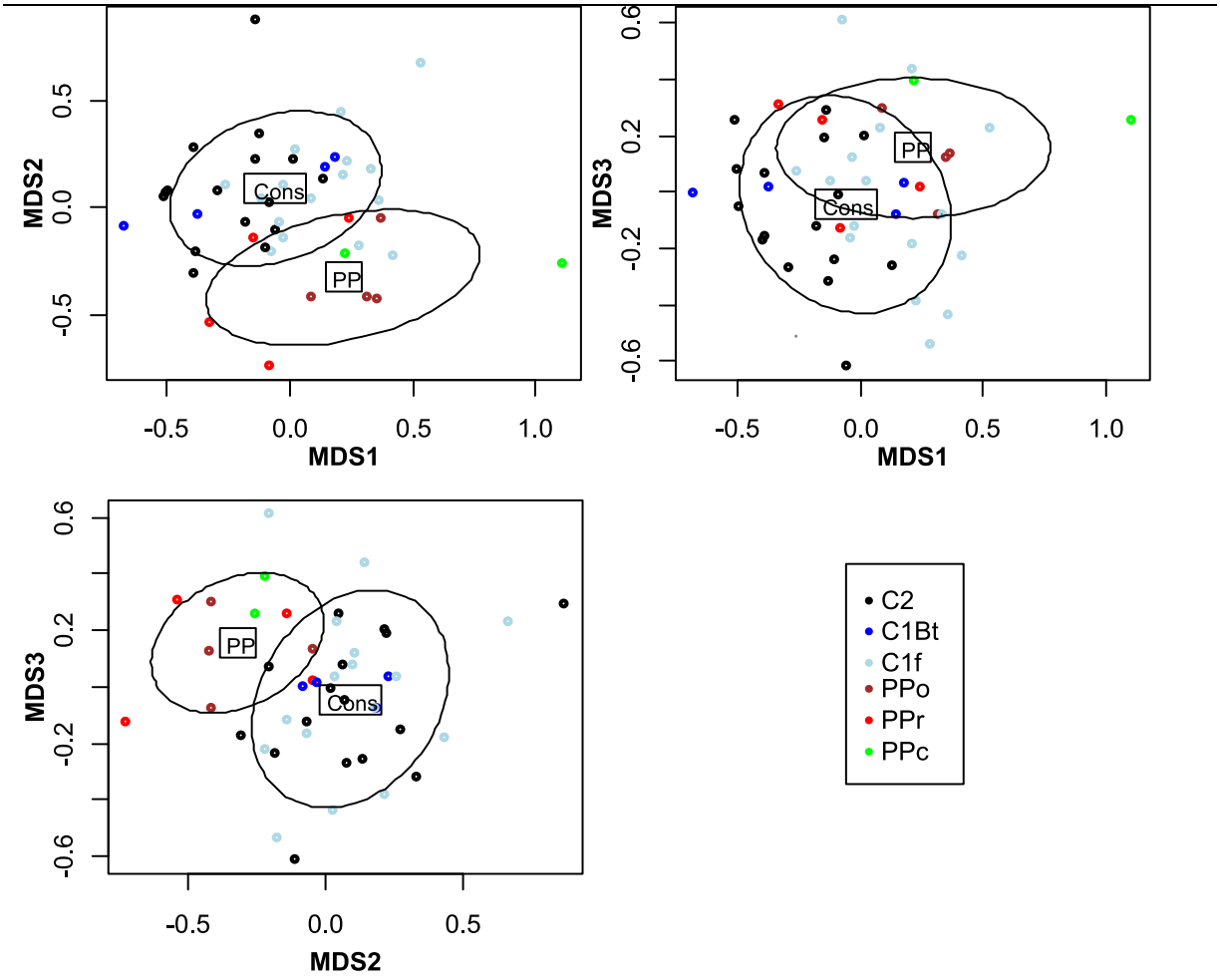


Figure 1 : non-Multi Dimensional Scale utilisant la distance de Bray-Curtis de la matrice de contribution des AG (% du total d'AG) des 46 espèces échantillonnées (stress = 0.17). Seuls les acides gras ayant une contribution supérieure à 0.3% ont été conservés dans l'analyse. Les données n'ont pas été transformées. PPr : Producteur primaire rhodophycées ; PPo : Producteur primaire ochrophycées ; PPc Producteur primaire chlorophycées ; C1f : Consommateur primaire filtreur ; C1Bt : Consommateur primaire brouteur ; C2 : Consommateur secondaire.

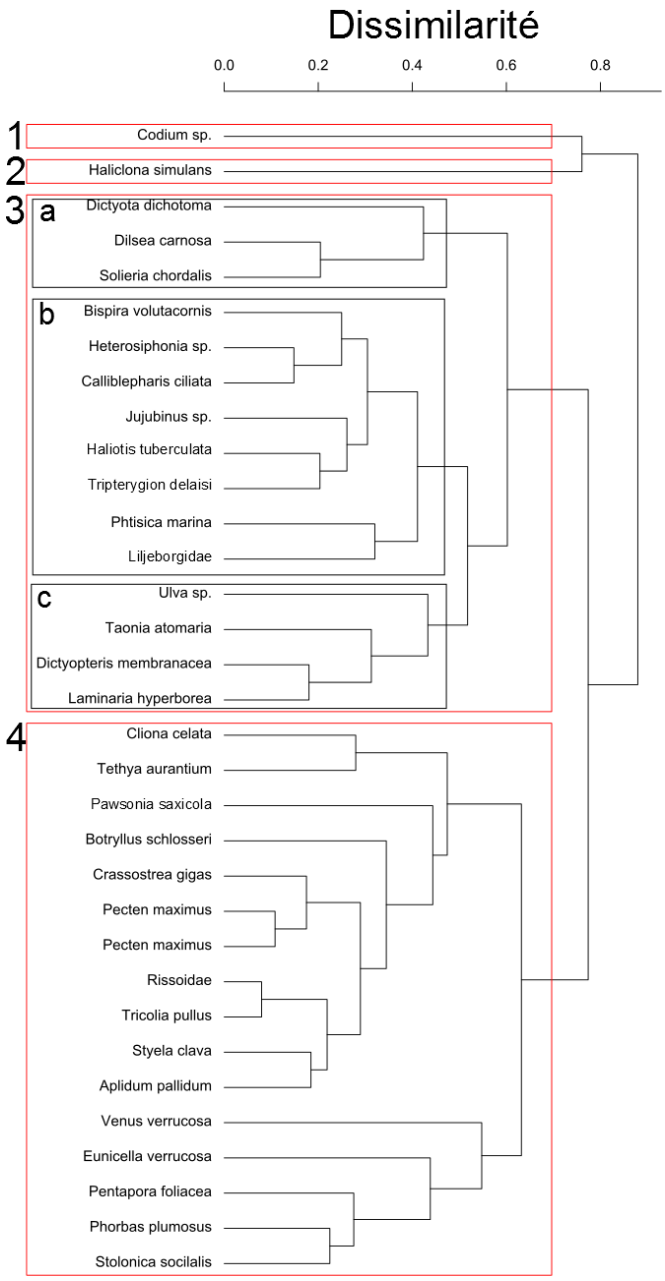


Figure 2 : Classification ascendante hiérarchique (CAH) basé sur les contributions des AG marqueurs des produteurs primaires (Tableau 4). Les données n'ont pas été transformées pour l'analyse. Seuls les consommateurs primaires et les producteurs primaires ont été conservés pour l'analyse.

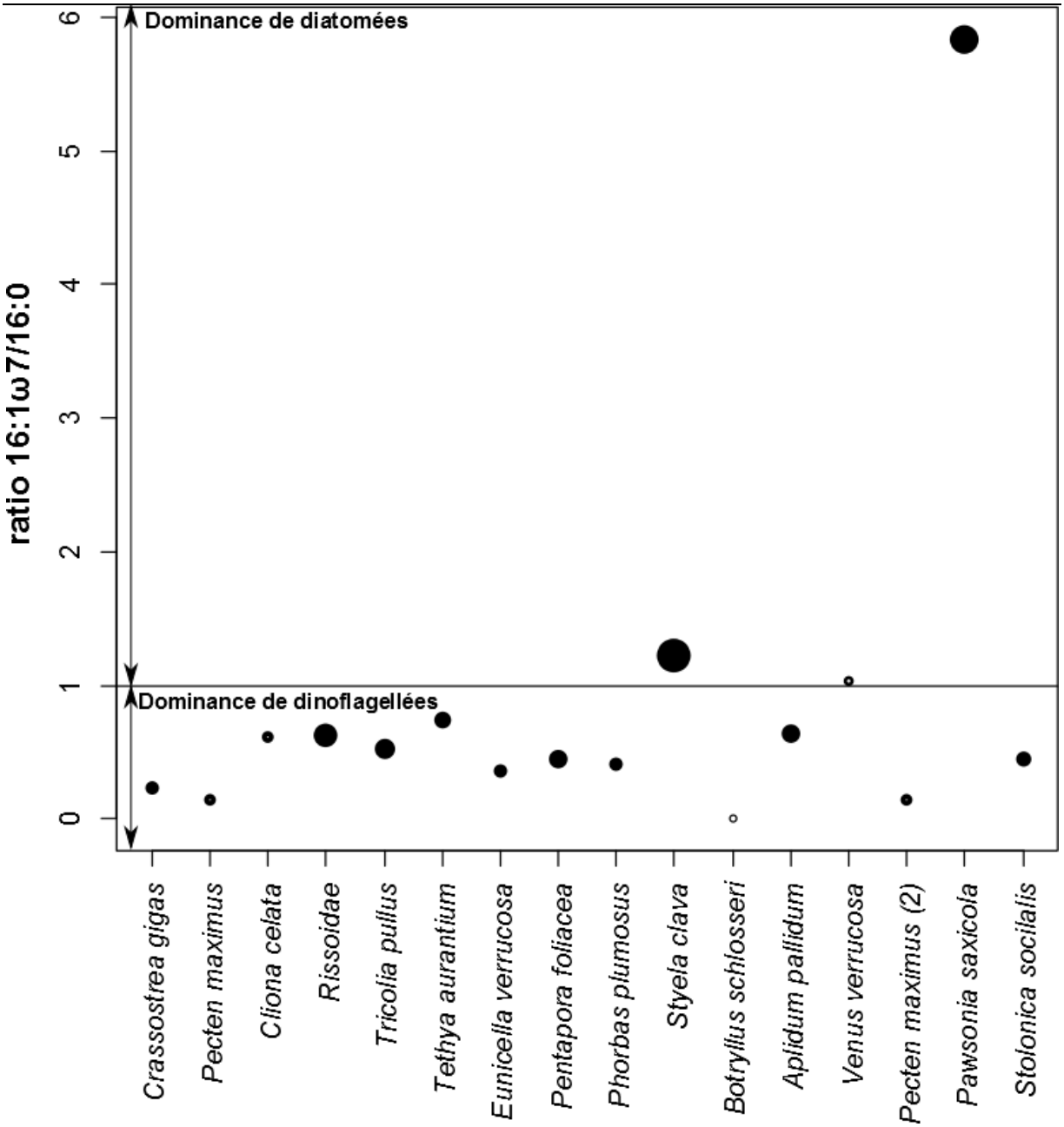


Figure 3 : Comparaison du ratio 16 :1ω7 / 16 :0 pour les consommateurs échantillonnées. La taille des points est proportionnelle à la quantité de 16 :1ω7.

DISCUSSION

Les compositions en AG des rhodophycées et des ochrophycées échantillonnées apparaissent similaires à celles décrites par Fleurence *et al.* (1994), Colombo *et al.* (2006) and Kelly & Scheibling (2012). Elles sont caractérisées par une forte abondance de 20 :5ω3, 20 :4ω6, 18 :1ω9 et 16 :1ω7. Néanmoins, dans notre étude, les ochrophycées et les rhodophycées se distinguent par 16 :0 qui est plus abondant dans les rhodophycées et le 18 :4ω3 qui est plus abondant dans les ochrophycées. Les chlorophycées quant à elles sont généralement composées d'AG polyinsaturés à 18 carbones (C_{18}) (Graeve *et al.* 2002, Kelly & Scheibling 2012). Dans notre étude, ce groupe se distingue principalement des deux groupes précédents par une faible concentration des AG polyinsaturés C_{20} et des AG saturés (14:0 et 16:0) et une forte abondance des AG polyinsaturées C_{18}. Les chlorophycées représentent la lignée macroalgale la plus évoluée, leur composition en AG est similaire aux plantes supérieures (Graeve *et al.* 2002).

Concernant les consommateurs, en prenant l'intégralité des signatures « acides gras », il est difficile de les catégoriser (Figure 2). Néanmoins, en se focalisant sur la signature des producteurs primaires, il est possible de discriminer les organismes se nourrissant principalement de microalgues (riche en 16:1ω7 et 20:5ω3) , des organismes se nourrissant de macroalgues (riche en 16:0, 18:3ω3 et moins riche en 20:5ω3) (Figure 3). Parmi, les organismes se nourrissant de microalgues, 3 espèces (*Styela clava*, *Venus verrucosa* et *Pawsonia saxicola*) se nourrissent préférentiellement de diatomées ; en effet le ratio 16 :1ω7/16 :0 supérieur à 1 traduit une forte contribution des diatomées dans le régime alimentaire (Dalsgaasd *et al.*, 2003, Budge & Parrish 1998). Généralement, les diatomées se retrouvent dans le compartiment benthique en tant qu'épiphytes (Latyshev et al. 2004, Richoux & Froneman 2008) ou dans la colonne d'eau. Les ratios inférieurs à 1, remarqués chez les autres espèces, traduisent une alimentation plus riche en dinoflagellés (Dalsgaasd *et al.*, 2003) Ces microalgues sont souvent capturées depuis la colonne d'eau par les filtreurs et depuis le sédiment par les déposivores (Howell et al. 2003 ; Guest et al. 2008). Il est intéressant de remarquer la présence deux espèces de mollusques (*Rissoidae* et *Tricollia pullus*) au sein de ce groupe ; en effet ces organismes sont souvent retrouvés sur les algues rouges (Obs. pers., Gallon 2010 ; Gallon et al., 2013) or leur signature AG semble montrer un comportement de microphagie et suggère un comportement de brouteur de biofilm.

Concernant les espèces se nourrissant de macroalgues, 6 espèces semblent s'alimenter préférentiellement de rhodophycées, ceci est bien documenté pour *Haliotis tuberculata*, les acides gras ultrainsaturés comme le 20:5ω7 et le 20:4ω6, très abondant dans les rhodophycées et certains ochrophycées (*Undaria pinnatifida*), accélèrent la croissance des individus (Mai et al 1996). Pour *Phtisica marina*, une étude récente de Guerra-García, J. M., & de Figueroa (2009) met évidence que les espèces du genre sont des prédateurs obligatoires se nourrissant de petits crustacés (copépodes). Par conséquent au vu de la signature Acides Gras analysés, on peut supposer que les individus échantillonnés se nourrissaient de petits crustacés brouteurs de rhodophycées ou de déposivores. Pour *Tripterygion delaisi*, la signature AG traduit une alimentation sur les rhodophycées or cette espèce est un prédateur de gastéropodes, petits annélides et petits crustacés (Zander and Berg 1984, Zander and Heimer 1992), par conséquent les proies potentielles de cette espèce doivent se nourrir de matière organique ayant une signature proche de celle des rhodophycées. Au vu des résultats de la CAH (Figure 3), *Bispira volutacornis* semble s'alimenter de matière organique en suspension issus de rhodophycées, cela traduirait un transfert très local de la matière organique.

L'intégration de la matière organique vers les consommateurs secondaires (prédateurs) apparaît difficile à caractériser. En effet, sur les substrats rocheux, une grande diversité de sources potentielles d'alimentation étant disponible, l'utilisation des traceurs AG reste très limitée (Kelly & Scheibling 2012). De plus, certains organismes sont capables de modifier certains AG à l'aide d'enzymes de type élongase ou désaturase (Hall et al. 2006).

En conclusion, les acides gras apparaissent être de bons traceurs de la matière organique à travers le réseau trophique. Leur utilisation nous a permis de distinguer les différents producteurs primaires entre eux : Chlorophycées riche en 17:1ω9 et 18:1ω11, Rhodophycées riches en 16:0 et 20:5ω3 et les Ochrophycées riches en 18:3ω3 et en 20:5ω3. De plus, parmi les consommateurs primaires, nous avons pu, en nous intéressant uniquement aux AG présents dans les producteurs primaires, distinguer les sources préférentielles de matière organique. D'un côté, une grande majorité de filtreurs et deux brouteurs (*Rissoidae* et *Tricollia pullus*) utilisent principalement les microalgues comme source et de l'autre côté, on retrouve des organismes qui se nourrissent principalement de macroalgues. Parmi eux, 3 espèces (*Haliotis tuberculata*, *Jujubinus sp*. et les *Liljijiborgae*) se nourrissent directement de rhodophycées, une espèce (*Bispira volutacornis*) se nourrit vraisemblablement de rhodophycées en dégradation probablement sous forme de macro déchets et de matière

organique particulaire en suspension dans l'eau. Pour finir deux espèces se nourrissent d'organismes brouteurs de rhodophycées.

Trophic class	*Rissoidae* Brouteurs	*Tricolia pullus* Brouteurs	*Haliothis tuberculata* Brouteurs	*Trypterigion delaisi* Brouteurs	*Hyppolyte sp.* Déposivores	*Crassostrea gigas* Filtreurs	*Pecten maximus* Filtreurs	*Cliona celata* Filtreurs	*Haliclona simulans* Filtreurs	*Pentapora foliacea* Filtreurs	*Phorbas plumosus* Filtreurs	*Styela clava* Filtreurs	*Bispira volutacornis* Filtreurs	*Botryllus schlosseri* Filtreurs	*Aplidium pallidum* Filtreurs	*Venus verrucosa* Filtreurs	*Pecten maximus* Filtreurs	*Pawsonia saxicola* Filtreurs	*Stolonica socilalis* Filtreurs	*Jujubinus sp.* Omnivores	*Calliostoma zizyphinum* Omnivores	*Dictyopteris membranacea* Ppo	*Laminaria hyperborea* Ppo
10:0	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
11:0	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,060	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
12:0	0,336	0,155	0,099	0,000	0,196	0,000	0,000	0,411	0,000	0,000	0,151	0,019	0,000	0,341	0,000	0,000	0,000	0,048	0,419	0,121	0,032	0,000	0,422
13:0	0,040	0,037	0,035	0,000	0,123	0,000	0,000	0,000	0,000	0,000	0,000	0,024	0,000	0,000	0,000	0,000	0,015	0,850	0,000	0,022	0,000	0,000	0,000
13:0anteiso	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
13:0iso	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
14:0	11,017	8,506	3,600	0,000	3,180	4,902	0,000	1,184	0,000	4,485	1,678	10,318	6,566	11,911	6,314	1,420	4,759	4,917	4,992	0,000	0,692	0,137	5,963
14:0iso	0,108	0,130	0,073	0,000	0,000	0,000	0,000	0,098	0,000	0,000	0,117	0,065	0,000	0,000	0,079	0,000	0,010	0,192	0,000	0,079	0,073	0,981	0,507
14:1ω3	1,399	1,016	0,022	0,000	0,000	0,000	0,000	0,000	1,055	0,000	0,062	0,024	0,000	0,895	0,000	0,000	0,000	12,404	0,000	0,000	0,000	0,000	0,000
14:1ω5	2,072	2,134	0,208	0,000	0,000	0,497	0,000	9,813	0,000	0,000	0,000	0,000	0,000	0,000	0,020	1,436	0,127	0,000	0,156	3,264	0,000	0,000	0,000
15:0	0,454	0,441	1,485	0,598	1,608	0,742	0,689	0,792	0,000	1,602	0,528	0,706	0,962	1,579	0,609	1,702	0,714	15,319	0,735	1,037	1,496	0,000	0,439
15:0anteiso	0,055	0,058	0,068	0,000	0,000	0,000	0,000	0,471	1,706	0,000	0,114	0,081	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,109	0,000	0,000	0,000
15:0iso	0,112	0,123	0,163	0,110	0,493	0,180	0,000	1,098	0,000	0,794	0,350	0,283	0,000	0,000	0,331	0,000	0,041	1,446	0,491	0,434	0,120	0,813	0,396
15:1ω1	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,222	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,042	0,000
16:0	15,481	15,689	20,467	25,731	23,415	18,214	22,478	5,929	2,445	18,895	11,760	13,225	21,091	14,645	11,453	2,066	20,067	2,271	12,029	21,468	15,135	20,391	23,395
16:0iso	0,349	0,287	0,143	0,134	0,477	0,185	0,000	1,037	0,000	0,262	0,252	0,264	0,000	0,000	0,573	0,000	0,064	0,902	0,323	0,581	0,757	0,000	0,000
16:1ω11	0,000	0,000	0,051	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,649	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,043	0,000	0,000	0,001	0,000
16:1ω5	0,714	0,626	0,283	0,000	0,126	0,260	0,311	0,092	1,681	0,000	2,154	0,922	0,997	0,749	0,603	2,155	0,334	0,116	0,389	0,648	0,000	0,000	0,000
16:1ω5	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
16:1ω7	9,763	8,144	1,532	0,018	5,631	4,204	3,289	3,596	1,654	8,483	4,801	16,119	7,898	0,000	7,352	2,132	4,723	13,264	5,326	4,505	2,297	0,269	3,629
16:1ω9	0,000	0,279	0,446	0,000	0,000	0,000	0,504	0,275	0,000	0,000	1,148	0,000	0,000	6,566	0,000	0,000	0,000	0,000	0,611	0,000	0,000	0,000	0,000
16:2ω4	0,739	0,680	0,049	0,000	0,122	0,249	0,000	0,103	2,251	0,494	0,000	1,121	1,385	0,000	0,000	2,299	0,208	1,377	0,369	0,365	0,000	0,000	0,000
16:2ω6	0,227	0,000	0,000	0,136	0,000	0,079	0,000	0,034	4,966	6,808	0,000	0,355	0,445	0,000	0,597	2,256	0,145	0,000	0,000	0,039	0,779	0,000	0,000
16:3ω3	0,599	0,512	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,272
16:3ω4	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
16:4ω1	1,328	1,075	0,078	0,000	0,000	0,118	0,000	0,500	5,073	0,000	0,133	1,168	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,094	0,000	0,000	0,000
17:0	0,645	0,675	2,135	1,738	2,495	1,140	0,959	0,343	0,000	2,383	0,702	0,658	0,000	1,570	1,116	2,371	0,833	0,285	1,152	2,026	3,350	0,306	0,000
17:0anteiso	0,236	0,170	0,000	0,000	0,449	0,173	0,000	0,713	1,038	0,000	0,444	0,074	0,000	0,000	0,438	0,000	0,000	0,639	0,217	0,283	0,000	0,000	0,000
17:0iso	0,979	0,793	0,171	0,082	1,029	0,429	0,443	1,852	0,000	0,532	1,481	0,350	0,000	0,000	0,890	2,206	0,375	0,171	0,538	1,534	1,456	1,202	0,000
17:1ω11	0,000	0,000	0,059	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
17:1ω7	0,000	0,100	1,769	0,363	0,000	0,000	1,629	0,000	0,000	0,000	1,052	0,000	0,000	0,000	2,061	2,450	0,306	0,000	0,566	0,000	3,886	0,000	0,000
17:1ω9	0,000	0,000	0,375	0,000	0,000	1,188	0,000	0,000	0,000	2,436	0,000	0,129	0,000	0,000	0,128	2,407	0,000	1,777	0,296	3,235	0,000	0,000	0,000
17:1ω9	0,120	0,767	0,000	0,000	0,000	0,000	0,000	0,091	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
18:0	3,765	3,682	6,889	0,001	6,744	4,678	8,309	2,185	11,034	6,974	3,021	4,275	1,416	4,445	3,703	2,741	7,074	5,806	7,002	0,081	8,601	0,491	3,058
18:01	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,727	0,000
18:0iso	0,118	0,181	0,118	0,000	0,000	0,053	0,000	0,161	0,000	0,000	0,465	0,105	1,285	0,000	0,000	0,000	0,000	0,000	0,000	0,442	0,000	0,000	0,000
18:1ω	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
18:1ω11	0,679	0,555	0,000	0,000	0,152	0,000	0,000	1,684	0,000	0,000	0,146	0,000	1,650	3,759	0,000	0,000	0,069	0,098	0,000	4,103	0,124	0,000	0,000
18:1ω5	0,181	0,174	0,155	0,000	0,171	0,199	0,000	0,127	0,000	0,000	0,000	0,000	1,488	0,000	0,176	2,853	0,133	0,059	0,267	0,282	0,138	0,000	0,000
18:1ω7	7,380	8,014	5,168	5,072	5,812	4,315	5,730	4,828	0,000	2,576	5,718	4,634	0,279	0,000	10,559	2,825	4,888	2,299	6,288	0,000	7,735	0,000	1,199
18:1ω9	3,176	3,523	6,571	9,186	10,971	3,830	1,704	1,271	1,205	3,149	1,272	1,618	8,478	4,968	1,167	2,789	1,132	2,673	4,483	6,995	4,432	0,000	12,691
18:2ω3	0,029	0,627	0,000	0,000	0,000	0,297	0,000	0,123	1,278	0,000	0,000	0,673	0,000	0,346	0,000	0,000	0,000	0,000	0,000	0,086	0,000	0,000	0,000
18:2ω4	0,827	0,920	0,000	0,000	0,000	0,000	0,000	0,305	0,000	6,827	0,000	0,000	0,000	0,128	0,000	0,000	0,000	0,000	0,000	1,604	0,000	12,855	5,409
18:2ω6	0,034	0,000	0,127	0,000	0,000	1,803	0,726	0,000	2,105	0,000	0,393	1,199	0,695	1,890	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
18:2ω9	0,000	0,000	0,407	0,000	1,719	0,000	0,916	0,000	0,000	0,000	0,000	0,000	0,000	0,000	2,420	2,935	0,698	0,254	1,553	0,000	2,070	0,000	0,000
18:3ω3	0,575	0,062	0,000	0,329	1,008	2,514	0,848	0,631	0,000	0,000	0,109	0,681	0,562	0,000	3,144	3,155	1,128	0,181	1,743	1,383	0,769	14,873	7,962
18:3ω6	0,236	0,149	0,063	0,223	0,136	0,212	0,000	0,114	0,000	0,000	0,280	0,754	0,000	0,479	0,347	3,007	1,040	0,291	0,200	0,221	0,132	0,000	1,196
18:4ω3	0,043	2,894	0,369	0,498	0,804	3,707	2,815	0,000	1,875	0,000	1,797	3,796	1,908	4,751	4,888	3,273	4,526	2,886	4,537	0,815	0,241	14,439	9,187
18;1ω7	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
19:0	0,091	0,000	0,071	0,095	0,161	0,101	0,000	0,271	0,000	0,000	0,436	0,000	0,501	0,000	0,620	3,032	0,138	0,204	0,279	0,258	0,072	0,000	0,000
19:1ω9	0,782	0,800	0,311	0,000	0,000	0,000	0,000	0,000	3,532	1,605	0,401	0,021	0,000	1,395	0,000	0,000	0,001	0,035	0,000	0,040	0,000	0,000	0,000
20:0	0,000	0,000	0,042	0,000	0,000	0,000	0,000	0,000	2,770	0,327	0,962	0,507	0,000	0,000	0,000	0,000	0,037	0,090	0,000	0,209	0,000	0,594	0,000
20:0	0,278	0,188	0,000	0,000	0,000	0,000	0,000	0,749	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,830
20:1ω11	0,004	1,774	0,000	0,000	0,000	1,529	0,000	0,351	0,000	2,698	0,000	0,057	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
20:1ω5	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
20:1ω7	1,585	1,239	0,257	0,000	0,000	3,902	0,000	0,897	0,000	0,000	0,474	0,017	3,320	0,000	0,303	3,476	1,514	0,900	0,135	1,455	0,335	0,000	0,000
20:1ω9	0,759	0,711	3,372	0,000	0,581	0,000	0,000	0,642	0,000	1,064	0,233	0,451	1,622	1,506	0,635	0,000	0,078	0,881	0,753	1,255	0,000	0,000	0,000
20:2ω6	0,960	0,786	0,292	0,285	0,304	0,202	0,812	0,537	4,957	1,713	0,231	0,073	0,000	0,000	0,000	3,629	0,633	0,339	0,173	0,465	0,451	0,802	0,000
20:2ω7	0,110	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
20:2ω9	0,541	0,508	0,145	0,380	0,393	0,487	0,000	0,080	0,000	0,000	0,000	0,000	0,000	0,000	1,788	3,508	1,536	0,456	0,532	0,306	0,265	0,000	0,000
20:3ω3	0,000	0,000	0,072	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,409	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
20:3ω6	0,334	0,328	0,117	0,151	0,177	0,208	0,150	1,578	0,000	0,628	0,138	0,224	0,000	0,000	0,264	3,712	0,408	0,000	0,239	0,222	0,091	0,000	0,000
20:3ω9	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
20:4ω3	0,986	0,774	0,060	0,530	0,237	0,601	1,012	2,498	16,044	1,071	0,337	0,317	0,000	0,000	0,553	3,936	1,174	0,940	0,323	0,127	0,098	0,000	0,000
20:4ω6	3,705	4,706	12,161	7,779	4,942	3,273	3,207	20,568	1,102	7,075	6,201	3,991	3,438	5,024	3,520	3,788	2,333	2,151	2,816	9,454	14,491	18,577	8,255
20:5ω3	16,579	15,795	9,939	11,873	14,842	17,352	23,342	19,578	1,030	10,368	6,893	22,748	17,029	18,950	22,590	4,035	21,845	15,194	10,061	11,727	7,321	0,908	11,495
21:0	0,000	0,000	0,150	0,000	0,000	0,000	0,433	0,884	0,000	0,000	0,387	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,446	0,000
21:5ω3	0,775	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
22:0	0,198	0,208	0,336	0,000	0,000	0,000	0,000	0,391	0,502	0,000	3,452	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,979	0,000	0,000	0,000
22:1ω11	0,122	0,000	0,062	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,146	0,000	0,130	0,804	0,409	0,000	0,044	0,000	0,000
22:1ω5	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
22:1ω7	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
22:1ω9	0,150	0,000	0,233	0,000	0,220	0,000	0,000	1,422	1,564	0,000	0,589	0,000	4,722	0,000	0,000	4,197	0,000	0,993	0,000	0,378	0,000	0,000	1,231
22:2ω6	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	13,128	0,000	0,000
22:2ω6	0,909	1,082	0,068	4,244	0,495	0,000	0,000	0,141	0,000	0,531	0,055	0,000	0,000	0,000	0,603	4,663	1,434	0,307	0,641	0,000	0,000	10,146	0,000
22:2ω9	0,527	0,553	6,517	0,000	0,000	4,354	0,000	0,000	2,759	0,000	0,086	0,000	4,899	0,000	0,000	4,216	0,140	0,115	0,203	2,638	5,735	0,000	0,000
22:4ω6	0,717	0,802	4,122	0,430	0,000	0,303	0,000	0,000	0,015	3,448	0,869	0,127	0,000	0,000	0,062	4,453	1,001	1,183	17,024	1,297	7,976	0,000	0,000
22:5ω3	1,159	2,296	7,619	0,000	0,000	1,015	1,792	0,061	4,725	1,601	1,376	0,574	0,000	0,000	0,000	0,000	0,000	0,000	0,000	9,443	0,000	0,000	0,584
22:5ω5	0,000	0,000	0,000	0,000	0,000	1,125	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
22:5ω6	0,246	0,430	0,171	1,587	0,839	0,357	0,000	0,000	2,396	2,001	2,074	0,202	0,000	0,000	0,183	4,541	0,595	0,252	0,425	1,344	3,379	0,000	2,035
22:6ω3	4,723	3,855	0,686	33,171	9,969	11,030	22,600	0,791	19,335	19,880	3,961	7,101	7,438	0,000	11,675	4,774	18,086	2,396	11,283	2,552	4,708	1,017	0,000
24:0	0,011	0,000	0,000	0,000	0,000	0,000	0,000	0,533	0,000	0,000	0,079	0,000	0,000	14,137	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
24:1ω5	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	2,247	0,000	0,000	0,000	0,000	0,000
24:1ω9	0,000	0,000	0,064	0,000	0,000	0,000	1,865	8,234	0,000	0,000	28,988	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
25:0	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,420	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000

PPo : Producteurs primaires ochrophycées; PPr : Producteurs primaires rhodophycées; PPc :Producteurs primaires chlorophycées

Taonia atomaria Ppo	*Heterosiphonia sp.* PPr	*Dilsea carnosa* PPr	*Calliblepharis ciliata* PPr	*Phyllophora crispa* PPr	*Ceramium sp.* PPr	*Phyllophora crispa* PPr	*Solieria chordalis* PPr	*Ulva sp.* PPc	*Codium sp.* PPc	*Torpedo marmorata* Predateurs	*Asterina gibbosa* Predateurs	*Cancer pagurus* Predateurs	*Anemonia sulcata* Predateurs	*Ocenebra erinacea* Predateurs	*Ctenolabrus rupestris* Predateurs	*Necora puber* Predateurs	*Dromia personata* Predateurs	*Inachus sp.* Predateurs	*Phtisica marina* Predateurs	*Liljijborgidae* Predateurs
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,336	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,327	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,055	0,000	0,685	0,089	18,209	0,000	0,000	0,195	0,197	1,236	0,000	0,401	0,049	0,000	0,000	0,000	0,261	0,000	0,000	1,036	0,876
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,119	1,598	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,000	0,030	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,000	0,032	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
7,168	4,781	19,062	10,741	11,049	7,052	4,987	5,536	2,123	1,773	1,261	0,805	0,289	1,318	2,057	2,224	4,050	0,000	0,000	5,691	2,663
0,483	0,852	0,000	0,000	0,000	0,000	0,000	0,000	0,000	1,238	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,071	0,071	0,000	0,000	0,000	0,000	0,000	0,000	0,163	0,000	0,000	0,000	0,000	0,000	0,000	0,135	0,123	0,000	0,000	0,000	0,000
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,778	0,000	0,000	0,000	0,000	0,000	0,076	0,198	0,000	0,000	0,000	0,083
0,760	0,433	0,524	0,508	0,000	0,000	1,087	2,260	0,000	0,000	0,602	0,316	0,344	0,000	0,350	0,598	0,708	0,603	0,477	1,178	0,795
0,034	0,203	0,000	0,092	0,000	0,000	0,000	0,000	0,000	0,000	0,033	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,799	0,648	0,330	0,292	0,000	0,000	0,000	0,000	0,000	0,000	0,244	0,596	0,000	0,000	0,000	0,000	0,143	0,000	0,113	0,000	0,361
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
17,919	27,285	48,150	26,310	43,808	64,092	63,998	53,211	19,840	1,328	33,649	1,676	13,388	35,748	13,776	23,371	18,929	12,650	18,215	39,134	21,448
0,271	0,436	0,188	0,157	0,000	0,000	0,000	0,000	0,000	0,000	0,354	0,516	0,125	0,000	0,954	0,201	0,265	0,000	0,000	0,000	0,359
0,000	0,000	0,000	0,000	0,000	0,000	0,000	1,572	0,000	1,463	0,000	0,000	0,000	0,000	0,000	0,100	0,000	0,000	0,000	0,000	0,000
9,144	0,000	0,000	0,164	0,000	0,000	0,000	4,303	1,537	0,848	0,000	0,000	0,000	0,167	0,000	0,193	0,180	0,000	0,000	0,000	0,120
0,000	0,582	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
5,142	10,922	1,697	6,696	0,000	1,845	7,739	0,866	0,366	4,316	4,159	1,444	5,655	0,237	1,925	5,693	11,981	3,787	0,036	7,432	3,954
2,453	0,731	0,192	0,388	0,000	0,000	0,000	1,933	3,436	0,000	1,511	0,000	0,074	0,000	0,000	0,444	0,000	0,000	0,000	0,000	0,241
0,459	0,831	0,054	0,222	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,284	0,000	0,000	0,000	0,348	0,627	0,000	0,000	0,215	0,202
0,041	0,507	0,000	0,110	0,000	0,000	0,000	0,000	0,000	0,029	0,958	0,000	0,000	0,771	0,000	0,000	0,273	0,367	0,216	0,000	0,000
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,000	2,215	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,161	0,549	0,000	0,248	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	5,778	0,000	0,253	0,000	0,000	0,000	0,000	0,000
0,428	0,444	0,348	0,348	0,000	0,000	0,000	0,276	0,000	0,000	0,000	0,501	0,684	0,000	0,351	0,906	1,005	0,948	2,065	2,681	1,624
0,155	0,140	0,000	0,000	0,000	0,000	0,000	0,000	0,067	0,000	0,418	0,377	0,203	0,000	0,000	0,235	0,000	0,000	0,000	0,289	0,386
0,989	0,583	0,172	0,175	0,000	0,000	2,234	0,619	0,948	3,766	0,000	0,372	0,491	0,419	0,000	0,534	0,565	0,471	0,079	0,845	0,691
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,262	0,084	0,000	0,000	0,000	0,000	0,000	5,149	2,953	0,000	1,934	5,958	3,200	0,000	1,088	0,519	0,683	1,204	1,151	0,000	0,418
0,000	0,317	0,000	0,000	0,000	0,000	0,000	5,485	0,000	13,858	0,504	0,000	0,000	0,000	0,000	0,202	0,618	0,000	0,000	0,000	0,144
0,420	0,000	0,182	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
1,257	2,983	3,459	2,323	20,042	9,184	0,686	1,988	1,967	1,393	18,992	7,847	0,000	10,844	6,195	6,737	4,793	8,122	10,025	0,231	2,680
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,094	0,000	0,000	0,000	0,000	0,000	0,000	0,437	0,303	0,000	0,000	0,000	0,390	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	12,469	0,000	0,000	0,000	0,000	0,000
0,000	0,144	0,000	0,000	0,000	0,000	5,054	0,135	0,000	16,353	0,000	0,997	6,332	0,000	1,034	0,000	0,259	0,000	0,000	0,000	0,000
1,147	0,972	0,000	0,527	0,000	0,000	0,000	1,496	0,000	0,000	0,190	1,204	5,823	1,695	0,000	0,256	0,242	0,000	0,000	0,000	0,000
2,547	9,040	0,000	4,185	0,000	0,000	1,251	0,000	8,779	0,000	8,165	5,154	14,855	0,000	0,000	0,018	7,734	5,952	7,097	5,751	2,803
0,278	5,279	3,406	4,670	0,000	4,989	0,000	3,583	3,562	2,050	16,340	1,135	0,000	0,441	3,524	5,004	11,193	16,586	11,973	14,236	31,139
0,000	1,250	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,128	0,000	0,000	0,000	0,354	0,000	0,000	0,000	0,000	0,000
1,629	0,000	0,734	0,960	0,000	0,000	0,000	0,000	7,002	0,000	0,000	0,266	0,979	0,000	0,000	0,961	0,000	0,000	0,000	0,000	0,000
0,668	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	7,119	0,000	0,386	0,000	0,872	0,456	0,069	0,000	0,000	0,000	0,000	0,000
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,387	0,000	0,000	0,000	0,000	0,000	2,009	0,911	0,000	0,767	0,767	0,000	1,105	0,000
1,480	0,655	0,000	0,000	0,000	0,000	0,000	0,000	22,007	18,393	0,121	0,000	0,000	0,461	0,000	0,000	0,322	0,244	0,000	0,000	0,484
1,943	0,508	0,000	0,801	0,000	0,000	0,000	0,000	1,378	2,039	0,000	0,000	0,000	0,000	0,000	0,198	0,710	0,000	0,000	0,000	0,061
8,828	1,439	0,000	0,000	0,000	0,000	0,000	0,000	6,044	0,000	0,210	0,000	0,000	0,000	1,190	0,000	1,430	0,000	1,214	0,413	0,533
0,000	0,000	0,000	0,000	0,000	0,000	0,000	2,409	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,000	0,139	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	1,888	0,000	0,339	0,000	0,000	0,204	0,000	0,000	0,000	0,147
0,437	0,958	0,000	0,278	0,000	0,000	0,000	0,000	0,017	0,000	0,346	0,209	0,110	3,180	0,000	0,485	0,044	0,235	0,832	0,644	0,103
0,000	0,217	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,131	0,000	0,000	0,000	0,000	0,907	0,000	0,000	0,000	0,000	0,000
0,196	0,000	0,090	0,206	0,000	0,000	0,000	0,000	0,256	0,000	0,000	0,000	0,000	0,272	1,650	0,000	0,000	0,000	0,000	0,000	0,000
0,262	0,624	0,000	0,000	0,000	0,000	0,000	0,000	0,393	0,000	0,000	0,000	0,000	0,000	0,000	1,150	0,000	0,000	0,000	0,000	0,000
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,059	0,000	0,000	0,000	0,000	0,000
0,067	0,433	0,000	0,329	0,000	0,000	0,000	0,000	0,070	0,000	0,000	0,000	0,000	0,000	3,648	0,000	0,978	0,000	1,063	1,850	1,638
0,268	0,261	0,000	0,543	0,000	0,000	0,000	0,000	0,112	0,000	0,000	15,188	0,333	0,000	7,265	1,084	0,339	0,000	0,995	0,503	0,234
3,031	0,270	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,832	1,119	0,343	1,057	0,453	0,777	1,653	1,301	0,682	1,770
0,326	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,000	0,275	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,363	6,821	0,423	0,000	0,000	0,000	1,404	0,000	0,000	0,909	0,418
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,456	0,299	0,000	0,355	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,767	0,000	0,000	0,234	0,000	0,000	0,000	0,000
0,000	0,106	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,660	0,000	1,412	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
2,010	0,312	0,000	0,276	0,000	0,000	0,000	0,000	0,000	5,389	0,000	0,000	0,000	0,764	0,000	0,658	0,413	0,000	0,000	0,000	0,000
9,429	12,295	8,794	13,333	0,000	0,000	7,406	5,179	1,974	0,000	13,009	16,501	8,844	0,000	4,159	4,607	2,854	10,066	10,787	2,033	4,310
9,314	13,898	3,274	15,738	0,000	0,000	2,106	1,963	5,778	4,029	2,833	22,017	23,207	6,061	20,375	17,130	14,897	28,244	26,477	7,966	6,393
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	7,019	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,348	0,000	0,000	0,496	0,000	0,000	0,000	0,000	0,000
0,000	0,500	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,744	0,000	0,439	0,367	0,091	7,055	0,180	0,000	0,000	0,000	0,000	0,053
0,000	0,034	0,000	0,000	0,000	5,883	1,992	1,062	0,000	0,000	0,194	0,479	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,470
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,931	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,764	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,403	1,243	1,749	3,133	0,000	0,000	0,000	0,000	2,087	0,000	0,738	0,199	0,350	0,263	0,000	0,283	0,819	0,000	0,000	0,000	0,000
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,327	0,049	0,000	1,829	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,131	0,000	0,000	1,300	0,000	1,081	0,990	0,134	0,000	0,285
0,000	0,194	0,000	0,000	3,213	0,000	0,000	0,000	1,559	0,401	0,000	0,759	0,000	0,000	6,597	0,272	0,476	0,000	0,000	0,000	0,000
2,892	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,642	0,000	0,000	0,318	0,352	3,558	0,838	0,533	0,452	0,000	0,000	0,000	0,000
1,363	0,391	0,000	1,120	0,000	0,000	0,000	0,000	1,184	1,527	3,124	0,289	2,030	14,701	6,542	2,358	0,000	0,000	0,000	0,000	0,000
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,138	1,168	6,956	0,694	3,792	7,103	1,534	0,000	0,000	0,000	1,315	0,147	0,402	0,000	0,000	0,802	0,311	0,260	0,659	5,233	7,681
2,034	4,525	0,000	2,173	0,000	0,000	0,000	0,000	3,145	0,000	0,000	1,541	9,246	7,217	5,713	15,847	6,686	9,876	14,887	0,020	4,442
0,000	0,005	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,480	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,000	0,069	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000

IV-3 Evolution temporelle de la structuration des réseaux trophiques dans les habitats à rhodophycées.

Au sein des systèmes côtiers, les macroalgues possèdent un rôle essentiel dans la fonction de production de matière organique (Mann 1973, Wienche and Bischof 2012). La matière synthétisée à partir de composés inorganiques par les producteurs primaires (autotrophes) peut alors être exportée dans les systèmes adjacents, on parle alors d'*outwelling*, (concept décrit par Odum en 1968 pour les phanérogames), ou bien consommée sur place par des organismes d'échelons trophiques supérieurs. Les analyses se basant sur les isotopes stables sont largement utilisées pour comprendre les transferts de matière des producteurs primaires vers les consommateurs primaires dans les écosystèmes complexes (Dubois et al. 2007 ; Schaal et al. 2008, 2010 ; Ouisse et al. 2012). Dans le cas des macroalgues, 10% de la production nette est consommé directement par les brouteurs alors que 90% entre par voie détritique dans les réseaux trophiques comme matière organique particulaire (MOP) ou comme matière organique dissoute (MOD) (Pomeroy, 1980; Mann, 1982). Wada (2008) a estimé que les macroalgues contribuent entre 1.5% et 34% au stock de la matière organique dissoute.

L'intégration de la matière organique issue des prairies à algues rouges est souvent méconnue, néanmoins ces algues sont très ubiquistes dans les zones côtières (Miller 2009). Ces formations se répartissent de l'infralittoral supérieur jusqu'au circalittoral inférieur et leur production peut atteindre 1kg $C.m^{-2}.an^{-1}$ (Miller 2009). Les analyses concernant l'intégration dans les réseaux trophiques de la matière organique produite par ces formations d'algues rouges restent relativement mal connues malgré la richesse en protéines de cette ressource due notamment aux pigments protéiques de ces algues. Quelques études s'intéressent aux algues rouges mais pour la plupart seul le $\partial^{13}C$ est étudié (Raven *et al.*, 1995; Raven *et al.*, 2002; Wang & Yeh, 2003; Mercado *et al.*, 2009) ou les algues rouges sont associées à d'autres macrophytes tel que les herbiers (Holmer *et al.*, 2004; Lepoint *et al.*, 2004; Kevekordes *et al.*, 2006) ou les laminaires (Fredriksen, 2003; Schaal *et al.*, 2009, 2010a; Schaal *et al.*, 2010b).

Dans ce contexte, cette partie vise à mettre en évidence les voies trophiques de la matière organique issue des communautés à algues rouges vers les niveaux supérieurs, et de suivre l'évolution saisonnière de l'architecture trophique des biocénoses à rhodophytes des habitats rocheux subtidaux.

MATERIEL ET METHODES

Site d'étude et échantillonnage

Bizeux (48°36.677N / 2°01.602O – WGS84) est un ilot granitique d'une surface approximative de 0.025 km². Il est situé à l'embouchure de la Rance, dans la baie de Saint Malo. Cet ilot est protégé des régimes de vents et de houles dominants et il est intégré dans un système turbide soumis à fort hydrodynamisme renforcé par les courants produits par l'usine marémotrice de la Rance.

Les échantillons ont été récoltés en plongée par les plongeurs scientifiques du service des stations marines du MNHN en juin et novembre 2011. Des quadrats de 0.1m² ont été jetés aléatoirement dans les habitats à algues rouges (i.e. zones où la densité d'algues rouges est supérieure à 5 ind/m²). Parmi les organismes échantillonnés, seuls les macroalgues, les éponges et mollusques ont été analysés parce qu'ils comprennent des niveaux trophiques bas de la biocénose (producteurs et consommateurs primaires) et parce que les consommateurs présentent a priori des comportements alimentaires contrastés : filtreurs pour les éponges et brouteurs et prédateurs chez les mollusques. Nous souhaitons aborder, au travers ce travail, la question du couplage benthos / pélagos des habitats à rhodophytes en faisant l'hypothèse que les brouteurs dépendent directement et exclusivement de la production primaire assurée par les rhodophytes tandis que les filtreurs (éponges) dépendent de la matière organique particulaire présente dans la colonne d'eau, dont la composition devrait composer un mélange complexe de matières organiques produites in situ par les macroalgues, mais également dans les étages supérieurs (algues brunes) ou distants (herbiers à phanérogames et marais salés) et par les microalgues benthiques ou pélagiques. Si les ratios isotopiques du C et du N sont relativement bien renseignés pour la plupart des producteurs primaires, ils restent peu décrits pour les macro-algues rouges.

Principe du fractionnement isotopique

Par définition, les isotopes sont des éléments dont la variation de la masse atomique est due aux différences de neutrons dans le noyau. Par conséquent, deux atomes sont dits isotopes s'ils ont le même nombre de protons mais un nombre de neutrons différent. Dans le milieu naturel, l'isotope le plus léger est largement majoritaire.

Tableau 1 : Abondances moyennes des principaux isotopes stables.

	Isotope 1		Isotope 2	
Eléments	Forme	Abondance (%)	Forme	Abondance (%)
Carbone	^{12}C	98,89	^{13}C	1,11
Azote	^{14}N	99,63	^{15}N	0,37
Hydrogène	^{1}H	99,98	^{2}H	0,01
Oxygène	^{16}O	99,76	^{18}O	0,2
Soufre	^{32}S	95	^{34}S	4,22

En écologie trophique, les rapports isotopiques du carbone ($^{13}C/^{12}C$) et de l'azote ($^{15}N/^{14}N$) sont communément utilisés pour comprendre la structuration des réseaux trophiques (Michener & Kaufman 2007). L'abondance de l'isotope lourd est rapportée à l'abondance de l'isotope léger puis comparée à un standard international. Les rapports isotopiques sont exprimés en δ (‰) :

$$\delta^{13}C = \left[\frac{\left(^{13}C/^{12}C\right)_{echantillon}}{\left(^{13}C/^{12}C\right)_{standard}} - 1\right] \times 10^3$$

$$\delta^{15}N = \left[\frac{\left(^{15}N/^{14}N\right)_{echantillon}}{\left(^{15}N/^{14}N\right)_{standard}} - 1\right] \times 10^3$$

Ces rapports reflètent le passé trophique des consommateurs. Lors du transfert de matière d'un producteur primaire vers un niveau trophique supérieur, la signature isotopique est altérée, c'est ce qu'on appelle le fractionnement isotopique. Le rapport $\delta^{13}C$ est enrichi entre les différents niveaux trophiques de moins de 1‰. Ce rapport est fortement lié à la photosynthèse, en effet les producteurs primaires acquièrent leurs signatures isotopiques de leurs sources minérales de carbone et d'azote. L'assimilation du carbone inorganique (CO_2 et HCO_3^-) via les différentes voies métaboliques (C3, C4, CAM) affecte d'autant plus la signature isotopique des producteurs primaires (Raven et al. 2002). Par conséquent le $\delta^{13}C$ apporte une information sur la source de carbone à la base du réseau et permet donc en milieu marin de différencier les apports benthiques (fortement négatif) des apports pélagiques et océaniques (faiblement négatif). Le rapport $\delta^{15}N$, s'enrichit, quant à lui, de 2 à 4‰, un fractionnement moyen de 2.5‰ est considéré entre producteur primaire et son consommateur et de 3.4‰ entre un consommateur primaire et un prédateur (Vander and Rasmussen, 2001). L'enrichissement de $\delta^{15}N$ à chaque niveau résulte de l'excrétion préférentielle d'azote appauvri en ^{15}N sous la forme d'urée, d'ammoniaque ou d'acide urique.

Préparation des échantillons

De retour au laboratoire, les algues ont été nettoyées des éventuelles épiphytes, rincées à l'eau distillée et lyophilisées pendant 24h. Les animaux ont été extraits de leur coquille par un rapide rinçage à l'acide chlorhydrique (HCl, 1N) pour limiter l'altération du $\delta^{13}C$ et du $\delta^{15}N$ (Mateo 2008). Ils sont ensuite rincés à l'eau distillée et lyophilisés (24h). Tous les échantillons séchés ont été réduits en poudre fine homogène grâce à un broyeur à billes.

Analyses statistiques

Comme le nombre d'individus analysés (entre 3 et 5 individus) n'est pas suffisant pour satisfaire les conditions de normalité, des tests non-paramétriques ont été réalisés. L'ensemble des tests statistiques ont été réalisés à l'aide du logiciel R (R-Team 2013).

RESULTATS

Ratio isotopiques des sources potentielles

Le $\delta^{13}C$ des producteurs primaires échantillonnés dans cette étude se situe entre -34,49‰ (*Phyllophora crispa*, novembre 2011) et -20.6‰ (*Calliblepharis ciliata*, juin 2011). Entre Juin et Novembre le $\delta^{13}C$ n'a pas varié significativement (Test U, p-value > 0.05), l'amplitude était de 13.4 et 12.43‰ respectivement pour juin et novembre 2011. La majorité des algues se situent entre -30 et -35‰ à l'exception de *Calliblepharis ciliata* qui présente des signatures moins négatives pour les mois de Juin et Novembre (resp. -20.6 et -22.1‰). Les valeurs de $\delta^{15}N$ pour les algues rouges sont comprises entre 6.75‰ (*Phyllophora crispa*, novembre 2011) et 10.32‰ (Solieria chordalis, novembre 2011). De plus, le $\delta^{15}N$ n'a pas évolué entre Juin et Novembre (Test U, p-value > 0.05).

Tableau 2 : $\delta^{13}C$ et $\delta^{15}N$ des producteurs primaires et des consommateurs échantillonnés sur Bizeux (PP : Producteurs primaire ; C1f : Consommateur primaire filtreur ; C1Bt : Consommateur primaire brouteur ; C2 : Consommateur secondaire)

Espèces	CT	δ13C ± SD		δ15N ± SD	
		Juin 2011	Nov. 2011	Juin 2013	Nov. 2011
Cryptopleura ramosa	PP	-33,85	-33,16	8,73	8
Phyllophora crispa	PP	-34,07±0,6	-34,49	7,33±0,61	6,75
Plocamium cartilaginum	PP	-32,74±0,2	-32,4±1,96	7,9±0,13	9,15±1
Calliblepharis ciliata	PP	-21,34±1,02	-21,18	8,15±0,49	8,14
Sphaerococcus coronopifolius	PP		-32,76		6,27
Bornetia secundiflora	PP		-29,88±1,8		8,3±0,12
Soliera chordalis	PP		-20,53		10,32
Halichondria panicea	C1f	-22,81	-22,7	8,81	9,653
Halichondria bowerbanki	C1f	-22,44		9,94	
Raspailia ramosa	C1f	-22,24		9,97	
Dysidea fragilis	C1f	-22,85	-21,24	9,14	10,44
Esperiopsis lobata	C1f	-22,5		8,69	
Stelligera stuposa	C1f		-21,86		9,7
Tricolia pullus	C1Bt	-20,8±0,35	-19,41	10,83±0,05	10,95
Jujubinus spp.	C1Bt	-21,01±1,67	-19,72±0,66	10,35±0,33	9,76±0,1
Rissoa spp.	C1Bt	-20,24±1,52	-20,23	9,86±0,32	9,66
Ocenebra erinacea	C2		-19,76±0,51		11,98±0,43
Hinia pygmae	C1Bt		-19,02		11,27
Gibbula cineraria	C2		-19,77		10,88

Ratios isotopiques des consommateurs

Au total, 12 espèces de consommateurs ont été échantillonnées pour représenter les premiers maillons trophiques (Tableau 2). Parmi les consommateurs primaires, deux groupes se distinguent significativement (Test U, $p < 0.05$). Les filtreurs sont représentés par 6 espèces d'éponges, leur signature isotopique est plus faible par rapport aux autres groupes trophiques (i.e. brouteurs et consommateur secondaire). Leur $\delta^{13}C$ est très proche de -22‰ alors que le $\delta^{15}N$ s'étend entre 8.69‰ (*Esperiopsis lobata*, juin 2011) et 10.44‰ (*Dysidea fragilis*, novembre 2011). Les brouteurs représentés par 4 espèces possèdent une signature $\delta^{13}C$ proche de -20‰ quelle que soit la saison et une signature $\delta^{15}N$ variant de 9.64‰ (*Rissoa* spp., juin 2011) à 10.88‰ (*Gibbula cineraria*, novembre 2011). Dans le même sens que pour les producteurs primaires, il n'y a pas de variations de la signature isotopique des consommateurs primaires entre juin et novembre.

En novembre 2011, 2 espèces de mollusques (*Ocenebra erinaceae* et *Hinia pygmae*) appartenant aux groupes des consommateurs secondaires ont été échantillonnées. Leur signature $\delta^{13}C$ est proche de celle des brouteurs (-20‰), par contre les valeurs de $\delta^{15}N$ sont plus élevées (resp. 11.68‰ et 11.27‰) ce qui semble cohérent pour un maillon trophique supérieur.

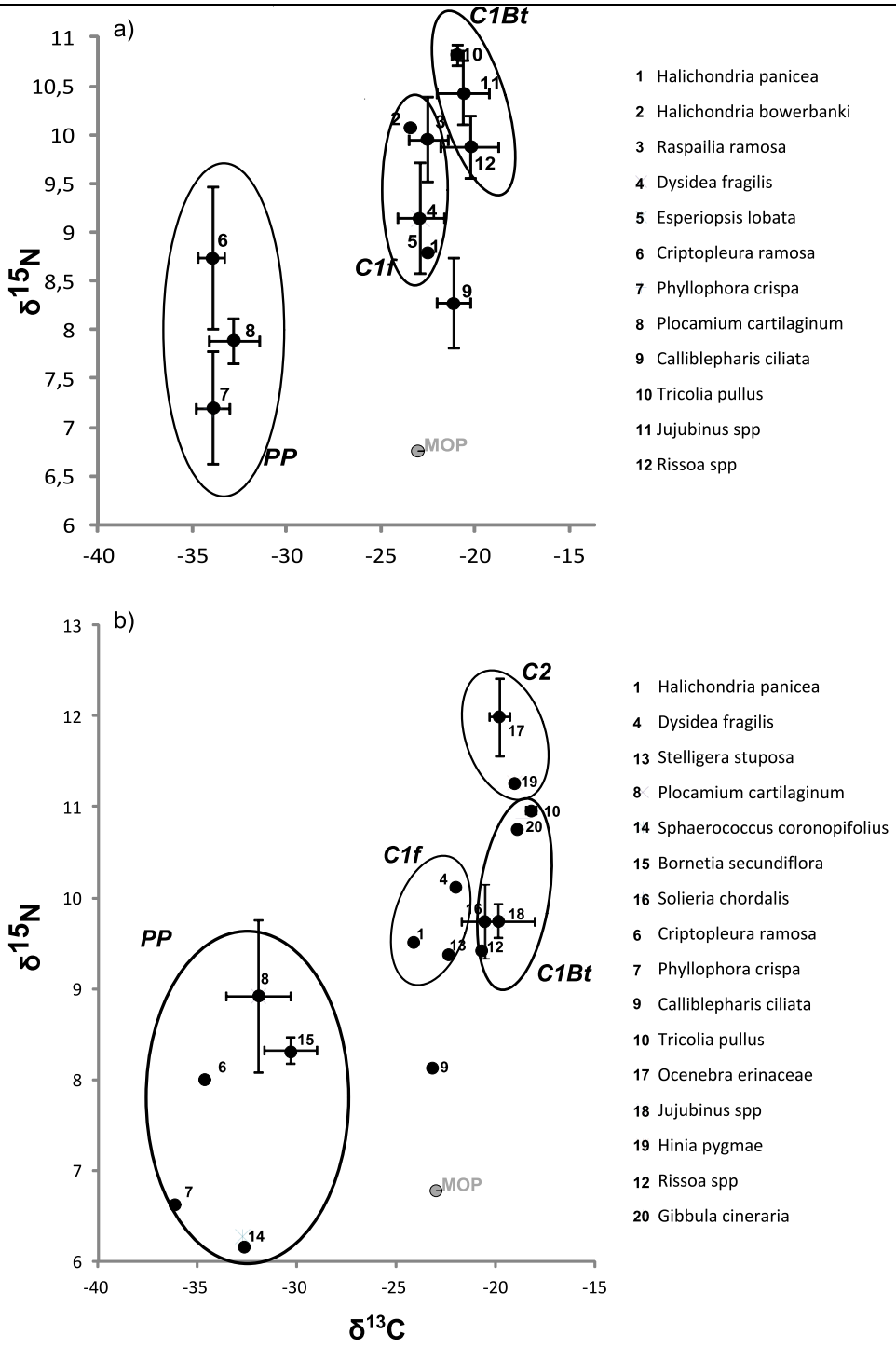


Figure 1 : Représentation du $\delta^{13}C$ vs. $\delta^{15}N$ des producteurs primaires et des consommateurs échantillonnés en Juin 2011 (a) et Novembre 2011 (b) sur l'ilot de Bizeux. Les ellipses rassemblent les organismes appartenant à un même groupe trophique (PP : Producteur primaire ; C1f : Consommateur primaire filtreur ; C1Bt : Consommateur primaire brouteur ; C2 : Consommateur secondaire ; MOP : Matière organique particulaire).

DISCUSSION

Signature des sources potentielles

La signature $\delta^{13}C$ des macroalgues peut être affectée par la disponibilité et la composition isotopique du carbone inorganique dissous. En effet, la valeur de $\delta^{13}C$ est liée à l'utilisation préférentielle du HCO_3^- plutôt que le CO_2 dissous en tant que source de carbone durant la production primaire (Raven *et al.* 2002). Parmi les macroalgues échantillonnées, deux groupes se distinguent par leur signature $\delta^{13}C$. Tout d'abord, un groupe avec une signature fortement négative (- 34‰ à -33‰) regroupe *Cryptopleura ramosa, Phyllophora crispa, Plocamium cartilagineum, Bornetia segundiflora*. Ces espèces intègrent principalement le CO_2 dissous par diffusion pour la photosynthèse et sont dépourvues d'un mécanisme de concentration du CO_2 (Raven *et al.* 2002, Hepburn *et al.* 2011). Le second groupe est constitué de *Calliblepharis ciliata* et de *Solieria chordalis* dont les signatures sont comprises entre -20‰ et -21‰. Ces espèces sont caractérisées à la fois par une assimilation de HCO_3^- et par la présence d'un mécanisme de concentration du CO_2 dissous (Hepburn *et al.* 2011). Les signatures isotopiques des producteurs primaires échantillonnés dans cette étude se retrouvent très proches des signatures isotopiques de producteurs primaires analysés dans d'autres systèmes côtiers comme la baie de Roscoff ou l'Archipel de Molène (Leclerc *et al.* 2013) ; la baie de Brest (Schaal *et al.* 2010), la baie d'Arcachon (Dubois *et al.* 2012).

Associée aux producteurs primaires, la matière organique particulaire (MOP) est aussi intégrée dans les réseaux trophiques. Cette MOP peut être issue de différentes sources marines, tel que : i) la matière organique sédimentaire (SOM) par remise en suspension lors de brassage total ou partiel de la colonne d'eau, ii) des macroalgues en dégradation, en effet 90% de la production des macroalgues entre par voie détritique dans les réseaux trophiques comme matière organique particulaire (MOP) ou comme matière organique dissoute (MOD) (Pomeroy, 1980; Mann, 1982), iii) des microalgues (non échantillonnées dans la présente étude) présentent des signatures isotopiques proches du MOP (Dubois *et al.* 2012).

Signature des consommateurs primaires

Les consommateurs primaires ne sont pas capables de se nourrir de toutes les sources de matières organiques. En effet, en fonction de leur physiologie et de leur localisation dans un habitat, ils vont devoir sélectionner une fraction de la matière organique disponible (Kasai *et al.* 2004, Dubois *et al.*2012). Néanmoins, certains consommateurs primaires tels que les

filtreurs sont capables d'assimiler plusieurs fractions de la matière organique (Schaal *et al.* 2010, Coma *et al.* 2011). Le fractionnement du ∂C entre les sources et les consommateurs est important, ce qui est observé dans de nombreux systèmes. Le fractionnement plus important chez les brouteurs que chez les filtreurs suggère que les sources de matières organiques sont différentes. Les filtreurs échantillonnés (exclusivement des éponges) présentent un enrichissement en ^{13}C par rapport à la MOP ce qui pourrait se traduire par une alimentation plus riche en phytoplancton/zooplancton ou de macroalgues intégrées dans le compartiment détritique. Le fort enrichissement en ^{13}C observé des brouteurs révèle une forte contribution macroalgues dans l'alimentation. La variabilité du $\delta^{15}N$ au sein des brouteurs met évidence un comportement omnivore de certains mollusques (*Tricolia pullus* et *Gibbula cineraria*). A contrario, on ne peut exclure que les filtreurs dépendent plus directement de la MOP formée par les algues rouges, tandis que les brouteurs consomment également des épiphytes… L'analyse des acides gras présentés dans le chapitre précédent plaide cependant en faveur de la première hypothèse, bien que la question reste ouverte et doive être tranchée par des études plus approfondies par espèces.

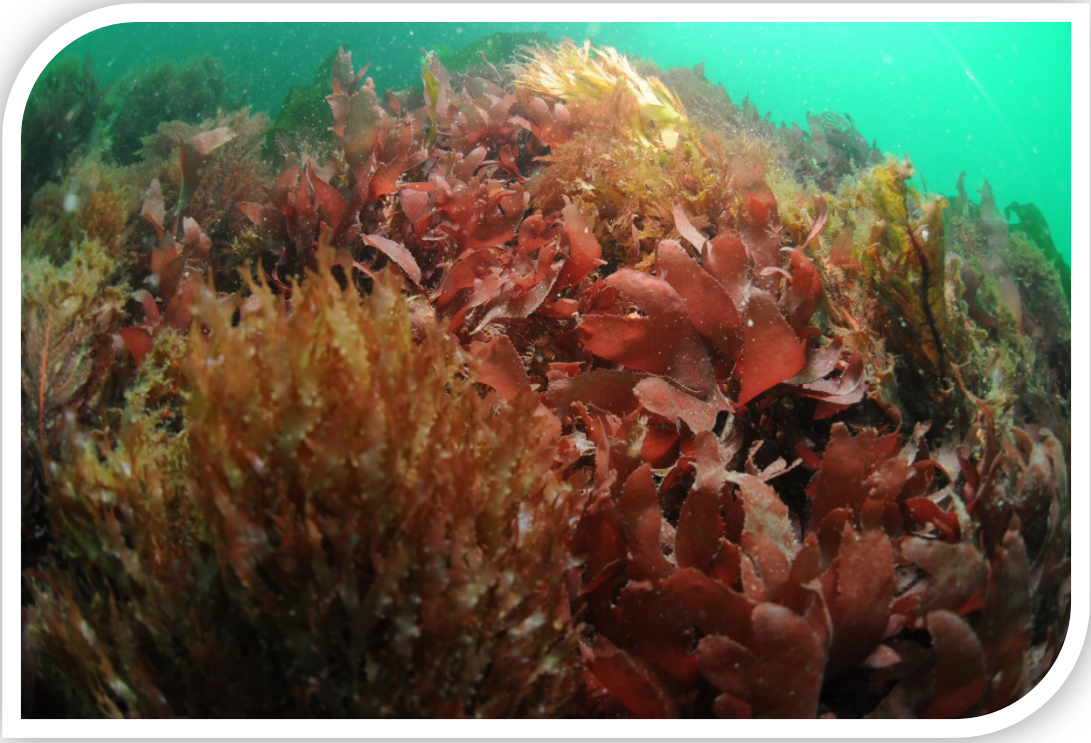
Structure du réseau trophique

L'organisation du réseau trophique n'a pas évolué entre les deux mois d'échantillonnage. Cette stabilité saisonnière suggère une certaine stabilité des sources trophiques à la base du réseau trophique. De plus, la grande diversité des comportements alimentaires des différents consommateurs permet de supporter l'absence d'une ressource durant une perturbation. La différence des signatures $\delta^{15}N$ et $\delta^{13}C$ entre les filtreurs et les brouteurs souligne que ces organismes se développent dans des microhabitats différents. Les filtreurs vont se localiser dans les zones où la matière organique particulaire est facilement accessible et les brouteurs vont quant à eux se réfugier dans les zones riches en matières organiques vivantes (macroalgues, biofilms).

En conclusion, cette étude préliminaire complète la vision globale des réseaux trophiques existant sur les substrats rocheux (Schaal 2010, Leclerc 2013). Au sein des habitats à dominance de rhodophycées, les macroalgues sont à la fois intégrées directement dans le réseau trophique par les brouteurs ou indirectement dans la matière organique particulaire consommée ensuite par les filtreurs. La stabilité saisonnière du réseau trophique suggère une redondance fonctionnelle des compartiments, c'est-à-dire une grande diversité des sources potentielles mais aussi une grande diversité des comportements alimentaires des

consommateurs. Néanmoins, une étude plus approfondie devra compléter ces résultats en intégrant plus d'espèces et par conséquent plus de compartiments trophiques.

DISCUSSION GENERALE & CONCLUSION



Les communautés à rhodophytes jouent un rôle essentiel au sein des écosystèmes côtiers de par la quantité de matière organique produite et l'intégration de cette matière dans le réseau trophique. Au total plus d'une centaine de plongées ont été réalisées totalisant au minimum 110 heures de plongée, et trois fois plus de temps en mer, grâce à une équipe composée de 15 plongeurs professionnels. Les études menées durant cette thèse ont permis de : 1) définir une méthodologie permettant de décrire les communautés benthiques vivant sur les substrat rocheux et d'évaluer la précision cette description ; 2) décrire les patrons d'organisation des assemblages à algues rouges à différentes échelles d'espace et de temps ; 3) comprendre le lien Diversité-Structure-Production existant au sein des communautés à rhodophytes ; 4) de suivre l'intégration des algues rouges dans le réseau trophiques.

Méthodologie de suivi des habitats rocheux

Avec pour objectif d'étudier à la fois la structuration et la production des communautés à rhodophytes, il a été nécessaire de mettre au point une méthodologie robuste afin de connaitre le lien entre effort d'échantillonnage et précision avec laquelle la communauté est décrite (Cf. Méthodologie). L'association d'échantillonnages qualitatifs et quantitatifs permet d'obtenir une description complète du système étudié ; les deux méthodes utilisées se complètent tant sur les échelles échantillonnées (macro-habitat ↔ micro-habitat) que sur les espèces observées et/ou récoltées (macrofaune ↔ méiofaune). L'échantillonnage au cours de la thèse s'est résumé à réaliser 5 couples quadrats + chasse à vue pour étudier la structuration des communautés à algues rouges depuis l'infralittoral inférieur en sous-strate des laminaires jusqu'au circalittoral supérieur où ces derniers dominent les assemblages macroalgaux. Par conséquent, au vu de l'abaque décrit par Gallon et al. (2013), pour les différents sites échantillonnés, 60 % la richesse spécifique a pu être évaluée, la structure observée par notre méthode présente 76% de similitude avec celle de la communauté totale. Avec un intervalle de confiance de 50%, la biomasse estimée par notre méthode est quant à elle moins précise. Cette précision apparait néanmoins suffisante pour détecter des variations spatiales voire temporelles (Gallon et al. 2013).

Distribution spatio-temporelles des communautés à rhodophytes.

Les différents travaux de cette thèse montrent que les communautés à rhodophytes sont très diversifiées, abondantes et largement répandues dans les habitats rocheux subtidaux du massif armoricain. Au total 80 espèces ont été recensées, les caractéristiques des assemblages (diversité, structure et biomasse) sont régies, à court terme, par les conditions

environnementales comme la température, la concentration en nutriment et, dans une moindre mesure, la turbidité. Il en résulte des patrons d'organisation qui se manifestent en fonction de la distance à la côte mais aussi en fonction des caractères physiques des microhabitats. Curieusement, si la composition et la structure des communautés n'est pas influencée par la profondeur, la biomasse quant à elle diminue en fonction de ce dernier paramètre.

A long terme dans un contexte de changements globaux, la distribution des assemblages est principalement contrôlée par les variations des températures moyennes alors que la composition des assemblages est plus sensible aux variations des amplitudes thermiques. Face à ces évolutions thermiques, les espèces, qu'elles soient d'affinité d'eau froide ou d'eau chaude, semble remonter vers le nord. De plus, ces travaux montrent que ces changements globaux varient en intensité le long des côtes bretonnes, le Golfe Normand Breton apparait être la région la plus touchée et la région incluant la mer d'Iroise la moins touchée. Bien que ces deux zones soient réputées pour leur fort hydrodynamisme, les caractéristiques hydrodynamiques de la première entrainent un isolement des masses d'eaux alors que ceux de la seconde entrainent alternativement en fonction de la saison un isolement ou un mélange des masses d'eaux.

Rôles et fonctions des communautés à rhodophytes au sein des systèmes rocheux.

Le lien Diversité-Structure-Production

Depuis les 20 dernières années, la compréhension du lien Diversité-Structure-Production au sein d'un écosystème est devenue une thématique majeure dans le domaine de l'écologie fonctionnelle (Loreau et al. 2001, Tillman 1999, Cardinal 2004, 2006). Classiquement, on attribue un lien positif-additif entre la richesse spécifique et la production de biomasse (Figure 1) (Tillman 1999, Balvaneara et al. 2006, Stachowicz 2007).

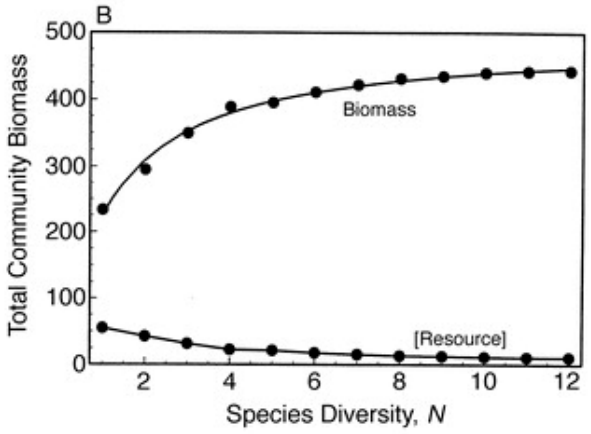


Figure 1 : Evolution de la biomasse en fonction de la diversité spécifique (issue de Tillman 1999)

Néanmoins, Loreau et Hector (2001) suggèrent de différencier deux mécanismes qui contribuent plus ou moins équitablement à l'effet de la diversité spécifique. D'un côté, l'effet de sélection « selection effect (SE)», qui se traduit par le fait que la biomasse d'une communauté ne peut pas excéder la biomasse de l'espèce la plus productive, et de l'autre côté, l'effet de complémentarité « complementary effect (CE) » qui représente l'équilibre de toutes les formes de niches pouvant influencer directement ou indirectement la biomasse. De plus, de récentes études ont montré que la diversité agit de manière variable sur la biomasse dans l'espace et dans le temps (Cardinal et al. 2007). Ce travail de thèse s'inscrit dans cette démarche en essayant de tester cette relation par des observations et des expérimentations *in situ*. Bien que l'étude de la relation Diversité-Structure-Production s'inscrit dans un continuum spatio-temporel, il était toutefois difficile voire impossible d'intégrer cette continuité dans le cas de cette thèse. Au cours de nos travaux, nous avons pu appréhender les relations entre diversité et production primaire à 3 niveaux d'un continuum espace-temps (Figure 2).

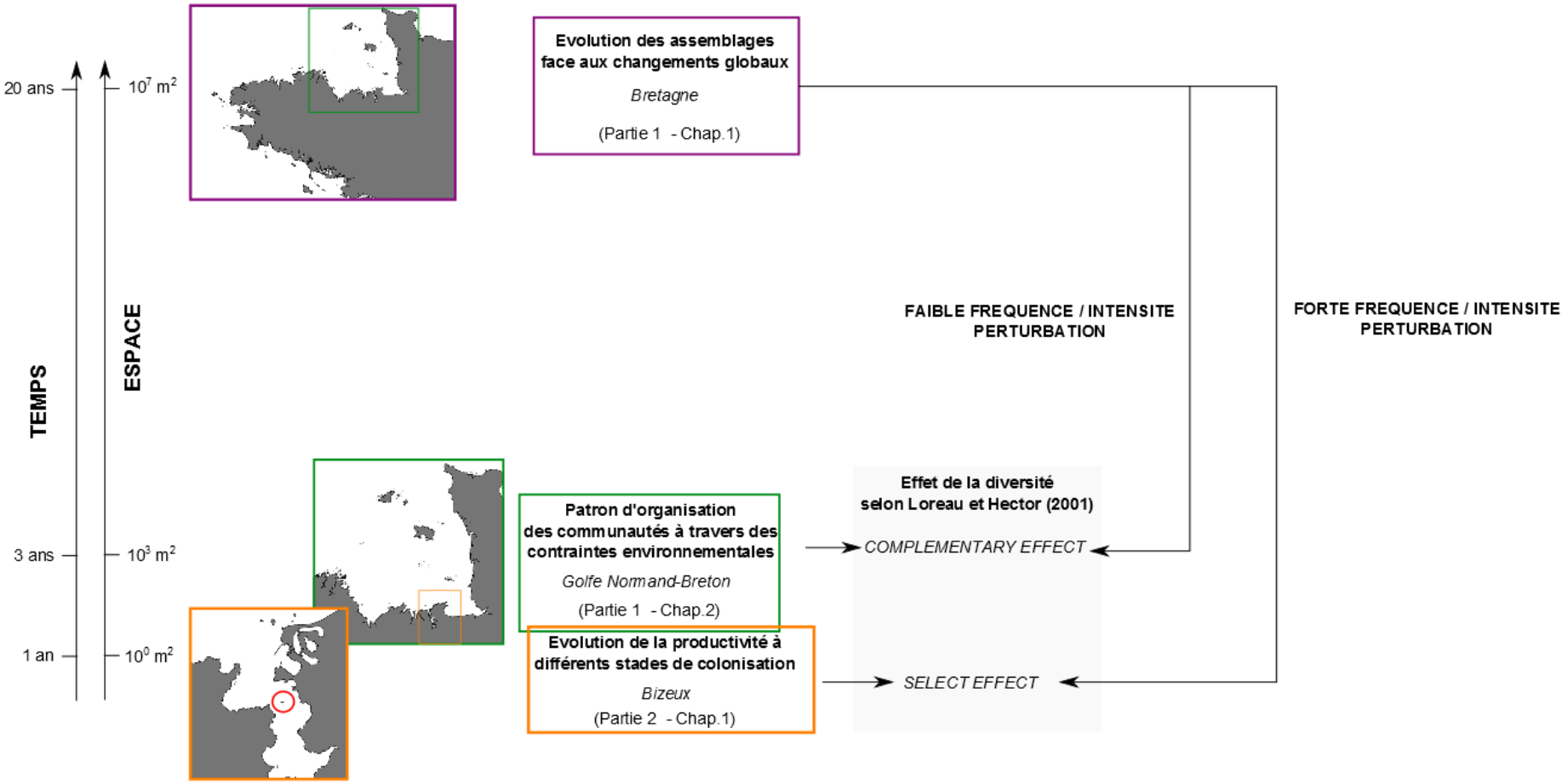


Figure 2 : Effet de la diversité à différentes échelles de temps et d'espace.

L'étude de suivi de colonisation, par la pose 34 plaques de granites sur Bizeux, a permis de proposer l'hypothèse que la biomasse macroalgale est liée principalement à une seule voire deux espèces reflétant un effet « selection species » et que ce sont les interactions intra-spécifiques (densité dépendantes) qui régulent la biomasse. Les espèces pionnières vont participer à la modification locale de l'habitat et contribuer à la création de nouvelles niches écologiques. Toutefois ces assemblages pionniers restent très instables du fait que la structure repose sur peu d'espèces. Associé à une augmentation de la diversité spécifique, une augmentation de la diversité fonctionnelle est essentielle pour renforcer la stabilité fonctionnelle des communautés.

Naturellement, on pourrait penser que la biomasse est aussi liée à la complexité de la structure des assemblages, une complexification de cette dernière se traduirait par une augmentation de la biomasse (Figure 3a). Or à l'échelle du Golfe Normand-Breton, l'étude du patron d'organisation a révélé qu'au niveau des communautés, la biomasse n'est pas liée à la structure des assemblages mais seulement à leur richesse spécifique, ce qui constitue un exemple de « complementary effect », grâce à la complémentarité des niches et à des mécanismes de redondance fonctionnelle (Figure 3b). Toutes les algues contribuent à la biomasse totale de la communauté, par contre leur contribution varie en fonction de facteurs biotiques et abiotiques.

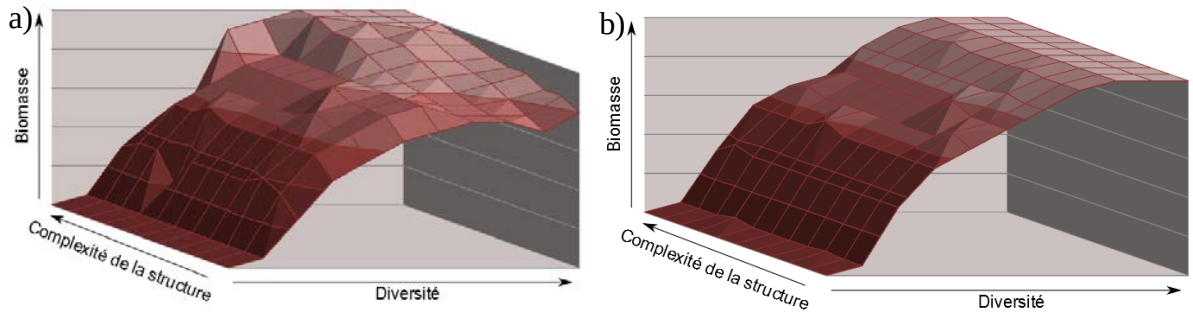


Figure 3 : Biomasse (z) en fonction de la diversité (x) et de la structure des communautés. a) relation théorique ; b) relation observée.

Comme nous l'avons montré précédemment, les évolutions à long terme des conditions environnementales peuvent avoir des conséquences plus ou moins important, en fonction de leur intensité, sur le fonctionnement des communautés macroalgales. En effet, des changements progressifs vont probablement entrainer un turn-over et/ou une acclimatation des espèces dans les communautés sans forcément bouleverser leur production de biomasse, la qualité de la matière organique photosynthétisée, son intégration dans les réseaux

trophiques et la valeur d'habitat d'espèces. Bien entendu cela n'est vrai que si les espèces de remplacement et/ou nouvellement installées possèdent des fonctions similaires à celle de la communauté originelle. Des changements plus brutaux ou plus récurrents peuvent quant à eux bouleverser profondément la structure et le fonctionnement par la disparition de cortège d'espèce ou l'apparition de nouvelles espèces compétitrices (exemple : *Sargassum muticum*, *Undaria pinnatifida*). L'introduction d'une nouvelle espèce dans un nouvel environnement résulte souvent en des bouleversements des interactions entre espèces. Lorsque l'envahisseur domine en abondance, ou détourne des ressources locales fondamentales à son profit, toute la chaîne d'interactions biologiques peut être perturbée. Dans certains cas, ceci conduit à la disparition de certaines, voire de toutes les espèces concernées par ces interactions. Ce phénomène est différent d'un processus purement lié au changement climatique que nous avons testé.

Intégration de la matière organique au sein communautés à rhodophytes

La connaissance sur les réseaux trophiques des habitats rocheux subtidaux s'améliore continuellement grâce au développement de nouveaux marqueurs trophiques et à une connaissance plus approfondie des mécanismes d'incorporation dans les réseaux. A l'heure actuelle, la grande majorité des études s'intéressant aux substrats rocheux se focalisent sur les habitats à Laminaires (e.g. Leclerc 2013a, 2013b, Schaal 2010, Fredriksen 2003, Miller 2011). Bien que la production des Laminaires reste l'une des plus importantes parmi les macroalgues, celles-ci ne recouvre que les strates supérieures (0m à 30m) des rochers immergés (obs. pers.).

Les deux études composant ce chapitre sont exploratoires. Elles n'ont pas pour objectif de décrire exhaustivement les réseaux trophiques des habitats à rhodophycées mais de poser des jalons quant à la réflexion sur l'intégration de la matière organique produite par ces algues dans les réseaux trophiques. Ces deux études confirment que la vision issue des marqueurs isotopiques et acides gras est complémentaire pour comprendre les transferts de matière végétale à travers les réseaux trophiques. Tout d'abord, l'utilisation des isotopes stables et plus précisément du $\delta^{15}N$ nous a permis de discerner clairement les différents compartiments trophiques (producteurs primaires, consommateurs primaires et consommateurs secondaires). Le $\delta^{13}C$ quant à lui a permis de différencier certaines algues rouges entre elles par leur affinité à fixer le CO_2 ou le HCO_3^-. Les marqueurs acides gras ont permis de différencier les différents producteurs primaires entre eux, des acides gras caractéristiques des algues rouges

(16:0), vertes (18:1ω11) et brunes (18:4ω3) ont pu être mis en évidence et suivi à travers les consommateurs primaires. L'utilisation pour les échelons supérieurs reste encore difficile en raison de la diversité des sources consommées par les prédateurs. Au final, ces travaux confirme que les algues rouges sont soit intégrer directement dans le réseau trophique par les brouteurs ou indirectement par voie détritique (Figure 4). De plus, il apparait que le réseau trophique associé aux habitats à algues rouges reste relativement stable dans le temps grâce à la grande diversité des sources potentielles et aux comportements alimentaires variés des consommateurs primaires et secondaires.

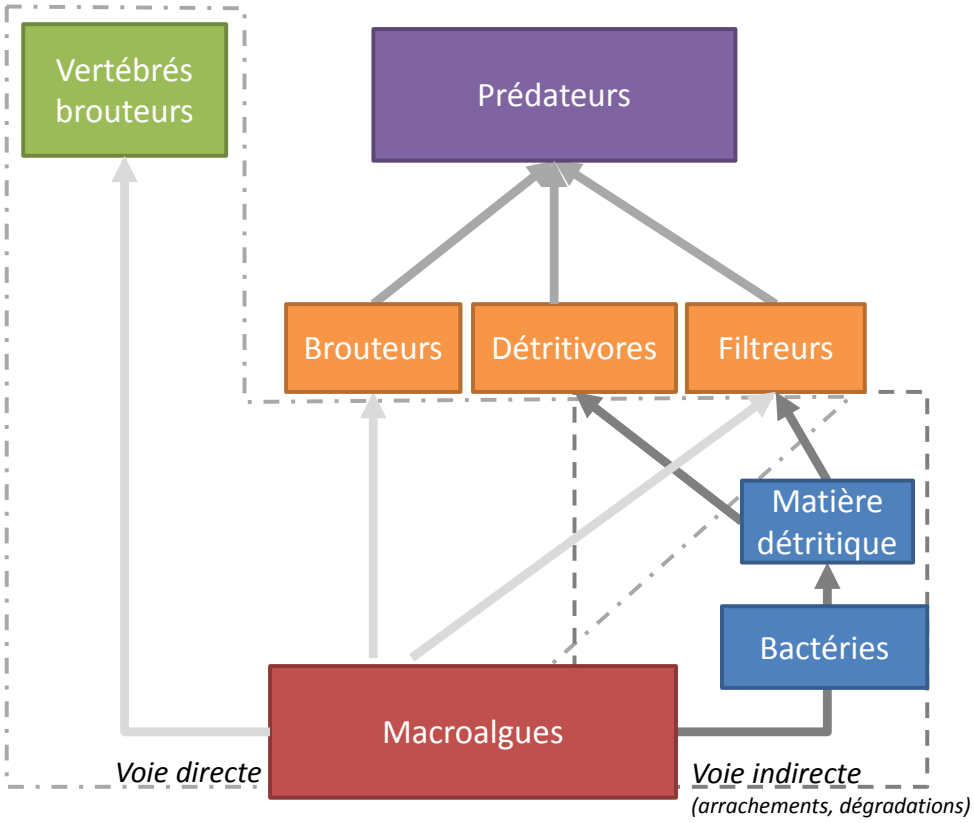


Figure 4 : Schémas du réseau trophique dans une communauté de macroalgues sur substrat rocheux

Limites et perspectives

Optimisation de la modélisation

Modéliser et/ou prédire la distribution d'espèces marines nécessite de constituer une base de donnée robuste pour regrouper à la fois les données de « présence » d'espèces et les données environnementales. Durant cette thèse, les données récoltées *in situ* n'étaient pas suffisantes pour développer des modèles robustes, par conséquent ces données ont été complétés par des

données d'occurrence provenant de bases extérieures (OBIS et GBIF). Le libre accès de ces bases de données « grande échelles » ouvre la porte à la modélisation de distribution à l'échelle du globe moyennant un support technique pouvant supporter de tels modèles. Néanmoins, l'utilisation de ces bases nécessite l'établissement de procédures préalables pour vérifier que: i) l'identification des espèces est correct, ii) les sites d'observation coïncident avec les aires de distributions, iii) la distribution de ces sites soit homogène au sein de la zone étudié. Dans le cas de cette thèse, le biais d'identification était au cœur de toute préoccupation lorsqu'il fallait combiner des bases de données, pour le réduire certaines espèces ont dû être éliminées, regroupées dans des groupes taxonomiques. Pour limiter la surreprésentation spatiale, les données ont été agrégées en cellules ayant une résolution compatible avec celle des données environnementales.

Le choix des variables environnementales est souvent conditionné à leur accessibilité, trouver et regrouper des données environnementales compatibles à la fois avec l'emprise spatiale et la période de l'étude est souvent imagé comme un parcours du combattant !! Dans notre cas, seules les données de température, de concentrations de chlorophylle a et de matière en suspension répondaient à ces critères et par conséquent les réponses prédites des espèces sont intimement liées à ces facteurs et peuvent être sensiblement différent si un nouveau paramètre est ajouté. A grande échelle, ce phénomène est plus atténué par l'accès à des bases de données libre, tel que BIO-Oracle (*www.oracle.ugent.be/)* regroupant des rasters de paramètres physiques et chimiques. Néanmoins, l'accès à ce genre de base de données n'exclut pas de renforcer la connaissance sur l'écophysiologie des espèces modélisées afin de se focaliser sur les paramètres essentiels allègent du coup les modèles.

Mesure du métabolisme en milieu subtidal

Dans le cas de l'étude du métabolisme associée aux communautés macroalgales, nous nous sommes confrontés à plusieurs difficultés. Tous d'abord, les mesures *in situ* sur le substrat naturel nécessitent de trouver un emplacement relativement horizontal pour poser les cloches et présentant peu d'irrégularité afin de limiter les fuites. Il aurait pu être possible d'aménager, du moins en zone intertidal, un support en ciment pour poser les plaques, mais en zone subtidal cela nécessite d'utiliser des bétons spéciaux riche en liant chimique pouvant être néfaste sur les communautés adjacentes. Nous avons donc décidé d'utiliser des plaques de granites pour mimer le substrat naturel. Ensuite, vient les difficultés liées à la variabilité des conditions environnementales, contrairement au milieu contrôlé, les mesures en milieu naturel

sont largement influencer par les conditions ambiantes, du coup nous avons dû nous plier aux aléas de « Mère Nature » pour réaliser notre expérimentation ce qui a limité les comparaisons de productivité aux différents stades de colonisation. Cependant, il serait intéressant de compléter les mesures relevées sur les plaques par des mesures prises directement sur le substrat naturel en développant un système de fixation non impactant et étanche. Cela permettrait de comparer les caractéristiques des assemblages sur substrat « artificiel » vs. « naturel » et de tester la redondance fonctionnelle d'une autre manière.

Suivi de la matière organique dans les réseaux trophiques

Il est bien évident que les données récoltées ne suffisent pas à décrire exhaustivement les réseaux trophiques d'un part parce que les données sont découplées dans l'espace : isotopes (Bizeux) et acides gras (les Haies de conches / les Hébihens) et d'autre part, en raison du nombre réduit d'échantillons par espèce. A l'origine, une analyse complémentaire par les acide gras et les isotopes stables aurait dû être réalisée sur les deux derniers sites mais des problèmes techniques liées à l'extraction des acides gras à réduit drastiquement le nombre d'échantillons pour l'isotopie. Pour compléter il faudrait multiplier le nombre de d'échantillons par espèces pour analyser la variation intra-spécifique des signatures, notamment pour les consommateurs primaires et secondaires. Il serait alors possible de faire ressortir leur signature acides gras « stable » afin de la suivre à travers le réseau trophique. Ces résultats couplés avec le $\delta^{15}N$, permettraient aussi d'identifier les signatures AG caractéristiques des différents compartiments trophiques. On obtiendrait alors à la fois des marqueurs taxonomiques et fonctionnels permettant de décrire plus précisément les réseaux trophiques à différentes échelles d'espaces et de temps.

CONCLUSION GENERALE

L'ensemble de cette étude a permis de décrire les patrons d'organisation des communautés à rhodophytes qui émergent aux travers des variations spatiales et temporelles des paramètres environnementaux. Il apparait que la température organise ces communautés le long des côtes bretonnes. Bien que la composition des communautés risque d'être profondément modifiée par les changements globaux, leurs fonctions restent relativement stables en fonction de l'intensité des perturbations grâce à des mécanismes de redondance fonctionnelle.

La biomasse produite estimée par ces communautés met en évidence leur rôle non négligeable au travers des systèmes rocheux voire même des systèmes côtiers, en raison de leur large distribution le long des massifs rocheux, mais aussi sur certains fonds meuble grossiers (Obs. pers.). Cette matière organique synthétisée est transféré dans les réseaux trophiques par voie direct ou indirect par voie détritique, des travaux spécifiques permettraient de quantifier la répartition de cette matière à travers ces deux voies trophiques.

Des études sur la fonction d'habitat pourront compléter les différents travaux réalisées dans cette thèse, dans le but mettre en évidence les liens exclusifs ou non entre certains vertébrés / invertébrés et les communautés à rhodophytes.

Le message le plus important, que nous avons illustré avec les différentes études de cette thèse, est que les communautés à rhodophytes ont un rôle non négligeable dans le fonctionnement des systèmes côtiers. Il est important de les prendre en compte dans le couplage pelagos/benthos des substrats rocheux.

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ANNEXES

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Improving occurrence-based rarity metrics in conservation studies by including multiple rarity cut-off points

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Abstract. 1. This study aims to develop a new method for assigning rarity weights to species in evaluations of the relative rarity of arthropod assemblages in conservation/monitoring studies.

2. A flexible characteristic was included in the rarity weighting method by introducing the possibility of fitting the method to a rarity cut-off point defined as the threshold of occurrence below which species are considered as being rare. This allows calculation of a rarity metric (index of relative rarity I_{RR}) with multiple rarity cut-off points.

3. The proposed weighting method was used and compared with three previously proposed methods in a theoretical analysis. I_{RR} values were then calculated for spider assemblages of a National Nature Reserve in France. Two methods of rankings were proposed: a local ranking between sites of the Nature Reserve, and a *regional ranking* in comparison to a reference database.

4. The proposed weighting method consistently weighted species according to the chosen rarity cut-offs. Species weights were less biased toward common species and rare species weights were less dispersed than with previous methods. Assemblages were consistently ranked according to the rarity of spiders in each assemblage. The index showed different patterns of rarity in assemblages which could not be detected by previous rarity metrics.

5. This method provides an improved understanding of assemblage rarity patterns relative to previous methods and can be consistently applied to other arthropod taxa in other geographic area and/or spatial scales.

Key words. Conservation scores, management monitoring, occurrence-based rarity, rare species, rarity cut-off points, spiders.

Introduction

Procedures for assessing areas for biodiversity conservation are usually based on two major methodological approaches: (i) complementarity-based approaches and (ii) scoring procedures. Complementarity-based methods assign values to areas on the basis of their contribution to selected biodiversity features that are not adequately represented in an existing set of areas (Margules *et al.*, 2002). These methods are thus best suited for systematic conservation planning. On the other hand, scoring procedures typically assign values to assemblages of species according to one or several criteria, including the presence of threatened, rare, or endemic species (Simaika & Samways, 2009).

Although the most appropriate methods used in systematic conservation planning are based on complementarity, scoring procedures are appropriate for identifying hotspots (Simaika & Samways, 2009), monitoring changes in land use and habitat disturbance (Basset *et al.*, 2008), comparing management

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practices (de Bello *et al*., 2010), as components of complex analyses (e.g. Samu *et al*., 2008), or when only one or a few sites need to be assessed. They are therefore appropriate tools in some of the central themes in the fields of arthropod conservation and diversity (Didham *et al*., 2010), for both aquatic (Simaika & Samways, 2009) and terrestrial taxa (Dapporto & Dennis, 2008).

This study focuses on rarity assessments of arthropod assemblages using scoring procedures. The vulnerability of arthropods remains poorly documented, with only 0.4% of described species evaluated by the IUCN criteria for endangered species (IUCN, 2010). Although arthropods represent 71–75% of globally described species (Chapman, 2009; IUCN, 2010), most invertebrate groups, including arthropods, are absent from national red lists (Zamin *et al*., 2010). Therefore, scoring procedures based on red lists or vulnerability status (e.g. Fattorini, 2009) can cover only a very limited number of arthropod taxa. In order to be suitable for most arthropod taxa, scoring methods should be based on criteria that reflect the rarity of species. The justification for focusing on rare species is primarily based on their greater risk of extinction relative to ecologically similar common species (Gaston, 1994; Flather & Sieg, 2007) and also because they serve as indicators for other species of concern with respect to conservation efforts (Lawler *et al*., 2003; Larsen *et al*., 2007).

Rare species are those with low abundance and/or small ranges relative to the abundances and/or distributions of other species within the considered taxon (Gaston, 1994). Although rarity is a continuous variable, species are often defined as *rare* when their abundance or geographic range decreases below a rarity cut-off point, which is defined in relation to the abundance or range of other closely related species (Flather & Sieg, 2007). Here, the rarity of a given species is assessed by the number of sites occupied in a given region, i.e. the regional occurrence of the species. Species occurrence is especially appropriate for assessing the rarity of assemblages of arthropods because the collection of presence–absence datasets requires less effort than collection of abundance datasets; in most cases, occurrence datasets are the only information available.

Because the rarity of a species depends upon the rarity of other (comparable) species, the rarity cut-off point may be highly variable among different taxa. Gaston (1994) recommended using the first quartile of the frequency distribution of species occurrence (i.e. the 25% species with the lowest occurrence). Yet, this first quartile can correspond to species whose occurrence is $< 5\%$ of all the sampled sites for a given region, as well as to species whose occurrence is equal to, for example, 20% of all the sampled sites in another region. This is due to the variations in species rarity among the different sample regions. Furthermore, the rarity cut-off point can differ according to taxa (Santoul *et al*., 2005; McCreadie & Adler, 2008), spatial scale (Flather & Sieg, 2007), and the choice of the investigators (e.g. for spiders: Buchar & Růžička, 2002; Harvey *et al*., 2002) and therefore must be flexible. However, species rarity is usually weighted with non-adjustable methods such as the inverse of their occurrence (i.e. the number of sites in which species have been found) or the inverse of their occurrence frequency (i.e. the percentage of sampled sites in which species have been found) (Kerr, 1997; Kier & Barthlott, 2001; Ysnel *et al*., 2008). These methods are not flexible and may not be relevant. The weight should not be an absolute value because the rarity of a given species depends on the rarity of other comparable species (Gaston, 1994). To improve the relevance of scoring procedures, flexibility should be included in the weighting of rarity.

This study aims to provide a rarity metric flexible enough to be applied to any arthropod taxa in any geographic area and at any spatial scale once biodiversity databases compiling previous samplings and/or species lists in a given region are available or can be quickly gathered (e.g. Keil & Konvicka, 2005; Pétillon *et al*., 2007a; McCreadie & Adler, 2008). For weighting species rarity, we propose a new method that depends upon the occurrence of the species with respect to a selectable rarity cut-off point. On the basis of species rarity weights, an index of relative rarity is then used to assign values to assemblages of species. Foremost, the new rarity weighting method is described along with the formula of the index of relative rarity. The advantages of the new weighting method are then analysed on the basis of a theoretical comparison with three existing weighting methods (Kerr, 1997; Sólymos & Fehér, 2005; and Dapporto & Dennis, 2008). To test the application of the index for conservation purposes, the method is applied and compared to the three previous methods in a case study of spiders in a French National Nature Reserve, which encompasses sites with different management practices.

Methods

Weighting of species rarity

Each species of the reference database is assigned a rarity weight calculated using a new weighting method. This weighting method is automatically adjusted depending on a rarity cut-off point selected by the user. Species rarity weights should increase exponentially as their occurrence falls below the rarity cut-off because it amplifies the weight of rare species and minimises the difference in weight between common species. This method should therefore enable integration of the intensity of rarity (i.e. the *level* of rarity) such that rarer species will have higher intensities of rarity. A low rarity cut-off point should assign high weights to species with high intensity of rarity (i.e. only very rare species), and progressively increasing this rarity cut-off point should progressively increase the weights of species of lower intensities of rarity.

The rarity cut-off point is expressed as a percentage of the maximal occurrence (i.e. the occurrence of the most widespread species $Q_{\max}$). Rare species (with an occurrence Q_i lower than the rarity cut-off) are expected to have a rarity weight (w_i) that increases exponentially with the distance between their occurrence and the rarity cut-off. Conversely, common species (with an occurrence Q_i higher than the rarity cut-off) are expected to have lower weights which vary only slightly. Common species whose occurrence is sufficiently distant from the rarity cut-off must have an almost null weight as they are assumed to be species that are not at risk. Species weight assignation can therefore be defined by the following relationship (graphical representation in Fig. 1a):

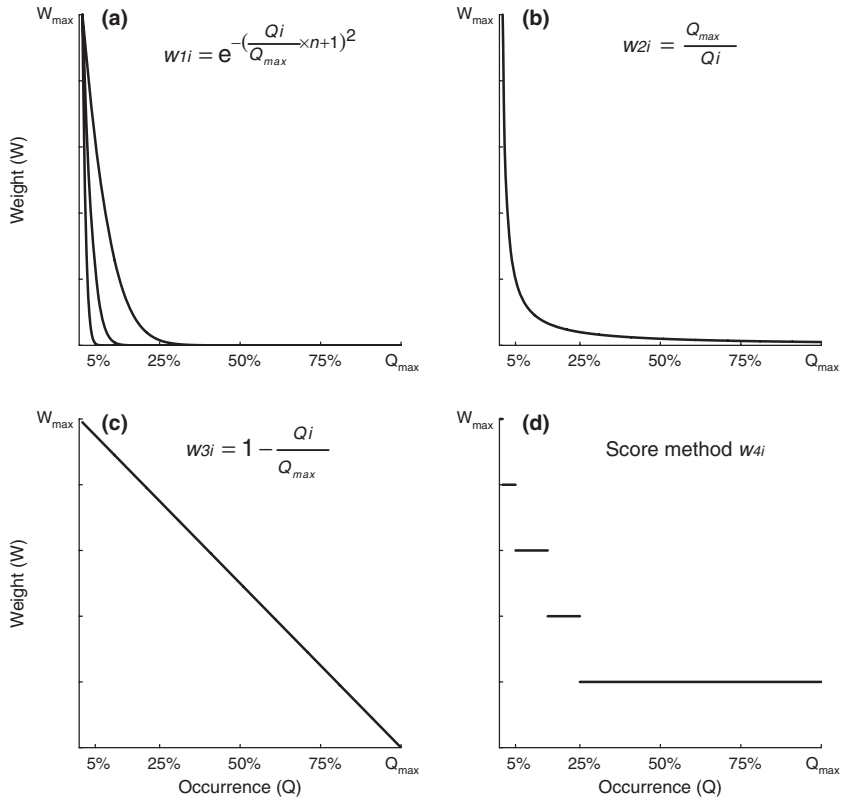

Fig. 1. Graphical representation of different weighting methods as a function of occurrence. (a) Weight assigned by the formula w_{1i} for three different rarity cut-off points. (b) Weight assigned by the inverse of the occurrence frequency (w_{2i}). (c) Weight assigned by the formula w_{3i} (from Dapporto & Dennis, 2008). (d) Weight assigned by a score related to the species occurrence class (w_{4i}) (modified from Sólymos & Fehér, 2005).

$$w_{1i} = \exp\left(-\left(\frac{Q_i}{Q_{\max}} \times n + 1\right)^2\right)$$

where n is an adjustment coefficient that can be adjusted to fit the rarity cut-off point (details on the calculation are provided in Appendix S1 in the Supporting Information). The squared exponential reduces any large dispersion of the weights of rare species.

Index calculation

The index assigns a value to a species assemblage on the basis of the rarity weights of its species. Weights of species of the assemblage are summed and then divided by the species richness so that the index is dependent on proportions of rare species but not on species richness. This division by the species richness makes the calculation similar to the Biodiversity Conservation Concern index (Fattorini, 2006). Because it is based on proportions of rare species, the index is called the Index of Relative Rarity (I_{RR}) and is calculated as follows:

$$I_{RR} = \left(\left(\sum(w_i)\right)/S - w_{\min}\right)/(w_{\max} - w_{\min})$$

where w_i is the weight of the ith species, S is the species richness of the assemblage, $w_{\min}$ is the minimum weight, assigned to the species of maximum occurrence of the large-scale dataset, and $w_{\max}$ is the highest weight assigned to the species of lowest occurrence of the large-scale dataset. The I_{RR} index ranges from 0 (all species of the assemblage have the minimum weight, i.e. ubiquitous species) to 1 (all species of the assemblage have the maximum weight, i.e. very rare species). Two I_{RR} values can only be compared when they are based on the same reference database and cut-off.

Theoretical analysis

The developed weighting method was compared to three other classical weighting methods: (i) weighting species with the inverse of their occurrence frequency: $w_{2i} = Q_{\max}/Q_i$; (ii) weighting species with the following formula: $w_{3i} = 1–Q_i/Q_{\max}$ (derived from Dapporto & Dennis, 2008); and (iii) assigning scores to categories of occurrence (w_{4i}) (e.g. Sólymos & Fehér, 2005). $Q_{\max}$ was

defined as the occurrence of the most widespread species. However, each method can be applied with a different definition of Q_{max}, as for instance the total number of sampled sites.

A sensitivity analysis and analysis of the correlation between species richness and index values are provided in Supporting Information (Appendix S2), as well as an illustration of the index values for different theoretical assemblages (Appendix S3).

Spider dataset

The index was applied to the spider database of western France. The ecological and indicator qualities of spiders have been demonstrated (Marc *et al*., 1999; Hendrickx *et al*., 2007), which makes them an appropriate model for testing the application of the index. Data in the original database was obtained from lists in existing literature (from 1820 to 2005), from species lists found in regional scientific reports, and from our own collection (for a detailed presentation, see Pétillon *et al*., 2007a). The reference database we used in this work is a subset of this database, which exclusively includes standardised samplings made between 1972 and 2005, 88.9% of which are biotope-informed (CORINE Biotope). This subset has 5703 records of 538 species found in 162 sampling stations. The most widespread species was found at 84 different stations (Q_{max}).

To assess whether the index is suitable for comparisons and rankings of assemblages of species, the assemblages of 10 stations sampled in a National Nature Reserve were extracted from the database and compared. This nature reserve is a coastal area of western France (Séné, 47°N, 2°W) that covers diverse terrain including salt marshes, sub-halophytic grasslands, wet meadows, fallow land, and heathlands surrounded by monospecific (dominated by *Prunus spinosa*) or diversified (deciduous) hedgerows. The different stations had different management regimes (grazed/ungrazed) and differed in salt concentration of the soil (non-halophytic, sub-halophytic, and halophytic vegetation); these two parameters influence the occurrence of rare spider species and the conservation value of spider assemblages (Bell *et al*., 2001; Pétillon *et al*., 2008).

Multiple rarity cut-off ranking

The indices of each assemblage of the Nature Reserve were calculated for a range of rarity cut-off points varying from a lower boundary to an upper boundary. The lower boundary corresponds to the minimum round cut-off that in turn corresponds to an occurrence >1. As there is no theoretical maximum rarity cut-off, Gaston's (1994) recommendation was applied because it is widely used in conservation and rarity assessment literature (Magurran, 2004; Flather & Sieg, 2007). Gaston (1994) recommended defining rare species as the lowest quartile of species in the assemblage. The upper bound was thus defined as the cut-off at which the mean proportion of rare species in the assemblages of our database was 25%. The indices for each assemblage were calculated from the lower round boundary to the upper round boundary with an interval of 1%.

The assemblages of the Nature Reserve were then ranked by two different methods. First, the median of the ranks of each assemblage was calculated over the range of rarity cut-offs. This first ranking constituted the ranking at the reserve's scale. To verify the consistency of this ranking with a ranking at the regional scale, the Nature Reserve's indices were compared with the quartiles of the indices of all of the assemblages of the reference database for each of the tested cut-offs. Nature Reserve assemblages that had indices above the third quartile of the indices of all of the assemblages of the reference database at most cut-offs were ranked first. Other assemblages were subsequently ranked depending on their indices relative to the median and the first quartile.

Finally, the ranks assigned to the Nature Reserve's assemblages on the basis of the new weighting method (w_1) were compared to the ranks obtained on the basis of (i) the other weighting methods (w_2, w_3, and w_4) and (ii) the proportion of rare species at each rarity cut-off.

All data analyses were performed using R (R Development Core, 2009 – scripts for the calculation of the index will be provided by the authors upon request).

Results

Theoretical analysis

Weighting of species by the inverse of their occurrence frequency (w_2) resulted in assignment of high weights only to species whose occurrence is lower than 10% of the maximum (Fig. 1b). Moreover, weights decreased significantly for species whose occurrence was between 1 and 5% of the maximum (i.e. only species with very low occurrence). In contrast, common species never had a null weight, and two common species could have different weights. The formula $w_{3i} = 1-Q_i/Q_{max}$ linearly assigned weight to species (Fig. 1c), such that a difference in occurrence resulted in an equivalent difference in weight. Assigning scores to categories of occurrence allowed a greater flexibility (Fig. 1d). However, the categories were defined arbitrarily, and two species of similar occurrence could have very different weights. Weighting species by the formula w_{1i} allowed for high weights to be assigned to different proportions of rare species depending on the selected cut-off, but with less dispersion of weights for very rare species than with the inverse of the occurrence frequency (Fig. 1a). Conversely, weight values decreased less significantly above the rarity cut-off, and the weight was almost null beyond a given distance from the cut-off.

The calculation of indices on a simulated set of assemblages revealed that the index values were not correlated with the species richness and varied consistently according to the intensity of rarity and the proportion of rare species (Appendices S2 & S3).

Application to assemblage ranking

The lower round rarity cut-off for an occurrence greater than 1 was 2% of the maximum occurrence. The mean proportion of

Table 1. Index of Relative Rarity (I_{RR}) values† of spider assemblages from the Nature Reserve (sampling stations S1–S10), calculated at 13 rarity cut-off points (2–14%‡) and corresponding rankings, quartiles§ of the indices of all the known assemblages of the reference database, and rankings of the reserve's assemblages based on these quartiles§.

	Assemblages of the National Nature Reserve of Séné										Quartiles of the indices of all the known assemblages of the reference region		
Biotope	Sub-halophytic meadows	Sub-halophytic meadows	Salt marshes	Salt marshes	Wet grasslands	Wet grasslands	Heathlands	Deciduous hedgerows	Monospecific hedgerows	Fallow land			
Station	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10			
Salinity degree	Sub-halophytic	Sub-halophytic	Halophytic	Halophytic	Non-halophytic	Non-halophytic	Non-halophytic	Non-halophytic	Non-halophytic	Non-halophytic			
Management	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Ungrazed	Ungrazed	Ungrazed	Ungrazed	1st Q.	Median	3rd Q.
I_{RR} 2%	0.018	*	*	*	*	*	*	0.037	0.027	*	*	*	*
I_{RR} 3%	0.018	*	*	0.001	*	*	0.001	0.039	0.027	0.001	*	*	0.004
I_{RR} 4%	0.018	*	0.003	0.008	*	*	0.007	0.045	0.027	0.004	*	0.001	0.012
I_{RR} 5%	0.018	*	0.005	0.017	*	0.001	0.016	0.055	0.029	0.008	*	0.006	0.019
I_{RR} 6%	0.018	0.001	0.009	0.027	*	0.003	0.026	0.066	0.031	0.012	0.001	0.012	0.027
I_{RR} 7%	0.019	0.004	0.012	0.037	*	0.005	0.037	0.077	0.033	0.017	0.002	0.018	0.035
I_{RR} 8%	0.020	0.007	0.016	0.047	*	0.008	0.049	0.088	0.036	0.022	0.006	0.024	0.041
I_{RR} 9%	0.022	0.012	0.020	0.057	0.001	0.010	0.061	0.099	0.039	0.027	0.010	0.033	0.050
I_{RR} 10%	0.025	0.017	0.024	0.066	0.001	0.013	0.074	0.110	0.043	0.032	0.013	0.039	0.058
I_{RR} 11%	0.028	0.023	0.028	0.075	0.003	0.017	0.086	0.121	0.047	0.038	0.018	0.046	0.069
I_{RR} 12%	0.033	0.030	0.033	0.084	0.005	0.021	0.098	0.132	0.052	0.044	0.024	0.052	0.081
I_{RR} 13%	0.037	0.037	0.037	0.093	0.009	0.025	0.110	0.144	0.057	0.051	0.030	0.059	0.092
I_{RR} 14%	0.043	0.044	0.042	0.101	0.013	0.030	0.123	0.155	0.063	0.058	0.038	0.068	0.103
Species richness	56	34	55	19	43	40	40	54	37	72			
% of rare species	12.5	14.7	12.7	21.1	14.0	15.0	37.5	38.9	18.9	18.1			
Reserve scale ranking	6	9	7	3	10	8	2	1	4	5			
% of I_{RR} > 3rd Q.	23.1	0.0	0.0	61.5	0.0	0.0	61.5	100	38.5	0.0			
% of I_{RR} > Median	23.1	0.0	23.1	38.5	0.0	0.0	38.5	0.0	38.5	38.5			
% of I_{RR} < Median	53.8	100	76.9	0.0	0.0	69.2	0.0	0.0	23.1	61.5			
% of I_{RR} < 1st Q.	0.0	0.0	0.0	0.0	100	30.8	0.0	0.0	0.0	0.0			
Regional scale ranking	5	8	7	2	10	9	2	1	4	6			

* I_{RR} values lower than 0.001.
† I_{RR} x%: Index (I_{RR}) adjusted at the rarity cut-off point x% of the maximum (see text). The values of I_{RR} can only be compared for the same cut-off.
‡The minimum 2% cut-off was chosen to have an occurrence > 1, and the maximum 14% cut-off corresponds to a mean proportion of 25% of rare species in the spider assemblages of western France.
§1st Q., first quartile; 3rd Q., third quartile.

25% of rare species for the assemblages of the database was reached at 14% of the maximum. The cut-off value of 14% of the maximum was thus identified as the upper boundary for the spider assemblages of western France.

For all assemblages of the Nature Reserve, the index values varied depending on the cut-off; higher cut-off values had higher indices (Table 1). This increase was monotonous but not linear, and its strength depended upon the assemblage. Four main patterns were distinguished (Fig. 2): (type 1) a single assemblage had indices higher than those of other assemblages regardless of the cut-off value (deciduous hedgerows S8); (type 2), two assemblages had indices higher than those of other assemblages at small cut-offs but not at high cut-offs (sub-halophytic meadows S1 and monospecific hedgerows S9); (type 3), two assemblages had low indices at small rarity cut-offs but high indices at higher cut-offs (salt marshes S4 and heathlands S7); and (type 4) five assemblages had lower rarity indices regardless of the rarity cut-off point (fallow land S10, ungrazed sub-halophytic meadows S2, grazed salt marshes S3, ungrazed S6 and grazed S5 wet grasslands).

S8 was ranked as the assemblage having the highest rarity index (Table 1; Reserve scale ranking row). Assemblages with high indices at higher cut-offs (type 3) were ranked second (S7) and third (S4). Assemblages with high indices mainly at small cut-offs (type 2) were ranked fourth (S9) and sixth (S1). Assemblages showing no major pattern (type 4) were assigned the lowest ranks, except for fallow land S10 that was ranked fifth.

Except for two inversions of ranks (S10 vs. S1 and S2 vs. S6), the ranking produced by comparing indices of the Nature Reserve to the quartiles of the indices from the database (Table 1; Regional scale ranking row) was similar to the ranking obtained using the scale of the Nature Reserve. The ungrazed salt marsh (S4), which was ranked third with the median-rank method, was tied for second with this quartile method.

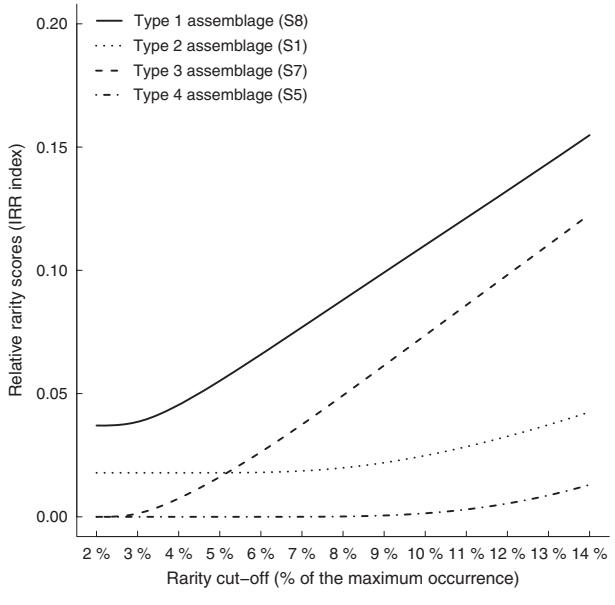

Fig. 2. Illustrations of the main patterns of variation of the I_{RR} values as a function of rarity cut-off points. Types 1, 2, 3, and 4 are illustrated by assemblages from deciduous hedgerows (S8), heathlands (S7), sub-halophytic grazed meadows (S1), and grazed wet grasslands (S5), respectively.

The simple rankings of the assemblages strongly differed depending upon the species weighting methods (Table 2). Indices based on method w_1 showed little variation among cut-offs (mean ± SD absolute variation in rank: 1.8 ± 1.2), with either a progressive gain in rank or a progressive loss of rank (except for heathlands S7 that both gained and lost ranks). Conversely, the proportion of rare species produced important variations between rarity cut-offs (mean ± SD absolute variation in rank: 8.7 ± 4.6) and never assigned a fixed ranking to an assemblage. Most assemblages both lost and gained ranks several times. Indices based on inverse of the occurrence frequency (w_2) produced the same rankings than the method w_1 between cut-offs 9 and 13%. Indices based on method w_3 produced rankings very different from the rankings obtained from the other methods. For instance, the grazed wet grassland (S5) was assigned the 4th rank but was ranked 10th by most of the other indices.

Discussion

Assets of the method

The index used here has several advantages: it varies from 0 (all species of the assemblage have the occurrence of the most widespread species) to 1 (all species of the assemblage have the same minimum occurrence). This aspect improves its readability. It is based on a proportion of species, which has the desirable property of making it independent of species richness and allowing comparisons among assemblages of different species richness. This property is verified by the lack of correlation between the index and species richness of randomly generated assemblages. This index integrates two parameters with respect to assemblages: the proportion of rare species and the intensity of rarity. Greater proportions of rare species and greater rarity produce a higher index value. The expected properties (rarity intensity and proportion of rare species) were verified using theoretical assemblages, and the values of the index were found to have a close fit.

The novelty of the method lies in the integration of a rarity cut-off point in the weighting method. This is a major improvement over previous methods. The analysis of several cut-offs showed that the assemblage rarity indices may be reversed depending upon the cut-off value. Therefore, an analysis based on a single cut-off or a non-flexible weighting method introduces a twofold risk: the risk of neglecting the majority of potentially interesting assemblages if the cut-off is too low and the risk of overlooking very rare species if the cut-off is too high. This twofold risk is present when species are weighted with the inverse of occurrence frequency (w_2), which is a commonly used method (e.g. Kerr, 1997; Kier & Barthlott, 2001; Ysnel *et al.*, 2008). Indeed, the rankings obtained by this method (w_2) produced the same rankings as method w_1 between cut-offs of 9 and 13%, thereby giving no sign of the presence of very rare species in both type 2 assemblages. Conversely, method w_1 does not overly

Table 2. Simple rankings of the assemblages of the Nature Reserve of Séné for the I_{RR} index between the 2 and 14% cut-offs*, for the proportion of rare species at each cut-off between 2 and 14%†, and for the I_{RR} index with weighting methods w_2, w_3, and w_4.

Station	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10
I_{RR} 2%	3	9	7	5	10	8	4	1	2	6
I_{RR} 3%	3	9	7	5	10	8	4	1	2	6
I_{RR} 4%	3	9	7	4	10	8	5	1	2	6
I_{RR} 5%	3	9	7	4	10	8	5	1	2	6
I_{RR} 6%	5	9	7	3	10	8	4	1	2	6
I_{RR} 7%	5	9	7	3	10	8	2	1	4	6
I_{RR} 8%	6	9	7	3	10	8	2	1	4	5
I_{RR} 9%	6	8	7	3	10	9	2	1	4	5
I_{RR} 10%	6	8	7	3	10	9	2	1	4	5
I_{RR} 11%	6	8	7	3	10	9	2	1	4	5
I_{RR} 12%	6	8	7	3	10	9	2	1	4	5
I_{RR} 13%	6	8	7	3	10	9	2	1	4	5
I_{RR} 14%	7	6	8	3	10	9	2	1	4	5
PR 2%	3	4	4	4	4	4	4	1	2	4
PR 3%	7	8	6	2	8	8	3	1	5	4
PR 4%	8	9	7	2	9	6	3	1	4	5
PR 5%	9	7	5	3	10	8	2	1	6	4
PR 6%	8	5	6	3	10	9	2	1	7	4
PR 7%	8	5	6	3	10	9	2	1	7	4
PR 8%	8	5	6	3	10	9	2	1	7	4
PR 9%	6	4	9	3	10	8	1	2	5	7
PR 10%	6	5	8	3	10	9	2	1	4	6
PR 11%	7	6	8	3	10	9	2	1	4	5
PR 12%	8	6	7	3	10	8	2	1	4	5
PR 13%	8	6	7	3	10	8	2	1	4	5
PR 14%	10	7	9	3	8	6	2	1	4	5
I_{RR} with w_2	6	8	7	3	10	9	2	1	4	5
I_{RR} with w_3	7	10	6	5	4	8	2	1	9	3
I_{RR} with w_4	7	6	8	4	10	9	2	1	5	3

*I_{RR} x%: Index (I_{RR}) adjusted at the rarity cut-off point x% of the maximum (see text).
†PR x%: Proportion of rare species at the cut-off x% of the maximum.

disperse the weight of rare species and assigns null weights above a certain threshold of occurrence, thus ensuring that species assumed to be not at risk have a null weight, and the proportion of species receiving high weights can be adjusted to avoid the above twofold risk.

The linear weighting method w_3 derived from Dapporto and Dennis (2008) assigns high weights to common species. This has a risk of assigning higher indices to assemblages containing no rare species than to assemblages actually containing some rare species. This risk has been confirmed in the comparison of the ranks. Weighting method w_4 is more flexible but arbitrary (Sólymos & Fehér, 2005) and introduces a risk that two species with close occurrences values will be assigned different weights. This risk is similar when the proportion of rare species alone is used and results in high variations in ranks between close cut-offs, which exacerbate the arbitrariness of the cut-off choice. Moreover, these discrete methods are sensitive to the drawback that species may change categories if ranges of other species change; therefore, their weight may strongly differ while their range remains constant (Gaston, 1994). Both methods (weighting method w_4 and the proportion of rare species) transform rarity into a discrete variable, although it is a continuous variable. The method we propose attempts to solve this problem: although rarity cut-off points are taken into account (discrete aspect), species with similar occurrences will always be given different, albeit similar weights (continuous aspect). Unlike the simple proportion of rare species, the continuous aspect of our weighting method prevents the possibility of obtaining very different results with different rarity cut-off points.

The number of cut-offs being compared has an impact on the accuracy of the analysis: if fewer cut-offs are compared, assemblages can be distinguished less precisely. We used an interval of 1% between cut-offs, but it is possible to use a smaller interval. However, that would not yield more information because the index monotonically increases with the cut-offs. The use of round cut-offs improves the readability of the index and enables practical standardisation.

Caveats of the method

Because our proposed index is based on occurrence data, the reliability of the estimate depends, at least in part, on the reliability of the dataset and methods of sampling. In addition, the estimation of rarity at a regional scale (in our case study, the area of the reference region is of approximately 65 000 km^2) may introduce some bias toward vagrant species. As a result, it is questionable whether the attribution of high weights to species of very

low occurrence is consistently valid. Some rare species in an assemblage may be vagrant species rather than rare species residing in the reference region, which might result in conserving atypical fauna of the region. In this case, it is possible to eliminate species of very low occurrence with a vagrancy cut-off point (e.g. McCreadie & Adler, 2008). Conversely, common species will not be highlighted by the index, although they can face high extinction risks. These caveats should be kept in mind when ranking assemblages on the basis of rarity criteria. The metric presented here is relevant if rarity is a decision target, but this does not exclude consideration of other metrics (see, for example, Basset *et al*., 2008).

The estimation of rarity may be biased if portions of the database are skewed towards particular geographic areas and/or biotope types. For example, artificial rarity may be attributed to species found in poorly sampled biotopes. Similarly, a trend toward sampling in nature reserves may result in overlooking of certain rare species subservient to other landscapes such as agricultural landscapes. When possible, the database should be optimised by evenly distributing samplings in space across the reference region. Likewise, proportions of samplings in each biotope type should be equivalent with respect to proportions of the biotope surfaces in the reference region, if such information is available.

In addition, an index based on proportions of rare species could be questionable, because, for example, an assemblage of 50 species with 14 rare species will have the same value as an assemblage of 70 species with 21 rare species (Appendix S3). This has been already discussed by Fattorini (2006), who indicated that a conservation index should not be dependent on species richness (and therefore be based on proportions of species). Indeed, in order to be meaningful, a comparison between assemblages should not introduce a bias toward particular assemblages. Because different types of biotopes have different native richness, an equitable comparison can only be achieved with an index based on proportions of species. Similarly, because of the species–area relationship, areas of different sizes should be compared with an index based on proportions of species in order to avoid a bias toward larger areas. Conversely, if assemblages are sampled in similar biotopes with similar area sizes, then they are compared on an equitable basis. In such less frequent situations, it may be more relevant to combine the new weighting method with an index based on the number of rare species (e.g. Kerr, 1997).

Rarity indices and ranking methods

It is impossible to obtain an absolute comparison of the observed rarity indices with notional indices of reference, describing an *ideal pattern of rarity*. The ranking produced by the median rank of each assemblage over the range of rarity cut-offs is therefore relative. Such a relative ranking implies the risk that assemblages considered of high value in a reserve would be considered of low value in another reserve, or would be of little interest to the reference region. The quartile method can then be applied to compensate for this risk. This method revealed that the ranking of stations in the National Nature Reserve of Séné was consistent with all of the known stations of the surrounding region. The observed inversions between local and regional rankings emphasise the role of using multiple rarity cut-offs. Although a given assemblage could have indices lower than those of another assemblage at most rarity cut-offs, its values at other cut-offs could be of high importance for the reference region (this was the case for the meadow S1). Furthermore, when monitoring the evolution of a site or when assessing the impact of land use change or habitat disturbances on assemblages, the quartile method offers a particularly relevant reference point.

The stations of the nature reserve highlighted by the index were globally consistent with existing knowledge. Heathlands represent the biotope with the greatest richness of spider species in Great Britain (Harvey *et al*., 2002) and with the highest proportion of rare species in western France (Pétillon *et al*., 2007a). Salt marshes are of important conservation value because of the stenotopic, halophilic species they host (Desender & Maelfait, 1999). On the other hand, hedgerows were not expected to be ranked first, but they contained the rarest species as well as the highest proportion of rare species. This result demonstrates the ability of such an index to show unexpected characteristics of interest in various assemblages. In addition, the index identified different stations with low rarity indices. These included stations subject to disturbances such as grazing, and areas with very low rarity indices, such as wet grasslands that are composed almost entirely of common and ubiquitous species (Pétillon *et al*., 2007a). The differences in rarity indices among grazed stations are due to different intensities of grazing. Although intensive grazing negatively affects assemblages of spiders, extensive grazing can have a beneficial effect (e.g. Bell *et al*., 2001; Pétillon *et al*., 2007b).

Flexibility of the index

Although the flexibility of the index is an appealing property, there may be an issue of subjectivity and the possibility of obtaining very different results as a result of arbitrary settings. The previous authors did not ponder this question as they used inflexible weighting methods (such as the inverse of occurrence frequency). However, as stated by Segan *et al*. (2010), objectivity does not emerge from the absence of choice. We argue that it is preferable to understand the patterns of rarity in assemblages and then make efficient choices rather than not carry out any selection and risk missing relevant conservation targets. In addition, such an index might be interpreted as a second step through a careful reading of species lists contributing to its rating. The choice of the settings of the index, i.e. the rarity cut-offs to be analysed, primarily depends on both the conservation targets and the mean proportion of rare species in the assemblages. When conservation targets focus on very rare species, small cut-offs will be preferred, thereby promoting assemblages of type 1 and 2. When conservation targets focus on high proportions of rare species, high cut-offs will be preferred, thereby promoting assemblages of type 1 and 3. The reserve ranking based on the boundaries proposed here represents a relevant compromise between the intensity of rarity and the proportion of rare species. The method first promoted the assemblage of type 1 and then assemblages of

type 2 and 3, in a manner depending on the balance between the proportion of rare species and the high intensity of rarity.

The meaning of cut-offs (especially *high cut-offs*), depends on the mean proportion of rare species in the assemblages. We chose an upper boundary corresponding to a mean proportion of 25% of rare species in assemblages because this is the most widespread definition of rarity (Flather & Sieg, 2007). This ensures a maximum cut-off sufficient to distinguish among assemblages and relevant to the taxon, area, and/or spatial scale being considered. Indeed, assemblages with almost no very rare species will be assigned high cut-offs. Conversely, assemblages with a high proportion of endemic species or containing a higher proportion of rare species (such as areas on a higher scale) will automatically be assigned a smaller maximum cut-off. The guidelines we propose to define the upper cut-off have been developed on and are therefore adapted for taxa having species-occurrence distribution curves that are right-skewed (most species are rare and few species are common). These patterns are the most frequently observed (Gaston, 2003), which makes the method suitable for most arthropod taxa.

Conclusions

The inclusion of flexibility in the weighting of species rarity provided two major improvements. First, given the relative nature of rarity, it ensures that the analysis is suitable and relevant for the studied taxon, the spatial scale, and/or the geographic area. Second, it provides a comprehensive analysis of the rarity patterns in assemblages of species and provides an improved understanding and fine discrimination between the different intensities of species rarity. Both these improvements are significant steps toward improving the *fitness for use* of rarity metrics. The fitness for use of this method will be useful in improving the relationship between objectives of studies and metrics, especially for lesser known taxa such as arthropods.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/j.1752-4598.2011.00148.x:

Appendix S1. Calculation of the adjustment coefficient *n*.

Appendix S2. Theoretical analysis of the I_{RR} index.

Appendix S3. Illustration of the index values for theoretical assemblages.

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Package 'G2Sd'

March 11, 2014

Type Package

Title Grain-size Statistics and Description of Sediment

Version 2.1

Date 2014-03-11

Depends R (>= 3.0.2), stats

Imports shiny, xlsx, rJava, xlsxjars,

Author Regis K. Gallon (MNHN), Jerome Fournier (CNRS|MNHN)

Maintainer Regis K. Gallon <reg.gallon@gmail.com>

Description G2Sd package gives full descriptive statistics and a physical description of sediment obtained with metric or phi sieves according to the grain size distribution.

License GPL-3

URL http://cran.r-project.org/web/packages/G2Sd/index.html,http://regisgallon.wordpress.com/r-software/

NeedsCompilation no

Repository CRAN

Date/Publication 2014-03-11 15:22:59

R topics documented:

coord_gran *Localisation of stations sampled*

Description

coord_gran is a dataframe of 2 observations and 21 variables. It corresponds to the localisation of the stations sampled.

Usage

```
data(coord_gran)
```

Format

A data frame with 21 observations on the following 2 variables.

X a numeric vector

Y a numeric vector

Source

Godet, L., Fournier, J., Toupoint, N., Olivier, F. 2009. Mapping and monitoring intertidal benthic habitats: a review of techniques and proposal of a new visual methodology for the European coasts. Progress in Physical Geography **33**, *378-402*

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Examples

```
data(coord_gran)
```

G2Sd *Grain-size Statistics and Description of Sediment*

Description

G2Sd package gives full descriptive statistics and a physical description of sediment obtained with metric or phi sieves according to the grain size distribution.

Details

The G2Sd package is an evolution of the Gradistat v.4.0 macro for MS Excel initially developped by Blott and Pye (2001) for phi sieves and Laser granulometer. This package is suited to analyse data obtained from metric (micrometer) or phi sieves. The user is required to input the weight of sediment retained on sieves spaced at any metric or phi intervals. Statistics are calculated using arithmetic and geometric Method of Moments (micrometer) and using logarithmic Folk and Ward (1957) Method (phi scale): mean, standard-deviation, skewness, kurtosis. The mode(s) is(are) determined graphically by the user (with a maximum of 4 modes). The determination of the mode is optional (no determination by default). Several percentiles and common index are calculated: D10, D50, D90, D90/D10, D90-D10, D75/D25, D75-D25, Trask(So) Index, Krumbein(Qd) Index. Physical description of texture, sorting, skewness or kurtosis are provided as such as the sediment name after Folk (1954). Are also included the percentage of particules falling into each predefined size fraction, modified from Blott and Pye (2001) scale, Udden (1914) and Wentworth (1922). There are four functions. `granstat` is a function which provides all results organized in two ways: a complete matrix (by default) or by separate items; `granplot` is a function which provides a histogramm with a cumulative percentage curve; `grandistrib` is a function which provides a barplot of the different fractions composing the sediment; `granmap` is a function which provides a georeferenced map of the sediment distribution.

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See Also

`granstat`, `granplot`, `grandistrib`

Examples

```
data(granulo)
data(coord_gran)
result=granstat(granulo)
granplot(granulo,1)
```

grandistrib *Composition of the sediment*

Description

This function provides a barplot of the different fractions composing the sediment

Usage

```
grandistrib(x, main="", scale = "fine", xlab = "Stations", ylab = "Percentage")
```

Arguments

x	A numeric matrix or data frame (see the shape of data(granulo))
main	a label for the title
scale	If fine, display the detailed composition; If large, display the simplify composition
xlab	a label for the x axis, defaults to a description of x.
ylab	a label for the y axis, defaults to a description of y.

Details

The obtained graph is commonly used by Sedimentologists

Value

A barplot with the composition of sediment for each station sampled

Author(s)

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See Also

granplot, grandistrib

Examples

```
data(granulo)
grandistrib(granulo, scale="fine")
```

granplot *Histogram with a cumulative percentage curve*

Description

This function provides a histogram of the grain-size distribution with a cumulative percentage curve

Usage

```
granplot(x, xc = 1, hist = TRUE, cum = TRUE, main = "",
col.cum = "red", col.hist="gray", cexname=0.9)
```

Arguments

x	A numeric matrix or data frame (see the shape of data(granulo))
xc	Define a column
hist	If TRUE, display a histogram; if FALSE, do not display a histogram
cum	If TRUE, display a cumulative percentage curve; if FALSE do not display a cumulative percentage curve
main	Add a title to the current plot
col.cum	Color in which cumulative percentage curve will be drawn
col.hist	Color in which histogram will be drawn
cexname	A numerical value giving the amount by which plotting text and symbols should be magnified relative to the default.

Details

The obtained graph is the most commonly used by Sedimentologists

Value

A histogram with a cumulative percentage curve

Author(s)

Regis K. Gallon (MNHN) <reg.gallon@gmail.com>, Jerome Fournier (CNRS) <fournier@mnhn.fr>

See Also

grandistrib

Examples

```
data(granulo)
granplot(granulo,xc=1,hist=TRUE,cum=TRUE,main="Grain-size Distribution",
col.hist="gray",col.cum="red")
```

granstat *Calculates all descriptive statistics*

Description

Statistics are calculated using arithmetic and geometric Method of Moments (micrometer) and using logarithmic Folk and Ward (1957) Method (phi scale): mean, standard-deviation, skewness, kurtosis. The mode(s) is(are) determined graphically by the user (with a maximum of 4 modes). The determination of the mode is optional (no determination by default). Several percentiles and common index are calculated: D10, D50, D90, D90/D10, D90-D10, D75/D25, D75-D25, Trask(So) Index, Krumbein(Qd) Index. Physical description of texture, sorting, skewness or kurtosis are provided as such as the sediment name after Folk (1954). Are also included the percentage of particules falling into each predefined size fraction, modified from Blott and Pye (2001) scale, Udden (1914) and Wentworth (1922). `granstat` is a function which provides all results organized in two ways: a complete matrix (by default) or by separate items.

Usage

```
granstat(x, web_interface=FALSE, statistic = "all", aggr = TRUE, modes = FALSE)
```

Arguments

`x`	A numeric matrix or data frame
`web_interface`	if TRUE, a simplified interface is displayed from your default web browser
`statistic`	Statistic used: "arithmetic", "geometric", "folk.ward", "all". If this argument is not used, all statistics are calculated
`aggr`	If TRUE, a complete matrix is provided. If FALSE, the results are organized in separate items: `$stat`, `$index`, `$mode`, `$sedim`. If this argument is not used, a complete matrix is provided
`modes`	If TRUE, the mode must be determinated graphically by the user. If FALSE, the mode is not determinated. If this argument is not used, no determination of the mode is proposed

Details

For the determination of the mode (`modes=TRUE`). All the samples are successively shown with a graph. The user can choose graphically the mode (1 in 4 maximum) by a click on the graph. If 4 modes are chosen, the following graph appears automatically. If 1, 2 or 3 modes are chosen, the user has to use the function stop locator in the graphic window.

If the weight of sediment retained on the broadest sieve exceeds 5 percent of the total mass of the sample, the Folk and Ward statistics cannot be computed.

Value

A matrix containing

mean.arith	the mean of grain-size distribution (arithmetic method of moments)
sd.arith	the standard-deviation of grain-size distribution (arithmetic method of moments)
skewness.arith	the skewness of grain-size distribution (arithmetic method of moments)
kurtosis.arith	the kurtosis of grain-size distribution (arithmetic method of moments)
mean.geom	the mean of grain-size distribution (geometric method of moments
sd.geom	the standard-deviation of grain-size distribution (geometric method of moments)
skewness.geom	the skewness of grain-size distribution (geometric method of moments)
kurtosis.geom	the kurtosis of grain-size distribution (geometric method of moments)
Sediment	physical description of the sediment, the sorting, the skewness and the kurtosis
Mean.fw.mm	the mean of grain-size distribution (logarithmic Folk and Ward method, mm scale)
Sd.fw.mm	the standard-deviation of grain-size distribution (logarithmic Folk and Ward method, mm scale)
Skewness.fw.mm	the skewness of grain-size distribution (logarithmic Folk and Ward method, mm scale)
Kurtosis.fw.mm	the kurtosis of grain-size distribution (logarithmic Folk and Ward method, mm scale)
Mean.fw.phi	the mean of grain-size distribution (logarithmic Folk and Ward method, phi scale)
Sd.fw.phi	the standard-deviation of grain-size distribution (logarithmic Folk and Ward method, phi scale)
Skewness.fw.phi	the skewness of grain-size distribution (logarithmic Folk and Ward method, phi scale)
Kurtosis.fw.phi	the kurtosis of grain-size distribution (logarithmic Folk and Ward method, phi scale)
Mode	the mode (mm scale), graphically defined by the user
D10(mm)	the 10th percentile
D50(mm)	the median
D90(mm)	the 90th percentile
D90/D10	ratio of the 90th percentile and the 10th percentile
D90-D10	difference between the the 90th percentile and the 10th percentile
D75/D25	ratio of the 75th percentile and the 25th percentile
D75-D25	difference between the the 75th percentile and the 25th percentile
Trask(So)	the Trask Index (So) defined as D25/D75 (mm scale)
Krumbein(Qd)	the Krumbein Index (Qd) defined as (D25-D75)/2 (phi scale)

Texture	physical description of the texture of the sediment
Boulder	percentage of sediment of the grain-size distribution retained in the Boulder class (upper to 63 mm)
Gravel	percentage of sediment of the grain-size distribution retained in the Gravel class (between 2 mm and 63 mm)
Sand	percentage of sediment of the grain-size distribution retained in the Sand class (between 63 micrometer and 2 mm)
Mud	percentage of sediment of the grain-size distribution retained in the Mud class (down to 63 micrometer)
Boulder	percentage of sediment of the grain-size distribution retained in the Boulder class (upper to 63 mm)
vcgravel	percentage of sediment of the grain-size distribution retained in the Very Coarse Gravel class (between 31.5 mm and 63 mm)
cgravel	percentage of sediment of the grain-size distribution retained in the Coarse Gravel class (between 16 mm and 31.5 mm)
mgravel	percentage of sediment of the grain-size distribution retained in the Medium Gravel class (between 8 mm and 16 mm)
fgravel	percentage of sediment of the grain-size distribution retained in the Fine Gravel class (between 4 mm and 8 mm)
vfgravel	percentage of sediment of the grain-size distribution retained in the Very Fine Gravel class (between 2 mm and 4 mm)
vcsand	percentage of sediment of the grain-size distribution retained in the Very Coarse Sand class (between 1 mm and 2 mm)
csand	percentage of sediment of the grain-size distribution retained in the Coarse Sand class (between 500 micrometer and 1 mm)
msand	percentage of sediment of the grain-size distribution retained in the Medium Sand class (between 250 micrometer and 500 micrometer)
fsand	percentage of sediment of the grain-size distribution retained in the Fine Sand class (between 125 micrometer and 250 micrometer)
vfsand	percentage of sediment of the grain-size distribution retained in the Very Fine Sand class (between 63 micrometer and 125 micrometer)
vcsilt	percentage of sediment of the grain-size distribution retained in the Very Coarse Silt class (between 40 micrometer and 63 micrometer)
silt	percentage of sediment of the grain-size distribution retained in the Silt class (lower than 40 micrometer)

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References

Blott, S., Pye, K. 2001. Gradistat: grain size distribution and statistics package for the analysis of unconsolidated sediment. Earth, Surface Processes and Landforms **26**, *1237-1248*

Folk, R.L. 1954. The distinction between grain size and mineral composition in sedimentary-rock nomenclature. Journal of Geology **62**, *344-359*

Folk, R.L., Ward, W.C. 1957. Brazos River bar: a study in the significance of grain size parameters. Journal of Sedimentary Petrology **27**, *3-26*

Krumbein, W.C., Pettijohn, F.J. 1938. Manual of Sedimentary Petrography. *Appleton-Century-Crofts, New-York*

Udden, J.A. 1914. Mechanical composition of clastic sediments. Bulletin of the Geological Society of America **25**, *655-744*

Wentworth, C.K. 1922. A scale of grade and class terms for clastic sediments. Journal of Geology **30**, *377-392*

Examples

```
#granulo is the data set
data(granulo)
granstat(granulo)
granstat(granulo,statistic="all",aggr=TRUE,modes=FALSE)
granstat(granulo,statistic="folk.ward",aggr=FALSE,modes=TRUE)

#to display the simplified interface
#granstat(web_interface=TRUE)
```

`granulo` *Data frame for G2Sd package*

Description

`granulo` is a data frame of 29 observations and 21 variables. The first column corresponds to the apertures sizes of AFNOR sieves, in micrometer (25000, 20000, 16000, 12500, 10000, 8000, 6300, 5000, 4000, 2500, 2000, 1600, 1250, 1000, 800, 630, 500, 400, 315, 250, 200, 160, 125, 100, 80, 63, 50, 40, 0). Warning ! the last sieve 0 corresponds to the material retained in the < 40 micrometer pan after sieving. The others columns corresponds to the weight of samples beside each size class

Usage

```
data(granulo)
```

Format

A data frame with 29 rows corresponding to the apertures sizes on the following 21 stations sampled

Details

This example provide a data frame of sedimentary data obtained with AFNOR sieves (in micrometer)

Source

Godet, L., Fournier, J., Toupoint, N., Olivier, F. 2009. Mapping and monitoring intertidal benthic habitats: a review of techniques and proposal of a new visual methodology for the European coasts. Progress in Physical Geography **33**, *378-402*

References

Fournier, J., Godet, L., Bonnot-Courtois, C., Baltzer, A., Caline, B. 2009. Distribution des formations superficielles de l archipel de Chausey (Manche). Geologie de la France **1**, *5-17*

Examples

```
data(granulo)
```

Index

Résumé :

Cette thèse aborde le lien structuration – fonction de ces communautés à travers différentes échelles spatio-temporelles. Pour réaliser ces études, nous nous sommes appuyés sur une méthodologie préalablement développée permettant d'évaluer la précision de nos paramètres en fonction de l'effort d'échantillonnage appliqué.
Dans un premier temps, nous avons décrit les patrons d'organisation existant à l'échelle de la Bretagne en comparant les assemblages observés entre 1992 et 1998 et ceux observés aujourd'hui. Puis, nous nous sommes concentrés sur les patrons d'organisation présents dans le Golfe Normand Breton et comment ceux-ci s'expriment a travers i) la composition spécifique ii) la structure, iii) la biomasse de ces communautés. La température organise les communautés le long des côtes bretonnes ; leur structure risque d'être modifiée dans le contexte des changements globaux par contre les fonctions associées se révèle relativement stable par la mise en place de mécanismes de redondance fonctionnelle.
Dans un second temps, nous avons suivi la composition spécifique et la structure des communautés algales durant un processus de colonisation ; la biomasse et la productivité ont été suivies pour ensuite être mises en relation avec les caractéristiques des communautés. La biomasse estimée par les communautés à algues rouges met en évidence un rôle non négligeable au travers des systèmes côtiers.
Pour finir, nous nous sommes intéressés au devenir de la matière organique produite par les communautés à rhodophytes. Nous nous sommes appuyés sur la complémentarité des marqueurs isotopes et acides gras pour tracer le cheminement de la matière organique au travers des réseaux trophiques. Il ressort que la matière organique synthétisée par les algues rouges est intégrée directement et/ou indirectement (par voie détritique) dans les réseaux trophiques.

Abstract:

This thesis approaches the link structure - function of these communities across different spatial and temporal scales. For these studies, we based our approach on a methodology previously developed to assess the accuracy of our parameters based on sampling carried effort.
First, we described the existing organization patterns across the Brittany coasts by comparing assemblages observed between 1992 and 1998 and those observed today. Then we focused on organization patterns present in the Normand Breton Gulf and how they are expressed through the i) the species composition , ii) structure , iii) the biomass of these communities. Red seaweeds communities are driven by the temperature, in the context of global changes their structure may be altered whereas their associated functions are relatively stable by the implementation of redundancy mechanisms.
In a second part, we followed the species composition and structure of macroalgal communities in a process of colonization, biomass and productivity were then set up relationship with the characteristics of communities. The estimated biomasses reveal an important role in the primary production of red seaweeds communities in coastal systems.
Finally, we examined the fate of organic matter produced by red seaweeds communities. We based on the complementarity of isotopes and fatty acid markers to follow organic matter through food webs. The organic matter produced by red algae is integrated directly and/or indirectly (detrital way) in benthic food webs.