



Production primaire et fonctionnement de communautés intertidales à canopée de Fucus

François Bordeyne

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Laboratoire Adaptation et Diversité en Milieu Marin (AD2M UMR7144)

Equipe Ecogéochimie et Fonctionnement des Ecosystèmes Benthiques (EFEB)

Production primaire et fonctionnement de communautés intertidales à canopée de *Fucus*

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Thèse de doctorat d'Océanographie Biologique

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INTRODUCTION



Introduction générale

La zone intertidale, également appelée estran, se définit classiquement comme la partie du littoral pouvant être découverte par la marée. Cette zone, qui correspond à l'interface entre le milieu terrestre et le milieu marin, se situe entre les limites extrêmes des plus hautes et des plus basses mers. Il s'agit donc d'un milieu très dynamique, rythmé quotidiennement par l'alternance des marées. A ce cycle de marée journalier, s'ajoute un cycle d'une période d'environ 14 jours, qui détermine l'alternance des marées de vive-eau (lorsque l'amplitude de marée est forte) et de morte-eau (lorsque l'amplitude de marée est faible). Les contraintes environnementales de cette zone sont donc particulièrement élevées et fluctuantes sur de courtes périodes.

Au sein de l'estran, la nature du substrat est variable et deux grands types de milieux se distinguent : les milieux meubles et les milieux rocheux. Les milieux rocheux abritent fréquemment une grande diversité de producteurs primaires et d'invertébrés benthiques, en particulier lorsque les conditions hydrodynamiques sont modérées (mode abrité). Cette diversité remarquable est liée à l'hétérogénéité importante de ces habitats, ainsi qu'à la complexité des structures biotiques et abiotiques qui les composent (McGuinness & Underwood 1986, Le Hir & Hily 2005, Schaal et al. 2011). La diversité de ces habitats suit néanmoins un gradient croissant depuis les hauts niveaux de marées jusqu'aux bas niveaux. Cette tendance résulte en partie de l'origine marine de la plupart des organismes vivant de façon permanente au sein de ces habitats, et qui requièrent donc une immersion régulière (Raffaelli & Hawkins 1999). La zone intertidale constitue donc un milieu présentant un gradient environnemental important sur de faibles distances. Le retrait de la marée expose en effet ces organismes à des périodes d'émersion plus ou moins prolongées, durant lesquelles l'intensité lumineuse et la température peuvent être très élevées et varier rapidement. Cette notion de gradient est un concept central de l'écologie en milieu intertidal (Fig. 0.1). Les différentes espèces y vivant ne tolèrent pas toutes de la même façon les changements des conditions environnementales liées à l'alternance des marées. Lorsque leurs limites de tolérance sont atteintes, il est possible d'observer une réduction significative de leur physiologie, voire leur mort (Bertness et al. 2014).

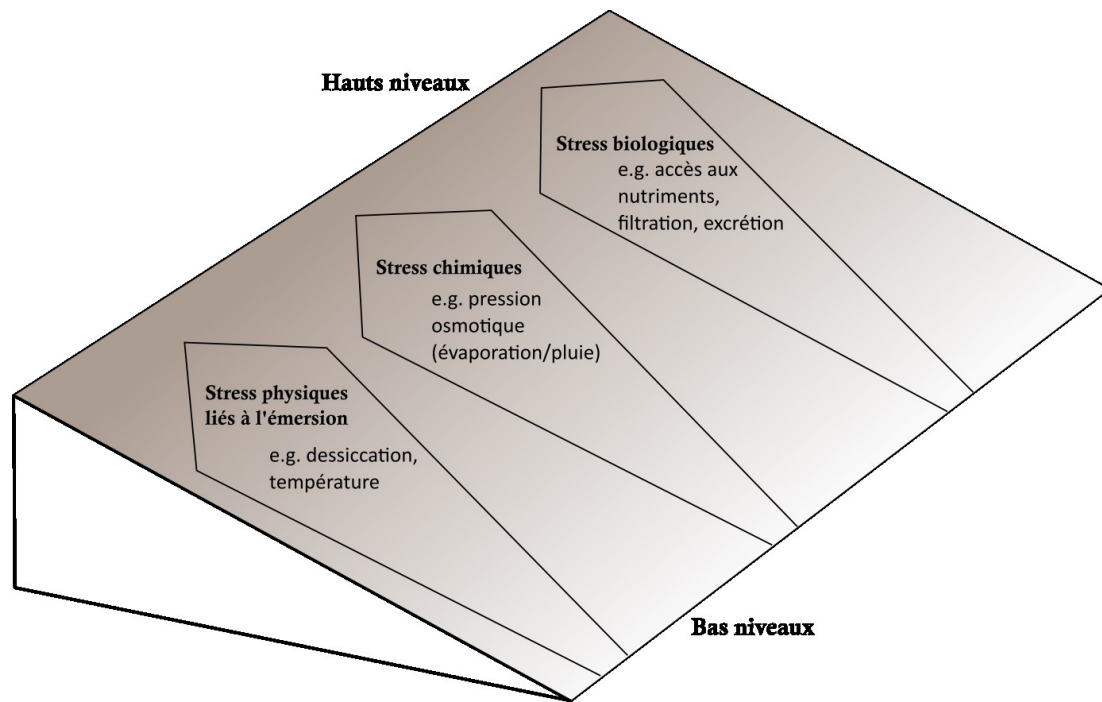


Fig. 0.1 Représentation conceptuelle des différents facteurs de stress liés au gradient d'émersion de la zone intertidale, depuis les bas niveaux jusqu'aux hauts niveaux de marée (simplifié d'après Raffaelli & Hawkins 1999).

Le long de ce gradient d'émersion, la distribution des espèces évolue rapidement, en particulier celle des espèces sessiles. Certaines espèces sessiles (par ex. balanes, algues brunes) forment d'ailleurs de véritables ceintures horizontales, nettement visibles, qui sont généralement caractéristiques d'un niveau marégraphique particulier. Ce patron de zonation verticale constitue l'une des plus évidentes particularités des estrans rocheux. Cela a été observé à de nombreux endroits du globe, et il est dorénavant admis que ces patrons de zonation présentent un caractère universel (Raffaelli & Hawkins 1999 et références incluses). Les raisons de ces zonations ont fait l'objet de nombreuses études au cours des dernières décennies (par ex. Underwood 1980, Hawkins & Hartnoll 1985, Somero 2002). De façon générale, il semble que les limites supérieures de distribution des espèces résultent principalement de leur tolérance face aux conditions environnementales (Foster 1971, Raffaelli & Hawkins 1999, Somero 2002), même si d'autres facteurs peuvent s'avérer significatifs, tels que l'herbivorie (Underwood 1980, Underwood & Jernakoff 1984) et la compétition inter-spécifique (Hawkins & Hartnoll 1985) par exemple. De nombreuses espèces ont ainsi développé un ensemble d'adaptations physiologiques (Tomanek & Helmuth 2002), morphologiques et/ou comportementales (Chelazzi & Vannini 1988), dont la mise en œuvre peut parfois se révéler complexe (Flores-Molina et al. 2014). Ces adaptations leur permettent par exemple de limiter les pertes en eau lors des périodes d'émersion, ou encore de

tolérer des variations de salinité importantes. Les limites inférieures de distribution seraient quant à elles principalement liées aux interactions biologiques, et en particulier à la compétition interspécifique (par ex. Schonbeck & Norton 1980, Lubchenco 1980, Raffaelli & Hawkins 1999). Malgré ces contraintes environnementales et biologiques fortes, l'espace libre constitue régulièrement le facteur le plus limitant pour l'installation et la croissance d'espèces sessiles, notamment dans les bas niveaux de mode abrité. Il n'est pas rare de voir, à marée basse, certaines algues recouvrir entièrement le substrat sur lequel elles sont établies. Ceci est particulièrement vrai pour les algues brunes évoquées précédemment, et formant des canopées (Fuciales, Phaeophyceae) (Fig. 0.2). Ces Fuciales sont considérées comme des espèces fondatrices (Bertness et al. 1999, Bruno & Bertness 2001). Par leur structure, elles modifient profondément les conditions environnementales, favorisant ainsi la survie et le développement de nombreuses espèces algales et animales (Stachowicz 2001, Dijkstra et al. 2012). Ces espèces fondatrices créent également de nouveaux habitats, offrant ainsi un substrat pour se développer à de nombreuses espèces associées (Dijkstra et al. 2012), ou bien encore une protection contre les prédateurs (Hawkins & Hartnoll 1985, Dijkstra et al. 2012). Ces espèces vont donc transformer les habitats naturels et favorisent la diversité et l'abondance de nombreuses espèces, de façon à former des communautés particulières.



Fig. 0.2 Communauté à *Fucus serratus* (Roscoff, France). ©Wilfried Thomas

Les communautés intertidales à canopée de macroalgues

Des systèmes productifs

Depuis plusieurs décennies, de nombreuses études ont été réalisées afin de quantifier la production primaire et la respiration des algues et de comprendre le rôle des facteurs environnementaux dans la régulation de ces processus. De par leur large distribution à l'échelle mondiale, leur relative facilité d'accès et leur rôle primordial pour les espèces associées évoqué précédemment, les algues brunes formant des canopées établies en milieu intertidal ont constitué, et constituent toujours, des modèles fortement utilisés lors d'études *in situ* ou en laboratoire. Ainsi, l'effet de la dessiccation (par ex. Quadir et al. 1979, Williams & Dethier 2005), de l'excès de lumière (par ex. Huppertz et al. 1990), ou bien encore de la disponibilité en nutriments sur la croissance et la photosynthèse (par ex. Raberg & Kautsky 2008, Nygård & Dring 2008) ont généralement été étudiés sur l'un de ces modèles. En se référant aux travaux de Mann (1973) ou plus récemment de Vadas et al. (2004), ces populations de Phaeophyceae peuvent être considérées parmi les systèmes les plus productifs par unité de surface à l'échelle mondiale, et pourraient jouer un rôle significatif dans les cycles biogéochimiques globaux (Smith 1981). L'ensemble de ces études apporte à la communauté scientifique des informations précieuses concernant la physiologie et le métabolisme des producteurs primaires dans leur environnement. Néanmoins, ces études ne tiennent pas toujours compte ni de l'ombrage de la canopée (Binzer & Sand-Jensen 2002b), ni de la forte diversité des espèces associées. Elles négligent ainsi l'ensemble des interactions se déroulant au sein des communautés. Ces interactions, bien trop souvent ignorées lors des mesures de production primaire en milieu marin, se révèlent pourtant particulièrement importantes. En effet, de nombreux exemples de complémentarité entre espèces ont été mis en évidence (par ex. Binzer & Middelboe 2005, Bracken & Stachowicz 2006, Gamfeldt et al. 2008, Tait & Schiel 2011a), au même titre que des interactions de compétition pour l'accès à certaines ressources fondamentales, telles que la lumière ou les nutriments (voir Wahl et al. 2011 et références incluses). L'échelle de la communauté semble donc être la mieux adaptée, et la plus réaliste, dans l'optique d'évaluer de façon précise le fonctionnement de tels milieux intertidaux (Migné et al. 2015a).

Toutefois, réaliser des mesures de métabolisme *in situ* et à l'échelle de la communauté en milieu intertidal représente un défi de taille, qui plus est lorsque l'objectif est de réaliser ces mesures à la

fois lors de périodes d'émersion et d'immersion. Des chambres d'incubation benthiques faciles à transporter et à mettre en œuvre en milieu intertidal pendant l'émersion ont été développées au cours des dernières années (Golléty et al. 2008, Tait & Schiel 2010). Leur utilisation a permis de préciser la part de la canopée dans le métabolisme global de la communauté (Golléty et al. 2008) et l'effet de paramètres environnementaux sur les taux de production primaire et de respiration (Golléty et al. 2008, Tait & Schiel 2013). De telles incubations en chambres benthiques ont également été réalisées afin d'évaluer les conséquences d'introduction d'espèces fondatrices sur le métabolisme des communautés intertidales (Tait et al. 2015), ou les effets, à plus ou moins long termes, de la perte ponctuelle des canopées suite à des perturbations ou des récoltes (Tait & Schiel 2011b, Stagnol et al. 2013). Il reste néanmoins de nombreux aspects concernant le métabolisme de ces communautés à explorer. En particulier, le rôle du gradient d'émersion est encore sujet à de nombreuses interrogations quant au fonctionnement des communautés, alors qu'il est clairement impliqué dans leur structure. En outre, la régulation du métabolisme lors de l'alternance de périodes d'émersion et d'immersion, qui implique des changements nets et rapides des conditions environnementales, doit encore être étudiée à cette échelle. Enfin, il n'existe pas à ma connaissance, de bilan annuel de production primaire précis pour les communautés intertidales d'algues brunes et les estimations basées sur des mesures régulières de biomasse ou de métabolisme d'individus extrapolées à la population (Cousens 1984, Ferreira & Ramos 1989, Vadas et al. 2004) demandent à être précisées.

Des systèmes complexes

Le devenir de la production primaire au sein de ces communautés se révèle essentiel pour l'appréciation du fonctionnement et de la dynamique de ces systèmes. En effet, les producteurs primaires occupent une position basale au sein des réseaux trophiques et constituent une ressource pour de nombreux consommateurs. L'établissement des relations d'ordre trophique représente un point central en écologie. Afin d'établir ces relations, des expériences de préférence alimentaire ont été réalisées, en particulier pour les herbivores (par ex. Lubchenco 1978, Van Alstyne et al. 1999), et complétées par l'analyse de contenus stomacaux (par ex. Sacchi et al. 1981). Même si la mise en œuvre et l'interprétation de ces expériences repose sur des connaissances solides de la diversité biologique et fonctionnelle des systèmes considérés (Riera 2006), ainsi que sur l'écologie et l'anatomie des espèces étudiées (Hawkins et al. 1989), leurs

résultats ne reflètent que partiellement le régime alimentaire des consommateurs et ne permettent pas une appréciation précise de l'assimilation des proies par les consommateurs. Ceci est d'autant plus vrai qu'il est commun d'observer chez les producteurs primaires, la mise en place temporaire de mécanismes de défense contre les herbivores (Molis et al. 2006), ou encore des variations saisonnières de la teneur en carbone et en azote des tissus (Carlson 1991, Brenchley et al. 1998, Lehvo et al. 2001), rendant complexes et fluctuantes les relations de préférence alimentaire et l'assimilation de leurs tissus par les consommateurs.

L'avènement des techniques de traçage trophique au cours des dernières décennies a apporté des outils complémentaires précieux dans l'étude des voies de transfert de matière et des relations d'ordre trophique. Parmi ces techniques, celles reposant sur les isotopes stables (Peterson & Fry 1987, Post 2002, Fry 2006) ont permis de nets progrès concernant la compréhension du fonctionnement trophiques des communautés intertidales de Phaeophyceae, aussi bien en milieu naturel (par ex. Riera et al. 2009, Steinarsdóttir et al. 2009, Golléty et al. 2010), qu'en milieu anthropisé (par ex. Riera et al. 2004, Schaal et al. 2010). Au-delà de leur relative complexité, il reste de nombreuses incertitudes sur les relations trophiques au sein de ces communautés. En particulier, le rôle de la saisonnalité a été relativement peu étudié à l'échelle de la communauté (Golléty et al. 2010), alors qu'elle constitue un élément clé des traits d'histoire de vie de nombreuses espèces en région tempérée. Du fait de l'opportunisme de certains consommateurs de ces communautés (Schaal et al. 2010), la structure trophique est susceptible de fluctuer de façon significative à l'échelle saisonnière. Par ailleurs, le niveau marégraphique auquel une communauté est établie peut avoir des conséquences significatives sur son architecture trophique, en raison des contraintes physiques liées à l'émersion et des différences d'abondance et de diversité liées au gradient d'émersion (Raffaelli & Hawkins 1999). Enfin, au-delà de leur fonction d'habitat, le rôle des algues brunes formant des canopées comme source de nourriture pour la communauté associée et les systèmes adjacents reste encore à évaluer avec précision.

Des systèmes dynamiques

En milieu intertidal, les communautés sont régulièrement soumises à des perturbations de plus ou moins forte intensité. Par définition, les perturbations affectent le fonctionnement des communautés (Boudouresque et al. 2009). Dans certains cas, elles conduisent à la création d'espace libre au niveau du substrat rocheux (Benedetti-Cecchi 2000). Dès lors, la colonisation et

les processus de succession peuvent être entamés au sein de ces espaces. En général, un petit nombre d'espèces opportunistes et à courte durée de vie forment une communauté faiblement diversifiée en traits fonctionnels en début de colonisation. Ces espèces sont remplacées progressivement par de nombreuses espèces plus exigeantes et à durée de vie plus longue, qui forment une communauté possédant une grande variété de traits fonctionnels en fin de colonisation (Noël et al. 2009). En milieu intertidal abrité, cette dernière est souvent caractérisée par la dominance d'une canopée, à laquelle sont associées de nombreux épibiontes ainsi qu'une sous-canopée comprenant des espèces encroûtantes et/ou gazonnantes (Noël et al. 2009). Historiquement, la succession était définie comme une séquence linéaire depuis les premiers stades de succession jusqu'à un stade ultime, le climax (Clements 1916, 1928). Cette vision ancienne a été revisitée, et il s'avère que ce processus démontre une très forte variabilité spatiale et temporelle, et dépend entre autres du moment où a lieu la perturbation et des conditions environnementales initiales (par ex. Sousa 1984, Farrell 1991, Jenkins et al. 2005, Jenkins & Martins 2009). En milieu intertidal, le gradient d'émersion pourrait donc constituer un facteur prépondérant pour la mise en place des communautés. Suite aux travaux fondamentaux de Connell & Slatyer (1977) qui ont décrit trois modèles alternatifs de succession basés sur la facilitation, l'inhibition ou la tolérance, les mécanismes de succession ont fait l'objet de nombreuses études. Ces études se sont notamment attachées à décrire les successions d'un point de vue taxonomique (par ex. Murray & Littler 1978) et à préciser les interactions et le rôle d'espèces clés (par ex. Hawkins 1981, Lubchenco 1983, Viejo et al. 2008). Ces processus de succession, en entraînant des changements de diversité spécifique et fonctionnelle, doivent influencer le fonctionnement des communautés (Noël et al. 2009). Une communauté comprenant de multiples espèces remplissant de nombreux traits fonctionnels est susceptible de présenter une production primaire par unité de surface plus importante qu'une communauté composée d'un petit nombre d'espèces aux traits fonctionnels identiques. L'évolution de la production primaire au cours de la succession a été peu étudiée en milieu marin (Martins et al. 2007), alors que ce processus est fondamental pour le fonctionnement des écosystèmes. En milieu terrestre, de telles études se sont avérées précieuses pour appréhender le fonctionnement des communautés forestières, indiquant par exemple que la productivité est maximale lors de stades de succession intermédiaires (par ex. Goulden et al. 2011).

Des systèmes exploités

L'utilisation des macroalgues par les populations côtière est un phénomène ancien (depuis le XVII^{ème} siècle en Europe, Jacob et al. 2012). Ces algues, récoltées en épave ou non, étaient utilisées à des fins variées, comprenant notamment l'amendement des sols ou encore la fabrication du verre. A l'heure actuelle, les algues de rives sont toujours récoltées et leur exploitation occupe une place non négligeable dans l'économie locale de nombreux pays européens. En particulier, les *Fucus* sont destinés principalement aux industries agroalimentaires, agricoles et cosmétiques. Sur les côtes bretonnes, la récolte de *F. serratus* est estimée de quelques centaines à quelques milliers de tonnes par an (Mesnildrey et al. 2012). Un suivi de la diversité et du métabolisme de la communauté après à une récolte expérimentale de *F. serratus* ne montre qu'un effet temporaire de la récolte qui se dissipe après une année environ (Stagnol et al. 2013). Néanmoins, cette étude doit être complétée en tenant compte notamment de différentes périodes de récolte de façon à intégrer les traits d'histoire de vie des espèces intertidales (par ex. le cycle de reproduction, qui dépend souvent de la saison).

Distribution des communautés de *F. vesiculosus* et de *F. serratus*

Le genre *Fucus* est représenté par plusieurs espèces répertoriées à de nombreux endroits du globe et formant des communautés le long des côtes de l'Océan Pacifique nord, de l'Océan Atlantique nord, ou encore dans l'Océan Arctique et en Mer Baltique (pour plus de détails sur la distribution mondiale des *Fucus*, voir Lüning 1990, Wahl et al. 2011, Neiva et al. 2016). En se focalisant sur l'Océan Atlantique nord, le genre *Fucus* est représenté par 8 espèces. Toutefois, quelques incertitudes demeurent quant à cette phylogénie (Neiva et al. 2016) et des processus d'hybridation ont été mis en évidence (Billard et al. 2005). Au sein de cette région, les communautés de *F. vesiculosus* et *F. serratus* sont distribuées sur une grande partie des côtes européennes (Fig. 0.3) et la Bretagne en particulier a constitué un refuge glaciaire pour ces deux espèces lors du dernier maximum glaciaire (0.026 – 0.019 Ma) (Coyer et al. 2003). Ces deux communautés sont également présentes sur les côtes ouest de l'Atlantique (Fig. 0.3). Néanmoins, *F. serratus* ne constituerait pas une espèce native sur ces côtes, ainsi qu'en Islande, et sa présence serait liée à d'anciens évènements d'introduction (Coyer et al. 2006b, Brawley et al. 2009).

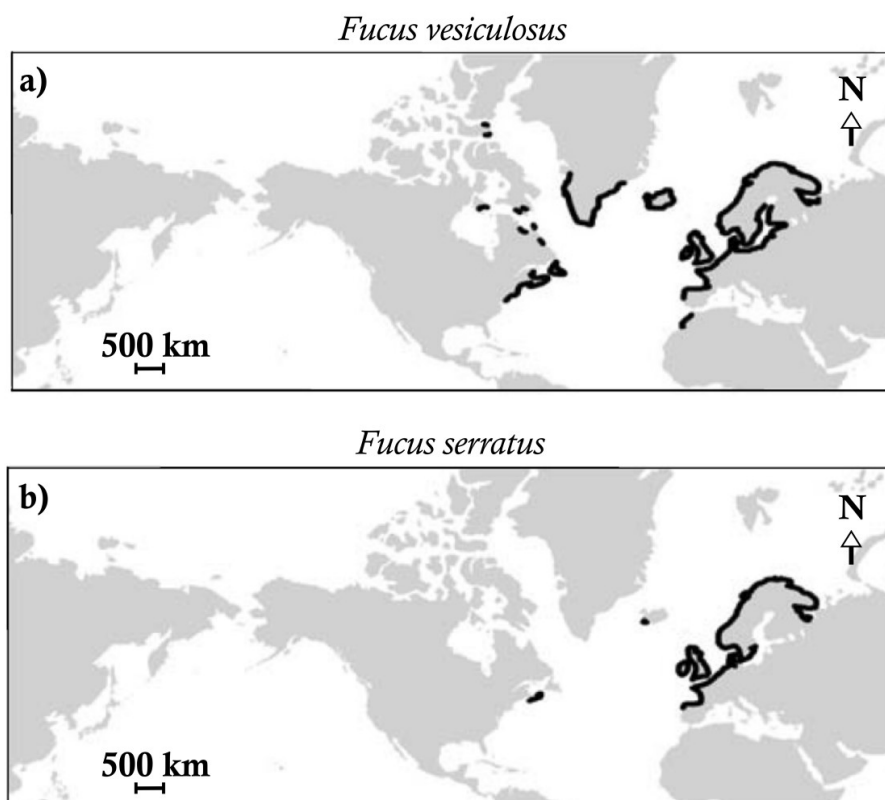


Fig. 0.3 Distribution mondiale de a) *Fucus vesiculosus* et b) *Fucus serratus* (d'après Coyer et al. 2006a).

La distribution des canopées d'algues brunes change en lien avec l'augmentation récente des températures (Nicastro et al. 2013, Duarte et al. 2013). Ainsi, Jueterbock et al. (2013) ont modélisé, sur la base de différents scénarios d'émission de gaz à effet de serre, l'évolution de la distribution de *F. vesiculosus* et *F. serratus* d'ici la fin du siècle. Cette modélisation prévoit essentiellement une extension de l'aire de distribution vers le nord pour ces deux espèces, et un déclin de *F. serratus* au sud de l'Europe (Fig. 0.4). Il semble donc fondamental d'améliorer nos connaissances sur le fonctionnement, la diversité et la dynamique de ces communautés dans leur milieu naturel. Enfin, il reste nécessaire d'évaluer l'effet des changements environnementaux sur les espèces clés de ces communautés, et sur les communautés dans leur ensemble.

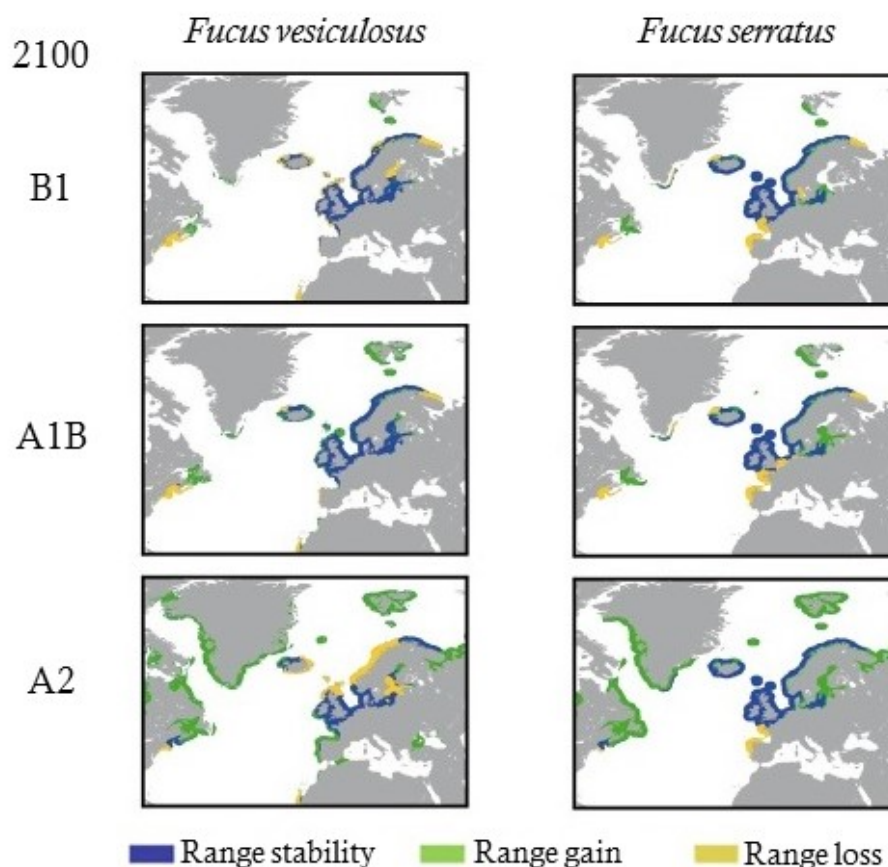


Fig. 0.4 Prédications de l'évolution des distributions de *F. vesiculosus* et de *F. serratus* d'ici à la fin du siècle, à partir de différents scénarios d'émissions de gaz à effet de serre (B1, A1B et A2, GIEC) (d'après Jueterbock et al. 2013).

Sur les côtes européennes, *Fucus vesiculosus* (Linnaeus) et *Fucus serratus* (Linnaeus) sont particulièrement abondants et forment de larges ceintures intertidales caractéristiques des étages médiolittoral moyen et médiolittoral inférieur. Ces deux espèces de *Fucus* peuvent atteindre une taille variant de plusieurs dizaines de centimètres à un mètre de long, pour une durée de vie généralement comprise entre 2 et 5 ans (Knight & Parke 1950). Leur biomasse peut atteindre plusieurs kilogrammes de poids frais par mètre carré (Dijkstra et al. 2012). *F. vesiculosus* se caractérise par la présence de vésicules aérifères au niveau du thalle (Fig. 0.5), qui peuvent toutefois être absentes dans des sites où l'hydrodynamisme est important. *F. serratus* se caractérise plutôt par un thalle plat, sans vésicule aérifère, et dont le bord est denté (Fig. 0.5).

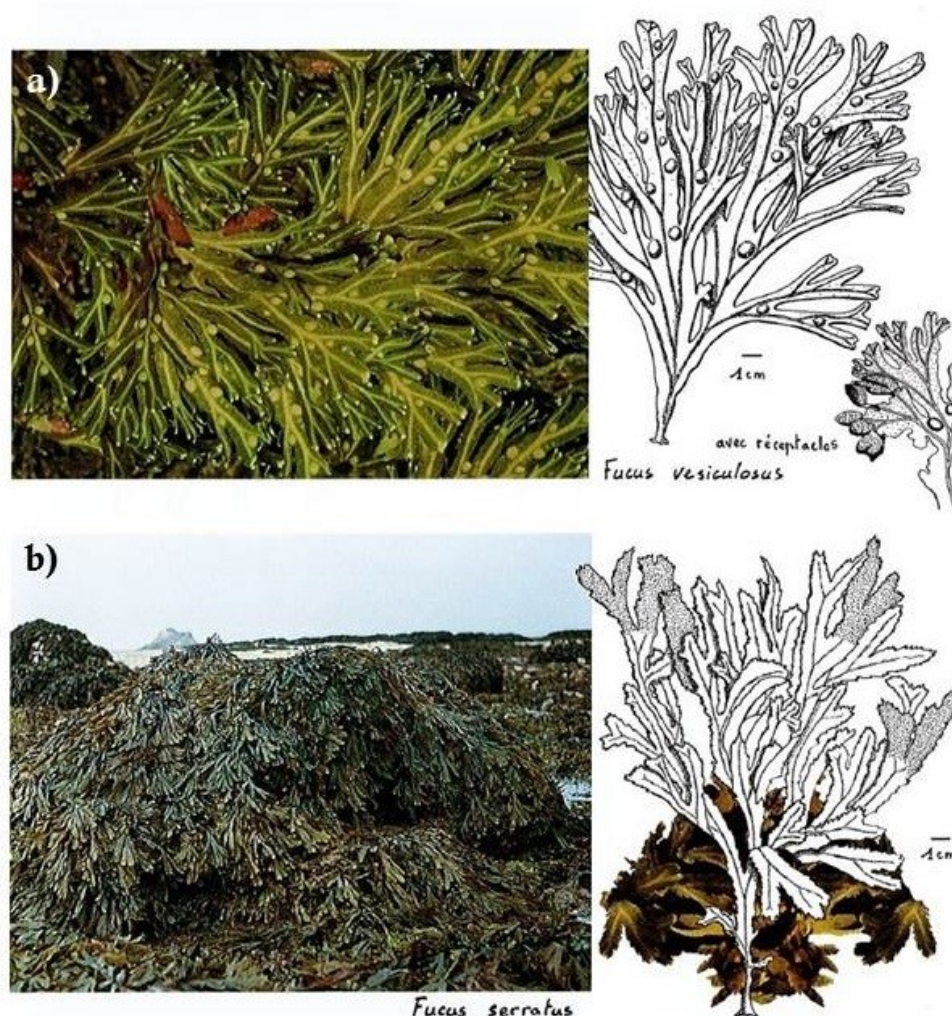


Fig. 0.5 Illustrations des caractéristiques morphologiques de a) *Fucus vesiculosus* et de b) *Fucus serratus*. © Susan de Goër et Marie-Claude Noailles

Problématiques de la thèse

Ce travail de thèse porte sur les deux communautés intertidales de *Fucus vesiculosus* et de *F. serratus*, dans le but d'approfondir les connaissances concernant leur structure et leur dynamique. Des mesures de métabolisme, des expérimentations et des suivis de leur composition spécifique ont été réalisés en milieu naturel à différentes périodes de l'année, et complétées par l'acquisition à haute fréquence de données environnementales du site d'étude. Cet ensemble d'éléments a été repris dans un modèle afin d'estimer précisément la production primaire annuelle de ces deux communautés. Les résultats obtenus sont discutés dans un contexte de zonation intertidale.

Ce manuscrit s'articule en trois parties.

La première partie vise à caractériser le fonctionnement et la dynamique saisonnière de ces communautés via le métabolisme (production primaire et respiration) lors des périodes d'émersion (chapitre 1) et le réseau trophique (chapitre 2).

La deuxième partie s'attache à décrire des processus de régulation du fonctionnement de ces communautés lors de l'alternance entre les périodes d'émersion et d'immersion (chapitre 3) et au cours de la succession suite à la colonisation de substrat vierge (chapitre 4).

La troisième partie présente le modèle conduisant à un bilan annuel de production primaire pour chacune de ces deux communautés (chapitre 5).

PARTIE I – FONCTIONNEMENT ET DYNAMIQUE

DES COMMUNAUTES A CANOPEE DE *FUCUS*



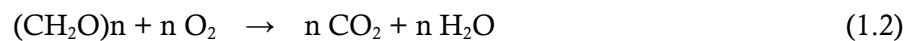
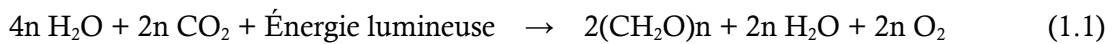
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Chapitre 1

Variations saisonnières du métabolisme à l'émersion et part de la canopée dans les flux de CO₂

Contexte général et résumé

La photosynthèse correspond à la conversion de l'énergie lumineuse en énergie chimique sous forme de composés organiques carbonés, à partir de dioxyde de carbone et d'eau (1.1). Elle permet donc la production de matière primaire par les organismes autotrophes. Seule une petite fraction des radiations électromagnétiques émises par le soleil ne peut être utilisée pour la photosynthèse (Fig. 1.1). Ces radiations, dites actives pour la photosynthèse (PAR) ont des longueurs d'ondes comprises entre 400 et 700 nm (= lumière visible). A l'inverse, la respiration des organismes (autotrophes et hétérotrophes) correspond à l'ensemble des processus métaboliques qui conduit à l'oxydation de composés organiques carbonés en CO_2 (1.2). Pour quantifier ces processus, il est donc possible de mesurer les flux d' O_2 ou de CO_2 .



Entre le lever et le coucher du soleil, la production primaire et la respiration (R) se déroulent simultanément, et les flux observés correspondent au bilan de ces deux processus. On distingue ainsi la production primaire brute (PPB) et la production primaire nette (PPN). La PPB correspond à la quantité totale de production primaire, alors que la PPN représente la PPB diminuée de la respiration (Fig. 1.2).

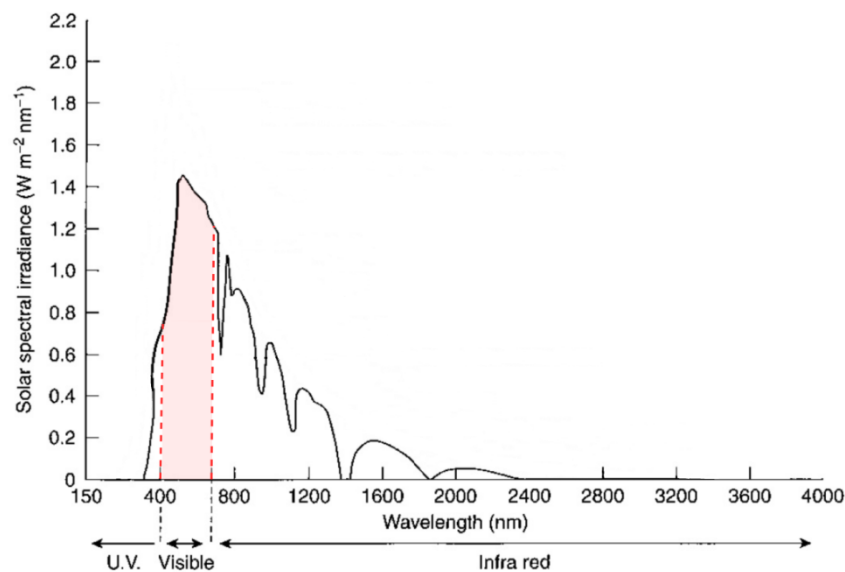


Fig. 1.1 Radiations solaires atteignant le niveau de la mer en fonction de leur longueur d'onde. Les radiations du visible (400 – 700 nm) sont présentées en rouge (modifié d'après Falkowski & Raven 2007).

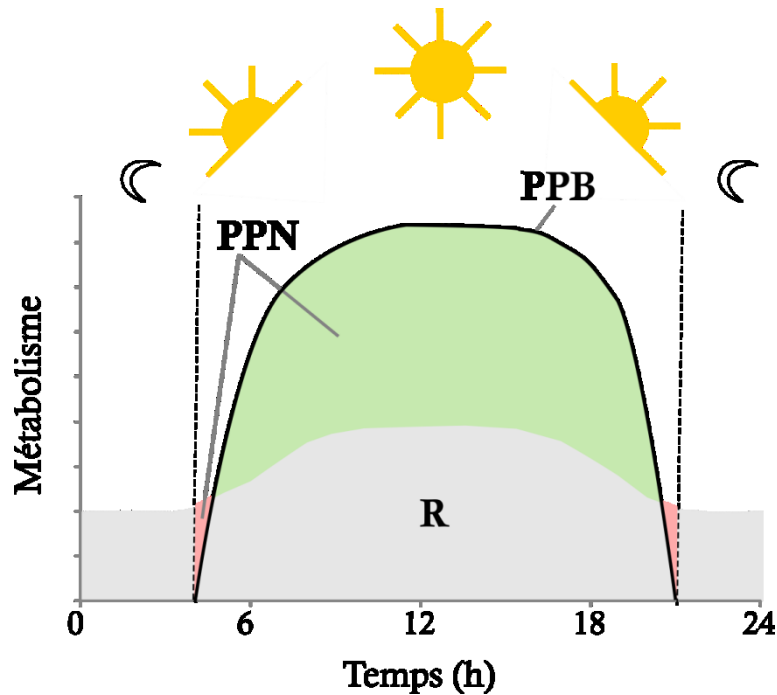


Fig. 1.2 Représentation schématisée de l'évolution de la respiration (R, en gris), de la production brute (PPB, en noir) et de la production primaire nette (PPN, en vert si $PPB > R$ et en rouge si $PPB < R$) au cours d'une journée théorique (modifié d'après Falkowski & Raven 2007).

Compte tenu de l'importance de la production primaire pour le fonctionnement et la dynamique des communautés intertidales à canopée de macroalgues, il semble fondamental de la quantifier et d'évaluer l'influence de différents facteurs environnementaux. Les études qui ont abordé cette problématique à l'échelle de la communauté sont rares (par ex. Golléty et al. 2008, Tait & Schiel 2011a) et demandent à être complétées. En région tempérée, l'alternance des saisons entraîne d'importantes fluctuations d'intensité lumineuse et de température. Ces fluctuations sont susceptibles d'influencer le métabolisme des communautés, puisque ces deux paramètres sont fondamentaux dans la régulation de la production primaire et de la respiration (Davison 1991, Kemp & Testa 2011, Staehr et al. 2012). En milieu intertidal, ces deux paramètres varient également de façon importante à l'échelle des cycles de marées. A cette échelle, s'ajoute l'alternance de la disponibilité en nutriments, puisque les organismes autotrophes intertidaux n'ont accès aux nutriments que lors des périodes d'immersion et doivent compter sur leurs réserves internes à l'émersion (voir Davison & Pearson 1996 et références incluses). L'aptitude des communautés à canopée de macroalgues à maintenir une production primaire nette positive lors des périodes d'émersion reste donc hypothétique.

Pour vérifier le maintien d'une PPN positive pendant l'émersion, il est indispensable de mesurer le métabolisme à l'échelle de la communauté. Golléty et al. (2008) ont ainsi adapté un système

permettant de mesurer les changements de concentration en CO_2 en milieu rocheux pendant l'émersion. Ce système est composé d'une chambre benthique reliée en circuit fermé à un analyseur de CO_2 à infrarouge (IRGA, Li-Cor Li820). Cette chambre benthique, d'une surface au sol de $0,09 \text{ m}^2$ et d'un volume de $17,7 \text{ L}$ permet d'isoler une partie de la communauté considérée et ainsi d'évaluer son métabolisme au cours de brèves incubations (quelques minutes) (Fig. 1.3). Les incubations sont réalisées soit à la lumière ambiante, pour déterminer la production primaire nette, soit à l'obscurité (après avoir couvert le système expérimental par une bâche opaque), pour déterminer la respiration.

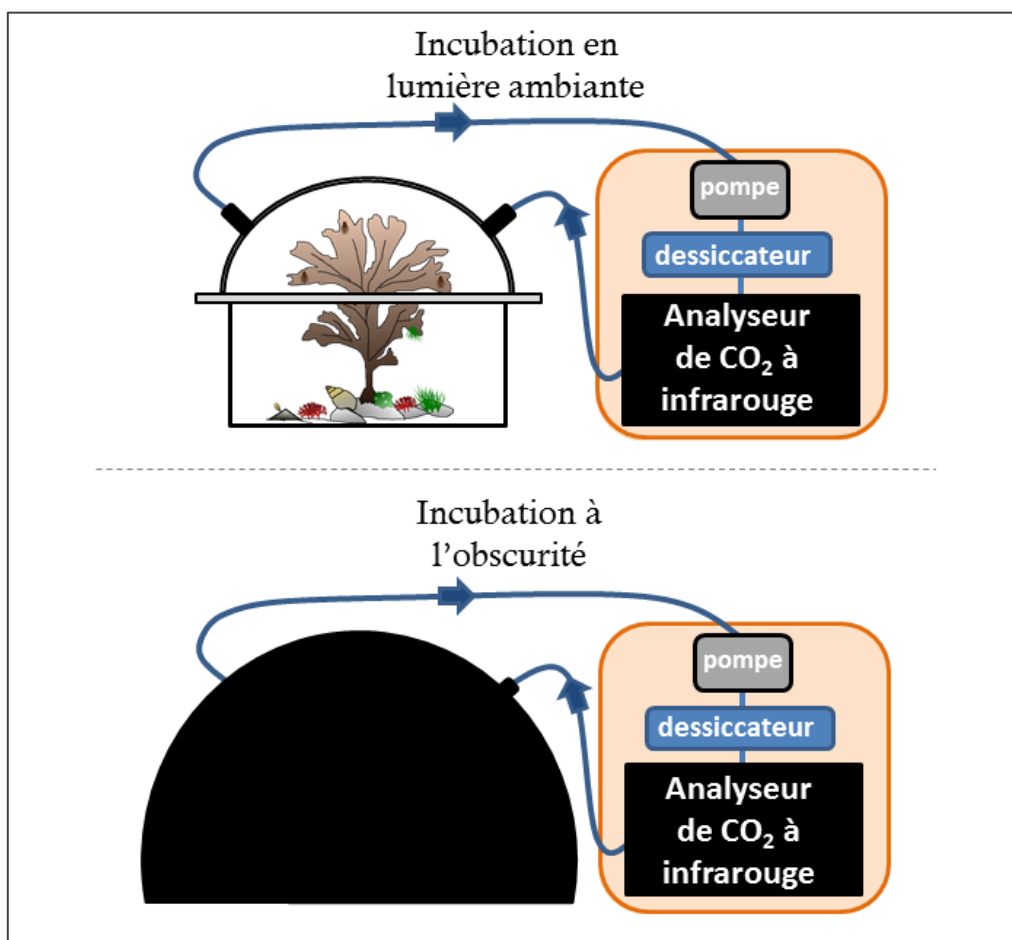


Fig. 1.3 Incubations *in situ*, pendant l'émersion, d'une communauté à canopée de macroalgue, comprenant une incubation en lumière ambiante pour évaluer la production primaire nette (en haut) et une incubation à l'obscurité pour évaluer la respiration (en bas).

Grâce à ce système, nous avons mesuré le métabolisme des communautés de *F. vesiculosus* et de *F. serratus* à 14 reprises d'octobre 2012 à décembre 2013, à raison d'une fois par mois (excepté en décembre 2012, où aucune mesure n'a pu être réalisée), de façon à évaluer l'influence des saisons

sur la production primaire et la respiration pendant l'émersion. Ces mesures ponctuelles ont été réalisées en début de périodes d'émersion dans l'optique d'éviter toute dessiccation susceptible d'affecter le métabolisme. Des fluctuations saisonnières marquées ont été mises en évidence, avec une production primaire et une respiration maximales en été et minimales en hiver. Les taux de métabolisme sont restés élevés toute l'année (PPB variant de 400 à 1 000 mgC m⁻² h⁻¹ ; R variant de 100 à 500 mgC m⁻² h⁻¹) et la production primaire s'est révélée supérieure à la respiration à chaque mesure. De façon intéressante, le rapport entre la R et la PPB a également montré des variations saisonnières significatives pour les deux communautés, étant lui aussi maximal en été et minimal en hiver. En parallèle, la teneur en carbone et en azote des tissus des deux espèces de *Fucus* a été analysée chaque mois. Ces contenus ont varié de façon saisonnière, mettant en évidence les tendances générales d'accumulation et d'utilisation des réserves énergétiques et des nutriments. A ce titre, il est vraisemblable que le métabolisme des canopées, et des communautés en général, a été limité par les nutriments en été.

Dans cette étude nous avons également cherché à évaluer la part de la canopée dans les flux de CO₂ de la communauté, à chaque période de l'année, en réalisant des mesures complémentaires de métabolisme (production primaire et respiration) après retrait de la canopée. Ces mesures ont permis de confirmer l'influence considérable de la canopée, qui a compté pour 77 à 97 % des flux globaux de CO₂. Cette influence s'est avérée relativement constante tout au long de l'année, et aucune variation saisonnière n'a pu être mise en évidence.

Enfin, la communauté de *F. vesiculosus*, la plus haute sur l'estran, a montré des taux de métabolisme plus faibles que la communauté de *F. serratus*.

Article n°1

Metabolic activity of intertidal *Fucus* spp. communities: evidence for high aerial carbon fluxes displaying seasonal variability

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Abstract: Semi-sheltered rocky shores are characterized by a typical succession of Phaeophyceae-dominated communities where canopy-forming algae are assumed to be very productive. However, metabolic activity of whole communities, integrating the main interactions that occur in these assemblages, still needs to be investigated more deeply, especially when communities are emerged. Thus, the metabolism of the mid-intertidal *Fucus vesiculosus* and *Fucus serratus* communities was surveyed once a month throughout a year in the Bay of Morlaix (France). *In situ* measurements of primary production and respiration were carried out at the onset of emersion periods, using benthic chambers coupled to CO₂-infrared gas analysers. Benthic measurements were performed successively on whole communities and after canopy removal, to assess the contribution of the canopies to the communities' carbon fluxes. Concurrently, nitrogen and organic carbon contents of the two *Fucus* species were evaluated monthly. Both communities exhibited high metabolic activity year-round (community gross primary production: 400-1 000 mgC m⁻² h⁻¹; community respiration: 100-500 mgC m⁻² h⁻¹), with canopies accounting for 77-97% of the global CO₂ fluxes. However, this relative canopies' contribution to global CO₂ fluxes did not follow seasonal fluctuations, whereas both metabolic activities and nitrogen and carbon contents did, confirming the importance of light and temperature in the regulation of metabolic processes. A nutrient limitation was also suggested to occur in summer, when seawater was nutrient-depleted. Finally, the *Fucus vesiculosus* community, located upper on the shore, exhibited lower photosynthetic activity than the *Fucus serratus* community, being consistent with the vertical zonation rules of intertidal habitats.

Keywords: Carbon fluxes; Community gross primary production; Community respiration; Emersion; *Fucus serratus*; *Fucus vesiculosus*; *In situ* monitoring; Phaeophyceae

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Introduction

Communities dominated by canopy-forming Phaeophyceae are particularly widespread along intertidal rocky shores of temperate regions. Such communities are usually considered to be very productive, although their metabolism has rarely been studied at the community scale (Golléty et al. 2008, Tait & Schiel 2010). Yet, these communities are constituted of numerous species (Rindi & Guiry 2004, Kersen et al. 2011, Migné et al. 2015b), giving rise to many interactions. For instance, numerous trophic relationships occur in these systems (Golléty et al. 2010, Duarte et al. 2015), as well as competition for light and space (Underwood 2000). Such interactions could lead to large variability in the metabolism of primary producers. They must for instance synthesize defence molecules against grazers, epibionts and/or biofilms (Brock et al. 2007, Wahl 2009) or are subjected to a reduced light due to epibionts, leading to a reduction of photosynthetic activity (Sand-Jensen 1977, Oswald et al. 1984). On the contrary, Tait and Schiel (2011a) demonstrated that the structural differences of primary producers, but also their location in the community assemblage could lead to an enhancement of the global primary production. Therefore, all these interactions play a fundamental role and need to be accounted for when investigating community metabolism, as highlighted by Migné et al. (2015a).

These communities also experiment large changes in abiotic conditions at various temporal scales. The most drastic change occurs at the tidal scale, due to the alternation of immersion and emersion periods. Although usually thought as stressful for intertidal organisms, emersion periods can, however, be a very useful time for algae to do photosynthesis (Golléty et al. 2008), with some of them exhibiting the major part of their production when emersed (Quadir et al. 1979). Thus, investigations of intertidal communities' metabolic activity should not neglect the low tide periods.

The study of Golléty et al. (2008) is to our knowledge the first one dealing with *in situ* metabolic activity of Phaeophycean dominated communities under emersed conditions. This pioneer study showed that primary production and respiration rates of the sheltered mid-intertidal *Ascophyllum nodosum* community followed a seasonal trend related to changes in light availability and temperature, and that the canopy and its epibionts were responsible for the huge majority of community' carbon fluxes.

Following the principles of the intertidal zonation of canopy-forming species and the general relationship between diversity of marine species and tidal level (Raffaelli & Hawkins 1999, Molina-Montenegro et al. 2005), it could be expected that the tidal level at which the communities are established is of paramount importance in controlling the magnitude and the seasonal variability of their metabolism, as well as the contribution (and its seasonal variability) of the canopy to the total metabolism. Furthermore, the hydrodynamism to which the communities are exposed and specific environmental conditions (e.g. nutrient depletion), could as well have an influence on these parameters. In the current context of harvesting of Phaeophyceae along European West coasts (Jacob et al. 2012), it appears crucial to better understand the year-round dynamic of the communities they form, but also the way these canopy-forming species contribute to this dynamic.

In addition, some essential information on algae-environment interactions could be obtained considering the elemental composition of canopy-forming Phaeophyceae, which was shown to reflect both assimilation and use of nutrients and organic compounds by the algae (Chapman and Craigie 1977; 1978). This appears to be particularly attractive in intertidal systems since algae have to rely on their own nitrogen reserves when emerged (Pedersen & Borum 1997).

Mid- and low-mid intertidal communities dominated respectively by canopy-forming algae *Fucus vesiculosus* Linnaeus and *Fucus serratus* Linnaeus are particularly widespread along European coasts (Jueterbock et al. 2013). This study focused on the metabolic activity of these two adjacent communities, using *in situ* carbon fluxes measurements performed at the onset of emersion periods, under saturating irradiance. We hypothesized that (1) while following temporal variations, their gross primary production and respiration remained substantial all over the year, that (2) canopies consistently acted as the major contributor of total carbon fluxes in the communities, with this contribution following seasonal pattern, and that (3) the nitrogen and organic carbon contents of the canopies also varied with seasons and environmental conditions. Finally, we also hypothesized that (4) the lower shore community exhibited a higher metabolic competitiveness than the upper shore community, in accordance with the principles of vertical zonation of canopy species.

Materials & methods

Study site

This study was performed on *F. vesiculosus* and *F. serratus* communities established on an intertidal semi-sheltered boulder reef located in front of the Station Biologique de Roscoff (Brittany, France) (48°43.743'N, 3°59.407'W), in the southwest part of the English Channel. On this reef, these communities form dense and multi-layer assemblages which frequently cover 100% of the substratum, making it an ideal place to study their metabolism. This shore is subjected to semi-diurnal tidal cycle with maximal range of about 9 m. It presents a typical vertical distribution of communities dominated by canopy-forming Phaeophyceae, where *F. vesiculosus* community is characteristic of the mid-intertidal (3.0 to 4.0 m above chart datum, corresponding to an annual emerged time of 20-35%) while *F. serratus* community is characteristic of the low mid-intertidal (2.5 to 3.0 m above chart datum, corresponding to an annual emerged time of 15-20%).

Environmental conditions

This site, located in the temperate part of Northern hemisphere, displays a seasonal day:night cycle varying from 9:15 in late December to 16:8 in late June. It is also subjected to seasonal variations of irradiance and temperature. The weather station of Brest-Guipavas (located at approx. 40 km of our study site) provided monthly maximal instantaneous irradiance (Max_{irr} , in W m^{-2}) and monthly mean air temperature (T_{air} , in °C) datasets (October 2012 – December 2013). The SOMLIT network (sampling site: Estacade, Roscoff, located at approx. 600 m of our study site) provided monthly mean seawater temperature (T_{seawater} , in °C) and monthly means seawater nutrient concentrations (NH_4^+ , NO_3^{2-} , NO_2^- and PO_4^{3-} , in $\mu\text{mol L}^{-1}$) datasets (October 2012 – December 2013).

Benthic metabolism measurements and sampling

Measurements of benthic metabolism of *F. vesiculosus* and *F. serratus* communities were performed once a month from October 2012 to December 2013, with the exception of December 2012. They were always done at the onset of emersion of a spring tide (around midday) to avoid a desiccation effect on metabolic rates. At each occasion, three intra-site replicates (2 to 5 m distance between each) of a 0.09 m² rock area were haphazardly selected for both communities (only two replicates in November 2013 for *F. serratus* community). A replicate included one to

several *Fucus* thalli (> 25 cm long) with the associated community, which was essentially made-up of *Fucus* epibionts (i.e. algae and sessile invertebrates directly attached to the *Fucus*, (Wahl 2009) and biofilms, as well as sub-canopy and encrusting macroalgae, rocky and sedimentary microphytobenthos and invertebrates, including the mobile ones on *Fucus* fronds. Each area was then enclosed in a custom-built incubation chamber (17.7 L) made of clear Plexiglas, connected to an infrared CO₂ gas analyzer (LiCor Li-820) in closed air circuit. Air motion of 1 L min⁻¹ was ensured by a pump in this closed circuit. CO₂ fluxes measurements were performed at the rock-air interface, as described by Migné et al. (2002), at ambient light and in darkness by covering up the chambers. These measurements allowed estimating the total community net primary production (NPP_t) and the total community respiration (CR_t), respectively, assuming that CO₂ fluxes measured in darkness after abrupt transition from ambient light reflected the respiration activity of the communities (del Giorgio & Williams 2005). Incubations were sufficiently short (i.e. 5 - 10 min) to avoid feedback of temperature and gas concentration changes on metabolic rates. Total community gross primary production (GPP_t) was calculated as $GPP_t = NPP_t + CR_t$. CO₂ fluxes were calculated from recorded data using the slope of CO₂ concentration ($\mu\text{mol}_{\text{CO}_2} \text{mol}_{\text{air}}^{-1}$) against time (min). Therefore, GPP_t and CR_t were expressed in carbon unit (mgC m² h⁻¹) assuming a molar volume of 22.4 L mol⁻¹ at standard temperature and pressure and a molar mass of 12 gC mol_{CO₂}⁻¹. Finally, the community metabolic balance was calculated each month for both communities as the ratio of CR_t to GPP_t.

After performing this first set of light and dark incubations, *Fucus* thallus and the associated epibionts and biofilms were removed from the incubation chambers, while mobile fauna being on the fronds was left inside of the chambers with the remaining organisms (including algae and invertebrates). A second set of light and dark incubations was performed on this residual community, in order to estimate residual community net primary production (NPP_r) and residual community respiration (CR_r). Residual community gross primary production (GPP_r) was calculated following the formula used previously ($GPP_r = NPP_r + CR_r$). These measurements allowed to determine the contribution of the canopy to the carbon fluxes of the community ($GPP_{\text{can}} = GPP_t - GPP_r$; $CR_{\text{can}} = CR_t - CR_r$).

Removed canopies were brought back to the laboratory to measure their dry masses after drying for 48 h at 60 °C. Dry masses were used to calculate the respiration rate of canopies ($R_{\text{can}}/DM_{\text{can}}$) and their productivity ($GPP_{\text{can}}/DM_{\text{can}}$) expressed in mgC g_{DM}⁻¹ h⁻¹.

Incident photosynthetically available radiation (400-700 nm) was recorded (LiCor QuantumSA-190, $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) close to the incubation chambers. Mean values during measurements at ambient light varied from 465 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ in December 2013 to 2094 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ in June 2013. Measurements were thus assumed to be done under saturating irradiance, based on the average value of 291 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ given for the onset of light saturation of coastal macroalgal communities (Middelboe et al. 2006).

Carbon and nitrogen content

Just before drying the removed canopies as mentioned previously, samples ($\approx 1\text{g}$ of fresh weight) were taken from *Fucus* fronds of each replicate, to assess their C and N contents. These sampling were done from January to December 2013. Samples were rinsed with distilled water before being dried (60°C, 48 h) and ground to a fine powder using a mortar and pestle. C and N mass percentages were determined at the Station Biologique de Roscoff using a Flash EA 1112 CHN analyzer (ThermoFinnigan) calibrated against nicotinamide and acetanilide reference materials.

Statistical analysis

Seasonal patterns of GPP_t , CR_t , CR_t/GPP_t , $\text{GPP}_{\text{can}}/\text{DM}_{\text{can}}$, $\text{R}_{\text{can}}/\text{DM}_{\text{can}}$, C and N contents were highlighted by fitting a sinusoidal curve (1.3) to the monthly mean values:

$$y = a + b \sin\left(\frac{2\pi}{365}x + c\right) \quad (1.3)$$

where y is the predicted value of the considered parameter, and x the time in days. F -test was used to test the fit, using R software, version 3.1.2 (R Core Team, 2014).

Comparisons of the two communities (community metabolism, canopy metabolism and C and N contents) were done using Wilcoxon signed rank test on the mean values for each month, performed with the R software, version 3.1.2 (R Core Team, 2014).

Correlations between monthly maximal instantaneous irradiance and PAR recorded during light incubations, and between N contents and seawater N-nutrients pool, were tested with Pearson coefficient using the R software, version 3.1.2 (R Core Team, 2014).

For both communities, the relationship between GPP_t or CR_t and environmental variables was analysed by linear multiple regression (Best procedure and AIC selection criteria) with p-values obtained by permutation, using PRIMER software, version 6.1.12 associated with

PERMANOVA+ for PRIMER, version 1.0.2. Predictor variables of GPP_t consisted of monthly maximal instantaneous irradiance, monthly means of air and seawater temperature and of nutrients seawater concentrations (NO_3^- , NO_2^- , NH_4^+ and PO_4^{2-}), and canopy dry mass. Predictor variables of CR_t consisted of monthly means of air and seawater temperature, and canopy dry mass.

Results

Environmental conditions

Monthly maximal instantaneous irradiance followed seasonal trend, with values ranging from 311 W m^{-2} in December 2012 to 1000 W m^{-2} in May 2013 (Fig. 1.4). Our records of incident photosynthetically available radiation during light incubations (data not shown) were significantly correlated with these values ($r = 0.885$, $p < 0.001$ for the *F. vesiculosus* community and $r = 0.784$, $p < 0.001$ for the *F. serratus* community). Monthly mean air and seawater temperatures also followed seasonal trends, with values ranging respectively from $5.8 \text{ }^\circ\text{C}$ in February 2013 to $18.2 \text{ }^\circ\text{C}$ in July 2013 and from $9.3 \text{ }^\circ\text{C}$ in March 2013 to $16.5 \text{ }^\circ\text{C}$ in August 2013 (Fig. 1.4). Nitrates (NO_3^-) dominated the seawater N-nutrient pool throughout the year, with concentration ranging from $0.19 \text{ } \mu\text{mol L}^{-1}$ at the end of July 2013 to $12.45 \text{ } \mu\text{mol L}^{-1}$ at the beginning of February 2013 (Fig. 1.5a). Ammonium (NH_4^+), nitrites (NO_2^-) and phosphates (PO_4^{2-}) seawater concentrations also fluctuated throughout the year, but remained lower than $0.75 \text{ } \mu\text{mol L}^{-1}$ (Fig. 1.5b).

Benthic metabolism

Fucus vesiculosus community exhibited a gross primary production (GPP_t , mean $\pm$ SE) ranging from $341.6 \pm 41.0 \text{ mgC m}^{-2} \text{ h}^{-1}$ in March 2013 to $962.9 \pm 195.4 \text{ mgC m}^{-2} \text{ h}^{-1}$ in June 2013 and respiration (CR_t , mean $\pm$ SE) ranging from $102.8 \pm 27.1 \text{ mgC m}^{-2} \text{ h}^{-1}$ in February 2013 to $562.7 \pm 117.1 \text{ mgC m}^{-2} \text{ h}^{-1}$ in August 2013. GPP_t of the *Fucus serratus* community ranged from $440.0 \pm 80.6 \text{ mgC m}^{-2} \text{ h}^{-1}$ in January 2013 to $1104.4 \pm 101.9 \text{ mgC m}^{-2} \text{ h}^{-1}$ in August 2013 and CR_t ranged from $74.3 \pm 7.9 \text{ mgC m}^{-2} \text{ h}^{-1}$ in January 2013 to $475.9 \pm 65.8 \text{ mgC m}^{-2} \text{ h}^{-1}$ in August 2013 (Fig. 1.6).

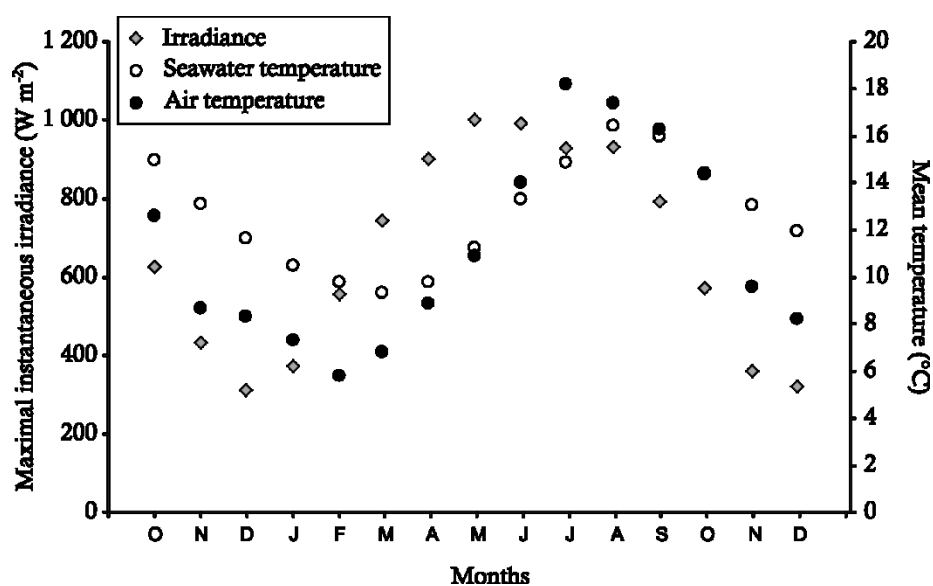


Fig. 1.4 Monthly maximal instantaneous irradiance, expressed in W m^{-2} , and monthly mean of seawater and air temperatures, both expressed in $^{\circ}\text{C}$, as a function of time.

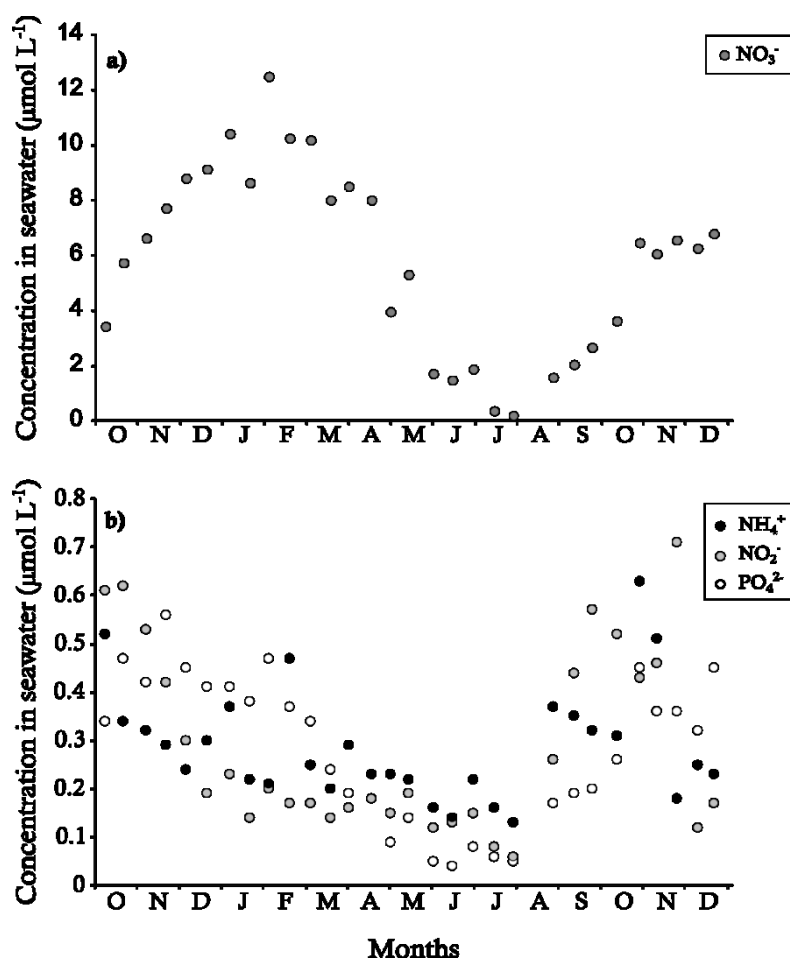


Fig. 1.5 Seawater concentration of (a) nitrates (NO_3^-) and (b) ammonium (NH_4^+), nitrites (NO_2^-) and phosphates (PO_4^{2-}), expressed in $\mu\text{mol L}^{-1}$, as a function of time.

Both GPP_t and CR_t of *F. vesiculosus* and *F. serratus* communities followed a seasonal pattern significantly fitted by sinusoidal curves (Table 1.1), with minimal values occurring during winter and maximal values occurring during summer, even though a metabolic depression was observed in July. While they followed the same seasonal fluctuations, the *F. vesiculosus* community exhibited significantly lower GPP_t than *F. serratus* community (20% lower on average) but significantly higher CR_t (25% higher on average) (Table 1.2). The metabolic balance (i.e. CR_t/GPP_t) was always lower than 1 during our measurements under saturating light conditions. It followed a significant seasonal pattern too (Table 1.1) with minimal values in winter and maximal values during late summer and early fall (from 0.23 to 0.73 for *F. vesiculosus* community and from 0.16 to 0.45 for *F. serratus* community) (Fig. 1.7). The metabolic balance was significantly higher for the *F. vesiculosus* community (Table 1.2), in agreement with the observed differences for both GPP_t and CR_t of these communities.

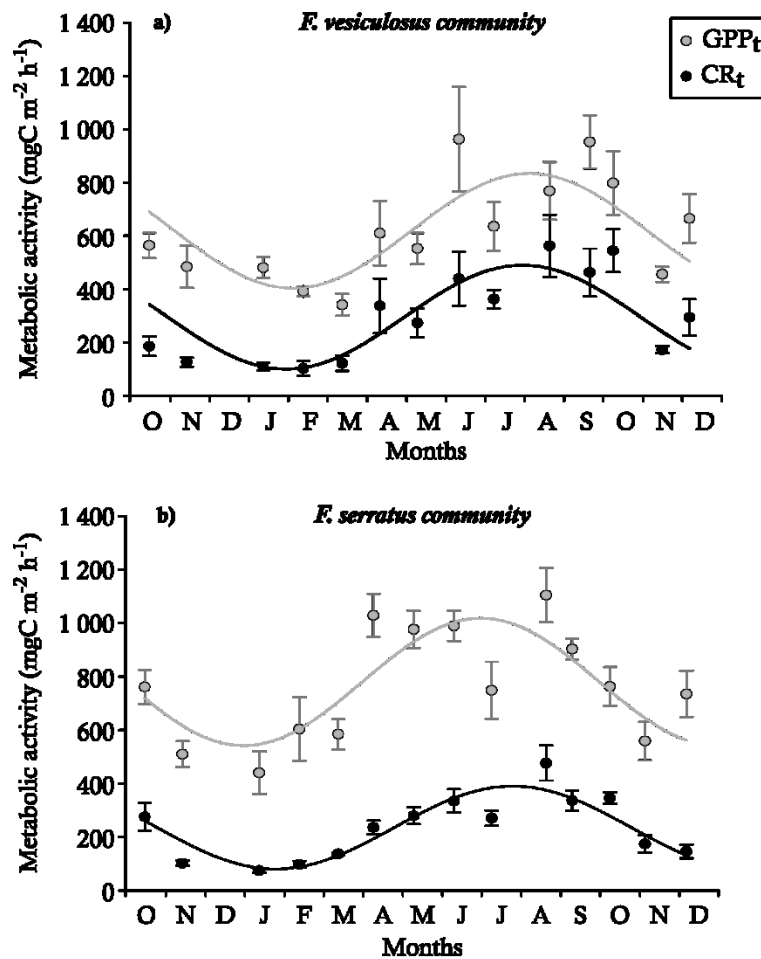


Fig. 1.6 Mean ($\pm$ SE) community gross primary production (GPP_t) and respiration (CR_t), both expressed in mgC m⁻² h⁻¹, as a function of time, for *Fucus vesiculosus* (a) and *Fucus serratus* (b) communities. Grey and dark lines represent the sinusoidal curves fitted on GPP_t and CR_t data sets, respectively.

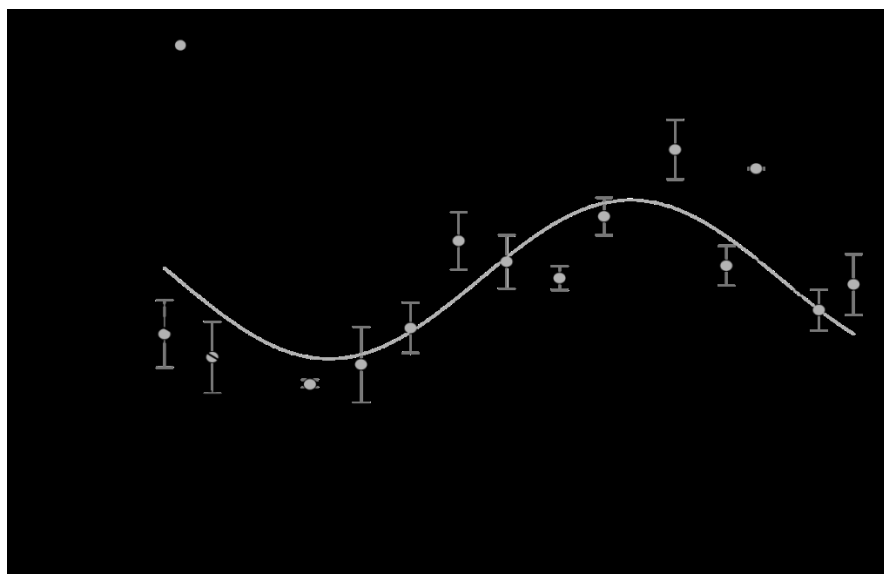


Fig. 1.7 Mean ($\pm$ SE) metabolic balance, calculated as CR_t/GPP_t , as a function of time, for *Fucus vesiculosus* (grey) and *Fucus serratus* (dark) communities. Grey and dark lines represent the sinusoidal curves fitted on *F. vesiculosus* and *F. serratus* communities metabolic balance data sets, respectively.

Table 1.1 Sinusoidal curve parameters (n , a , b , c and R^2) and F -test significant level (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$) for *Fucus vesiculosus* and *Fucus serratus* community gross primary production (GPP_t), community respiration (CR_t), metabolic balance (CR_t/GPP_t), canopy productivity (GPP_{can}/DM_{can}), canopy respiration rate (R_{can}/DM_{can}), C content (% C), N content (% N).

Community/canopy		n	a	b	c	R^2	p
CR_t	<i>F. vesiculosus</i>	14	295.6	-194.8	7.4	0.634	**
	<i>F. serratus</i>	14	235.2	154.8	4.3	0.787	***
GPP_t	<i>F. vesiculosus</i>	14	618.9	-214.9	7.3	0.555	*
	<i>F. serratus</i>	14	779.7	238.2	17.3	0.604	*
CR_t/GPP_t	<i>F. vesiculosus</i>	14	0.4487	0.1678	4.3259	0.556	*
	<i>F. serratus</i>	14	0.2930	0.1238	4.0211	0.804	***
R_{can}/DM_{can}	<i>F. vesiculosus</i>	14	0.1187	-0.0772	1.2554	0.851	***
	<i>F. serratus</i>	14	0.1210	-0.0686	1.8345	0.779	***
GPP_{can}/DM_{can}	<i>F. serratus</i>	14	0.4330	0.1810	-0.5001	0.668	**
% C	<i>F. vesiculosus</i>	12	38.80	0.89	4.91	0.766	**
	<i>F. serratus</i>	12	39.99	1.45	4.39	0.807	**
% N	<i>F. vesiculosus</i>	12	1.64	-0.60	3.52	0.873	***
	<i>F. serratus</i>	12	1.49	-0.53	3.46	0.878	***

The variability of GPP_t was best explained by NO_3^- seawater concentration and DM_{can} taken together for the *F. vesiculosus* community whereas it was best explained by Max_{irr} , T_{air} and all seawater nutrient concentrations for the *F. serratus* community (Table 1.3). The variability of CR_t was best explained by the three predictor variables taken together (T_{air} , $T_{seawater}$ and DM_{can}) for the *F. vesiculosus* community whereas it was best explained by T_{air} alone for the *F. serratus* community (Table 1.3).

Table 1.2 Wilcoxon signed rank test results (V , p) for differences between *Fucus vesiculosus* and *Fucus serratus* in mean community gross primary production (GPP_t), community respiration (CR_t), metabolic balance (CR_t/GPP_t), canopy productivity (GPP_{can}/DM_{can}), canopy respiration rate (R_{can}/DM_{can}), C content (% C), N content (% N).

	V	p
CR_t	15	0.017
GPP_t	12	0.009
CR_t/GPP_t	3	< 0.001
R_{can}/DM_{can}	50	0.903
GPP_{can}/DM_{can}	13	0.011
% C	78	< 0.001
% N	9	0.016

The metabolism of these two communities was consistently dominated by the canopies (i.e. the dominant species and their epibionts) since they accounted for the huge majority of the global CO_2 fluxes (77-97% of CR_t and 83-95% of GPP_t). Nevertheless, no seasonal pattern was observed for the relative contribution of canopies, neither for respiration nor for primary production (F -test, $p > 0.05$). The productivity (GPP_{can}/DM_{can} , mean $\pm$ SE) of *F. vesiculosus* canopy ranged from 0.172 ± 0.029 mgC $g_{DM}^{-1} h^{-1}$ in November 2013 to 0.473 ± 0.072 mgC $g_{DM}^{-1} h^{-1}$ in June 2013 and its respiration rate (R_{can}/DM_{can} , mean $\pm$ SE) from 0.043 ± 0.010 mgC $g_{DM}^{-1} h^{-1}$ February 2013 to 0.217 ± 0.053 mgC $g_{DM}^{-1} h^{-1}$ in June 2013. The productivity of *F. serratus* canopy ranged from 0.083 mgC $g_{DM}^{-1} h^{-1}$ in November 2013 to 0.740 ± 0.112 mgC $g_{DM}^{-1} h^{-1}$ in April 2013 and its respiration rate from 0.040 ± 0.008 mgC $g_{DM}^{-1} h^{-1}$ in November 2012 to 0.240 ± 0.027 mgC $g_{DM}^{-1} h^{-1}$ in June 2013 (Fig. 1.8). As for whole communities, both productivity and respiration rate of the canopies followed a significant seasonal pattern (Table 1.1), except for the *F. vesiculosus*

productivity (F -test, $p > 0.05$). Finally, the productivity of *F. vesiculosus* was significantly lower than the one of *F. serratus* (30% lower on average). No significant difference was found for respiration rate (Table 1.2).

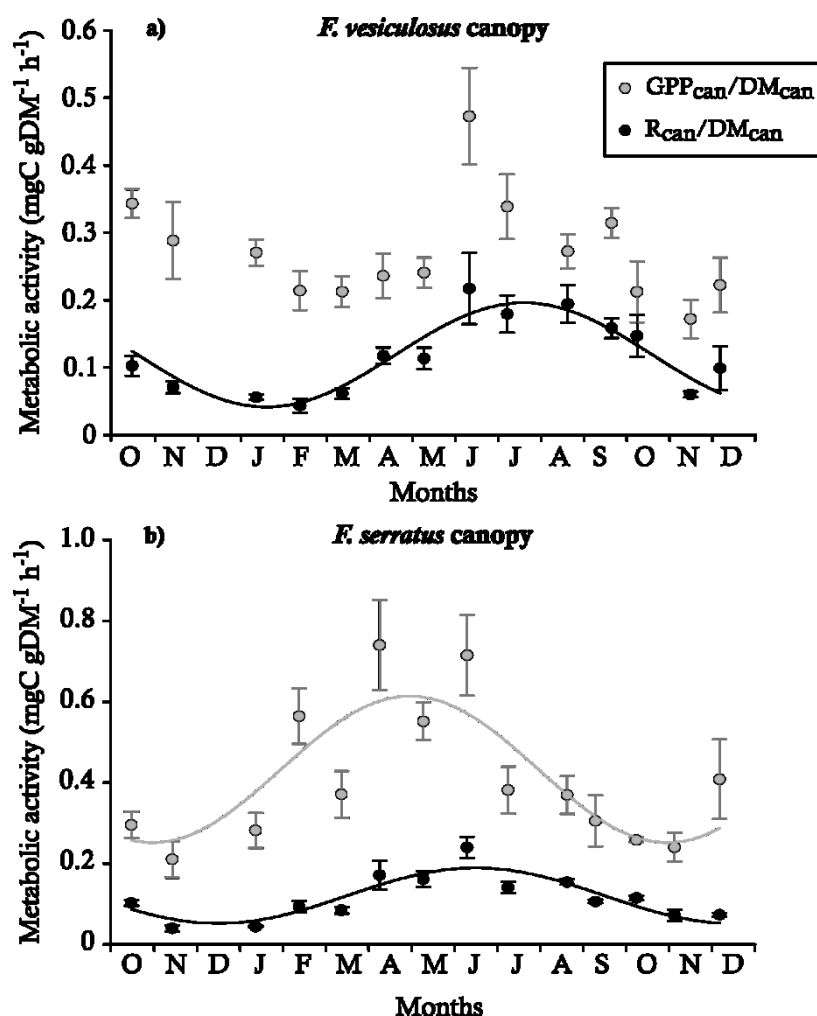


Fig. 1.8 Mean ($\pm$ SE) gross canopy productivity (GPP_{can}/DM_{can}) and canopy respiration rate (R_{can}/DM_{can}), both expressed in $mgC\ gDM^{-1}\ h^{-1}$, as a function of time, for *Fucus vesiculosus* (a) and *Fucus serratus* (b) canopies. Grey and dark lines represent the sinusoidal curves fitted on productivity and respiration data sets, respectively.

Carbon and nitrogen contents

C and N contents measured from *Fucus* thallus samples exhibited a seasonal pattern significantly fitted by sinusoidal curves (Fig. 1.9, Table 1.1). For both *Fucus* species, C content was the lowest in autumn and the highest in summer, ranging from 37.5 to 39.7% of DM for *F. vesiculosus* and from 37.8 to 41.7% of DM for *F. serratus*. On the contrary, N content was the lowest in summer and the highest in spring, ranging from 0.88 to 2.39% of DM for *F. vesiculosus* and from 0.99 to

2.16% of DM for *F. serratus* (Fig. 1.9). *F. serratus* held significantly higher C content but lower N content than *F. vesiculosus* (Table 1.2). N content was significantly correlated with seawater N-nutrient pool, both for *F. vesiculosus* ($r = 0.694$, $p = 0.012$) and *F. serratus* ($r = 0.665$, $p = 0.018$).

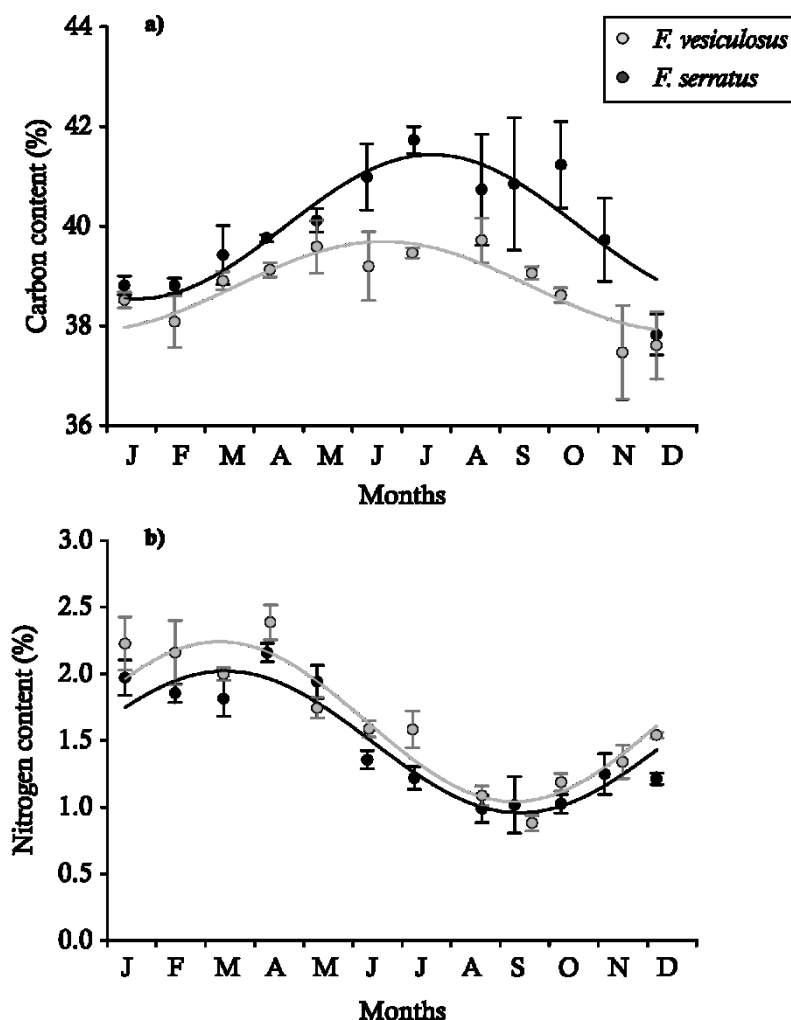


Fig. 1.9 Mean ($\pm$ SE) C content (a) and N content (b), both expressed in % of DM_{can}, as a function of time, for *Fucus vesiculosus* (grey) and *Fucus serratus* (dark). Grey and dark lines represent the sinusoidal curves fitted on *F. vesiculosus* and *F. serratus* data sets, respectively.

Discussion

By measuring *in situ* metabolism of intertidal *Fucus vesiculosus* and *F. serratus* communities under saturating irradiance, this study highlights that, whatever the season, these communities display a substantial metabolic activity at the beginning of emersion periods. Our results of metabolic activity overlapped those previously obtained for *Ascophyllum nosodum* community (188–846 mgC m⁻² h⁻¹ for GPP_t and 122–616 mgC m⁻² h⁻¹ for CR_t, Goll  ty et al. 2008). Consequently, in such

latitudes, intertidal Phaeophycean-dominated communities appear to be photosynthetically active and efficient throughout the year, even though measurements were performed under emerged conditions, which are often considered to be very stressful (Wahl et al. 2011). This study also confirms that Phaeophycean-dominated communities are the most productive systems of intertidal habitats. Indeed, *F. vesiculosus* and *F. serratus* communities displayed considerable higher year-round mean GPP_t (in mgC m⁻² h⁻¹) than those obtained in studies using the same *in situ* measurement method, i.e. 7 to 9 times higher than a *Zostera noltei* bed (Ouisse et al. 2010), 15 to 20 times higher than a muddy-sand community (Migné et al. 2004) or 35 to 44 times higher than a sandy beach community (Hubas et al. 2006). All these studies were conducted at the community scale, integrating the interactions between species and their responses to a broad range of local conditions, especially of incident light (Middelboe et al. 2006, Tait & Schiel 2011a, Migné et al. 2015a), and accounting for the contribution of biofilms which is known to be highly significant, both for autotrophic and heterotrophic activities (Golléty & Crowe 2013).

Table 1.3 Results of linear multiple regressions (R^2 , p) analyzing relationships between GPP_t or CR_t and environmental variables, for both community. Max_{irr} = monthly maximal instantaneous irradiance; T_{air} = monthly mean air temperature; T_{seawater} = monthly mean seawater temperature; NO₃⁻ = monthly mean nitrates concentration in seawater; NO₂⁻ = monthly mean nitrites concentration in seawater; NH₄⁺ = monthly mean ammonium concentration in seawater; PO₄²⁻ = monthly mean phosphates concentration in seawater; DM_{can} = canopy dry mass.

	Community	Environmental variables	R ²	p
GPP _t	<i>F. vesiculosus</i>	NO ₃ ⁻ , DM _{can}	0.684	0.002
	<i>F. serratus</i>	Max _{irr} , T _{air} , NO ₃ ⁻ , NO ₂ ⁻ , NH ₄ ⁺ , PO ₄ ²⁻	0.84	0.016
CR _t	<i>F. vesiculosus</i>	T _{air} , T _{seawater} , DM _{can}	0.898	< 0.001
	<i>F. serratus</i>	T _{air}	0.749	< 0.001

As expected, both GPP_t and CR_t exhibited a seasonal pattern, with minima in winter and maxima in summer, in each community. Such seasonal pattern is in agreement with the general idea that light availability and temperature act as the major drivers of community metabolism (Davison 1991, Golléty et al. 2008, Ouisse et al. 2010, Kemp & Testa 2011). However, inorganic seawater nutrient concentrations also act as a key factor of metabolic regulation of marine systems. Photosynthesis can be limited by low nutrient concentrations which affect algal growth

and lead to changes in the structure and the food webs of the communities (Bosman et al. 1987). In this study, a gross primary production depression was observed in July for both *F. vesiculosus* and *F. serratus* communities and matched with the lowest records in seawater nutrient concentrations close to the study site, suggesting that a nutrient limitation has occurred during this period. The same depression in primary production was observed in summer for the *A. nodosum* community (Golléty et al. 2008), also matching with the lowest seawater nutrient concentrations (SOMLIT network data), strengthening this nutrient limitation hypothesis. Furthermore, the multiple correlations analyses showed that the variability of GPP_t was best explained by incident light, air temperature and seawater nutrient concentrations in *F. serratus* community, and by NO_3^- concentration and canopy dry mass in *F. vesiculosus* community. Surprisingly, neither incident light nor temperature appeared in the best model of regressions for GPP_t of *F. vesiculosus* community. It can be hypothesized that as the *F. vesiculosus* community is located upper on the shore than the *F. serratus* community, it has a more restricted access to seawater nutrients, inducing a higher susceptibility to nutrient limitation, and particularly to nitrates, which dominate the nutrient pool.

The GPP_t depression observed in July could also be related to the highest irradiances as an excess of light could act as significant stress for photo-autotrophic organisms (e.g. Huppertz et al. 1990; Häder and Figueroa 1997; Bischof et al. 2000). However, Creis et al. (2015) have demonstrated that the exposition of *F. vesiculosus* individuals to UV-B conditions approximately two times more important than the maximal conditions occurring in Brittany only led to a slight reduction in the maximal efficiency of PSII after 1 and 4 weeks of chronic exposure. In addition, as we were working at the community scale, only the upper layer of the community (mainly composed of *Fucus* spp.) was exposed to high light, and could have suffer from it. This layer acted as a protective layer for the other components of the community, which benefited from the attenuation of incident light and could have maintained a high metabolic activity. The canopy biomass appeared to be a good predictor of metabolic variations of the *F. vesiculosus* community GPP_t . Binzer and Sand-Jensen (2002b) demonstrated that at high density, photosynthetic tissues have the ability to fully use incident light. This would imply an optimal distribution and utilisation of incident light among all photosynthetic tissues in the community. Nevertheless, at

very high canopy density, photosynthetic activity could be limited under high light due to uneven distribution of photons (Binzer & Sand-Jensen 2002b).

During our measurements, *F. vesiculosus* and *F. serratus* communities always performed as autotrophic entities, with a CR_t/GPP_t ratio strictly lower than 1. Interestingly, this metabolic balance fluctuated according to a seasonal pattern, as did photosynthesis and respiration. Such pattern could be related to the seasonal fluctuations of the biomass of these communities, as the metabolic balance was maximal in summer when maximal biomass accumulation occurred. Indeed, community gross primary production is limited at high canopy density while its respiration rate is linearly related to its density (Binzer & Sand-Jensen 2002b). Finally, this seasonal variation implies that metabolic balance has to be used with caution if measured punctually, particularly when dealing with the annual carbon budget of an ecosystem.

By removing *F. vesiculosus* and *F. serratus* canopies, we showed that they were responsible for the great majority of CO_2 fluxes (77-97% of CR_t and 83-95% of GPP_t). This confirms that the role of canopy-forming macroalgae in the community is not restricted to facilitation for associated species, but is also fundamental in the community metabolism, all over the year. No seasonal pattern emerged however, even though diversity and abundance of epibionts and others species, like the opportunistic ones, are known to exhibit a strong seasonal variability (e.g. Rindi and Guiry 2004). Being substantial productive entities, canopy-forming algae can control the community processes they dominate, to constitute one of the major suppliers of organic carbon for coastal food webs (Paine 2002, Goll  ty et al. 2008). By this way, the global current decline of canopy-forming macroalgae (Airoidi & Beck 2007, Duarte et al. 2013) and the predicted shift of European *F. vesiculosus* and *F. serratus* communities northward (Jueterbock et al. 2013; 2014) are likely to have dramatic effects on the dynamics of coastal ecosystems (Thompson et al. 2002).

As major metabolic component of their communities, the *F. vesiculosus* and *F. serratus* canopies rationally exhibited high productivity and respiration rate (in $mgC\ g_{DM}^{-1}\ h^{-1}$). These rates were found to be in the same range as those obtained for other slow-growing Phaeophyceae (e.g. Quadir et al. 1979; Williams and Dethier 2005; Goll  ty et al. 2008). Yet, some previous studies on *Fucus* spp. indicated productivity 2 to 10 times higher than our results (Brinkhuis et al. 1976, Maberly & Madsen 1990, Kawamitsu & Boyer 1999) whereas respiration rates were quite similar.

These high productivities might be explained by the use of fucoids segments under laboratory conditions, contrasting with our *in situ* conditions, where the canopies consisted of multi-layer assemblages subjected to strong self-shading, at least for the basal layers. Furthermore, canopies were considered as a multi-specific complex, composed of *Fucus* thalli associated with their epibionts (e.g. Chlorophyta, Rhodophyta, Bryozoa, Tunicates, etc.) and biofilms. These species probably acted as productivity inhibitors due to light attenuation, at least for the heterotrophic ones, as demonstrated by Sand-Jensen (1977) on eelgrass leaves. Considering this, our results appeared to be realistic about what really happened on the field. As for whole communities, a seasonal pattern of productivity and respiration rate was observed, except for *F. vesiculosus* productivity, confirming the previous hypothesis about metabolic drivers. The C contents of both species followed a clear seasonal pattern, as those well described for *Laminaria* species (e.g. Gagné et al. 1982; Gevaert et al. 2001), with the highest C content in summer, when C assimilation by photosynthesis exceeds C requirements, leading to a storage of carbohydrates (Gomez & Wiencke 1998, Lehvo et al. 2001) and the lowest in winter when photosynthesis was not sufficient to supply C requirements, leading to a gradual use of carbohydrate reserves (Hatcher et al. 1977, Lehvo et al. 2001). Any variation in C content due to reproduction investment was detected while both species are known to exhibit seasonal trend in their reproductive strategy (Knight & Parke 1950, Brenchley et al. 1998). Yet, this reproductive process is known to be spread over several months (Knight & Parke 1950), with resources investment rarely exceeding 55% and fertile individuals found year-round (Brenchley et al. 1998). The N contents also followed seasonal variations, which are well documented in the literature too (e.g. Asare and Harlin 1983; Carlson 1991; Brenchley et al. 1998; Young et al. 2007). For both species, N content was highest in winter and lowest in summer, and was significantly correlated with seawater N-nutrient concentrations, as already observed by Young et al. (2007). This is also consistent with the N turnover rate of approximately 2 to 3 weeks exhibited by *F. vesiculosus* (Viana et al. 2015). High seawater nutrient availability in winter allowed a substantial N assimilation and storage by *Fucus* species. Stored N is gradually used to support an active growth during spring and summer, when N-seawater is depleted. Nutrients limitation of metabolic activity, supposed to occur at community scale, is strengthened by N contents values. Indeed, Pedersen and Borum (1997) have calculated a critical N tissue content of 1.71% of DM to support maximum growth rate for *F. vesiculosus*. Lower contents were observed during several months in

our *F. vesiculosus* and *F. serratus* individuals. Yet, we could expect a seasonal fluctuation of critical N concentration and/or N-requirements for these species, which could restrict N-limitation during summer months, when both N tissue and seawater nutrient concentrations were the lowest.

This study allowed the comparison of the metabolism, at the beginning of the emersion period and under saturating irradiance, of two adjacent communities along the vertical zonation. The upper community exhibited the lowest GPP_t and the highest CR_t , and as a consequence, the highest metabolic balance. The canopy productivity was also lower for *F. vesiculosus* than for *F. serratus*. This is consistent with the C content values, significantly lower in *F. vesiculosus* than in *F. serratus*. Differences in C content were particularly pronounced during summer and fall, when a higher net primary production for *F. serratus* was observed. Moebus et al. (1974) have evidenced that lower C contents in upper species could be a consequence of a higher organic C release during low tide in response to a higher desiccation degree. Finally, *F. serratus* appeared to be more competitive than *F. vesiculosus* in a metabolic point of view, in agreement with the vertical zonation rules (Raffaelli & Hawkins 1999). The latter species has probably achieved more efficient, but costly, protecting mechanisms to deal with abiotic stresses, such as temperature or desiccation, to the detriment of its competitiveness. This could cause high differences in the annual carbon balance of adjacent communities and needs to be investigated in details further.

Conclusion and perspectives

This study showed that the two widespread *Fucus vesiculosus* and *F. serratus* communities exhibited high rates of both gross primary production and respiration all over a year, confirming their importance in the intertidal area. Nevertheless, as our measurements were achieved at the beginning of emersion for each community, further investigations need to be performed, using complementary methods, to survey the metabolism of these intertidal communities during tidal and daily cycles. This is essential to assess accurately the annual carbon balance of such Phaeophycean-dominated systems to bring some insights about their functional ecology, but also to carry on such measurements with the prospect to get fundamental information about ecosystem functioning modifications due to the large and complex changes that occur on the biosphere (Staehr et al. 2012).

Chapitre 2

Fonctionnement trophique des communautés

à canopée de *Fucus*

Contexte général et résumé

Les résultats du chapitre précédent mettent en évidence une fluctuation saisonnière de la production primaire pour les deux communautés de *Fucus* lors de mesures à l'émersion. Les biomasses algales totales et de la canopée mesurées régulièrement à Roscoff (4 périodes de mesures de mars à novembre 2014 pour la communauté de *F. vesiculosus* et 7 périodes de mesures de mars 2014 à février 2015 pour la communauté de *F. serratus* ; 5 quadrats aléatoires de 0,25 m² par période de mesure et par communauté) montrent la même tendance (Fig. 2.1). D'autre part, la concentration en chlorophylle *a* dans l'eau de mer mesurée à environ 600 m de la zone d'étude indique une forte saisonnalité de la biomasse phytoplanctonique (Fig. 2.2, données SOMLIT, point Estacade, <http://somlit-db.epoc.u-bordeaux1.fr/bdd.php>).

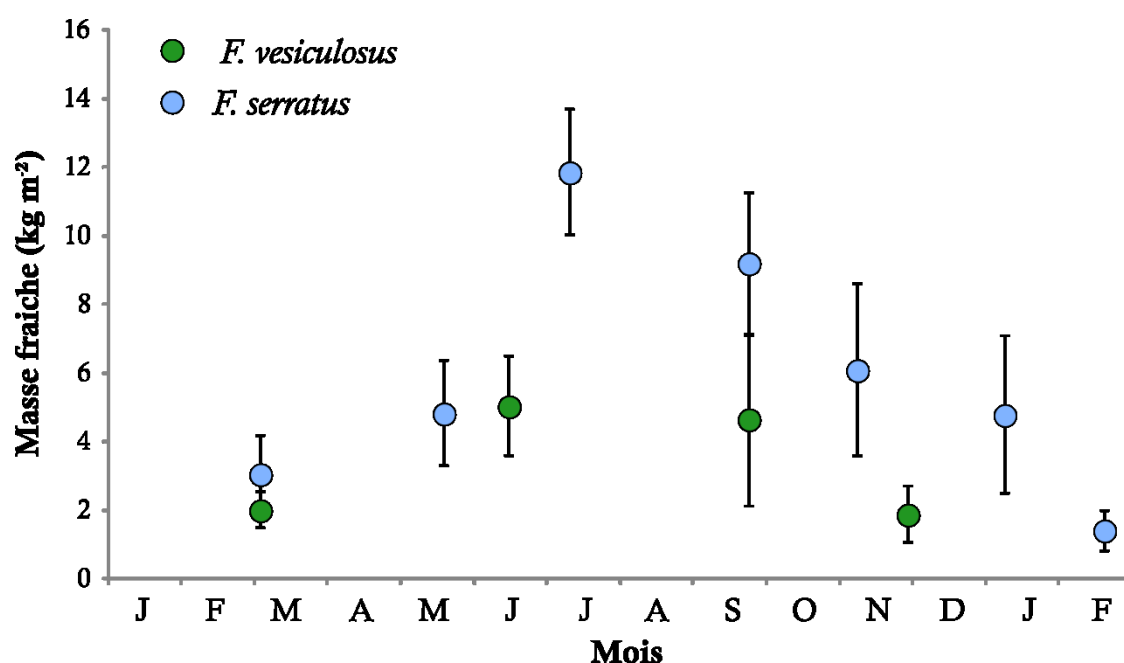


Fig. 2.1 Variations de biomasse fraîche moyenne ($\pm$ SD, en kg m⁻²) des canopées de *F. vesiculosus* (en vert) et de *F. serratus* (en bleu), entre mars 2014 et février 2015.

Les producteurs primaires, macroalgues et phytoplancton, constituent les ressources trophiques des consommateurs primaires associés aux communautés intertidales à canopée de macroalgues (Dauby et al. 1998, Riera et al. 2009). La variation saisonnière de leur biomasse pourrait donc entraîner d'importantes modifications dans la structure trophique et les voies de transfert de la matière, comme cela a été observé au sein de communautés côtières arctiques par exemple (Forest et al. 2008, Darnis et al. 2012). Ainsi, il semble fondamental, si l'on souhaite appréhender

de façon précise le fonctionnement trophique des communautés de *Fucus*, de tenir compte de l'influence des saisons.

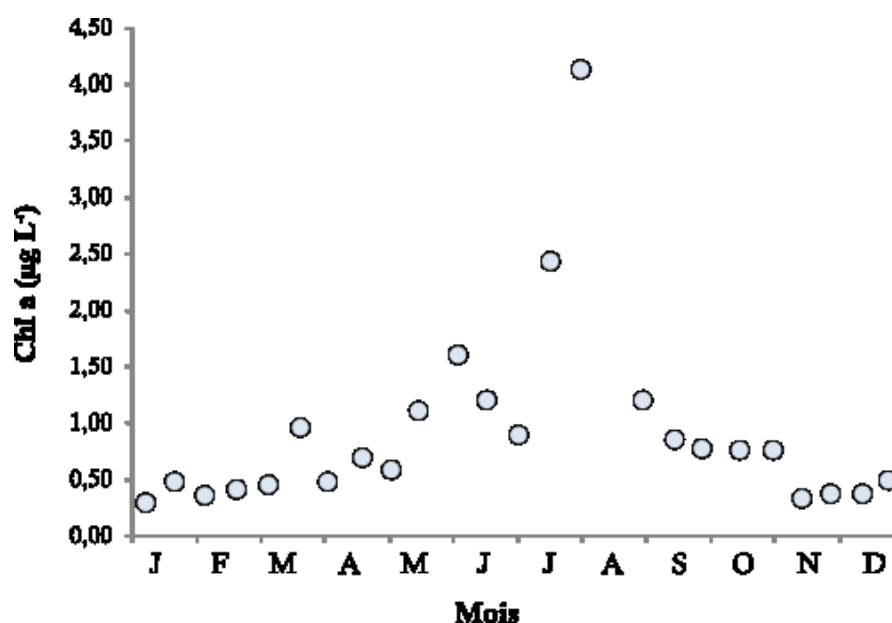


Fig. 2.2 Evolution de la concentration en chlorophylle *a* (en $\mu\text{g L}^{-1}$) dans l'eau de mer, entre janvier et décembre 2013, à proximité du site d'étude (données SOMLIT, point Estacade).

La composition taxonomique de ces deux communautés de *Fucus* varie en fonction du niveau marégraphique auquel elles sont établies. De plus, en milieu intertidal, l'accès aux ressources pour les producteurs primaires et les filtreurs est restreint aux périodes d'immersion (Raffaelli & Hawkins 1999). Ces communautés pourraient donc avoir des réseaux trophiques différents du fait de leur niveau marégraphique. L'analyse de réseaux trophiques dans un contexte de zonation intertidale a été rarement réalisée (Steinarsdóttir et al. 2009) mais s'avère nécessaire pour la compréhension du fonctionnement général des communautés à canopée de macroalgues.

Ce chapitre a donc pour objectifs de décrire la structure trophique des communautés de *F. vesiculosus* et de *F. serratus* au cours de différentes saisons et de les comparer dans un contexte de zonation intertidale. Cette étude se base sur l'analyse des isotopes stables du carbone et de l'azote.

Par définition, les isotopes d'un même élément chimique divergent par leur nombre de neutrons, occasionnant des différences de masse. Les isotopes sont dit stables s'ils ne se modifient pas au cours du temps, à la différence des isotopes dit instables ou radioactifs dont le noyau se désintègre

spontanément au cours du temps. Les isotopes stables sont naturellement présents dans l'environnement et sont utilisés comme éléments de traçage trophique. L'abondance de chaque isotope stable présent dans un organisme est déterminée par spectrométrie de masse. Cette analyse consiste en une séparation magnétique des isotopes en fonction de leur masse, et permet de déterminer leur ratio ($^{13}\text{C}/^{12}\text{C}$ pour le carbone et $^{15}\text{N}/^{14}\text{N}$ pour l'azote). Ce ratio est ensuite rapporté à un standard international, le Pee Dee Belemnite pour le carbone et l'azote atmosphérique pour l'azote. Ce ratio s'exprime alors en unité δ (‰) (2.1 et 2.2) :

$$\delta^{13}\text{C} = \left(\frac{(^{13}\text{C}/^{12}\text{C})_{\text{échantillon}}}{(^{13}\text{C}/^{12}\text{C})_{\text{standard}}} - 1 \right) \times 1000 \quad (2.1)$$

$$\delta^{15}\text{N} = \left(\frac{(^{15}\text{N}/^{14}\text{N})_{\text{échantillon}}}{(^{15}\text{N}/^{14}\text{N})_{\text{standard}}} - 1 \right) \times 1000 \quad (2.2)$$

En raison de leur différence de masse, les isotopes d'un même élément ne sont pas utilisés dans les mêmes proportions par les organismes. Ainsi, au cours de la photosynthèse, les producteurs primaires ont tendance à favoriser l'assimilation d'isotopes légers. Néanmoins, la diversité des mécanismes de photosynthèse mis en œuvre par ces producteurs primaires participe à ce qu'ils soient caractérisés par des signatures isotopiques qui leurs sont propres (Raven et al. 2002).

Lors du transfert de matière d'un niveau trophique à un autre, un processus de fractionnement isotopique (ou facteur d'enrichissement trophique) conduit à un enrichissement en isotopes lourds (^{13}C , ^{15}N) dans les tissus du consommateur par rapport à sa source (Peterson & Fry 1987). Ce fractionnement isotopique résulte des processus d'assimilation de la matière organique d'une part et de l'élimination de différents composés via la respiration et l'excrétion d'autre part. L'enrichissement en isotopes lourds s'avère donc particulièrement variable d'une espèce à l'autre. Il peut tout de même être moyenné au sein de groupes trophiques ou taxonomiques distincts : entre 0 et 1 ‰ pour le ^{13}C (Caut et al. 2009) et entre 2,5 et 3,5 ‰ pour le ^{15}N (Zanden & Rasmussen 2001, Post 2002, Vanderklift & Ponsard 2003). Les signatures isotopiques en carbone et en azote des différents organismes présents dans les communautés sont donc liées à leurs relations trophiques et permettent de mettre en évidence les principales voies de transfert de la matière (Fig. 2.3).

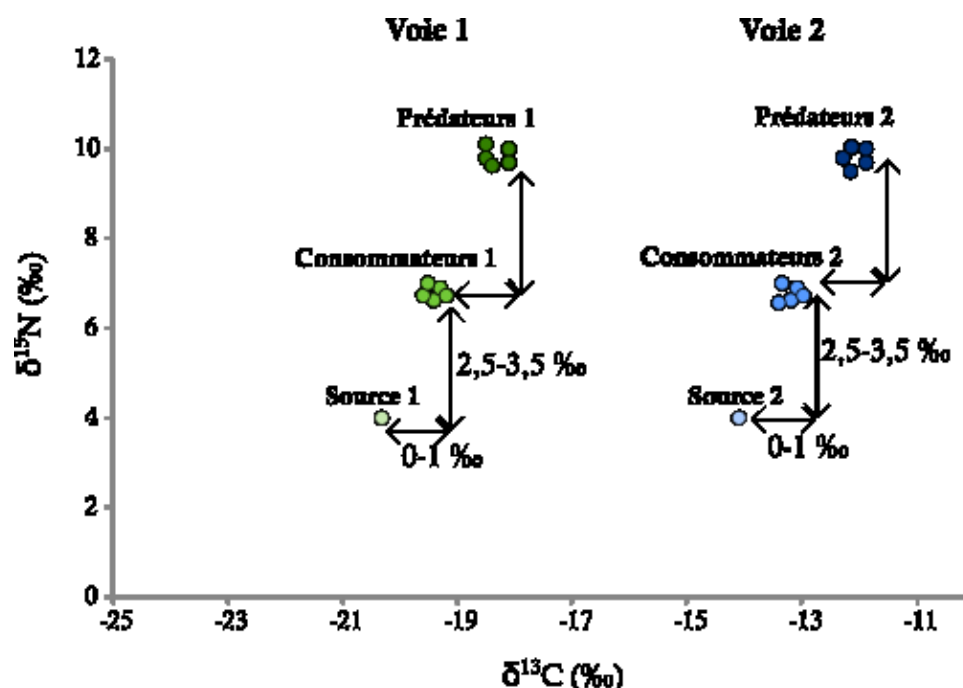


Fig. 2.3 Illustration du principe d'enrichissement trophique au sein de deux voies de transfert théoriques comprenant une source, des consommateurs primaires et secondaires (prédateurs).

Les réseaux trophiques des communautés de *F. vesiculosus* et de *F. serratus* ont été analysés au cours de quatre saisons successives (septembre et décembre 2013, mars et juin 2014) en collaboration avec Pascal Riera (UPMC, Station Biologique de Roscoff). Pour chaque saison, les producteurs primaires et les consommateurs les plus communs ont été échantillonnés au cours d'une marée basse de vive-eau. Les sources sont composées de différentes espèces de macroalgues dressées et encroûtantes et du biofilm épilithique, mais aussi de la matière organique particulaire en suspension. Celle-ci a été échantillonnée à proximité du site d'étude, dans le cadre du réseau d'observation SOMLIT. Pour les consommateurs, une attention particulière a été apportée pour prélever, à chaque saison et dans chacune des deux communautés, des taxons appartenant aux différents groupes trophiques (i.e. filtreurs, herbivores et prédateurs). La signature isotopique ($\delta^{13}\text{C}$ et $\delta^{15}\text{N}$) de chaque échantillon a été déterminée par spectrométrie de masse, par Cédric Leroux (responsable de la plateforme isotopes stables à la Station Biologique de Roscoff).

Ces analyses ont permis de mettre en évidence, pour chacune des deux communautés et à chaque saison, des réseaux trophiques complexes, composés de différentes voies de transfert et de plusieurs niveaux trophiques. Globalement, il s'avère que ces deux communautés sont constituées de nombreux taxons opportunistes et/ou généralistes. Les *Fucus* ne représentent pas la

source dominante de nourriture pour les herbivores, malgré leur très forte biomasse comparée aux autres producteurs primaires. Il n'y a pas de différences saisonnières marquées de la structure trophique de ces deux communautés, bien que de la variabilité saisonnière puisse être observée pour quelques taxons. Par exemple, les filtreurs utilisent principalement la matière organique particulière au printemps et en été, et les débris de macroalgues en automne et en hiver.

La structure trophique de ces deux communautés apparaît similaire, malgré leurs niveaux marégraphiques différents. Les taxons de consommateurs communs aux deux communautés présentent ainsi des signatures isotopiques non significativement différentes en fonction de la communauté dans laquelle ils ont été échantillonnés.

Article n°2

Trophic structure of two intertidal *Fucus* spp. communities along a vertical gradient: similarity and seasonal stability evidenced with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

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Abstract: Intertidal communities dominated by canopy-forming macroalgae typically exhibit some differences in their specific composition that are related to their location along the emersion gradient of rocky shores. Tidal level is also expected to affect resource availability for both primary producers and consumers, potentially leading to divergence in the trophic structure of these communities. Furthermore, in temperate areas, the alternation of seasons has usually a large influence on the primary production and on life-history traits of numerous species, which may induce some changes in the food webs of intertidal communities. Thus, this study aimed to investigate the trophic structure of two intertidal communities located at different tidal levels, over several seasons. Focusing on the dominant species of primary producers and consumers, the food webs of the *Fucus vesiculosus* (Linnaeus, 1753) and *Fucus serratus* (Linnaeus, 1753) communities were studied during four successive seasons, using an isotopic ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) approach. Due to the diversity of primary producers and consumers living in these two communities, food webs were relatively complex and composed of several trophic pathways. These food webs remained rather conserved over the successive seasons, even though some variability in isotopic signature and in diet has been highlighted for several species. Finally, despite their location at different tidal levels, the two *Fucus* spp. communities exhibited nearly the same trophic structure, with common consumer species displaying similar isotopic signature in both of them.

Keywords: Intertidal zonation; Seasons; Stable isotopes; Trophic groups

Highlights

- Food webs of intertidal furoid communities included several trophic pathways
- Trophic structure of furoid communities remained highly conserved over the year
- Furoid communities from different tidal heights exhibited similar food webs

Acknowledgments: The authors thank the SOMLIT network for providing isotopic data of particulate organic matter of our study area. Two anonymous reviewers are thanked for constructive comments. This work benefited from the support of the Brittany Regional Council and of the French Government through the National Research Agency with regard to the investment expenditure programme IDEALG ANR-10-BTBR.

Introduction

Along intertidal rocky shores of temperate areas, sheltered habitats are usually dominated by canopy-forming brown algae (Phaeophyceae) that can cover almost all the substratum. These species are established along a vertical gradient and are typically associated with numerous species of primary producers and consumers in such a way that intertidal rocky shores are composed of a succession of distinct communities from high to low tide levels (Raffaelli & Hawkins 1999). Trophic structure of these intertidal communities has been the focus of intensive research during the past decades, due to the emergence of the stable isotopic approach (Dauby et al. 1998, Sarà et al. 2007, Riera et al. 2009, Duarte et al. 2015). To our knowledge, only one study was however carried out in the context of vertical zonation (Steinarsdóttir et al. 2009). Tidal zonation is, yet, expected to be a significant driver of community trophic structure. For instance, shore level usually controls resource access for primary producers (e.g. $\text{CO}_2/\text{HCO}_3^-$ and nutrients, Raven & Hurd 2012), sessile fauna (as some species can only feed when immersed, Raffaelli & Hawkins 1999) and mobile fauna (as the amount of available food might decrease from low to high shore levels, Underwood 1984). Trophic relationships are considered as an important component of community functioning and should be defined more accurately in the context of tidal zonation. The use of stable isotopes seems particularly powerful for this purpose, as they act as chemical tracers of energy flow (Peterson & Fry 1987, Fry 2006). Thus, $\delta^{13}\text{C}$ of a consumer usually provides information about its diet sources while its $\delta^{15}\text{N}$ value is often related to its trophic position in the food web (Zanden & Rasmussen 2001, Caut et al. 2009).

In temperate areas, abiotic factors such as light and temperature display significant seasonal fluctuations. As a consequence, intertidal communities show seasonal pattern in their metabolism (Golléty et al. 2008, Bordeyne et al. 2015), as well as in their species richness and/or abundance (Rindi & Guiry 2004, Dethier & Williams 2009). These seasonal fluctuations potentially influence species interactions and may therefore lead to modification in their food webs. Furthermore, seasonal changes in isotopic composition of both primary producer and consumer species are regularly evidenced in coastal communities (Nordström et al. 2009, Hyndes et al. 2013), including intertidal habitats (Golléty et al. 2010, Ouisse et al. 2011b). These changes, which could be related to numerous biotic and abiotic factors (Jennings et al. 2008, Vanderklift & Bearham 2014, Viana et al. 2015), may also reflect important modifications in the trophic structure of these communities over time (McMeans et al. 2015). In this context, it appears

essential to understand how seasonal variations can structure the food webs of benthic communities, and also how these communities respond to existing environmental variations (Hyndes et al. 2013).

Using a $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ approach, this study focuses on the main taxa inhabiting two communities that are established at adjacent tidal levels. These two communities, widespread in temperate rocky shores, are respectively dominated by the canopy-forming species *Fucus vesiculosus* Linnaeus and *Fucus serratus* Linnaeus. This study aimed to describe the trophic structure of these communities, considering the alternation of seasons. Comparisons between communities were also carried out, and the results of these comparisons were interpreted in the context of vertical zonation of intertidal rocky shores.

Materials & methods

Study site

The study site is located in front of the Station Biologique de Roscoff, in the southwestern part of the English Channel (Brittany, France) (48°43.743'N, 3°59.407'W). It consisted of an intertidal boulder reef subjected to semi-diurnal tidal cycle, with maximal amplitude of about 9 m. This semi-sheltered rocky shore is characterized by a vertical succession of communities dominated by canopy-forming Phaeophyceae, where the *Fucus vesiculosus* and *F. serratus* communities are characteristic of the mid-intertidal (3.0 to 4.0 m above chart datum) and low mid-intertidal (2.5 to 3.0 m above chart datum) respectively. These communities are mainly composed of dense *Fucus* spp. canopies, covering up to 100 % of the substratum, which are associated with miscellaneous epibionts (i.e. algae and sessile invertebrates directly attached to the *Fucus*, see (Wahl 2009). They are also made up of sub-canopy and encrusting algae, as well as microphytobenthos, and phytoplankton during high tide. Finally, these communities also support a diverse pool of mobile invertebrates (Raffaelli & Hawkins 1999, Migné et al. 2015b).

Sampling and preparation for stable isotopes analysis

For both *F. vesiculosus* and *F. serratus* communities, the most representative taxa of food sources (i.e. erect and encrusting algae, and epilithon) and consumers were collected by hand during low tide, in four successive seasons (September and December 2013 and March and June 2014, see Supplementary material for the list of sampled taxa). After collection, samples were frozen at

-18 °C for later processing. Particular attention was taken to collect consumers from the main trophic groups (filter-feeders, grazers and predators), based on literature knowledge (Dauby et al. 1998, Riera et al. 2009, Golléty et al. 2010). Stable isotope data for marine suspended particulate organic matter (POM) were obtained from the SOMLIT network, in a place located at approximately 600 m of our study site (Estacade sampling point, Roscoff, France, data available at <http://somlit-db.epoc.u-bordeaux1.fr/bdd.php>).

In the laboratory, erect algae were carefully cleaned in filtered seawater (0.45 µm) to remove detrital fragments and attached organisms. The encrusting ones were scrubbed in filtered seawater, which was then filtered onto pre-combusted filters (Whatman GF/F glass microfiber filters). In order to remove inorganic carbon of the encrusting Rhodophyta *Phymatolithon lenormandii*, HCl 1N was added to seawater prior to filtration. Epilithon was gently removed from small boulders using a smooth brush and collected in filtered seawater, then filtered onto pre-combusted filters. Regarding consumers, organisms belonging to the Cnidaria (except campanulariidae), Mollusca, Arthropoda (except amphipods) and Echinodermata phyla were treated at the individual level, while for colonial taxa (i.e. campanulariidae, Bryozoa and Ascidiacea), *Spirorbis* sp. and amphipods, several organisms were pooled together to get enough material for accurate stable isotope analyses. Gastropods were extracted from their shell to take off foot muscle, whereas for decapods, muscle was taken off from their pereopods. For *Asterina gibbosa*, amphipods, campanulariidae and polyclinidae, half of the samples were acidified to remove inorganic carbon (HCl 1N) while the other part remained untreated. $\delta^{13}\text{C}$ measurements were performed on acidified samples and $\delta^{15}\text{N}$ on untreated ones, as advised by Schlacher & Connolly (2014). Finally, all samples were rinsed with distilled water, before being dried (60°C, 48h) and ground to a fine homogeneous powder using an agate mortar and pestle.

Carbon and nitrogen stable isotopes ratios were determined using a Flash EA 1112 CHN analyzer (ThermoFinnigan) coupled with a Finnigan Delta Plus mass spectrometer, via a Finnigan Con-Flo III interface. Data are expressed in the standard δ unit (2.3):

$$\delta X(\text{‰}) = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 10^3 \quad (2.3)$$

With X is ^{13}C or ^{15}N and R is $^{13}\text{C}/^{12}\text{C}$ ratio for carbon or $^{15}\text{N}/^{14}\text{N}$ ratio for nitrogen.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were calculated in relation to the certified reference materials Vienna-Pee Dee Belemnite-limestone (V-PDB) and atmospheric di-nitrogen (N_2). The V-PDB and N_2 at air-scales

were achieved using in-house protein standards, calibrated against NBS-19 and IAEA N3 reference materials. The standard deviation of repeated measurements of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the laboratory standard was 0.10 ‰ versus V-PDB and 0.05 ‰ versus at-air, respectively.

Taxonomic diversity and density of gastropod grazers

Gastropod grazers (hereafter referred to as “grazers”) constitute the most abundant group of consumers in these communities (approx. 95% of the countable fauna) and likely play a significant role in organic matter fluxes within the food webs. The taxonomic diversity of these grazers was monitored in the same areas and at the same periods than sampling for stable isotopes analyses (i.e. September and December 2013, and March and June 2014). Thus, at each season, grazers were identified at the species level and counted in five replicates of 0.1 m² randomly chosen in each community. To account for spatial variability, intra-community replicates were 3 to 10 m away one from each other.

Data analysis

The trophic structure of each community, its temporal fluctuations, and the potential trophic relationships between diets and consumers, were investigated by drawing dual-isotope plots at each sampling period. The “community-wide” isotopic metrics developed by Cucherousset & Villéger (2015) (i.e. isotopic richness, divergence, dispersion, evenness and uniqueness) were used as a complement to these dual-isotope plots. The isotopic richness is related to the area of the bi-dimensional isotopic space that is filled by all the taxa while the isotopic divergence, dispersion, evenness and uniqueness are related to the distribution of taxa in this space, providing information about trophic diversity and redundancy. These metrics have the benefit to be mathematically independent of the number of replicates used and allow accounting for abundance/biomass of taxa, when available. They were calculated at each sampling period and for each community, using the R functions computed by Cucherousset & Villéger (2015), with R software, version 3.2.2 (R Core Team 2015). Their coefficient of variation across seasons was used to discuss about the seasonal variability in the trophic structure of these two communities.

Bayesian stable isotope mixing models (SIAR, Parnell et al. 2010, Parnell & Jackson 2013) were implemented to estimate the relative contribution of food sources to the diet of several consumers, at each season, and for each community. To do so, trophic enrichment factors of

0.28 ± 0.23 ‰ for $\delta^{13}\text{C}$ and of 2.5 ± 0.68 ‰ for $\delta^{15}\text{N}$ were assumed (Caut et al. 2009). Thus, these mixing models were run for a set of filter-feeders selected for each community, implementing POM and erect algae as potential food sources. Erect algae were used considering that they may be consumed by filter-feeders through detritus (Leclerc et al. 2013), despite that degradation process might affect their isotopic composition (Lehmann et al. 2002). Mixing models were also run for a set of grazers selected for each community, implementing epilithon and erect algae as potential food sources. Grazer selection was realized according to Hawkins et al. (1989), in such a way that diversity of feeding behaviours and of radula types was maximised. In the *F. serratus* community, some erect Rhodophyta were pooled together according to their characteristics, to limit the number of potential food sources (Phillips et al. 2014).

For comparisons between communities, we first calculated the overall level of isotopic overlap between the two communities using the isotopic overlap metrics (isotopic similarity and nestedness) developed by Cucherousset & Villéger (2015), from the average isotopic signature of each taxon. We also focused on consumer taxa present in both communities (i.e. shared consumers, see Supplementary Material for their identities). Their average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ obtained in the *F. vesiculosus* community were plotted against those obtained in the *F. serratus* community. Slopes and intercepts of a Model II regression were then calculated according to the major axis method, using the “lmodel2” R package version 1.7-2 (Legendre 2014), for both $\delta^{13}\text{C}_{\text{Fves}}$ vs $\delta^{13}\text{C}_{\text{Fser}}$ and $\delta^{15}\text{N}_{\text{Fves}}$ vs $\delta^{15}\text{N}_{\text{Fser}}$ plots. Student’s t-tests were performed to test if slopes and intercepts of regressions were significantly different from 1 and 0, respectively. If not, it would indicate that, on average, the shared consumers’ exhibited similar isotopic signature in the two communities.

Focusing on grazers, potential differences between communities were first investigated in terms of taxonomic diversity (i.e. distribution of abundances among taxa) using clustering analysis (group average) and one-way ANOSIM test (for each community, the four seasonal samples were considered as replicates). These analyses were performed on similarity matrix calculated from Bray-Curtis similarity index on square-root transformed abundances, using PRIMER software, version 6.1.12 (Clarke & Gorley 2006). Then, potential difference between communities in term of isotopic diversity of grazers was investigated using the isotopic diversity metrics (isotopic richness, divergence, dispersion, evenness and uniqueness, Cucherousset & Villéger 2015). These

isotopic metrics were calculated at each season and for each community, from grazer isotopic signatures, with and without weighting them by their abundances. Clustering analysis and one-way ANOSIM tests were then performed for each condition on similarity matrices calculated using Bray-Curtis similarity index on the five metrics, following the procedure previously described.

Results

*Trophic structure of *Fucus* spp. communities and seasonal variability*

For each community, primary sources were distributed over a large range of $\delta^{13}\text{C}$ over the sampling seasons. For the *F. vesiculosus* community, *Caulacanthus ustulatus*, POM and epilithon were the most ^{13}C -depleted sources, and displayed $\delta^{13}\text{C}$ ranging from -20.3 to -24.0 ‰, according to sampling seasons. *Ascophyllum nodosum*, *F. vesiculosus*, *Ulva* spp. and *Hildenbrandia rubra* were more ^{13}C -enriched and showed $\delta^{13}\text{C}$ values ranging from -13.0 to -18.4 ‰, according to sampling seasons. These sources were mainly discriminated by their $\delta^{15}\text{N}$, with *A. nodosum* and *F. vesiculosus* being on average more ^{15}N -depleted (5.1 to 7.4 ‰) than *Ulva* spp. and *H. rubra* (6.2 to 8.9 ‰, Fig. 2.4). For the *F. serratus* community, *C. ustulatus*, *Chondracanthus acicularis*, POM and epilithon were the most ^{13}C -depleted sources, and displayed $\delta^{13}\text{C}$ values ranging from -19.5 to -25.0 ‰, according to sampling seasons. The other sources were more ^{13}C -enriched (-14.8 to -19.9 ‰). Among them, *F. serratus* was the most ^{15}N -depleted (3.0 to 5.7 ‰), while *Ulva* spp., *H. rubra*, *Mastocarpus stellatus* and *P. lenormandii* were more closely related ($\delta^{15}\text{N}$ ranging from 6.5 to 9.7 ‰, Fig. 2.5). Regarding consumers, filter-feeders were on average the most ^{13}C -depleted, with $\delta^{13}\text{C}$ values ranging from -16.5 to -20.8 ‰ for the *F. vesiculosus* community and from -15.2 to -21.2 ‰ for the *F. serratus* community, according to sampling seasons. In comparison, grazers were more ^{13}C -enriched, with values ranging from -13.9 to -16.4 ‰ for the *F. vesiculosus* community and from -13.1 to -17.0 ‰ for the *F. serratus* community, according to sampling seasons. Predators occupied the top of the food webs, and were the most ^{15}N -enriched consumers. They displayed $\delta^{15}\text{N}$ values ranging from 9.2 to 13.0 ‰ for the *F. vesiculosus* community (filter-feeders and grazers: 7.2 to 10.8 ‰, Fig. 2.4) and from 7.7 to 14.0 ‰ for the *F. serratus* community (filter-feeders and grazers: 6.0 to 10.3 ‰, Fig. 2.5), according to sampling seasons.

F. vesiculosus community

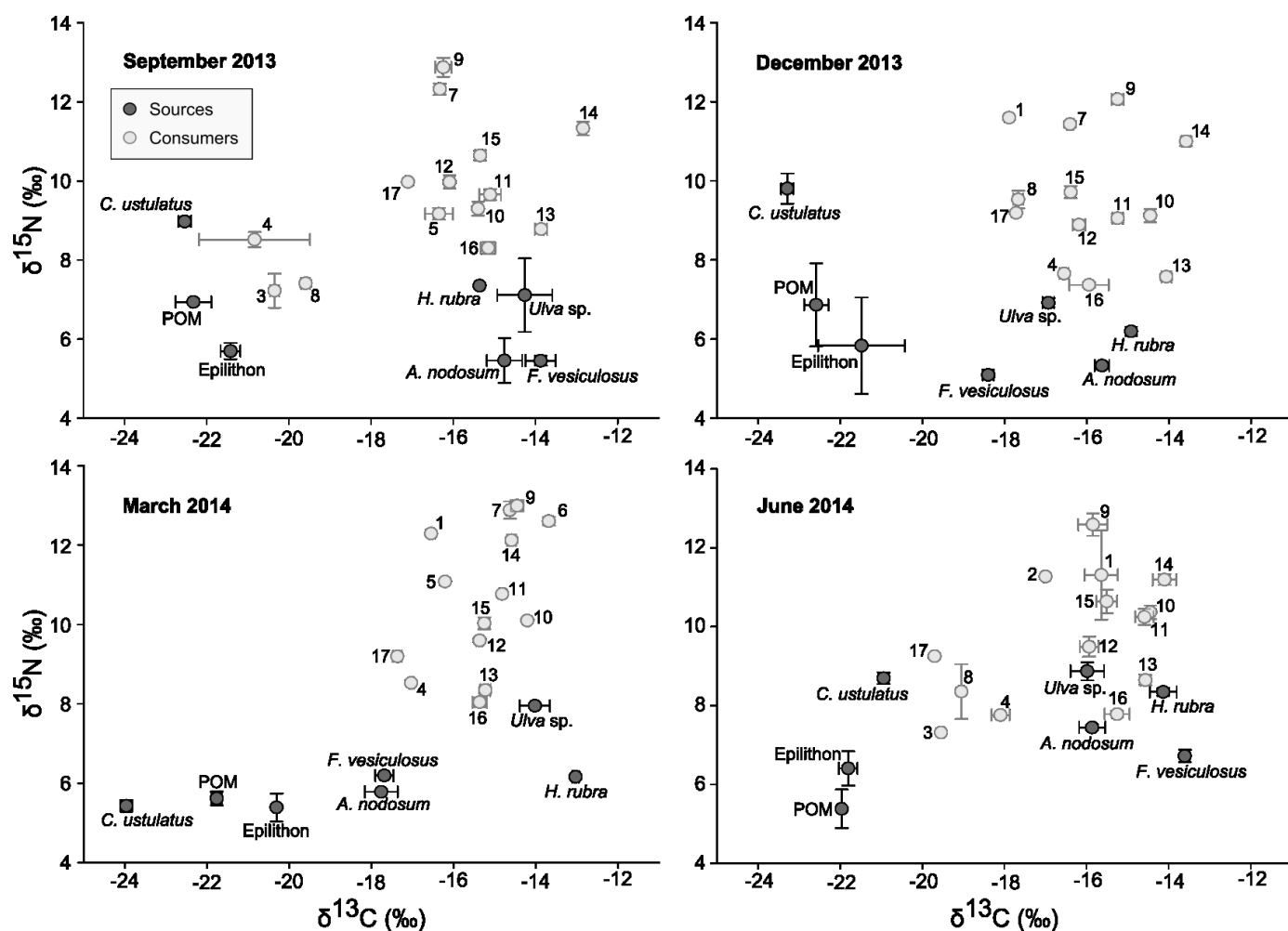


Fig. 2.4 Mean $\pm$ SE of $\delta^{15}\text{N}$ (‰) vs $\delta^{13}\text{C}$ (‰) for primary producers and consumers of the *Fucus vesiculosus* community, sampled in September and December 2013 and March and June 2014. Sources are represented by dark-grey rounds and their names are indicated nearby, while consumers are represented by light-grey rounds. Consumers: 1 *Actinia equina*; 2 *Actinia fragacea*; 3 *Alcyonidium* sp.; 4 Amphipods; 5 *Anemonia viridis*; 6 *Asterina gibbosa*; 7 *Calliostoma zizyphinum*; 8 Campanulariidae; 9 *Carcinus maenas*; 10 *Gibbula pennanti*; 11 *Gibbula umbilicalis*; 12 *Littorina littorea*; 13 *Littorina obtusata*; 14 *Nucella lapillus*; 15 *Phorcus lineatus*; 16 *Patella vulgata*; 17 *Spirorbis* sp. Values are given in Supplementary Material 2.1.

F. serratus community

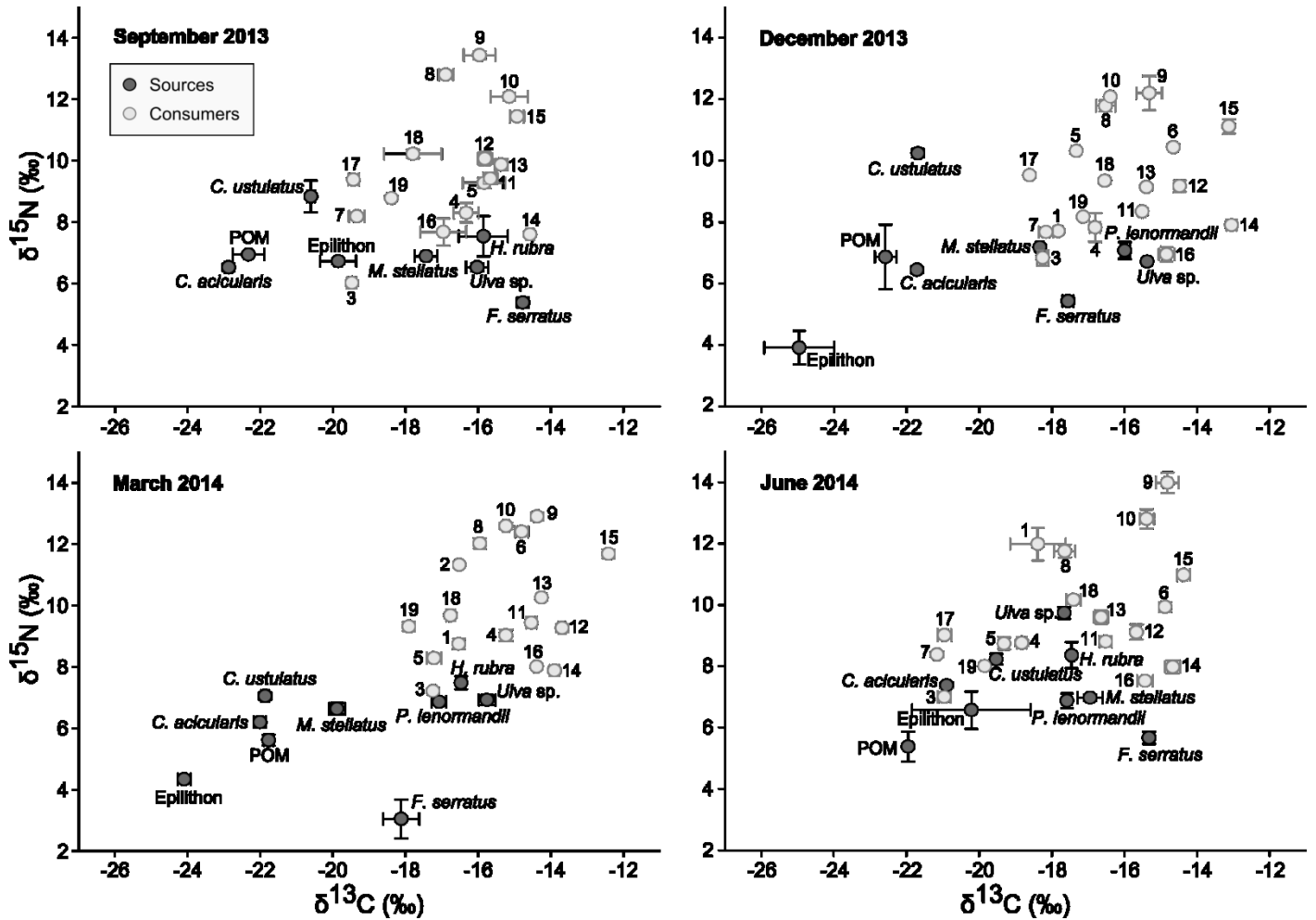


Fig. 2.5 Mean $\pm$ SE of $\delta^{15}\text{N}$ (‰) vs $\delta^{13}\text{C}$ (‰) for primary producers and consumers of the *Fucus serratus* community, sampled in September and December 2013 and March and June 2014. Sources are represented by dark-grey rounds and their names are indicated nearby, while consumers are represented by light-grey rounds. Consumers: 1 *Actinia equina*; 2 *Actinia fragacea*; 3 *Alcyonidium* sp.; 4 Amphipods; 5 *Anemonia viridis*; 6 *Asterina gibbosa*; 7 *Botryllus schlosseri*; 8 *Calliostoma zizyphinum*; 9 *Cancer pagurus*; 10 *Carcinus maenas*; 11 *Gibbula cineraria*; 12 *Gibbula pennanti*; 13 *Gibbula umbilicalis*; 14 *Littorina obtusata*; 15 *Nucella lapillus*; 16 *Patella vulgata*; 17 Polyclinidae; 18 *Porcellana platycheles*; 19 *Spirorbis* sp. Values are given in Supplementary Material 2.2.

The five isotopic metrics showed low variability across seasons, as their coefficient of variation varied between 3.8 and 14.6% in the *F. vesiculosus* community and between 2.4 and 25.4% in the *F. serratus* community (Table 2.1). Only isotopic richness and uniqueness of the *F. serratus* community exhibited a coefficient of variation higher than 15%. This was mainly due to the high ^{13}C and/or ^{15}N depletions of two basal sources in some seasons (i.e. epilithon was ^{13}C and ^{15}N depleted in both December and March, and *F. serratus* was ^{15}N depleted in March, Fig. 2.5).

Table 2.1 Isotopic diversity metrics calculated at each season and for each community, and their associated coefficient of variation (CV, in %).

<i>F. vesiculosus</i> community	Date	Sept	Dec	March	June	CV
	Isotopic richness	0.590	0.565	0.528	0.413	13.3
	Isotopic divergence	0.765	0.729	0.695	0.743	3.8
	Isotopic dispersion	0.607	0.535	0.429	0.461	13.1
	Isotopic evenness	0.785	0.791	0.774	0.844	4.0
	Isotopic uniqueness	0.455	0.349	0.394	0.500	14.6
<i>F. serratus</i> community	Date	Sept	Dec	March	June	CV
	Isotopic richness	0.269	0.415	0.389	0.308	25.4
	Isotopic divergence	0.709	0.701	0.681	0.722	2.4
	Isotopic dispersion	0.503	0.334	0.400	0.447	14.3
	Isotopic evenness	0.828	0.737	0.743	0.801	5.4
	Isotopic uniqueness	0.538	0.274	0.249	0.425	25.2

Relative contributions of potential food sources to the diet of consumers were highly variable between sampling seasons (Table 2.2). In the *F. vesiculosus* community, the contribution of POM to the diet of filter-feeders was maximal in September and June (17.2 to 49.4% on average) and minimal in December and March (8.8 to 13.1% on average). In contrast, erect macroalgae were the main resources to filter-feeders in December and March (86.9 to 91.2% on average, Table 2.2). For grazers, no clear seasonal trend in diet was evidenced, even though *Ulva* spp. and *F. vesiculosus* constituted their main trophic resources in March (27.0 to 77.6% on average) and in June (42.9 to 71.2% on average), respectively. In the *F. serratus* community, the contribution of POM to the diet of filter-feeders was maximal in September and June (29.5 to 77.6% on average) and minimal in December and March (6.1 to 16.1% on average) as well. Erect macroalgae were their main resources in December and March (83.9 to 93.9% on average, Table 2.2). No clear

Table 2.2 Ranges (1st - 99th percentiles) and mean of potential contributions (%) of primary sources to the diet of several species of filter-feeders and grazers, according to SIAR mixing models. Analyses were carried out for each community and during all sampling seasons.

<i>F. vesiculosus</i> community						
	Date	<i>A. nodosum</i>	<i>F. vesiculosus</i>	<i>C. ustulatus</i>	Epilithon	<i>Ulva</i> spp.
Filter-feeders						
<i>Campanulariidae</i>	September	0.2 - 32.2 (12.3)	0.2 - 28.3 (10.9)	2.3 - 62.5 (31.5)	5.7 - 67.5 (36.2)	0.2 - 28.3 (9.2)
	December	1.9 - 55.9 (28.2)	0.3 - 45.1 (15.6)	0.6 - 33.6 (14.7)	0.2 - 29.9 (8.8)	2.6 - 69.4 (32.8)
	June	0.3 - 36.5 (13.4)	0.3 - 27.8 (10.9)	0.8 - 56.2 (24.9)	11.7 - 63.8 (39.4)	0.2 - 34.4 (11.5)
<i>Spirorbis</i> sp.	September	0.6 - 45.4 (19.0)	0.7 - 43.1 (19.1)	1.2 - 40.5 (21.5)	0.5 - 39.8 (17.2)	1.6 - 47.3 (23.3)
	December	3.4 - 57.2 (29.9)	0.5 - 46.3 (18.6)	0.4 - 25.7 (11.4)	0.2 - 28.9 (9.7)	2.4 - 61.5 (30.5)
	March	0.7 - 47.1 (20.6)	0.9 - 52.5 (23.1)	0.3 - 28.2 (10.7)	0.3 - 34.1 (13.1)	14.1 - 50.8 (32.5)
	June	0.2 - 46.5 (14.4)	1.4 - 39.0 (23.3)	0.1 - 20.5 (5.6)	36.3 - 59.7 (49.4)	0.1 - 29.6 (7.3)
Grazers						
<i>Gibbula umbilicalis</i>	September	0.5 - 50.3 (19.8)	1.0 - 51.8 (24.3)	0.7 - 32.4 (12.2)	0.1 - 20.6 (5.9)	10.1 - 64.2 (37.7)
	December	3.2 - 64.5 (30.5)	0.3 - 41.0 (15.5)	0.4 - 28.8 (12.7)	0.1 - 30.0 (8.1)	3.1 - 67.7 (33.1)
	March	0.1 - 23.5 (6.6)	0.1 - 26.4 (8.1)	0.1 - 10.6 (3.3)	0.1 - 15.3 (4.4)	63.0 - 89.3 (77.6)
	June	0.4 - 52.7 (18.5)	14.3 - 71.3 (44.4)	0.1 - 22.5 (4.9)	0.1 - 15.6 (3.3)	2.3 - 53.5 (28.9)
<i>Littorina obtusata</i>	September	0.5 - 47.3 (17.8)	17.9 - 77.3 (48.7)	0.1 - 7.8 (2.0)	0.1 - 7.4 (1.9)	8.7 - 51.1 (29.6)
	December	20.1 - 94.4 (67.6)	0.4 - 64.9 (21.1)	0.1 - 5.8 (1.4)	0.1 - 21.4 (4.5)	0.1 - 20.4 (5.4)
	March	0.5 - 57.2 (20.4)	0.3 - 45.6 (15.9)	0.1 - 26.6 (4.2)	0.1 - 38.0 (9.0)	2.0 - 76.4 (50.5)
	June	0.2 - 41.7 (12.8)	49.1 - 84.2 (71.2)	0.1 - 12.7 (3.5)	0.3 - 15.1 (7.3)	0.1 - 24.3 (5.2)
<i>Patella vulgata</i>	September	2.1 - 58.6 (28.4)	8.5 - 68.5 (38.1)	0.1 - 15.5 (5.8)	0.5 - 22.8 (10.6)	0.7 - 41.4 (17.1)
	December	9.2 - 86.7 (52.3)	0.8 - 70.0 (27.8)	0.1 - 11.8 (2.4)	0.1 - 32.5 (7.9)	0.1 - 41.9 (9.6)
	March	0.6 - 59.2 (23.3)	0.5 - 50.8 (19.7)	0.1 - 43.3 (12.0)	0.2 - 51.0 (18.0)	0.3 - 73.5 (27.0)
	June	0.6 - 60.1 (25.0)	13.8 - 72.2 (42.9)	0.1 - 24.1 (6.8)	0.2 - 26.6 (8.6)	0.3 - 49.2 (16.7)
<i>F. serratus</i> community						
	Date	<i>F. serratus</i>	<i>C. ustulatus</i> & <i>C. acicularis</i>	<i>M. stellatus</i>	Epilithon	<i>Ulva</i> spp.
Filter-feeders						
<i>Alcyonidium</i> sp.	September	0.2 - 27.3 (9.5)	0.8 - 56.2 (23.9)	0.4 - 42.5 (16.1)	15.2 - 60.2 (39.2)	0.2 - 32.2 (11.2)
	December	1.5 - 66.7 (28.1)	0.2 - 35.2 (13.1)	0.5 - 49.2 (19.5)	0.6 - 35.4 (16.1)	1.2 - 45.0 (23.3)
	March	8.5 - 61.5 (41.2)	0.1 - 17.3 (5.0)	0.1 - 27.3 (8.2)	0.1 - 21.5 (6.1)	17.4 - 61.2 (39.5)
	June	0.1 - 18.2 (4.2)	0.1 - 39.1 (9.7)	0.1 - 20.1 (4.7)	36.5 - 91.9 (77.6)	0.1 - 16.8 (3.8)
<i>Spirorbis</i> sp.	September	0.9 - 40.8 (19.7)	0.4 - 39.4 (15.4)	0.4 - 47.4 (18.2)	10.8 - 46.7 (29.5)	0.4 - 44.1 (17.2)
	December	2.4 - 75.5 (37.4)	0.1 - 21.7 (6.2)	0.2 - 43.8 (14.1)	0.1 - 21.5 (6.7)	8.6 - 62.9 (35.7)
	March	0.2 - 36.7 (9.3)	0.3 - 37.2 (13.1)	0.6 - 51.6 (22.3)	0.2 - 32.8 (10.5)	19.3 - 61.8 (44.9)
	June	0.3 - 27.6 (11.0)	0.3 - 49.1 (16.1)	0.2 - 36.3 (12.0)	29.9 - 73.3 (54.1)	0.1 - 25.3 (6.9)
Grazers						
<i>Gibbula pennanti</i>	September	1.1 - 62.5 (29.4)	0.2 - 45.1 (12.7)	0.4 - 48.4 (18.9)	0.1 - 30.8 (7.7)	1.5 - 76.1 (31.4)
	December	0.5 - 45.4 (18.9)	0.2 - 33.1 (10.7)	0.5 - 53.6 (22.4)	0.1 - 23.5 (5.6)	4.8 - 88.2 (42.5)
	March	0.1 - 20.0 (4.9)	2.7 - 50.9 (17.4)	0.5 - 57.8 (23.1)	0.1 - 20.7 (5.0)	10.6 - 87.4 (49.6)
	June	45.2 - 83.1 (69.2)	0.1 - 11.5 (3.1)	0.3 - 42.2 (13.6)	0.1 - 10.7 (2.6)	0.4 - 26.3 (11.5)
<i>Littorina obtusata</i>	September	76.6 - 97.1 (89.9)	0.1 - 4.3 (1.1)	0.1 - 9.7 (2.5)	0.1 - 6.0 (1.5)	0.1 - 18.1 (5.0)
	December	7.3 - 74.8 (37.8)	0.1 - 14.3 (3.6)	0.2 - 31.5 (10.1)	3.0 - 44.8 (26.4)	1.2 - 46.1 (22.1)
	March	9.3 - 41.5 (26.2)	0.2 - 34.0 (12.3)	0.5 - 39.9 (16.8)	0.3 - 38.8 (15.7)	5.8 - 57.9 (30.0)
	June	60.8 - 96.9 (86.3)	0.1 - 10.5 (2.3)	0.1 - 28.4 (6.0)	0.1 - 13.0 (2.9)	0.1 - 10.6 (2.5)
<i>Patella vulgata</i>	September	2.3 - 55.9 (27.1)	0.2 - 35.4 (12.1)	0.4 - 48.2 (19.5)	0.6 - 45.6 (20.0)	0.7 - 50.5 (21.3)
	December	1.1 - 64.8 (27.6)	0.1 - 34.7 (9.1)	0.3 - 45.3 (15.6)	0.3 - 64.2 (20.4)	0.7 - 79.2 (27.4)
	March	3.9 - 40.1 (22.4)	0.4 - 38.9 (15.6)	0.6 - 43.4 (18.9)	0.3 - 41.2 (16.1)	2.9 - 57.3 (27.0)
	June	35.9 - 93.3 (76.7)	0.1 - 17.0 (3.8)	0.2 - 42.8 (10.3)	0.1 - 22.2 (5.0)	0.1 - 20.5 (4.2)

seasonal trend in diet of grazers was evidenced, even though *F. serratus* constituted their main trophic resources in June (69.2 to 86.3% on average).

Comparisons between communities

No seasonal trend in trophic structure has been observed for these two intertidal communities. As well, when comparisons between communities were performed at each season, any difference were evidenced, neither considering the functional isotopic space of whole communities (i.e. high isotopic similarity and isotopic nestedness), nor considering the isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of consumers species present in both communities. Therefore, comparisons between communities were performed using an average isotopic signature of each taxon, obtained after pooling the stable isotope values of the different sampling periods. Considering these year-round means in isotopic signature, the two communities presented an isotopic similarity of 0.779 and an isotopic nestedness of 0.894 (Fig. 2.6). Almost all the taxa (43 of 52) were included in the intersection of the two isotopic spaces. Regarding the consumers shared by the two communities, the model II regressions of dual plots exhibited significant Pearson's coefficient (For $\delta^{13}\text{C}_{\text{Fves}}$ vs $\delta^{13}\text{C}_{\text{Fser}}$, $n = 14$, $R = 0.876$, $p < 0.001$; for $\delta^{15}\text{N}_{\text{Fves}}$ vs $\delta^{15}\text{N}_{\text{Fser}}$, $n = 14$, $R = 0.953$, $p < 0.001$) (Fig. 2.7). The slopes of regressions were equal to 1.2 and 1.0 for $\delta^{13}\text{C}_{\text{Fves}}$ vs $\delta^{13}\text{C}_{\text{Fser}}$ and $\delta^{15}\text{N}_{\text{Fves}}$ vs $\delta^{15}\text{N}_{\text{Fser}}$, respectively, while intercepts were equal to 2.9 and 0.3, respectively. These slopes and intercepts were not significantly different from 1 and 0, respectively (For $\delta^{13}\text{C}_{\text{Fves}}$ vs $\delta^{13}\text{C}_{\text{Fser}}$, $t = 1.42$, $p = 0.091$ for the slope and $t = 1.49$, $p = 0.080$ for the intercept; for $\delta^{15}\text{N}_{\text{Fves}}$ vs $\delta^{15}\text{N}_{\text{Fser}}$, $t = 0.13$, $p = 0.450$ for the slope and $t = 0.40$, $p = 0.349$ for the intercept).

In both communities, *Gibbula* spp., *Littorina* spp. and *Patella vulgata* were the most dominant taxa of grazers: *G. umbilicalis* being the most abundant species in the *F. vesiculosus* community (96 to 208 individuals per m^2) and *G. pennanti* was most abundant species in the *F. serratus* community (130 to 508 individuals per m^2 , Table 2.3). Clustering analysis performed on the taxonomic diversity of grazers discriminated the two communities (Fig. 2.8a), which were significantly different according to the ANOSIM test ($R = 0.75$, $p = 0.029$). When performed on isotopic diversity metrics, these analyses did not allow to significantly discriminate the two communities, neither when they were conducted on unweighted data (ANOSIM test, $R = 0.26$, $p = 0.083$, Fig. 2.8b), nor when conducted on data weighted by abundance of grazers (ANOSIM test, $R = 0.12$, $p = 0.229$, Fig. 2.8c).

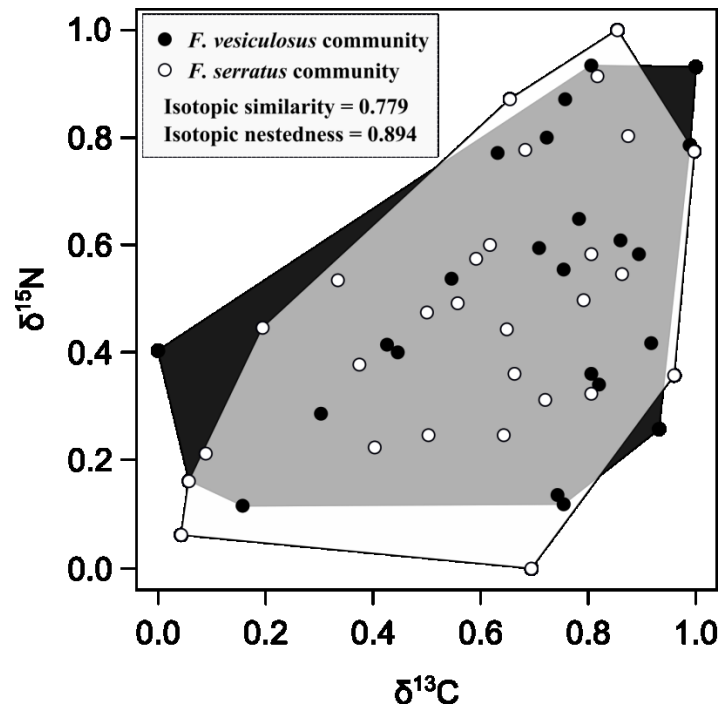


Fig. 2.6 Annual mean of scaled $\delta^{15}\text{N}$ vs scaled $\delta^{13}\text{C}$ for primary producers and consumers of the *F. vesiculosus* (black rounds) and *F. serratus* (white rounds) communities. Isotopic spaces are represented in dark-grey for the *F. vesiculosus* community and in white for the *F. serratus* community. The light-grey space represents the intersection of these two isotopic spaces.

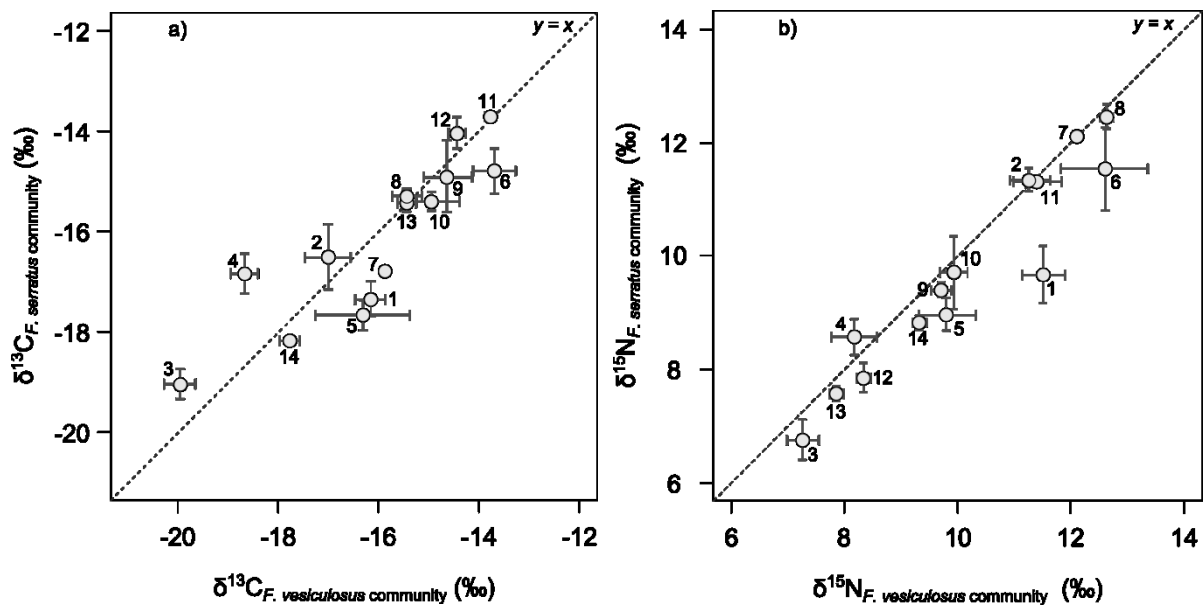


Fig. 2.7 Annual mean of a) $\delta^{13}\text{C} \pm \text{SE}$ (‰) of shared taxa obtained in the *F. vesiculosus* community vs those obtained in the *F. serratus* community, and of b) $\delta^{15}\text{N} \pm \text{SE}$ (‰) of shared taxa obtained in the *F. vesiculosus* community vs those obtained in the *F. serratus* community. Dashed lines represent the function $f(x) = y$. Shared taxa: 1 *Actinia equina*; 2 *Actinia fragacea*; 3 *Alcyonidium* sp.; 4 Amphipods; 5 *Anemonia viridis*; 6 *Asterina gibbosa*; 7 *Calliostoma zizyphinum*; 8 *Carcinus maenas*; 9 *Gibbula pennanti*; 10 *Gibbula umbilicalis*; 11 *Nucella lapillus*; 12 *Littorina obtusata*; 13 *Patella vulgata*; 14 *Spirorbis* sp.

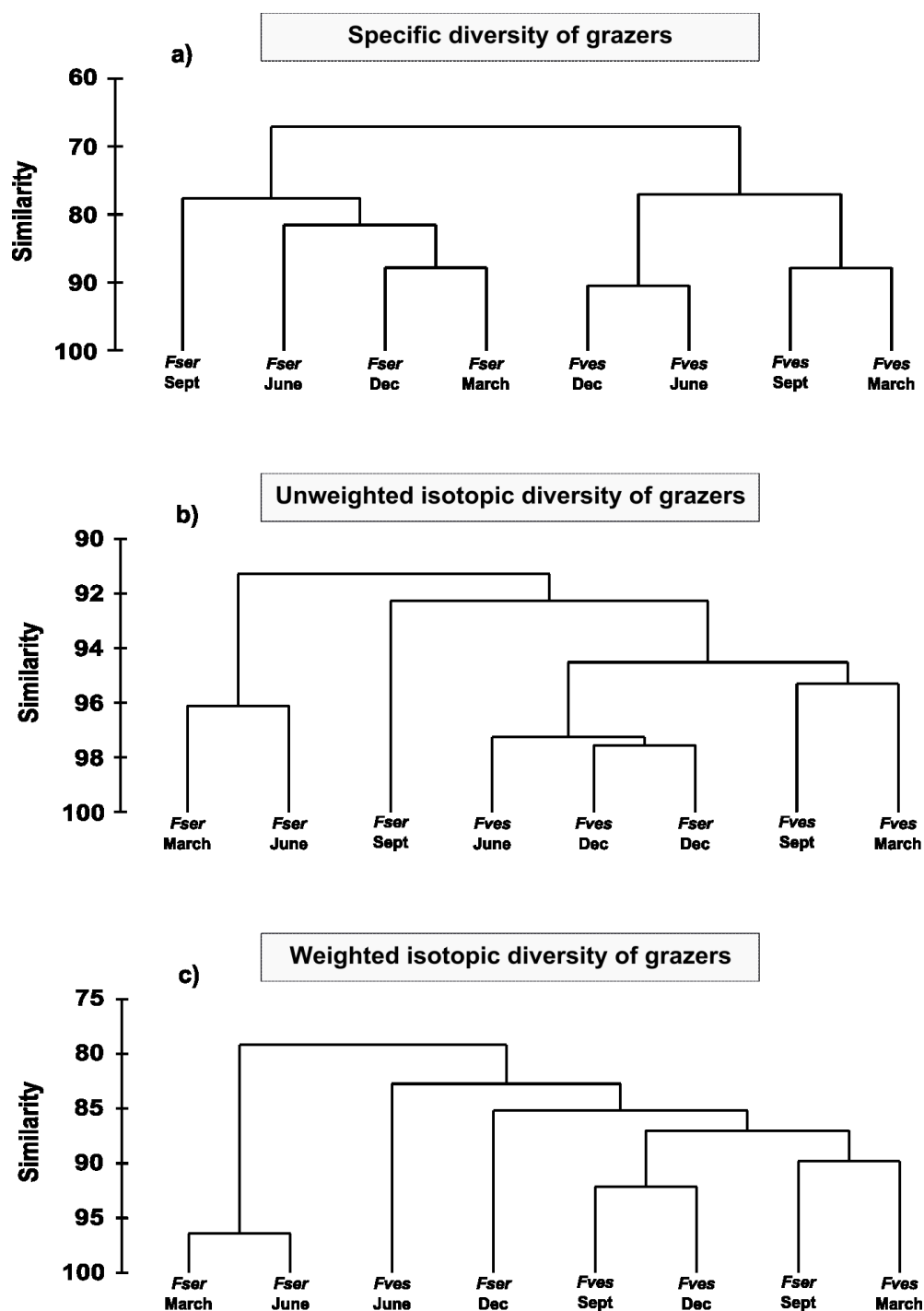


Fig. 2.8 Dendrograms from clustering analyses conducted on the grazers' data; a) on square-root transformed abundances, b) on isotopic diversity metrics calculated from unweighted isotopic data, and c) on isotopic diversity metrics calculated from isotopic data weighted by grazers' abundances.

Table 2.3 Abundance of grazers recorded at each period of observation in the two communities.

	Date	Sept	Dec	March	June
<i>F. vesiculosus</i> community	<i>Gibbula cineraria</i>	0	2	0	2
	<i>Gibbula pennanti</i>	58	170	32	226
	<i>Gibbula umbilicalis</i>	208	106	174	96
	<i>Littorina littorea</i>	6	12	16	2
	<i>Littorina obtusata</i>	172	76	118	86
	<i>Littorina saxatilis</i>	4	0	0	0
	<i>Patella vulgata</i>	32	62	20	22
	Date	Sept	Dec	March	June
<i>F. serratus</i> community	<i>Gibbula cineraria</i>	20	26	54	26
	<i>Gibbula pennanti</i>	130	430	508	240
	<i>Gibbula umbilicalis</i>	36	38	24	46
	<i>Lamellaria perspicua</i>	0	4	0	0
	<i>Littorina obtusata</i>	94	80	70	18
	<i>Patella vulgata</i>	2	12	36	32
	<i>Tricolia pullus</i>	0	0	2	0

Discussion

Trophic structure of Fucus spp. communities

By analysing isotopic composition of the main taxa inhabiting the *Fucus vesiculosus* and *F. serratus* communities, we attempted to depict their global trophic structure. Thus, for each community, functional groups of consumers are well discriminated one from each other whatever the season, despite some overlap. As expected, filter-feeders were the most ^{13}C -depleted consumers, while predators were the most ^{15}N -enriched and occupied the top of the food webs. Both sources and consumers were distributed over large $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges, suggesting that the *Fucus* spp. communities are characterized by a complex trophic structure (Golléty et al. 2010). This complexity may have been however underestimated during this study, as the ultimate top predators of these communities (i.e. fishes and shore birds, Ellis et al. 2007), as well as one potential food source (epibiotic biofilms) were not sampled. Despite that, the large $\delta^{15}\text{N}$ range of consumers (i.e. $\delta^{15}\text{N}$ extended over 4.7 to 7.4 ‰ according to the sampling period) reveals the presence of several trophic levels within the *Fucus* spp. communities. The heterogeneous distribution in $\delta^{15}\text{N}$ of primary consumers prevented, however, to attribute an accurate trophic position to each consumer (Post 2002, Riera et al. 2009). As well, their large $\delta^{13}\text{C}$ range is

characteristic of the occurrence of several trophic pathways, as previously reported in rocky shore habitats (Golléty et al. 2010, Leclerc et al. 2013). This likely results from the high diversity of food sources and feeding behaviors of invertebrates (Riera et al. 2009), which are favored by the multitude of microhabitats that usually characterized rocky shores (Schaal et al. 2010, 2011). Mixing models also highlighted the occurrence of several trophic pathways in fucoid communities. Thus, filter-feeders were supposed to rely mainly on POM and on several species of erect algae through the detrital pathway. As well, the diet of grazers was mainly based on a mix of different species of algae (i.e. *Fucus*, *Ulva* spp., *A. nodosum*, *M. stellatus*). According to these results, filter-feeders and grazers can be considered as generalist species. Therefore, *Fucus* species did not constitute the cornerstone of these food webs, supplying the vast majority of organic carbon for primary consumers (with the exception of June for grazers), as we might reasonably expect from their abundance (i.e. 1.50 to 11.80 kg of fresh weight m⁻² for *Fucus* canopies; 0.02 to 0.28 kg of fresh weight m⁻² for all other erect macroalgae, Bordeyne et al., unpublished data). However, fucoid species are usually considered to have poor nutritional values and can induce anti-grazing defence that may repel primary consumers (Molis et al. 2006). Therefore, primary consumers may show food preference toward more nutritional species (Lubchenco 1978, Littler & Littler 1980, Watson & Norton 1985), despite their lower abundance. Epibiotic biofilms, while not sampled here, may also constitute a complementary trophic resource for some species of grazers, notably those living on fucoid fronds such as *Littorina obtusata* (see Norton et al. 1990). Interestingly, according to its isotopic signature and the results of mixing models, the introduced alga *C. ustulatus* has very low contribution to the diet of grazers. This species, first recorded close to our study site almost 30 years ago (Rio & Cabioch 1988), was suggested to be unpalatable for native consumers due to production of secondary metabolites (Smith et al. 2014). However, filter-feeders may rely on this species through the detrital pathway. Finally, we should mention that the wide ranges in specific contributions obtained from mixing models reveal some uncertainties, and have to be considered with caution (Phillips et al. 2014).

Seasonal variability of trophic structure

The year-round analysis of the isotopic composition of the main taxa inhabiting the *F. vesiculosus* and *F. serratus* communities revealed an overall preservation of their food webs across seasons. This trend, depicted by comparing the biplots drawn at each season, was supported by the low

values of the coefficient of variation across seasons for isotopic diversity metrics, especially in the *F. vesiculosus* community. Such preservation of trophic structure across seasons has already been noticed for a *Fucus*-dominated community (Schaal et al. 2010), even though the studied community was subjected to a strong anthropogenic pressure, which may have influenced isotopic composition of both sources (Viana et al. 2015) and consumers (Warry et al. 2016). Thus, the year-round preservation of food webs we observed in non-impacted fucoid communities could have major implications regarding our knowledge of their dynamics. Indeed, temporal modification of species richness and/or abundance is generally considered as a key process in temperate habitats (Dethier & Williams 2009) and could potentially lead to a seasonality in resource availability, as observed in the Arctic environments. Such seasonality finally leads to large modifications of food webs in these extreme environments (Forest et al. 2008, Darnis et al. 2012). In the present study, however, most of the common macroalgae are perennial (e.g. *Fucus* spp., *M. stellatus*), providing constant resources for grazers, despite the fall to spring decrease in abundance of ephemeral alga *Ulva* spp. (Migné et al. 2015b). Therefore, grazers do not need to switch their diet over the course of the year, explaining their temporal conservation within food webs. In contrast, filter-feeders showed a partial switch in diet over the year, according to the results of mixing models. They were found to rely mainly on phytoplankton-dominated POM during summer and on macroalgae-derived organic matter during winter, which is consistent with seasonal variations in abundance of phytoplankton observed close to our study area (SOMLIT data). Such switch in diet has already been observed in kelp forests of Brittany (Leclerc et al. 2013), and strengthens the idea that macroalgae-derived detritus are a significant food source for filter-feeders (Sarà et al. 2007, Crawley et al. 2009, Schaal et al. 2010, Miller & Page 2012). They are therefore suggested to be opportunistic species relying on the most abundant food source (Ricciardi & Bourget 1999, Schaal et al. 2010). In spite of this temporal diet variability, the average trophic position of this functional group in the two communities remained unchanged, and filter-feeders stayed ^{13}C -depleted compared to grazers, all over the year. The relative seasonal conservation of predators within the food webs was probably due to the seasonal consistency of their potential diet (i.e. primary consumers) but should also result from a relative degree of omnivory and opportunism (Thompson et al. 2007, Silva et al. 2010, Duarte et al. 2015). Finally, the overall preservation of trophic structure across seasons observed despite some seasonal changes in taxonomic diversity of consumers, suggests that some

redundancy in the feeding behaviour of these species (Hawkins et al. 1989, Golléty et al. 2010) helps to keep a relative food web stability over time (Christie et al. 2009).

The high degree of conservation of their trophic structures exhibited by furoid communities during the sampling year could lead to further new insights about dynamics of these habitats. These results should, however, be complemented by the addition of densities or biomasses for each taxa, as this may thoroughly modify the vision we have of trophic relationships (Rigolet et al. 2015).

Comparisons between communities

By analysing isotopic composition of taxa living in these communities, we had the prospect to do comparisons in the context of vertical zonation of intertidal habitats. Using community-wide metrics, we highlighted an important similarity in the average trophic structure of the two *Fucus* spp. communities. This was supported by the large number of taxa present in the common isotopic space. Despite some differences in the species richness and composition between these two communities (Davoult et al., unpublished data), they shared a roughly similar isotopic functional space, suggesting that the same trophic functions are undertaken by different species in the *F. vesiculosus* and *F. serratus* communities. This is consistent with the fact that intertidal communities are mostly composed of generalists and opportunistic species, that rely mainly on the most abundant food sources (Steinarsdóttir et al. 2009). Such plasticity in diet could favour growth rates of consumers, as demonstrated by Lee et al. (1985), providing them some benefit in intertidal habitats. However, the two *Fucus* spp. communities exhibited significant differences in their photosynthetic activity over the year (Bordeyne et al. 2015), potentially leading to important differences in the amount of carbon accumulation at the base of the food webs, and in carbon fluxes toward top predators. Again, further investigations taking into account taxon abundances are needed to understand more faithfully the trophodynamics of these communities.

Although the *F. vesiculosus* and *F. serratus* communities exhibit some differences in their specific composition, several taxa of consumers live commonly in the two communities. These taxa were found to exhibit, on average, similar isotopic composition, whether they were found in the *F. vesiculosus* community or in the *F. serratus* one. Steinarsdóttir et al. (2009) observed a similar pattern on a few number of invertebrate species from Icelandic coast. These results are particularly interesting since most of the considered taxa are sessile or slow moving invertebrates.

Therefore, this suggests that they used similar diet resources in both locations. The case of the green crab *Carcinus maenas* is slightly different, as for this highly mobile species, migration toward higher intertidal levels for foraging activity has been shown to be usual during high tide (Silva et al. 2010). This species can thus be considered as a coupler that underlie landscape level food webs, as defined by Rooney et al. (2008).

Finally, we focused on grazers, which constitute the most abundant group of invertebrates in the two communities. Diversity monitoring highlighted significant differences in the composition of this group between the two communities, in accordance with the tidal control of species distribution and abundances (Raffaelli & Hawkins 1999). Furthermore, the high diversity of radula types and feeding mechanisms of grazers within a community indicated some functional complementarity (for instance, *P. vulgata* is considered as a scraper of hard substrata, while *Gibbula* spp. seem rather to brush algae, Hawkins et al. 1989), and is likely to reduce interspecific competition and promote species coexistence in relatively high abundances. However, when considering isotopic composition, no significant difference between communities has been highlighted, whether the abundance of grazers was accounted for or not. These results suggest that the two groups of grazers have almost the same trophic functions within the two communities, despite some differences in species identities and abundances.

By focusing on grazers, the present study confirms that considering species abundance or biomass in association with stable isotope approach is a fresh opportunity to bring some new insights about community functioning (Cucherousset & Villéger 2015, Rigolet et al. 2015). In this study, this approach allowed us to exclude significant difference in the trophic structure of grazers between the two communities, as discussed before. Without this, any evident conclusion would have been drawn, as the doubt could still subsist with a p-value of 0.08 (obtained for unweighted isotopic data of grazers), especially when specific composition and abundance varied between the two communities.

Conclusion

This study highlighted that the two widespread *Fucus vesiculosus* and *F. serratus* communities exhibited trophic structures that remained highly conserved over a year, despite some seasonal fluctuations in physiological processes and in species composition and abundance. Thus, such food web approaches should be carried on, not only at the seasonal scale but also at various

temporal scales (McMeans et al. 2015), to better understand the dynamics of food webs, especially according to the specific features of their environment. Furthermore, the two *Fucus* spp. communities exhibited similar trophic structure while they are located at different shore levels and exhibit some differences in their specific composition. In this context of vertical zonation, it would be interesting to go further, and for instance have a look to the specific composition and food webs of several communities dominated by canopy-forming macroalgae that are established on the whole intertidal gradient.

Supplementary material 2.1 Mean $\pm$ SE (‰) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of sources and consumers of the *F. vesiculosus* community, with the number of replicates (n) analysed for each sampling period (September and December 2013 and March and June 2014). Groups: ER = Erect alga; EN = Encrusting alga; G = Grazer; FF = Filter-feeder; P = Predator.

		September			December			March			June		
	Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n
<i>Ascophyllum nodosum</i>	ER	-14.8 $\pm$ 0.4	5.5 $\pm$ 0.6	3	-15.6 $\pm$ 0.2	5.3 $\pm$ 0.1	3	-17.8 $\pm$ 0.4	5.8 $\pm$ 0.1	3	-15.9 $\pm$ 0.3	7.4 $\pm$ 0.1	3
<i>Caulecanthus ustulatus</i>	ER	-22.5 $\pm$ 0.2	9.0 $\pm$ 0.1	3	-23.3 $\pm$ 0.1	9.8 $\pm$ 0.4	3	-24.0 $\pm$ 0.2	5.4 $\pm$ 0.1	3	-20.9 $\pm$ 0.1	8.7 $\pm$ 0.1	3
<i>Fucus vesiculosus</i>	ER	-13.9 $\pm$ 0.4	5.5 $\pm$ 0.1	3	-18.4 $\pm$ 0.1	5.1 $\pm$ 0.1	3	-17.7 $\pm$ 0.2	6.2 $\pm$ 0.1	3	-13.6 $\pm$ 0.1	6.7 $\pm$ 0.2	3
<i>Hildenbrandia rubra</i>	EN	-15.4	7.4	1	-14.9 $\pm$ 0.1	6.2 $\pm$ 0.2	3	-13.0 $\pm$ 0.1	6.2 $\pm$ 0.1	2	-14.1 $\pm$ 0.3	8.3 $\pm$ 0.1	3
<i>Ulva</i> sp.	ER	-14.3 $\pm$ 0.7	7.1 $\pm$ 0.9	3	-16.9 $\pm$ 0.1	6.9 $\pm$ 0.1	3	-14.0 $\pm$ 0.4	7.9 $\pm$ 0.1	3	-16.0 $\pm$ 0.4	8.9 $\pm$ 0.2	3
Epilithon		-21.4 $\pm$ 0.2	5.7 $\pm$ 0.2	2	-21.5 $\pm$ 1.1	5.8 $\pm$ 1.2	2	-20.3 $\pm$ 0.1	5.4 $\pm$ 0.4	2	-21.8 $\pm$ 0.2	6.4 $\pm$ 0.4	2
POM		-22.3 $\pm$ 0.4	6.9 (1)	2	-22.6 $\pm$ 0.3	6.9 $\pm$ 1.1	3	-21.8 $\pm$ 0.1	5.6 $\pm$ 0.2	3	-22.0 (1)	5.4 $\pm$ 0.5	2
<i>Actinia equina</i>	P				-17.9	11.6	1	-16.5	12.3	1	-15.6 $\pm$ 0.4	11.3 $\pm$ 1.1	4
<i>Actinia fragacea</i>	P										-17.0	11.3	1
<i>Anemonia viridis</i>	P	-16.3 $\pm$ 0.3	9.2 $\pm$ 0.1	2				-16.2	11.1	1			
Campanularidae	FF	-19.6 $\pm$ 0.1	7.4 $\pm$ 0.1	4	-17.7 $\pm$ 0.1	9.5 $\pm$ 0.2	3				-19.0 $\pm$ 0.1	8.4 $\pm$ 0.7	3
<i>Spirorbis</i> sp.	FF	-17.1	10.0	1	-17.7	9.2	1	-17.4 $\pm$ 0.1	9.2 $\pm$ 0.1	3	-19.7	9.3	1
<i>Celliostoma zizyphinum</i>	P	-16.3 $\pm$ 0.1	12.3 $\pm$ 0.1	2	-16.4 $\pm$ 0.1	11.4 $\pm$ 0.1	3	-14.6 $\pm$ 0.1	12.9 $\pm$ 0.2	2			
<i>Gibbula pennanti</i>	G	-15.4 $\pm$ 0.1	9.3 $\pm$ 0.2	6	-14.4 $\pm$ 0.1	9.1 $\pm$ 0.2	6	-14.2 $\pm$ 0.1	10.1 $\pm$ 0.1	6	-14.5 $\pm$ 0.1	10.4 $\pm$ 0.2	6
<i>Gibbula umbilicalis</i>	G	-15.1 $\pm$ 0.3	9.7 $\pm$ 0.1	6	-15.2 $\pm$ 0.1	9.1 $\pm$ 0.1	6	-14.8 $\pm$ 0.1	10.8 $\pm$ 0.1	6	-14.6 $\pm$ 0.2	10.2 $\pm$ 0.2	6
<i>Littorina littorea</i>	G	-16.1 $\pm$ 0.1	10.0 $\pm$ 0.2	6	-16.2 $\pm$ 0.2	8.9 $\pm$ 0.1	6	-15.4 $\pm$ 0.1	9.6 $\pm$ 0.1	6	-15.9 $\pm$ 0.2	9.5 $\pm$ 0.2	6
<i>Littorina obtusata</i>	G	-13.9 $\pm$ 0.2	8.8 $\pm$ 0.1	10	-14.1 $\pm$ 0.1	7.6 $\pm$ 0.1	10	-15.2 $\pm$ 0.1	8.3 $\pm$ 0.1	10	-14.6 $\pm$ 0.1	8.6 $\pm$ 0.1	10
<i>Nucella lapillus</i>	P	-12.8 $\pm$ 0.1	11.3 $\pm$ 0.2	6	-13.6 $\pm$ 0.1	11.0 $\pm$ 0.1	6	-14.6 $\pm$ 0.1	12.1 $\pm$ 0.1	6	-14.1 $\pm$ 0.3	11.2 $\pm$ 0.1	6
<i>Patella vulgata</i>	G	-15.1 $\pm$ 0.2	8.3 $\pm$ 0.1	6	-15.9 $\pm$ 0.5	7.4 $\pm$ 0.1	6	-15.4 $\pm$ 0.2	8.0 $\pm$ 0.1	5	-15.3 $\pm$ 0.3	7.8 $\pm$ 0.1	6
<i>Phorcus lineatus</i>	G	-15.3 $\pm$ 0.1	10.6 $\pm$ 0.1	6	-16.4 $\pm$ 0.1	9.7 $\pm$ 0.2	6	-15.3 $\pm$ 0.1	10.0 $\pm$ 0.2	6	-15.5 $\pm$ 0.2	10.6 $\pm$ 0.3	6
<i>Alcyonidium</i> sp.	FF	-20.3 $\pm$ 0.1	7.2 $\pm$ 0.4	6							-19.5 $\pm$ 0.1	7.3 $\pm$ 0.1	6
Amphipods	FF	-20.8 $\pm$ 1.4	8.5 $\pm$ 0.2	6	-16.5 $\pm$ 0.1	7.7 $\pm$ 0.1	3	-17.0 $\pm$ 0.1	8.5 $\pm$ 0.1	3	-18.1 $\pm$ 0.2	7.8 $\pm$ 0.1	3
<i>Carcinus maenas</i>	P	-16.2 $\pm$ 0.2	12.9 $\pm$ 0.2	5	-15.2 $\pm$ 0.2	12.1 $\pm$ 0.1	5	-14.5 $\pm$ 0.2	13.0 $\pm$ 0.1	5	-15.8 $\pm$ 0.4	12.6 $\pm$ 0.3	4
<i>Asterina gibbosa</i>	P							-13.7 $\pm$ 0.1	12.6 $\pm$ 0.1	2			

Supplementary material 2.2 Mean $\pm$ SE (‰) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of sources and consumers of the *F. serratus* community, with the number of replicates (n) analysed for each sampling period (September and December 2013 and March and June 2014). Groups: ER = Erect alga; EN = Encrusting alga; G = Grazer; FF = Filter-feeder; P = Predator.

	Group	September			December			March			June		
		$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n
<i>Caulacanthus ustulatus</i>	ER	-20.6 $\pm$ 0.1	8.8 $\pm$ 0.5	3	-21.7 $\pm$ 0.1	10.2 $\pm$ 0.1	3	-21.9 $\pm$ 0.1	7.1 $\pm$ 0.1	3	-19.5 $\pm$ 0.1	8.2 $\pm$ 0.2	3
<i>Chondracanthus acicularis</i>	ER	-22.9 $\pm$ 0.1	6.5 $\pm$ 0.1	3	-21.7 $\pm$ 0.1	6.4 $\pm$ 0.1	3	-22.1 $\pm$ 0.2	6.2 $\pm$ 0.2	3	-20.9 $\pm$ 0.1	7.4 $\pm$ 0.1	3
<i>Fucus serratus</i>	ER	-14.8 $\pm$ 0.1	5.4 $\pm$ 0.2	3	-17.6 $\pm$ 0.1	5.4 $\pm$ 0.1	3	-18.1 $\pm$ 0.5	3.0 $\pm$ 0.6	3	-15.3 $\pm$ 0.1	5.7 $\pm$ 0.2	3
<i>Hildenbrandia rubra</i>	EN	-15.9 $\pm$ 0.7	7.5 $\pm$ 0.7	2				-16.5 $\pm$ 0.1	7.5 $\pm$ 0.2	2	-17.5 $\pm$ 0.1	8.4 $\pm$ 0.4	3
<i>Mastocarpus stellatus</i>	ER	-17.4 $\pm$ 0.3	6.9 $\pm$ 0.1	3	-18.3 $\pm$ 0.1	7.2 $\pm$ 0.1	3	-19.9 $\pm$ 0.2	6.6 $\pm$ 0.2	3	-16.9 $\pm$ 0.3	7.0 $\pm$ 0.1	3
<i>Phymatolithon lenormandii</i>	EN				-16.0 $\pm$ 0.1	7.1 $\pm$ 0.3	3	-17.1 $\pm$ 0.2	6.9 $\pm$ 0.1	3	-17.6 $\pm$ 0.1	6.9 $\pm$ 0.2	3
<i>Ulva</i> sp.	ER	-16.0 $\pm$ 0.3	6.5 $\pm$ 0.1	3	-15.4 $\pm$ 0.1	6.7 $\pm$ 0.1	3	-15.8 $\pm$ 0.2	6.9 $\pm$ 0.2	3	-17.7 $\pm$ 0.1	9.7 $\pm$ 0.2	3
Epilithon		-19.9 $\pm$ 0.5	6.7 $\pm$ 0.1	2	-25.0 $\pm$ 1.0	3.9 $\pm$ 0.6	2	-24.1 $\pm$ 0.2	4.3 $\pm$ 0.1	2	-20.2 $\pm$ 1.6	6.6 $\pm$ 0.6	2
POM		-22.3 $\pm$ 0.4	6.9 (1)	2	-22.6 $\pm$ 0.3	6.9 $\pm$ 1.1	3	-21.8 $\pm$ 0.1	5.6 $\pm$ 0.2	3	-22.0 (1)	5.4 $\pm$ 0.5	2
<i>Actinia equina</i>	P				-17.8	7.7	1	-16.5 $\pm$ 0.1	8.7 $\pm$ 0.2	3	-18.4 $\pm$ 0.8	12.0 $\pm$ 0.5	2
<i>Actinia fragacea</i>	P							-16.5 $\pm$ 0.1	11.3 $\pm$ 0.1	2			
<i>Anemonia viridis</i>	P	-15.8 $\pm$ 0.6	9.3 $\pm$ 0.2	2	-17.3	10.3	1	-17.2 $\pm$ 0.2	8.3 $\pm$ 0.1	2	-19.3 $\pm$ 0.1	8.7 $\pm$ 0.2	3
<i>Spirorbis</i> sp.	FF	-18.4	8.8	1	-17.1	8.2	1	-17.9 $\pm$ 0.1	9.3 $\pm$ 0.2	3	-19.9	8.0	1
<i>Calliostoma zizyphinum</i>	P	-16.9 $\pm$ 0.2	12.8 $\pm$ 0.1	6	-16.5 $\pm$ 0.3	11.8 $\pm$ 0.2	5	-16.0 $\pm$ 0.1	12.0 $\pm$ 0.2	5	-17.6 $\pm$ 0.3	11.6 $\pm$ 0.2	6
<i>Gibbula cineraria</i>	G	-15.7 $\pm$ 0.2	9.4 $\pm$ 0.2	6	-15.5 $\pm$ 0.1	8.3 $\pm$ 0.1	6	-14.5 $\pm$ 0.1	9.4 $\pm$ 0.1	6	-16.5 $\pm$ 0.2	8.8 $\pm$ 0.1	6
<i>Gibbula pennanti</i>	G	-15.8 $\pm$ 0.2	10.1 $\pm$ 0.2	6	-14.5 $\pm$ 0.1	9.2 $\pm$ 0.2	6	-13.7 $\pm$ 0.1	9.3 $\pm$ 0.1	6	-15.7 $\pm$ 0.1	9.1 $\pm$ 0.3	6
<i>Gibbula umbilicalis</i>	G	-15.4 $\pm$ 0.2	9.9 $\pm$ 0.2	6	-15.4 $\pm$ 0.1	9.1 $\pm$ 0.1	6	-14.3 $\pm$ 0.1	10.3 $\pm$ 0.1	6	-16.6 $\pm$ 0.2	9.6 $\pm$ 0.2	6
<i>Littorina obtusata</i>	G	-14.6 $\pm$ 0.1	7.6 $\pm$ 0.1	10	-13.1 $\pm$ 0.1	7.9 $\pm$ 0.1	10	-13.9 $\pm$ 0.1	7.9 $\pm$ 0.1	10	-14.7 $\pm$ 0.2	8.0 $\pm$ 0.2	10
<i>Nucella lapillus</i>	P	-14.9 $\pm$ 0.2	11.4 $\pm$ 0.1	6	-13.1 $\pm$ 0.1	11.1 $\pm$ 0.2	6	-12.4 $\pm$ 0.1	11.7 $\pm$ 0.1	6	-14.4 $\pm$ 0.2	11.0 $\pm$ 0.1	6
<i>Patella vulgata</i>	G	-17.0 $\pm$ 0.6	7.7 $\pm$ 0.4	6	-14.8 $\pm$ 0.2	7.0 $\pm$ 0.2	5	-14.4 $\pm$ 0.1	8.0 $\pm$ 0.1	6	-15.4 $\pm$ 0.2	7.5 $\pm$ 0.1	6
<i>Alcyonidium</i> sp.	FF	-19.5 $\pm$ 0.1	6.0 $\pm$ 0.1	6	-18.3 $\pm$ 0.2	6.8 $\pm$ 0.2	6	-17.2 $\pm$ 0.1	7.2 $\pm$ 0.1	5	-21.0 $\pm$ 0.2	7.0 $\pm$ 0.1	6
Amphipods	FF	-16.3 $\pm$ 0.3	8.3 $\pm$ 0.3	2	-16.8 $\pm$ 0.1	7.8 $\pm$ 0.5	2	-15.2 $\pm$ 0.1	9.0 $\pm$ 0.2	3	-18.8 $\pm$ 0.1	8.8 $\pm$ 0.1	3
<i>Cancer pagurus</i>	P	-16.0 $\pm$ 0.4	13.4 $\pm$ 0.1	3	-15.3 $\pm$ 0.4	12.2 $\pm$ 0.6	2	-14.4 $\pm$ 0.1	12.9 $\pm$ 0.1	5	-14.8 $\pm$ 0.3	14.0 $\pm$ 0.3	3
<i>Carcinus maenas</i>	P	-15.1 $\pm$ 0.5	12.1 $\pm$ 0.1	6	-16.4	12.1	1	-15.2 $\pm$ 0.1	12.6 $\pm$ 0.1	6	-15.4 $\pm$ 0.2	12.8 $\pm$ 0.3	5
<i>Porcellana platycheles</i>	FF	-17.8 $\pm$ 0.8	10.2 $\pm$ 0.1	5	-16.5 $\pm$ 0.1	9.3 $\pm$ 0.1	5	-16.6 $\pm$ 0.1	9.7 $\pm$ 0.1	5	-17.4 $\pm$ 0.2	10.2 $\pm$ 0.1	5
<i>Botryllus schlosseri</i>	FF	-19.3 $\pm$ 0.2	8.2 $\pm$ 0.1	3	-18.2 $\pm$ 0.2	7.7 $\pm$ 0.1	5				-21.2 $\pm$ 0.1	8.4 $\pm$ 0.1	3
Polyclinidae	FF	-19.4 $\pm$ 0.1	9.4 $\pm$ 0.1	6	-18.6 $\pm$ 0.1	9.5 $\pm$ 0.1	5				-21.0 $\pm$ 0.2	9.0 $\pm$ 0.1	5
<i>Asterina gibbosa</i>	P				-14.7	10.4	1	-14.8 $\pm$ 0.2	12.4 $\pm$ 0.1	5	-14.9 $\pm$ 0.1	9.9 $\pm$ 0.2	2

**PARTIE II – PROCESSUS DE REGULATION DU
FONCTIONNEMENT DES COMMUNAUTES A
CANOPEE DE *FUCUS***



Chapitre 3

Variation du métabolisme au cours du cycle de marée

Contexte général et résumé

Les mesures ponctuelles de métabolisme réalisées en début de périodes d'émersion ont démontré l'importance qu'ont les fluctuations saisonnières des conditions environnementales sur la production primaire et la respiration des communautés de *Fucus* (Chapitre 1). En milieu intertidal, les conditions environnementales fluctuent aussi de façon considérable à plus petite échelle de temps, et en particulier à celle du cycle de marée. Ainsi, les communautés intertidales sont alternativement émergées et immergées, ce qui les expose à deux environnements particulièrement contrastés. A l'émersion, les communautés peuvent être exposées à de fortes lumières, des températures extrêmes, ou encore au vent, ce qui favorise la dessiccation. Au contraire, à l'immersion les conditions environnementales sont plus tamponnées mais les températures estivales et l'intensité lumineuse sont généralement faibles. L'alternance des périodes d'émersion et d'immersion au cours du cycle de marée est donc susceptible de générer de fortes variations du métabolisme pour les communautés de macroalgues. A notre connaissance, aucune étude n'a évalué à ce jour le métabolisme de ce type de communautés à la fois lors de périodes d'émersion et d'immersion. Quelques études réalisées en laboratoire sur des morceaux de thalle de *Fucus* ou des individus entiers ont mis en évidence que leur métabolisme varie effectivement selon qu'il soit mesuré dans l'air ou dans l'eau (par ex. Johnson et al. 1974, Madsen & Maberly 1990, Williams & Dethier 2005). Néanmoins, ces études ne permettent pas de comprendre le métabolisme en conditions naturelles et à l'échelle de la communauté. Plus récemment, Clavier et al. (2011) et Ouisse et al. (2011a) ont mesuré le métabolisme d'herbiers de zostères *in situ* au cours du cycle de marée et ont montré qu'il était plus important dans l'eau que dans l'air. Bien que le fonctionnement des herbiers de zostères soit différent de celui des communautés à canopée de macroalgues, ces résultats originaux nous ont encouragés à poursuivre dans cette voie, afin de mieux appréhender le fonctionnement des communautés intertidales.

En général, les périodes d'émersion sont considérées comme les plus contraignantes, notamment en raison de la dessiccation qui affecte les organismes intertidaux. Cette dessiccation pourrait entraîner d'importantes diminutions de la production primaire et de la respiration, comme cela a été démontré par des mesures en laboratoire (par ex. Quadir et al. 1979) ou en milieu naturel

(Lamote et al. 2012) sur des individus isolés. Cela reste à vérifier sur des communautés à canopées de macroalgues, en particulier lorsqu'elles sont denses.

Le métabolisme de la communauté de *F. serratus* a été mesuré *in situ* lors de périodes d'émersion et d'immersion, à l'aide de chambres benthiques. Ces mesures ont été réalisées à 13 reprises, de façon à couvrir l'ensemble des saisons entre avril 2014 et février 2016. La production primaire et la respiration ont été évaluées en début d'émersion par la mesure des flux de CO₂, comme présenté dans le Chapitre 1, et à l'immersion, par la mesure des flux de carbone inorganique dissous. Ce suivi montre que le métabolisme varie de façon saisonnière à l'émersion comme à l'immersion. La production primaire et la respiration de la communauté de *F. serratus* apparaissent significativement plus élevées dans l'air que dans l'eau, en particulier en hiver. L'analyse des paramètres environnementaux (lumière, température) mesurés durant les incubations suggère une limitation de la production primaire par le manque de lumière à l'immersion. En complément, le métabolisme de cette communauté a été mesuré à 7 reprises au cours de périodes complètes d'émersion de vive-eau (séries d'incubations successives, depuis le retrait de la marée jusqu'à son retour), d'avril 2014 à avril 2015. Les résultats indiquent que la production primaire et la respiration demeurent globalement élevées pendant toute la durée de l'émersion. Ces résultats suggèrent donc que les périodes d'émersion jouent un rôle fondamental pour le fonctionnement de la communauté de *F. serratus*, et pourraient contribuer de façon considérable à son bilan énergétique, bien qu'elle ne soit émergée que 15 à 25 % du temps.

Article n°3

Variation of furoid community metabolism during the tidal cycle: insights from *in situ* measurements of seasonal carbon fluxes during emersion and immersion

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Article en révision dans *Limnology and Oceanography*

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Abstract: Intertidal communities dominated by canopy-forming brown seaweed are typically highly productive systems. However, their metabolism can vary significantly over time, due to fluctuations in abiotic parameters. If tidal and/or seasonal cycles play an important role in the regulation of metabolism in these communities, they may therefore strongly influence community functioning and dynamics. Here, we investigated the low mid-intertidal *Fucus serratus* community, measuring *in situ* carbon fluxes of its primary production and respiration during different seasons. To perform direct comparisons of its underwater and aerial metabolism, these measurements were carried out during immersion and emersion, analyzing the changes in dissolved inorganic carbon and in CO₂ concentrations under closed benthic chambers. Our results show that during both tidal periods, community gross primary production and respiration varied seasonally with minimum values in winter and maximum values in summer. These values were, on average, 5 and 3.5 times higher when the community was exposed to air than when immersed, due to the large changes that occur in abiotic environmental conditions during the tidal cycle. Primary production fluctuated greatly during immersion and was generally limited by underwater light availability. In contrast, primary production remained high during emersion, partly because canopies limit the water loss of their understory layers. During both tidal periods, community respiration was mainly driven by temperature. Our results suggest that the relatively high metabolism during emersion contributes substantially to the total energy budget of furoid mid-intertidal communities, even those that are low on the shore and spend most of their time underwater.

Keywords: Carbon fluxes; Community gross primary production; Community respiration; Emersion; *Fucus serratus* community; Immersion; *In situ* metabolism; Intertidal; Seasons; Tidal cycle

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Introduction

Intertidal communities are by definition exposed to two alternating, contrasting environments (i.e. air and seawater), with markedly different abiotic conditions. Such abrupt changes in abiotic environmental conditions, and especially in light and temperature, are likely to influence community metabolism (e.g. Clavier et al. 2011; Ouisse et al. 2011a). When exposed to air, intertidal primary producers can undergo numerous stresses (*sensu* Wahl et al. 2011), such as desiccation (leading to hydric stress) and extreme light intensity and temperature. These potential stressors may inhibit their photosynthetic efficiency (Quadir et al. 1979, Huppertz et al. 1990, Hanelt et al. 1993), and the activation of protective mechanisms may have physiological costs for primary producers (Tomanek & Helmuth 2002). When immersed in water, intertidal primary producers may face low light conditions due to the attenuation of light by seawater, potentially limiting their photosynthesis (Tait & Schiel 2011a). Large species that undergo self-shading may therefore be particularly affected by these low light conditions (Binzer & Sand-Jensen 2002b). The duration of aerial and underwater exposure may significantly drive the metabolism of intertidal primary producers, and thus play a substantial role in their organic carbon acquisition (Williams & Dethier 2005, Dethier & Williams 2009). Nevertheless, within macroalgal-dominated communities, dense canopy-forming species may buffer these environmental constraints for the understory layers (Tait & Schiel 2013). Furthermore, in this type of complex assemblage, numerous species interact and may complement each other, notably for light use (Tait & Schiel 2011a). Such natural assemblages cope efficiently with the harsh environmental conditions they experience throughout a tidal cycle.

Among intertidal macroalgal communities, those dominated by canopy-forming brown seaweed (Phaeophyceae) are particularly ubiquitous in temperate regions (e.g. Lüning 1990; Jueterbock et al. 2013). These complex habitats fulfill some essential ecological roles, including food supply for other habitats and nurseries for numerous invertebrate species (Crawley et al. 2009, Schmidt et al. 2011). Although intertidal macroalgal systems have been recognized as highly productive for several decades (Mann 1973), their metabolism has not been extensively studied to date. Only a few studies have investigated community metabolism *in situ*, but only either during emersion periods (e.g. Golléty et al. 2008; Bordeyne et al. 2015) or during immersion (e.g. Tait and Schiel 2010), and there are no direct comparisons of aerial and underwater community metabolism (Migné et al. 2015a). However, such comparisons can provide insight into the relationship

between environmental constraints and community metabolism (Pedersen et al. 2013), and therefore into the functioning and dynamics of such communities.

Here, we investigated the large intertidal community dominated by *Fucus serratus* Linnaeus. Its aerial and underwater rates of primary production and respiration were compared by measuring *in situ* carbon fluxes both during emersion and immersion. This comparison was carried out at different periods of the year to study the effect of the seasonal variations in environmental parameters (Rheuban et al. 2014). Light intensity and temperature were also surveyed in an attempt to determine their role in the regulation of community metabolism. Because the *F. serratus* community is established at the low mid-intertidal level, it is exposed to air for only approximately 15 to 25% of time. Thus, we tested whether this community exhibits higher primary production during immersion than during emersion.

Materials & methods

Study site

This study was performed on an intertidal boulder reef located in front of the Station Biologique de Roscoff (48°43.778'N, 3°59.770'W) in the southwestern part of the English Channel. This reef is located in the temperate part of the Northern hemisphere and therefore has seasonal variations in incident irradiance and temperature (Supplementary material 3.1). This semi-sheltered reef experiences a semi-diurnal tidal cycle with maximal amplitude of about 9 m. Several communities dominated by canopy-forming algae are established on this shore according to a vertical zonation pattern. The low mid-intertidal level of this shore (from 2.5 to 3.5 m above chart datum) is typically characterized by a dense belt of the *F. serratus* community, where the thallus of the dominant species frequently covers 100% of the substratum.

Measurement of community metabolism

Within this area, three concrete quadrats were set in place (2-3 m apart, internal surface area of ca. 0.07 m²) so that they all contained one to several *F. serratus* thalli (> 25 cm long), understory and encrusting algae as well as invertebrates (Fig 3.1a). Community net primary production (NPP) and community respiration (CR) were examined using short incubations under a benthic chamber performed in ambient light and in darkness, respectively, during emersion and immersion. To do so, custom-built incubation chambers made of clear (NPP) or opaque (CR)

Plexiglas were set down on the concrete quadrats (total volume of ca. 20 L) and secured using elastic straps (Fig. 3.1b & c). It was assumed that respiration rates measured in darkness after an abrupt transition from ambient light reflect the respiration activity of the community (del Giorgio & Williams 2005, Tait & Schiel 2013).

For immersion measurements, incubation chambers were placed on the concrete quadrats by scuba divers, ensuring that any air bubbles remained inside. Mixing of seawater within the chambers was ensured by autonomous stirrers (Fig. 3.1b). Seawater samples were collected at the beginning and the end of incubations to estimate changes in dissolved inorganic carbon (DIC). pH and temperature of these samples were measured immediately using a pH meter (HQ40d portable pH, Hach®, Loveland, CO, USA) coupled with a pH electrode (Intellical™ PHC101 standard gel filled electrode, Hach®). Samples were then filtered on cellulose acetate filters (0.8 μm) and poisoned with HgCl_2 . In the laboratory, total alkalinity of each sample was determined on three 20 mL subsamples using 0.01 N HCl potentiometric titration with an automatic titrator (Titroline alpha, Schott SI Analytics, Mainz, Germany). DIC was calculated from temperature, salinity, pH and total alkalinity using CO_2SYS software (Lewis et al. 1998) with the constants from Mehrbach et al. (1973) refitted by Dickson and Millero (1987). Inorganic carbon fluxes were then calculated from the difference between the final and initial DIC concentrations.

For emersion measurements, the chambers were connected to infrared CO_2 gas analyzers (Li-Cor Li820, LI-COR®, Lincoln, Nebraska, USA), to form closed air-circuits, where an air circulation rate of 1 L min^{-1} was ensured by pumps (Fig. 3.1c). CO_2 concentration ($\mu\text{mol}_{\text{CO}_2} \text{ mol}_{\text{air}}^{-1}$) within the chambers was recorded every 5 s. These data were then used to determine carbon fluxes during each incubation (mgC h^{-1}), assuming a molar volume of 22.4 L mol^{-1} at standard pressure and temperature, and a molar mass of $12 \text{ g C mol}_{\text{CO}_2}^{-1}$, as described by Migné et al. (2002).

The metabolism of the *F. serratus* community was measured on 13 occasions from April 2014 to February 2016. Underwater measurements were always carried out around midday, during the rising tide of neap tide, and consisted of the succession of one dark incubation and one light incubation, performed simultaneously on the three quadrats (only two in November 2014). Dark and light incubations were performed respectively at a mean depth of $2.4 \pm 1.0 \text{ m}$ and $3.0 \pm 0.6 \text{ m}$, and were carried out for ca. 20 to 75 min, according to the time of the year. Measurements during emersion were always carried out during the following spring tide, a few days later. At each occasion, three light incubations (only two in November 2014) and a dark incubation were

performed successively from the onset of the emersion period (around midday). These incubations were sufficiently short (ca. 3 to 5 min) to avoid any feedback of temperature and CO₂ concentration changes on metabolic rates.

At the end of each incubation, benthic chambers were opened to allow complete seawater or air replenishment before the beginning of a new incubation. Metabolic rates were calculated according to the internal surface area of the concrete quadrats and expressed in carbon units for the community (mg C m⁻² h⁻¹). During emersion and immersion, NPP and CR measurements were used to calculate the community gross primary production (GPP), as $GPP = NPP + CR$. The metabolic balance of the community was also calculated for each set of measurements, as the ratio of mean CR to mean GPP (except when GPP was equal to 0).

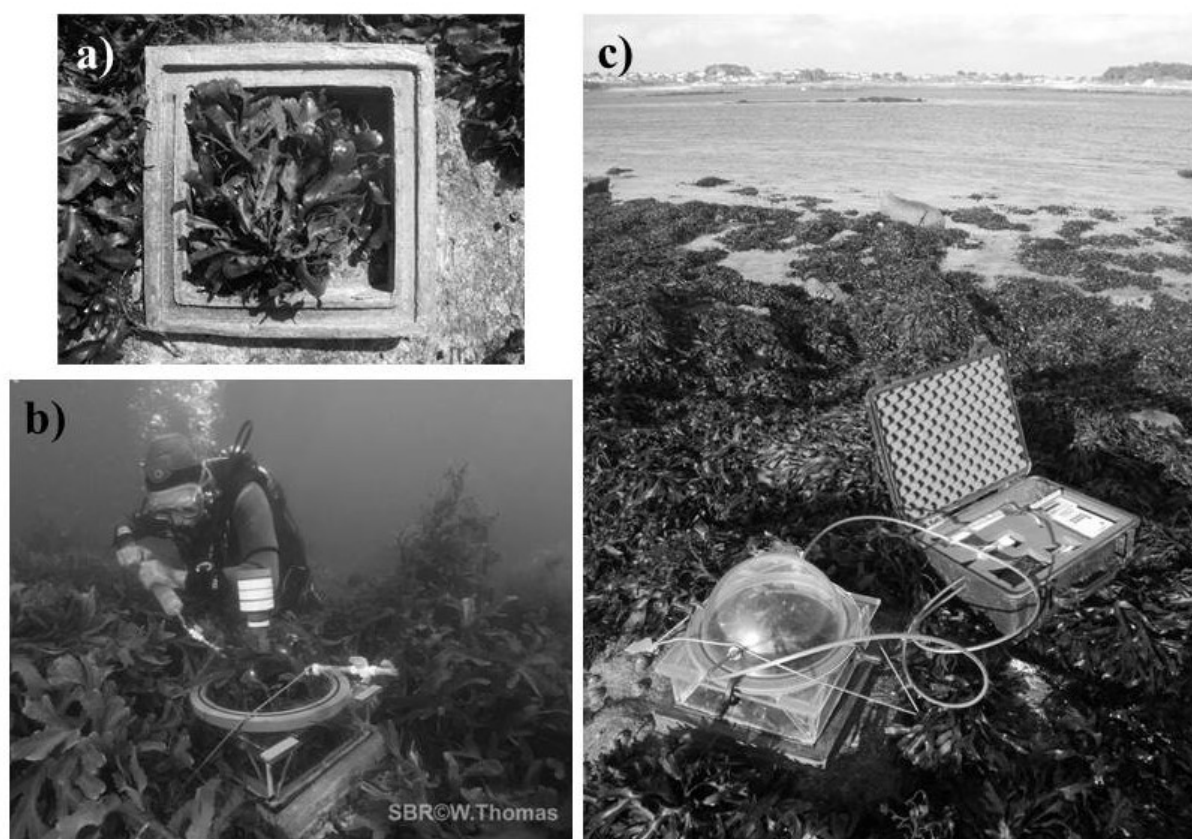


Fig. 3.1 a) Concrete quadrat. b) Incubation in ambient light during an immersion period. c) Incubation in ambient light during an emersion period.

In addition, a series of four underwater incubations were performed in ambient light (hereafter referred to as “underwater incubation series”) in July 2014 to evaluate the fluctuation of GPP during an immersion period (approx. 80, 145, 240 and 290 minutes after the rising tide flooded

the quadrats, corresponding to a seawater height above the quadrats of approx. 1.6, 3.0, 4.1 and 4.5 m, respectively). To do so, the CR values obtained a few days before were used, assuming they remain identical over a two-week interval (from 7 to 24 of July) and that they do not fluctuate during an immersion cycle.

Likewise, the metabolism of the *F. serratus* community was studied during entire emersion periods of spring tide (hereafter referred to as “aerial incubation series”), on haphazardly selected areas of 0.09 m² containing one to several *F. serratus* thalli and their associated community. Seven aerial incubation series were performed from April 2014 to April 2015. At each occasion, successive sets of light and dark incubations were carried out from the onset of the emersion period to the return of seawater at intervals of ca. 25 to 40 min. The first measurements of GPP and CR were considered as an estimation of community metabolism without any desiccation, and the following measurements were expressed as a percentage of these first values. At the end of the incubation series, the canopies were sampled to estimate the degree of desiccation they experienced during emersion. To do so, canopies were weighed a few minutes after removal (FW_{end}). They were then immersed in seawater overnight to fully recover their water content, and weighed the following day (FW_{full}). Finally, canopies were dried (60°C, 48h) and weighed (DW). Loss of water at the end of emersion period was estimated according to the following equation (3.1):

$$\text{Water loss (\%)} = \left(1 - \frac{\text{FW}_{\text{end}} - \text{DW}}{\text{FW}_{\text{full}} - \text{DW}} \right) \times 100 \quad (3.1)$$

During all incubations, temperature and irradiance (PAR, 400 – 700 nm) were measured close to the incubation chambers. Temperature was recorded every 5 min using HOBO® Pendant® Temperature/Light data loggers (Onset Computer Corporation, Bourne, MA, USA) and irradiance was recorded every minute using a spherical sensor (ultra-miniature MDS-MKV) in seawater and a planar sensor (Li-Cor QuantumSA-190) in the air. Simultaneous spherical and planar (Compact-LW ALW-CMP sensor, JFE Advantech Co., Ltd., Hyogo, Japan) sensor measurements were used to calculate a conversion factor (0.746, $R^2 = 0.937$, $n = 877$, $p < 0.001$) for underwater irradiance.

Statistical analyses

The 13 means of GPP, CR and CR:GPP ratios measured in the quadrats were compiled over a calendar year according to the day of measurement, for emersion and immersion separately. Sinusoidal curves were then fitted to these values to demonstrate seasonal patterns, according to the following equation (3.2):

$$y = a + b \sin\left(\frac{2\pi}{365}x + c\right) \quad (3.2)$$

where y is the predicted value of the considered parameter, and x is the time in days. For GPP during immersion, the model was constrained in such a way that a and b were equal, to avoid negative predicted values. A F -test was used to test the fit, using R software, version 3.2.2 (R Core Team 2015). Comparisons between emersion and immersion values of GPP, CR, CR:GPP, incident irradiance, and temperature during both light and dark incubations were performed using Wilcoxon signed rank tests on the mean values from each set of measurements.

Correlation between CR values and temperature during dark incubations was tested using Pearson's coefficient, for emersion and immersion separately.

GPP values obtained during emersion and immersion, as well as those of the underwater incubations series, were pooled and plotted against the mean irradiance measured during these incubations. A global photosynthesis versus light curve (P-I curve) was then fitted to these values, according to the mathematical model of Webb et al. (1974) (3.3):

$$GPP = GPP_{\max} \left(1 - e^{\left(-\frac{I}{I_k}\right)}\right) \quad (3.3)$$

where GPP is the observed gross primary production, $GPP_{\max}$ is the theoretical maximal gross primary production, I is the irradiance during light incubations and I_k is the irradiance at which $GPP_{\max}$ would be reached if GPP had continued to increase in a linear way with increasing PAR.

An F -test was used to test the fit.

Regarding the aerial incubation series, a two-degree polynomial curve was fitted to the GPP values according to the duration of aerial exposure, and relationship was tested using an F -test.

The linear relationship between CR and duration of exposure was also tested using an F -test.

Results

During immersion, the community GPP (mean $\pm$ SE) ranged from 0 to 962.2 ± 430.4 mg C m⁻² h⁻¹ and CR (mean $\pm$ SE) from 19.5 ± 5.4 to 266.4 ± 84.5 mg C m⁻² h⁻¹ (Fig. 3.2a). During

emersion, the *F. serratus* community GPP ranged from 620.0 ± 36.5 to $1\,515.5 \pm 478.3$ mg C m⁻² h⁻¹ and CR from 95.0 ± 41.0 to 685.5 ± 398.1 mg C m⁻² h⁻¹ (Fig. 3.2b). GPP and CR displayed seasonal patterns that showed significant fit with sinusoidal curves, reaching their maximum values during summer and their minimum values during winter, for both emersion and immersion measurements (Fig. 3.2a & 3.2b, Table 3.1). GPP and CR values were significantly higher during emersion than during immersion (Table 3.2), being on average 5 and 3.5 times higher when the community was exposed to the air, respectively. Likewise, irradiance and temperature recorded during the incubations also showed strong seasonal changes (Fig. 3.2c & 3.2d) and were significantly higher during emersion than during immersion (Table 3.2). The metabolic balance, calculated as the ratio of CR to GPP, ranged from 0.08 to 0.55, except in February when it reached 1.11 during immersion (Fig. 3.3). This ratio showed a seasonal pattern that fit significantly with a sinusoidal curve (Table 3.1) during emersion but not during immersion ($F_{3,9}$, $p > 0.05$). The metabolic balance did not show any significant differences when determined during emersion or during immersion (Wilcoxon signed rank test, $p > 0.05$).

Table 3.1 Sinusoidal curve parameters (n, a, b, c, R² and p) for *Fucus serratus* community respiration (CR), gross primary production (GPP) and metabolic balance (CR:GPP), during immersion and emersion.

		n	a	b	c	R²	p
CR	Immersion	13	100.2	83.5	4.6	0.701	0.006
	Emersion	13	304.6	262.1	4.4	0.864	< 0.001
GPP	Immersion	13	387.4	387.4	1.2	0.881	< 0.001
	Emersion	13	1 000.5	307.7	4.5	0.637	0.014
CR:GPP	Emersion	13	0.2777	0.1659	1.3120	0.858	< 0.011

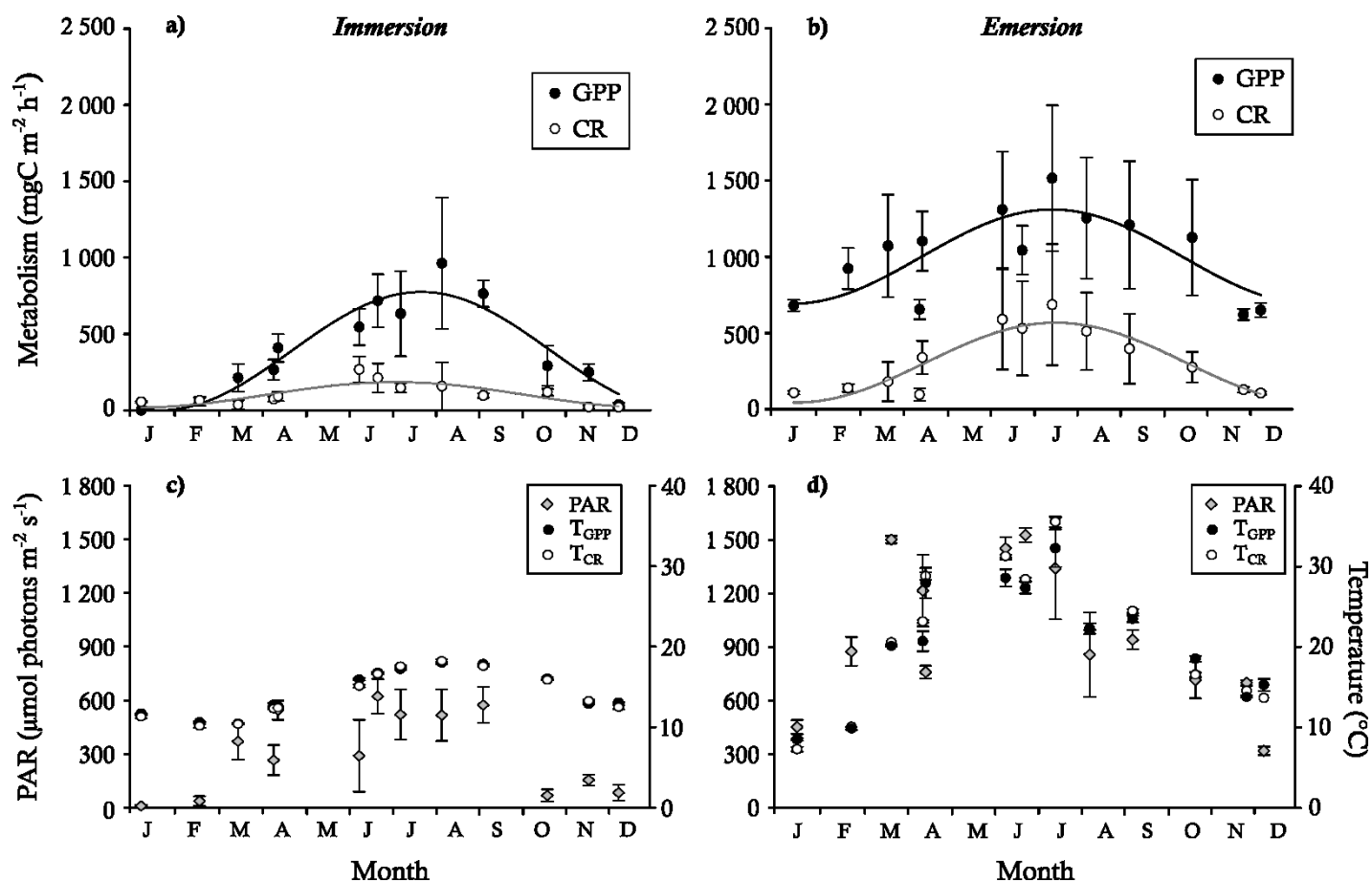


Fig. 3.2 Mean ($\pm$ SE) gross primary production (GPP, black circles) and respiration (CR, white circles), both expressed in $\text{mg C m}^{-2} \text{h}^{-1}$, as a function of time, both during immersion (a) and emersion (b). Black and gray lines represent the sinusoidal curves fitted on the GPP and CR datasets, respectively. Mean ($\pm$ SD) irradiance (PAR, in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, gray diamonds), temperature (T_{GPP} , in $^{\circ}\text{C}$, black circles) during incubations in light and temperature (T_{CR} , in $^{\circ}\text{C}$, white circles) during incubations in the dark, are also indicated for both immersion (c) and emersion (d).

Table 3.2 Wilcoxon signed rank test results (V , p) for differences between emersion and immersion, for mean community respiration (CR), community gross primary production (GPP), metabolic balance (CR:GPP), irradiance (PAR) and temperature during dark and light incubations (T_{CR} and T_{GPP} , respectively).

	V	p
CR	91	< 0.001
GPP	91	< 0.001
CR:GPP	37	0.910
PAR	91	< 0.001
T_{CR}	83	0.006
T_{GPP}	85.5	0.006

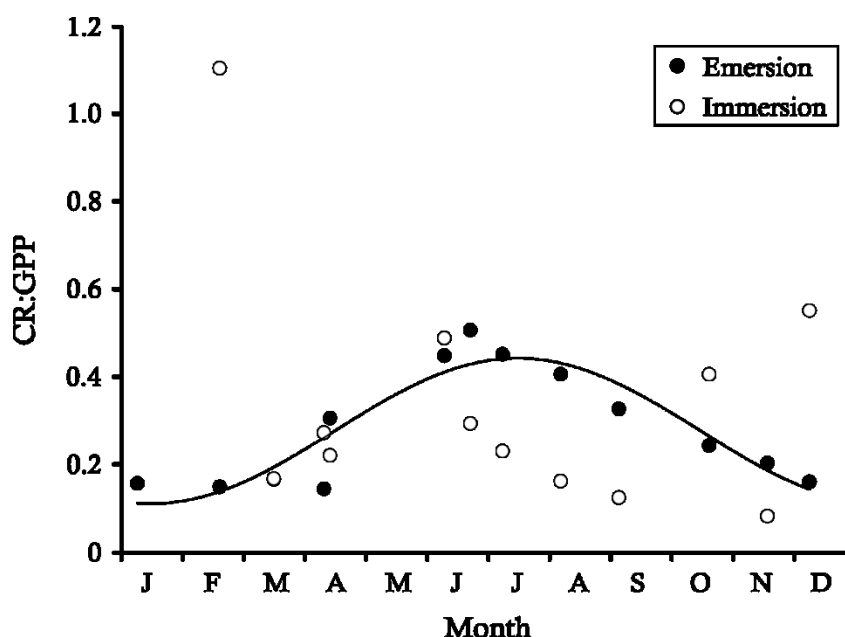


Fig. 3.3 Mean metabolic balance, expressed as ratio of community respiration (CR) to community gross primary production (GPP), during a calendar year for both immersion (white circles) and emersion (black circles). The black line represents the sinusoidal curve fitted on metabolic balance measured during emersion.

During the underwater incubation series, surface irradiance remained stable for the first three incubations. However, underwater irradiance decreased gradually, mainly due to a rise in seawater level above the benthic chambers (Fig. 3.4). Increases in surface and underwater irradiances observed during the last incubation resulted primarily from changes in cloud cover. Finally, GPP measured during these incubations exhibited the same fluctuations as underwater irradiance (Fig. 3.4).

Based on all the data points for mean GPP versus irradiance, the P-I curve showed significant fit with the (Webb et al. 1974) model (Fig. 3.5, $F_{2,28}$, $R^2 = 0.916$, $p < 0.001$), with a GPP_{max} of $1\,310.7\text{ mg C m}^{-2}\text{ h}^{-1}$ and an I_k of $696\text{ }\mu\text{mol photons m}^{-2}\text{ s}^{-1}$. CR was significantly correlated with the temperature recorded during dark incubations, for emersion (Fig. 3.6, $F_{1,11}$, $r = 0.829$, $p < 0.001$) and immersion (Fig. 3.6, $F_{1,11}$, $r = 0.678$, $p = 0.011$).

During the aerial incubation series, GPP increased slightly for the first 70 min and then decreased reaching approx. 80% of initial GPP after more than 200 min of emersion (Fig. 3.7a, $F_{3,114}$, $R^2 = 0.327$, $p < 0.001$). In contrast, CR decreased continuously from the onset of emersion reaching approx. 75% of initial CR after more than 200 min of emersion (Fig. 3.7b, $F_{1,115}$, $R^2 = 0.296$, $p < 0.001$). The canopies lost on average $18.7 \pm 4.4\%$ of their water content at the end of the emersion period.

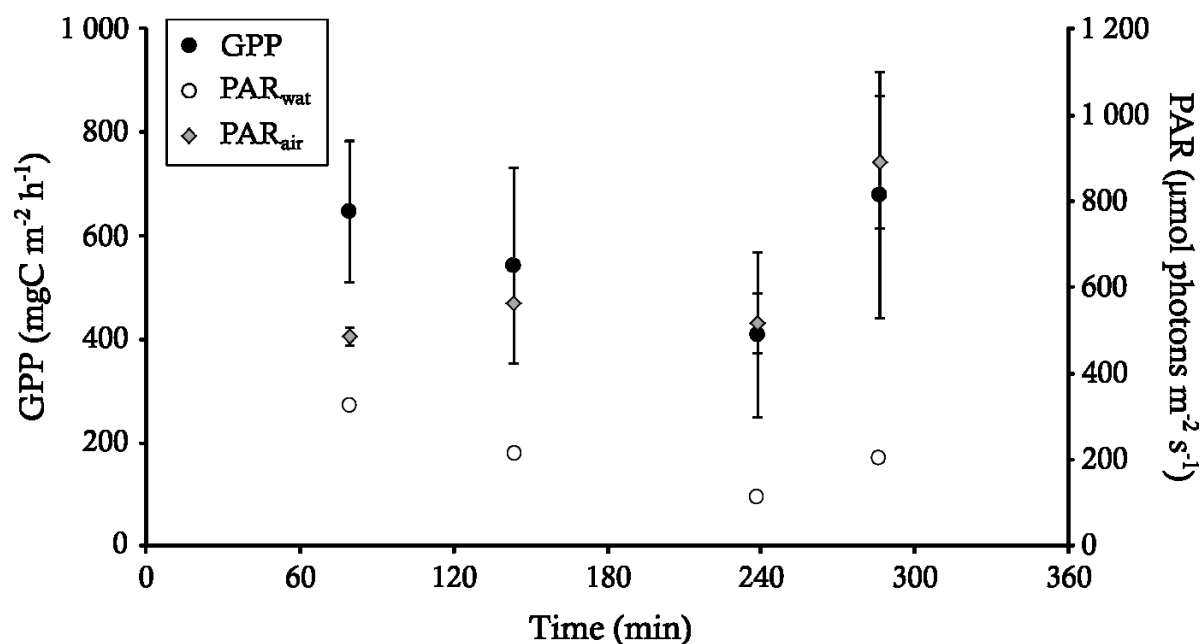


Fig. 3.4 Mean ($\pm$ SE) gross primary production (GPP, in $\text{mg C m}^{-2} \text{h}^{-1}$, black circles) and mean ($\pm$ SD) surface irradiance (PAR_{air} , in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, gray diamonds) and underwater (PAR_{wat} , in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, white circles) during the underwater incubation series. Time indicates the length of time (in minutes) since the flood tide first immersed the quadrats. Surface irradiance was provided by the SOMLIT network, and was measured on the roof of the Station Biologique de Roscoff.

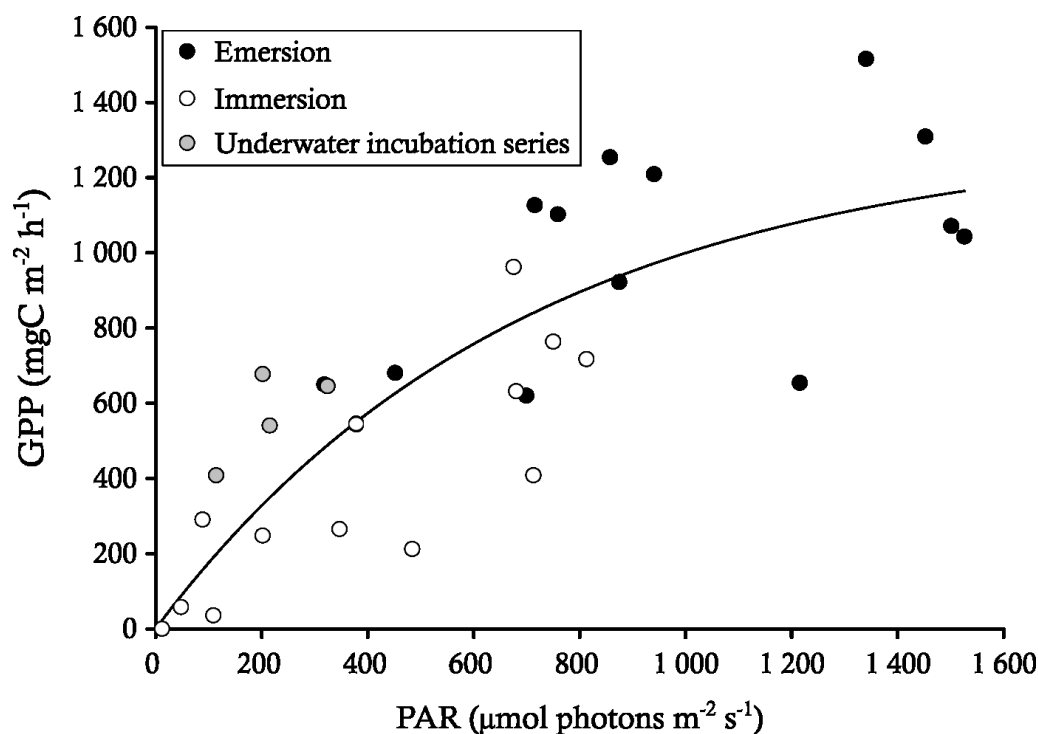


Fig. 3.5 Global relationship between community gross primary production (GPP, in $\text{mg C m}^{-2} \text{h}^{-1}$) and irradiance (PAR, in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$), established from the values obtained during emersion (black circles) and immersion (white circles) and from underwater incubation series (gray circles), and according to the mathematical model of Webb et al. (1974) (black line).

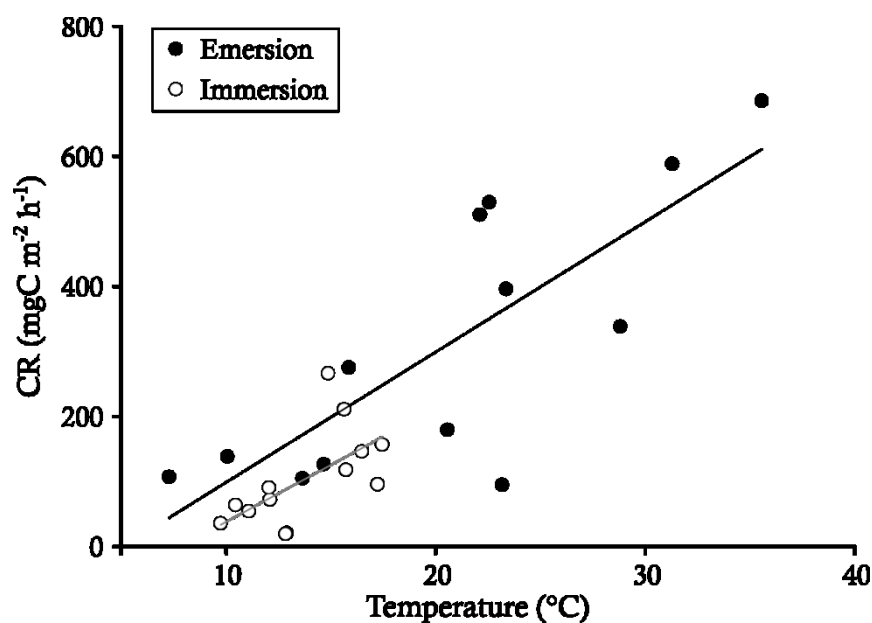


Fig. 3.6 Linear relationships between community respiration (CR, in $\text{mg C m}^{-2} \text{ h}^{-1}$) and temperature ($^{\circ}\text{C}$), established from the values obtained either during emersion (black circles, black line) or during immersion (white circles, gray line).

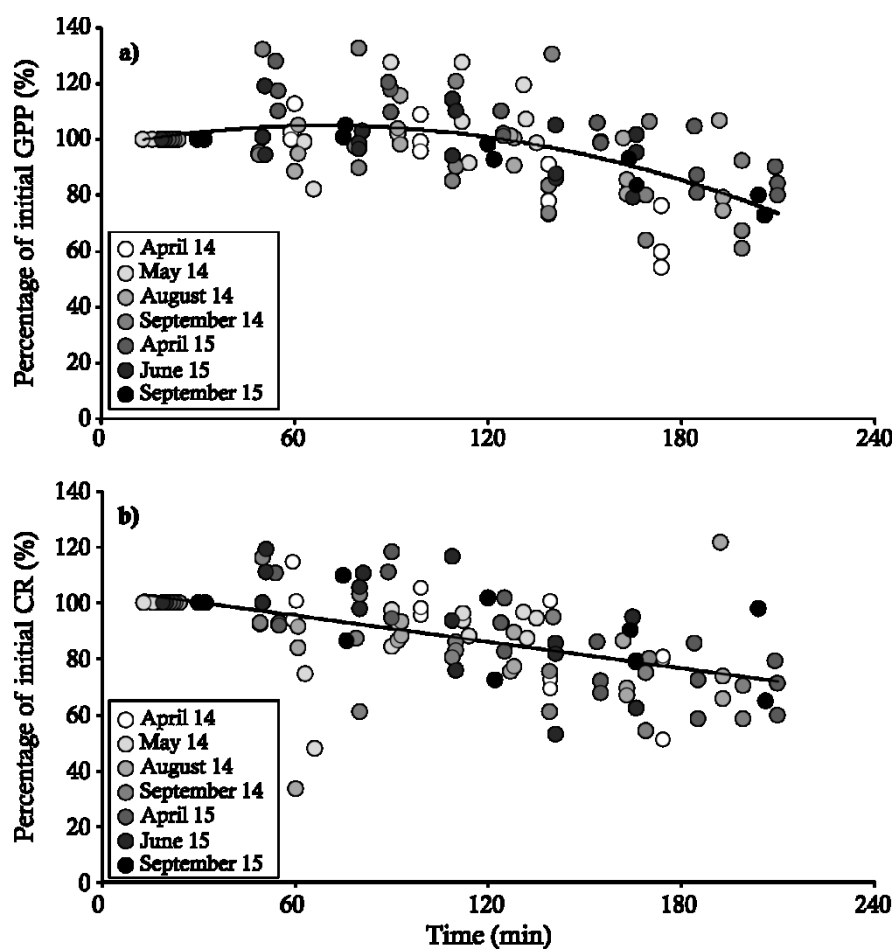


Fig. 3.7 Fluctuations in community gross primary production (a) and respiration (b) during the aerial incubation series, at different moments during the 2014-2015 study years, from the beginning of aerial exposure to the return of seawater with the flood tide.

Discussion

To our knowledge, this study is the first to investigate the *in situ* metabolism of an intertidal macroalgal community, during both emersion and immersion, and throughout the year. Results highlighted that the *F. serratus* community displayed, during both tidal periods, high rates of primary production and respiration that fluctuated throughout the year according to a seasonal pattern well-established for such communities in temperate areas (e.g. Cheshire et al. 1996; Golléty et al. 2008; Bordeyne et al. 2015). Accordingly, either when exposed to the air or immersed in seawater, the metabolism of this community was at its highest in summer, when both light availability and temperature were at their highest annual levels, and at its lowest in winter. This pattern confirms that the dynamics of community metabolism respond to the year-round fluctuations of climatic conditions, with light availability and temperature constituting the main drivers of GPP and CR, respectively (Davison 1991, Kemp & Testa 2011, Tait & Schiel 2013). The metabolic balance (i.e. the CR:GPP ratio) also showed a significant seasonal trend when calculated from measurements during emersion. The values of the metabolic balance and its seasonal trends are in agreement with those previously observed for the same community (Bordeyne et al. 2015), indicating that the underlying processes are highly conserved from year to year. The metabolic balance between primary production and respiration may thus depend on the combination of the seasonal fluctuations of two main elements: algal biomass and temperature. The summertime increase in biomass usually leads to changes in community structure, which are characterized by an increase in self-shading, limiting primary production (Binzer & Sand-Jensen 2002a, b). Furthermore, the summertime rise in temperature increases the respiration rate more strongly than primary production (López-Urrutia et al. 2006, Tait & Schiel 2013). However, no seasonal trends in metabolic balance were detected from immersion measurements. In immersion, the annual range of GPP was larger than that of community respiration. Thus, during summer, GPP and CR were both high and, consequently, the metabolic balance was relatively low (i.e. from 0.13 to 0.49). In contrast, during winter, the metabolic balance was high due to the extremely low GPP values. The low light environment experienced in winter during immersion led to a metabolic balance that exceeded unity, indicating that the community acted as a heterotrophic system during the measurement period.

Both primary production and respiration rates of the *F. serratus* community were significantly higher during emersion than during immersion. Numerous studies have attempted to describe

how intertidal macroalgae living at various shore levels respond to the alternation of emersion and immersion periods (see Migné et al. 2015a and references therein). Most studies illustrate that upper-shore species exhibit greater metabolic rates in air than in water, contrary to lower-shore species. However, these studies are carried out either on small fragments of algae or on entire individuals, but not on whole communities. The environmental constraints that fragments or individuals experience may, however, greatly differ from those experienced by whole communities (Pedersen et al. 2013). Furthermore, such natural assemblages are usually thought to show higher physiological performance when intact (e.g. Tait and Schiel 2011a), due to the degree of complementarity between layers. This complementarity between layers and species may even be amplified when these complex assemblages are exposed to air. Indeed, isolated algae usually suffer from desiccation and/or high solar radiation when exposed to air, potentially affecting their physiology (e.g. Williams and Dethier 2005; Lamote et al. 2012). In a multilayered community, the upper layer acts as a natural filter, protecting the other layers of the community from desiccation, extreme light and high temperature, thereby facilitating metabolic activity. For instance, at the end of emersion periods during which the aerial incubation series were performed, the upper layer was almost dried out whereas the lower understory remained moist, limiting the total water loss for the whole community. These observations reflect those reported for a *Fucus gardneri* assemblage (Haring et al. 2002). Furthermore, photoinhibition was also avoided, as shown by the P-I curve. In these conditions, a high rate of primary production was maintained throughout emersion periods, regardless of the time of the year, even though the light distribution for the understory layers was probably uneven and sub-optimal (Binzer and Sand-Jensen 2002b). Therefore, from an ecological point of view, aerial exposure constitutes a favorable environment for primary production of this type of intertidal community due to the canopy effect and to a significant complementarity between layers and species.

For practical reasons, underwater light incubations began on average 140 min after tidal flooding, when benthic chambers were submerged under on average 3.0 m of seawater. These conditions are not optimal for the primary production of the *F. serratus* community because light intensity is significantly attenuated by seawater. Thus, GPP is probably higher a few minutes just after tidal flooding, when the underwater light level is maximal. The large changes in primary production measured during the underwater incubation series are consistent with the fluctuation in underwater light availability. Thus, primary production appears to be a highly fluctuating process

when underwater, due to the continuous and rapid changes in light intensity caused by ebbing and rising tides. Finally, the higher rates of primary production observed during emersion than during immersion are likely due to the higher light intensity reaching the community. These results challenge those obtained for intertidal macrophyte-dominated systems in which light distribution is assumed to be more favorable underwater (Clavier et al. 2011, Ouisse et al. 2011a). A significant P-I curve was fitted on all data points for GPP versus irradiance (i.e. for both emersion and immersion). An annual I_k of nearly $700 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ was calculated for the *F. serratus* community. This value is in the upper range of those previously obtained for submerged macrophyte communities (i.e. 5-95th percentiles were $203\text{-}795 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$, (Binzer et al. 2006), but substantially higher than those obtained for the mid-intertidal *Ascophyllum nodosum* community when exposed to air (i.e. $192 \pm 156 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$, Goll  ty 2008). The P-I curve also shows that GPP did not reach saturation, even under maximal irradiance. This lack of saturation has already been demonstrated on other natural macroalgal assemblages using underwater incubations (e.g. Middelboe et al. 2006; Tait and Schiel 2011a), and results from sub-optimal light distribution among assemblage layers. The primary production of the *F. serratus* community is thus mainly regulated by light availability, regardless of the time of year and the tidal period. In other words, other regulating factors (e.g. desiccation) are of only secondary importance. Furthermore, this observation indicates that there are efficient stress protection mechanisms at the community scale. The metabolism of the intertidal community is efficient in aerial and underwater environments, providing that there is sufficient light, even though light is often considered as one of the most variable abiotic components of coastal shores (Schubert et al. 2001). Nevertheless, further investigations are needed to better understand the regulation of primary production in intertidal fucoid communities, especially when exposed to extreme environmental conditions that were not encountered during this study, such as low light environments when exposed to air and, conversely, to high light environments when underwater. The respiration of the *F. serratus* community was mainly driven by temperature, as indicated by the highly significant correlations between CR and temperature during dark incubations. This pattern is in agreement with the general opinion that temperature has a strong effect on respiration rates (Kemp & Testa 2011, Tait & Schiel 2013). However, in winter, when seawater temperature was higher than air temperature, CR was higher when the community was exposed to air than when underwater. Although this observation does not challenge the general

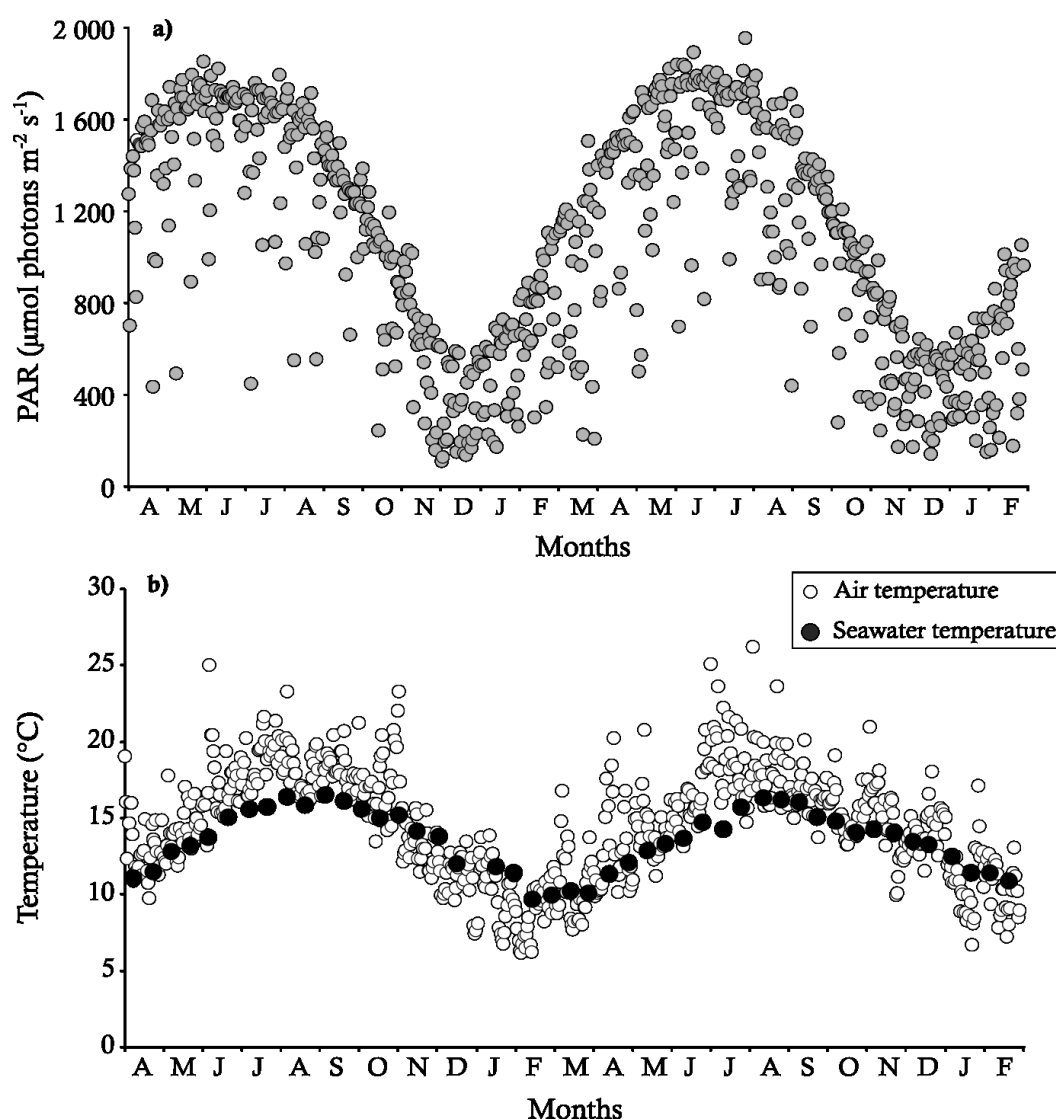
conclusion on the dynamics of community metabolism, there appears to be a slight difference in respiration activity during emersion and immersion. This difference may be related to the physiological activity of epibiotic and heterotrophic microorganisms. It is now widely accepted that macroalgae, and *Fucus* species in particular, are associated with a wide variety of epibiotic microorganisms (e.g. Stratil et al. 2013; Saha and Wahl 2013). These microorganisms may depend on the release of algal exopolymer substances (EPS). When algae are exposed to the air, EPS remain on the fronds, constituting an important source of energy for heterotrophic microorganisms (Wyatt et al. 2010, 2014), and leading to enhanced community respiration (Goll  ty et al. 2008, Goll  ty & Crowe 2013). However, when the algae are immersed, the EPS are released in the surrounding seawater, as dissolved organic carbon, and rapidly removed by water motion.

Overall, this study highlights that air is not the least favorable environment for primary production in intertidal macroalgae assemblages. Emersion periods may thus substantially contribute to the annual carbon budget of the *F. serratus* community. For instance, light intensities during underwater incubations rarely reached the I_k determined during this study, indicating that GPP was generally light-limited during an immersion period. Our results complement those of Middelboe et al. (2006), which demonstrated that shallow-water macroalgal communities are strongly light-limited during most of the year (Pedersen et al. 2013). Emersion periods are thus essential for the organic carbon requirements of photosynthetic organisms, especially in winter when intertidal communities rapidly encounter a low-light environment with the rising of the tide. Without these periods of air exposure, intertidal algae in temperate regions would completely drain their organic carbon stocks (Bordeyne et al. 2015). Thus, while Maberly and Madsen (1990) calculated that emersion periods can substantially contribute to the overall energy budget of a single species inhabiting high shore levels (i.e. *Fucus spiralis*), our results support the idea that they can also substantially contribute to the energy budget of whole intertidal communities, even those spending most of their time underwater.

Conclusion

By analyzing carbon fluxes of the *F. serratus* community at different seasons and during emersion and immersion periods, we highlight the main drivers of community metabolism. Primary production was mainly driven by light availability whether the community was exposed to air or

underwater, and respiration was mainly driven by temperature, with a slight difference between the two tidal periods. This study also demonstrated that the community maintains high rates of primary production throughout an emersion period, despite potentially high stress levels. Emersion periods thus appear to contribute substantially to the annual carbon budget of this type of intertidal community. The next step is to determine a realistic and accurate annual carbon budget for this community, using a modelling approach based on the present metabolism measurements.



Supplementary material 3.1 a) Daily maximal irradiance in air (PAR, 400-700 nm, $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) in Roscoff, as a function of time from April 2014 to February 2016. b) Seawater temperature (black circles) and daily maximal temperature in air (open circles) in Roscoff, both expressed in $^{\circ}\text{C}$ during the study period from April 2014 to February 2016. Datasets come from the SOMLIT Network and are available at <http://somalit-db.epoc.u-bordeaux1.fr/bdd.php?serie=ST>.

Chapitre 4

Métabolisme et structure des communautés à canopée de *Fucus* durant la succession

Contexte général et résumé

Les communautés de *Fucus* sont soumises à des perturbations, naturelles ou induites par l'homme, qui sont susceptibles d'affecter un ou plusieurs compartiment(s) particulier(s) (perte de la canopée par ex.), voir l'ensemble de ces communautés et ainsi créer des espaces libres pour la colonisation. Dans tous les cas, la structure et le fonctionnement des communautés peuvent en être profondément modifiés. Compte tenu de l'importance de la production primaire de ces communautés (apport de nourriture aux consommateurs associés par ex.), il semble essentiel d'étudier son évolution suite à ces perturbations.

Lors du processus de colonisation, l'installation et la persistance des différentes espèces dépendent de la disponibilité des propagules, de la survie et de la croissance des juvéniles. Il apparaît donc important de comprendre l'écologie des jeunes stades de vie, et en particulier des espèces fondatrices telles que les *Fucus* si l'on souhaite comprendre la dynamique, le fonctionnement et la distribution des communautés (Lamote et al. 2007). En général, les juvéniles sont plus exposés aux prédateurs que les adultes (Lubchenco 1983, Santelices 1990) et moins tolérants face aux conditions d'émersion (dessiccation, forte température par ex., Fogg 2001). En l'absence de protection, leur survie et/ou leurs performances physiologiques sont donc susceptibles d'être profondément affectées.

Ainsi, l'objectif de ce chapitre est d'examiner les variations de la structure et du métabolisme des assemblages de *F. vesiculosus* et de *F. serratus*, depuis les premiers stades de colonisation (substrat vierge). Pour cela, nous avons fixé 21 plaques de granit vierges (de 0,16 m² de surface) dans la zone de *F. vesiculosus* et 20 dans la zone de *F. serratus* (Fig. 4.1) en février 2013. La structure des assemblages (richesse taxonomique et densité de *Fucus*) colonisant ces plaques a été observée tous les 3 mois pendant 3 ans et demi. Le métabolisme à l'émersion (production primaire et respiration) a, quant à lui, été évalué tous les 2 à 5 mois sur un nombre restreint de plaques ($1 \leq n \leq 6$), à l'aide des chambres benthiques présentées précédemment. En parallèle, la structure et le métabolisme des communautés de *F. vesiculosus* et de *F. serratus* alentours ont été évalués tous les 3 mois (5 quadrats aléatoires de 0,1 m² pour la structure et 3 quadrats de 0,09 m² pour le métabolisme).



Fig. 4.1 Plaques de granit vierges fixées dans la zone de *Fucus serratus*.

La colonisation des plaques s'est avérée très variable et sur certaines d'entre elles, aucun *Fucus* ne s'est installé durablement au cours des 3 ans et demi du suivi. Le gradient intertidal semble avoir joué un rôle important sur la colonisation par les *Fucus* puisque 42 % des plaques de la zone de *F. vesiculosus* n'ont pas été colonisées contre seulement 10 % des plaques de la zone de *F. serratus*. Sur les autres plaques, *F. vesiculosus* a été la première des deux espèces de *Fucus* à s'installer, quelle que soit la zone considérée. *F. vesiculosus* est même resté plus abondant que *F. serratus* sur les plaques de la zone de bas niveau durant les 3 premières années du suivi. Des expériences de colonisation complémentaires, réalisées dans différentes conditions initiales (i.e. élimination des *Fucus serratus* ou élimination complète de la communauté), indiquent que la survie et la croissance des juvéniles de *F. serratus* sont favorisées par la présence d'autres espèces (sous-canopée par ex.). Ces résultats suggèrent donc que les juvéniles de *F. serratus* sont relativement sensibles aux conditions environnementales et que les juvéniles de *F. vesiculosus* sont plus tolérants.

En ne considérant que les plaques où des *Fucus* se sont installés, la structure des assemblages s'approche petit à petit de la structure observée pour la communauté de *Fucus* alentours, mais en diffère toujours après 3 ans et demi de colonisation, dans chacune des deux zones. Le métabolisme a quant à lui atteint un niveau similaire à celui des communautés alentours après environ 24 mois de colonisation. Sur les plaques de la zone située en bas niveau marégraphique, *F. vesiculosus* a donc régulièrement rempli le rôle de *F. serratus* d'un point de vue du métabolisme.

Article n°4

Changes in community structure and primary production over the course of succession for two intertidal furoid communities at different shore heights

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Abstract: Small scale disturbances regularly create bare spaces in intertidal communities dominated by canopy-forming brown algae, allowing succession to occur. To date, this process has been widely investigated in a perspective of transition of species from early to late successional stages. In contrast, very few studies have assessed changes in primary production and respiration over successional sequence, while these functions are essential for macroalgal communities. To investigate this issue, we placed several bare granite slabs in the *Fucus vesiculosus* and *F. serratus* communities, which are established at different tidal levels. Thus, the influence of emersion gradient on succession was also evaluated. The structure of assemblages settling on the slabs (i.e. density of *Fucus* spp. and taxonomic diversity) was assessed every three months over a 42 months period, and compared with what was recorded in *Fucus* communities. Measurements of primary production and respiration of slabs assemblages were carried out every two to five months during emersion periods and were also compared with metabolism of *Fucus* communities. Succession was highly variable during this survey, and some slabs remained uncolonized by *Fucus* species. For each tidal level, and regarding the slabs where *Fucus* settled, the structure of assemblages developed toward *Fucus* communities but remained still different after 42 months. In contrast, primary production and respiration of slabs assemblages were similar to those of *Fucus* communities after approximately 24 months, indicating that, due to rapid growth of *Fucus*, these functions were rapidly filled in. Interestingly, emersion gradient had a weak influence on successional sequence once *Fucus* is settled, even if in the lowest tidal level *F. vesiculosus* fulfilled the role of *F. serratus*.

Keywords: Emersion gradient; *Fucus serratus*; *Fucus vesiculosus*; Gross primary production; Recruitment; Succession.

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Introduction

Communities dominated by canopy-forming brown algae (Phaeophyceae) established on intertidal rocky shores are widely distributed around the world (Lüning 1990, Neiva et al. 2016). These communities are of critical importance for coastal areas, as they contribute substantially to nutrient cycling and production of organic matter through photosynthesis (e.g. Tait and Schiel 2010; Tait et al. 2015). This organic matter benefits to a large variety of species inhabiting these communities permanently (Riera et al. 2009) or temporarily (Silva et al. 2010), as well as to other coastal ecosystems (Crawley et al. 2009), through the export of detritus by water movement (Duarte & Cebrian 1996).

Intertidal rocky shores are regularly subjected to disturbances resulting from both physical and biological processes, either natural or man-induced, that may affect community functioning (Sousa 1984). These disturbances, which take part in the large temporal and spatial variability that characterizes rocky shores (e.g. Dethier 1984; Benedetti-Cecchi 2000), can release new spaces in these habitats, depending on their magnitude. Within these bare spaces, successional sequences occur and usually consist in a transition from a community made of a few opportunistic and ephemeral species, tolerant to harsh environmental conditions but characterized by a low diversity in functional traits, to a more complex community, made of numerous species with a more diverse and complementary pool of functional traits (Noël et al. 2009). This process is, however, highly variable in time and space (Jenkins et al. 2005). In particular, successional sequences are expected to vary according to the vertical zonation, which is known as a fundamental driver of community structure and species distribution (Underwood 1980, Raffaelli & Hawkins 1999). According to shore height, species interactions (Bertness et al. 1999) and primary production of benthic assemblages (Migné et al. 2015a) may also greatly vary, influencing therefore their dynamics.

A mosaic of patches of different successional ages may be commonly observed on rocky shores, as a consequence of series of disturbances. These patches, which can strongly differ in species composition (Dethier 1984), may therefore exhibit large discrepancies in term of community functioning, and especially in productivity. Such changes in primary production over successional sequences have rarely been addressed on rocky shores (Martins et al. 2007), while succession has been the focus of intensive research during the past decades (e.g. Connell and Slatyer 1977; Lubchenco 1983; McCook and Chapman 1993; Benedetti-Cecchi 2000). Yet, the

short life expectancy of the majority of organisms involved in the successional sequence of intertidal communities makes them an ideal place to investigate such issues.

Thus, the present study associates diversity and primary production measurements over successional sequences. It was conducted on two widespread intertidal communities dominated by canopy-forming Phaeophyceae, *Fucus vesiculosus* Linnaeus and *F. serratus* Linnaeus, respectively. These communities, which are adjacent in the vertical pattern of rocky shores, usually consist of dense and complex assemblages mainly composed of *Fucus* spp. associated with epibionts, understory and encrusting algae, as well as invertebrates. The successional sequences were investigated in these communities during a period of three years and a half, corresponding approximately to the life span of both *F. vesiculosus* and *F. serratus* (Fish & Fish 1989). During this period, we tested the hypotheses that (1) primary production varies over successional sequences according to the identity of settled species, and that (2) both taxonomic diversity and primary production are comparable to those of established communities of the same areas at the end of the survey. Then, we hypothesized that (3) the timing of successional sequences differs according to the shore height, being faster in low shore than in high shore, due to more favorable environmental conditions.

Materials & methods

Study sites

This study was carried out on an intertidal boulder reef located in the southwestern part of the English Channel, in front of the Station Biologique de Roscoff (Brittany, France). The tidal cycle is semi-diurnal in this place, with a maximal amplitude of about 9 m. Owing to its situation in the temperate part of the Northern Hemisphere, this reef is subjected to seasonal fluctuations in environmental conditions, and especially in incident irradiance and temperature. This study was carried out in two distinct sites within this reef, which are separated by approx. 350 m: Karreg Ar Vraz (48°43.754'N, 3°59.420'W) and Roc'h Fañchig (48°43.772'N, 3°59.781'W). The mid-intertidal level (3.0 to 4.0 m above chart datum) is characterized by a *Fucus vesiculosus* community (40 to 60% substratum coverage) at Karreg Ar Vraz, and by a dense *Ascophyllum nodosum* community (75 to 100% substratum coverage) at Roc'h Fañchig. In both sites, the low mid-intertidal level (2.5 to 3.0 m above chart datum) is characterized by a *F. serratus* community, where the canopy-former covers 75 to 100% of the substratum.

Structure and metabolism of assemblages during succession

To study the successional sequences of the *F. vesiculosus* and *F. serratus* communities, several bare granite slabs (40 cm × 40 cm) were haphazardly attached to large boulders of the Karreg Ar Vraz site, in February 2013. Thus, twenty-one slabs were placed in the mid-intertidal level (area where *F. vesiculosus* is dominant) and twenty in the low mid-intertidal level (area where *F. serratus* is dominant). The slabs were arranged to be 1 to 3 m away one from each other within areas, and were separated by a distance of approx. 30 m between areas.

The structure of assemblages settled on the slabs was monitored every 3 months from September 2013 to June 2016. Organisms were identified in the field to the lowest possible taxonomic level, being usually the species level, except for some colonial taxa (e.g. bryozoans, ascidians), algal recruits and group of species morphologically similar (e.g. amphipods). *Fucus* spp. individuals were counted when large enough to be identified to the species level. Identification and counting were performed on all the slabs of the *F. vesiculosus* area at each sampling period. This survey effort was also carried out in the *F. serratus* area until June 2015. After that, it had to be reduced to only 10 randomly chosen slabs, as assemblages were too dense to monitor the overall area within expected time limits. In addition, identification and counting were carried out in the *F. vesiculosus* and *F. serratus* communities established a few hundred meters away from areas containing granite slabs (hereafter referred to as “established communities”), using five randomly chosen 0.1 m² quadrats per community every three months from September 2013 to March 2016 (with the exception of December 2015).

The aerial metabolism of assemblages settled on the slabs was measured on randomly chosen slabs every two to five months from March 2013 to June 2016. Measurements were carried out on one to four slabs during the first year, and five to six slabs during the following months. At each occasion, carbon fluxes at the air-slab interface were measured at the onset of emersion period of spring tides (around midday). Net primary production (NPP) and respiration (R) of assemblages were examined successively using short incubations (i.e. 5-15 min) under closed chambers, which were carried out in ambient light and in darkness, respectively. Incubation chambers, which are made of transparent Plexiglas, have a covering surface of 30 cm x 30 cm and a total volume of ca. 17.7 or 26.5 L, depending on the amount of organisms settled on the slabs. These chambers were connected to infrared CO₂ gas analyzers (Li-Cor Li820, LI-COR®, Nebraska, USA), to form closed air-circuits, where an air circulation rate of 1 L min⁻¹ was

ensured by pumps. CO₂ concentration ($\mu\text{mol}_{\text{CO}_2} \text{mol}_{\text{air}}^{-1}$) within the chambers was recorded every 5 s. These data were then used to determine carbon fluxes during each incubation (mgC h^{-1}), assuming a molar volume of 22.4 L mol^{-1} at standard pressure and temperature, and a molar mass of $12 \text{ gC mol}_{\text{CO}_2}^{-1}$, as described by Migné et al. (2002). Metabolic rates were calculated according to the covering surface of incubation chambers (i.e. 0.09 m^2) and expressed in carbon units for the benthic assemblage ($\text{mgC m}^{-2} \text{ h}^{-1}$). The gross primary production (GPP) of benthic assemblage was then calculated as the sum of NPP and R. For each period of measurement, the mean metabolic balance was also calculated, as the ratio of R to GPP. As well, the aerial metabolism of the established *F. vesiculosus* and *F. serratus* communities was monitored every three months from March 2013 to June 2015. This monitoring was carried out on 3 haphazardly selected replicates per community, according to the method described previously. During all incubations in ambient light, photosynthetically available radiations (PAR, in $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) were regularly measured close to the incubation chambers, using a planar sensor (Li-Cor Quantum SA-190), to ensure that measurements were performed under saturating irradiance (assuming that the onset of light saturation for coastal macroalgal communities is reached, on average, at $291 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$, Middelboe et al. 2006).

Recovery of metabolism in a F. serratus community after harvesting

To evaluate the duration of metabolism recovery after harvesting, a ca. 50 m^2 zone located within the *F. serratus* area of the Karreg Ar Vraz site was harvested in February 2013, by cutting fucoids longer than ca. 10 cm. After that, measurements of aerial metabolism within this harvested area were carried out every 2 to 5 months from March 2013 to September 2014, using the methodology previously described. At each occasion, these measurements were performed on 3 to 4 replicates that were haphazardly selected.

Recruitment of F. serratus after experimental treatments

The recruitment of *F. serratus* was studied in experimental plots of the Roc'h Fañchig site, from February 2015 to June 2016. To do so, 20 plots of $40 \text{ cm} \times 40 \text{ cm}$ containing several *F. serratus* and separated by 1 to 3 m one from each other, were selected within the study site. Five randomly-selected plots were assigned as control plots, and the fifteen remaining were assigned to three different experimental treatments (i.e. five plots/treatment). The first experimental

treatment consisted of *F. serratus* removal (assuming that, in this site, all *Fucus* individuals were *F. serratus*) without damaging associated community. Indeed, encrusting and understory algae may provide some shelter from canopy sweeping or desiccation for instance for zygote and embryos of *F. serratus*, thereby facilitating their establishment. Second treatment consisted of complete community removal, and was done by scraping the substratum using wire brushes and paint scrapers until no visible fragments of algae and sessile animals remained. Last treatment also consisted of complete community removal and was done by scraping and burning the substrate, to suppress all existing life, including biofilms and potential zygotes and embryos of *F. serratus*. Prior to experimental treatments, the number of *F. serratus* and of juveniles (i.e. small *Fucus* sp., assumed to be *F. serratus*) visible with naked eye were counted in each plot and did not differ between treatments (one-way ANOVA, *F. serratus* individuals: $F_{3,16} = 0.513$, $p > 0.05$; Juveniles of *F. serratus*: $F_{3,16} = 1.871$, $p > 0.05$). Experimental treatments were carried out during two consecutive days in spring tides, at the beginning of February 2015. After that, the abundance of *F. serratus* visible with naked eye was evaluated in all plots and at each spring tides until June 2016, according to their size (i.e. 3 size classes: juveniles < 50 mm, young *F. serratus* of 50-250 mm and large *F. serratus* > 250 mm and 5 abundance classes: 0 ind., [1:10 ind.], [11:100 ind.], [101:1 000 ind.], > 1 000 ind.). A mean index of *F. serratus* abundance was then calculated for each class size of all treatments. To do so, a number from 0 to 4 has been assigned to each abundance class (i.e. 0 being assigned to abundance class 0 ind. and 4 being assigned to the abundance class > 1 000 ind.). The mean index of abundance calculated for each class size of each treatment was then determined as the average value obtained for the five plots per treatment.

Evaluation of Fucus spp. maturity

In order to estimate the potential presence of gametes, and therefore of zygotes and embryos of both *F. vesiculosus* and *F. serratus* species, their sexual maturity was evaluated year-round. During each spring tide from March 2015 to March 2016, 39 to 48 individuals (> 20 cm) of each species were randomly selected on the field (Karreg Ar Vraz) and the most developed receptacle of each individual was sampled. In the lab, these receptacles were briefly rinsed with freshwater, wrapped individually in wet paper towel and put in the dark at 4°C for 48h. They were then put individually in petri dishes filled with filtered seawater and exposed to light for 2 h (approx. 1 000

μmol of photons $\text{m}^{-2} \text{s}^{-1}$, Metal halide lamp, Sylvania BRETILUX HSI-TSX 400W 4K). The percentage of receptacle that had spawn gametes during light exposure was then evaluated under a binocular magnifier.

Data analyses and statistical tests

The slabs where any furoid was settled at the end of survey (i.e. after 3 ½ years) were not included in data analyses (i.e. 9 slabs in the *F. vesiculosus* area and 2 in the *F. serratus* one), as they were assumed to be not representative of the succession process. Difference in the mean number of taxa between assemblages settled on the slabs and established communities was tested at each period of measurement using Student's *t*-test after normality (Kolmogorov-Smirnov test, $p > 0.05$) and homoscedasticity (Levene test, $p > 0.05$) have been checked. When homoscedasticity was not verified, the Welch correction was applied. In addition, difference in the mean number of taxa settled on the slabs of the *F. vesiculosus* area and of the *F. serratus* one was tested using paired *t*-test on average values, after normality has been checked.

Fluctuations of assemblages' composition during the successional process were investigated using non-metric multidimensional scaling (nMDS) based on Bray-Curtis similarities, calculated from average presence-absence data. The structure of these assemblages was also compared with those of established communities using ANOSIM test, considering the sampling carried out during the last year of survey as replicates (i.e. from June 2015 to June 2016, $n = 5$ for slabs and $n = 3$ for established communities). nMDS and ANOSIM tests were performed using PRIMER software v6 (Clarke & Gorley 2006).

Difference in fertility between furoid species was tested using paired *t*-test on percentage values of fertile individuals, after normality has been checked. All statistic tests were performed using R software v.3.2.2 (R Core Team 2015).

Results

Structure of assemblages during succession

On 11 of the slabs placed in the *F. vesiculosus* area in February 2013, the density of *F. vesiculosus* progressively increased from 1 ± 1 ind m^{-2} in September 2013 to 131 ± 33 ind m^{-2} in June 2015, and then decreased to 84 ± 24 ind m^{-2} in June 2016 (Fig. 4.2a). *F. serratus* was first recorded on these slabs in March 2016 (1 ± 1 ind m^{-2}) and reached a mean density of 4 ± 3 ind m^{-2} in June

2016 (Fig. 4.2a). On 18 of the slabs placed in the *F. serratus* area in February 2013, *F. vesiculosus* was the first furoid to settle and increased from 1 ± 1 ind m⁻² in September 2013 to 88 ± 21 ind m⁻² in June 2014. Then, the density of *F. vesiculosus* decreased to 44 ± 13 ind m⁻² in June 2016 (Fig. 4.2b). *F. serratus* was first recorded on these slabs in June 2014 (22 ± 8 ind m⁻²) and reached a maximal density of 39 ± 18 ind m⁻² in March 2016 (Fig. 4.2b).

In the *F. vesiculosus* area, the mean number of taxa increased from the beginning to the end of the succession survey, when it reached, on average, 20 ± 2 taxa per slab ($n = 11$, Fig. 4.3a). The mean number of taxa recorded during the monitoring of established *F. vesiculosus* community fluctuated from 9 ± 1 to 18 ± 2 taxa per quadrat ($n = 5$), showing some seasonal variability. The mean number of taxa settled on the slabs differed significantly from established community in some occasions, being lower than established community at the beginning of the survey and higher at the end of the survey (Fig. 4.3a). In the *F. serratus* area, the mean number of taxa also increased from the beginning to the end of the succession survey, when it reached, on average 24 ± 3 taxa per quadrat ($n = 18$, Fig. 4.3b). The mean number of taxa recorded on established community varied from 12 ± 1 to 23 ± 2 taxa per quadrat ($n = 5$), and showed some seasonal variability. In the *F. serratus* area, the mean number of taxa settled on the slabs differed significantly from established community in some occasions, and especially during the first year of the survey, where it was lower than in established community (Fig. 4.3b). Analyses of assemblages' composition showed that the successional sequences of both areas followed a similar trajectory (Fig. 4.4). Assemblages settled on the slabs significantly differed from established communities during the last year of survey (ANOSIM test, *F. vesiculosus* slabs: *Global R* = 0.846, $p = 0.002$; *F. serratus* slabs: *Global R* = 0.959, $p = 0.002$). The mean number of taxa per slab was significantly lower in the *F. vesiculosus* area than in the *F. serratus* one (paired *t*-test, $t = -3.7$, $df = 11$, $p = 0.003$).

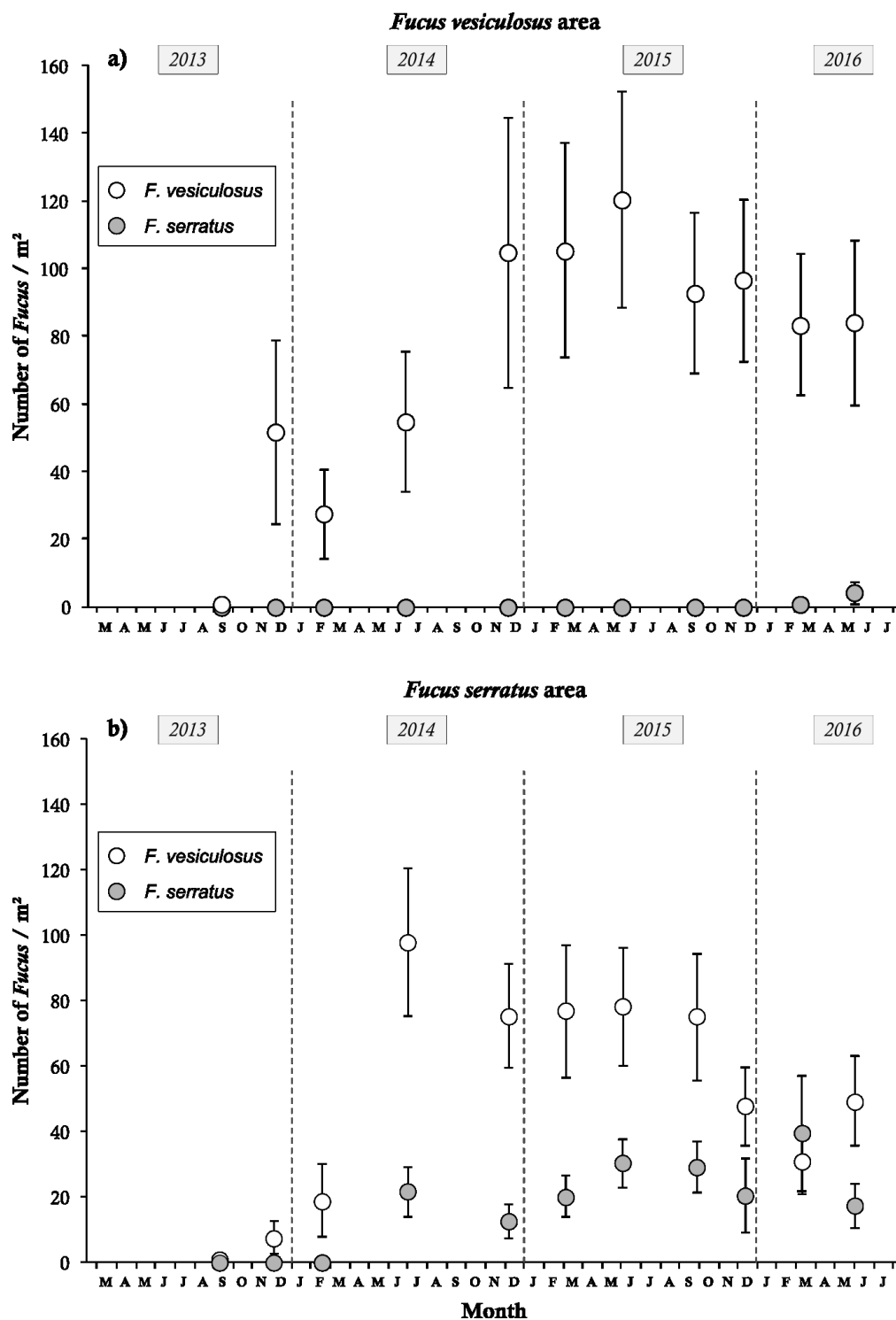


Fig. 4.2 Mean ($\pm$ SE) density (in ind m⁻²) over time of *F. vesiculosus* (white circles) and *F. serratus* (gray circles) settled on the slabs placed in the *F. vesiculosus* ($n = 11$) (a) and *F. serratus* ($8 \leq n \leq 18$) (b) areas.

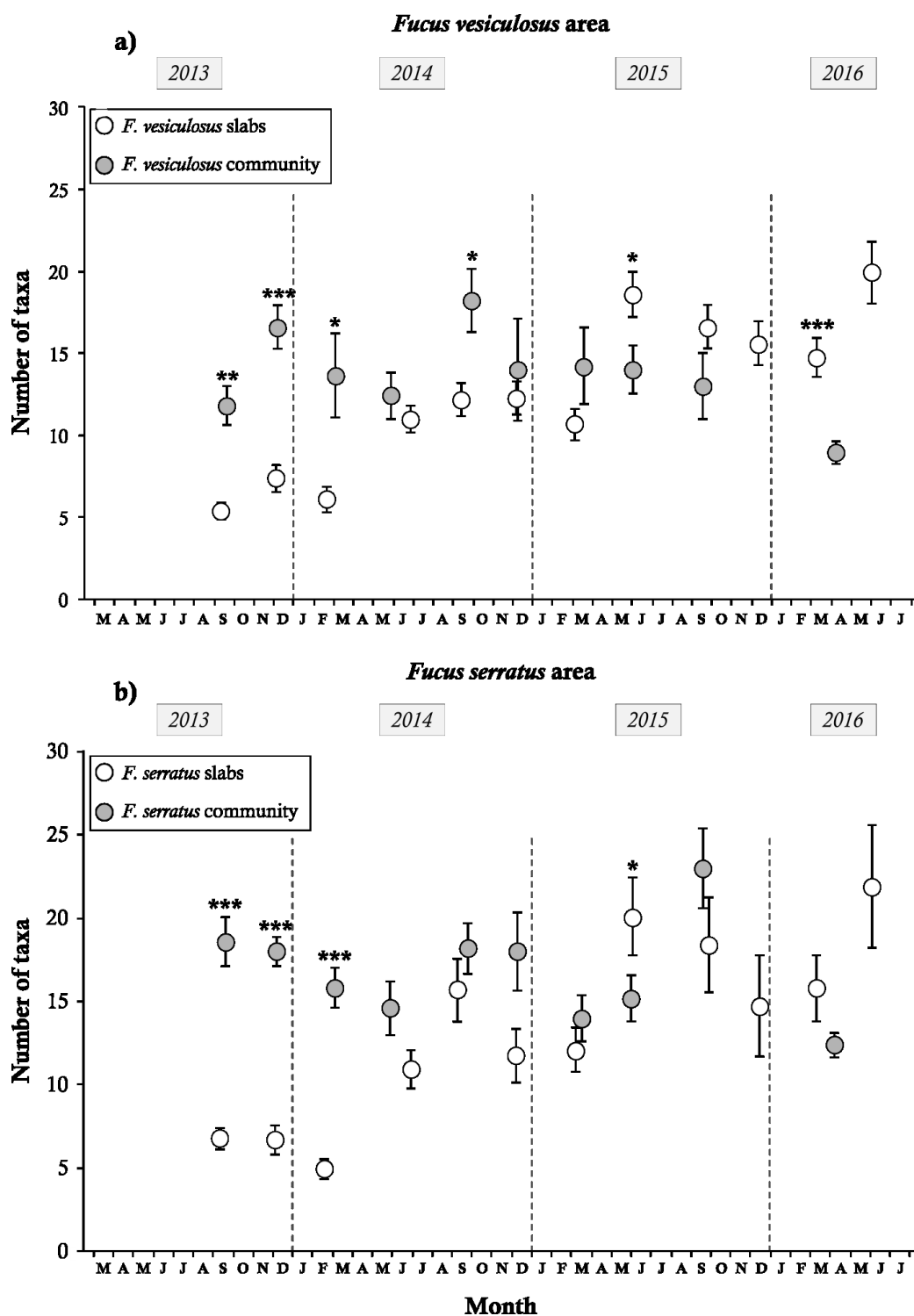


Fig. 4.3 Mean ($\pm$ SE) number of taxa over time **a)** on the *F. vesiculosus* slabs ($n = 11$, white circles) and the established *F. vesiculosus* community ($n = 5$, gray circles) and **b)** on the *F. serratus* slabs ($8 \leq n \leq 18$, white circles) and the established *F. serratus* community ($n = 5$, gray circles). Asterisks above bars indicated the results of Student's *t*-test (* for $p < 0.05$, ** for $p < 0.01$ and *** for $p < 0.001$).

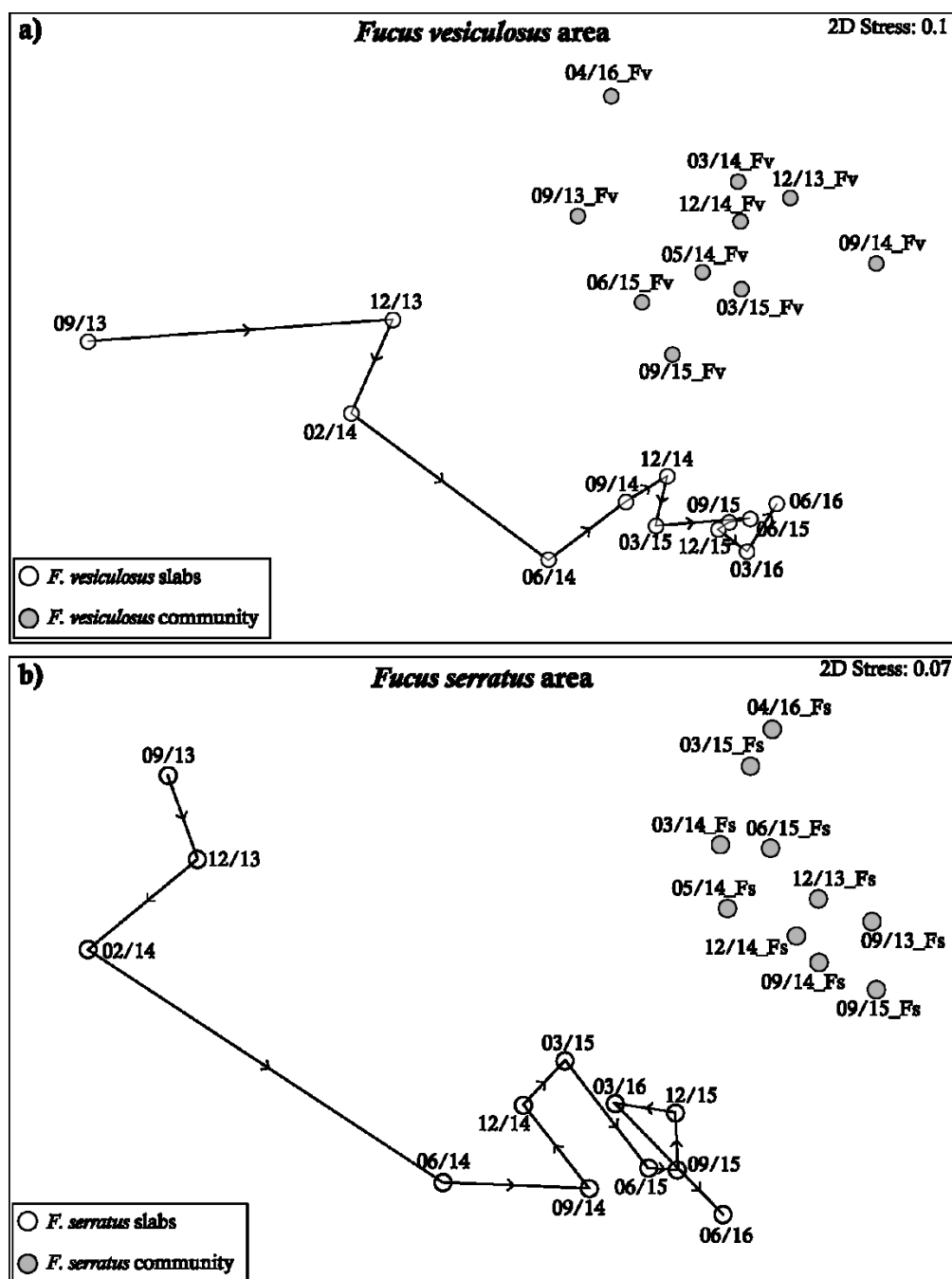


Fig. 4.4 Two-dimensional non-metric multidimensional scaling plots showing (a) the trajectory of assemblages settled on the slabs of the *F. vesiculosus* area over time ($n = 11$, white circles), as well as the temporal variation of taxonomic composition of the established *F. vesiculosus* community ($n = 5$, gray circles); and (b) the successional trajectory of assemblages settled on the slabs of the *F. serratus* area over time ($8 \leq n \leq 18$, white circles) as well as the temporal variation of taxonomic composition of the established *F. serratus* community ($n = 5$, gray circles).

Metabolism during succession process

Assemblages settled on the slabs of the *F. vesiculosus* area exhibited a GPP that increased during the survey, ranging from 2.1 mgC m⁻² h⁻¹ in May 2013 (n = 1) to 850.1 ± 193.6 mgC m⁻² h⁻¹ in May 2015 (n = 3) (Fig. 4.5a). Then, GPP fluctuated between 507.6 ± 251.0 (n = 3) and 680.4 ± 177.9 (n = 3) mgC m⁻² h⁻¹. The GPP of the established *F. vesiculosus* community showed some seasonal variability, and ranged from 329.0 ± 60.4 mgC m⁻² h⁻¹ to 1 016.6 ± 171.9 mgC m⁻² h⁻¹ (Fig. 4.5a). In the *F. serratus* area, assemblages settled on the slabs exhibited a GPP that increased from 5.6 mgC m⁻² h⁻¹ in March 2013 (n = 1) to 1 003.2 ± 321.11 mgC m⁻² h⁻¹ in May 2015 (n = 5) (Fig. 4.5b). Then, GPP fluctuated between 538.3 ± 93.4 (n = 5) and 952.6 ± 316.2 (n = 4) mgC m⁻² h⁻¹. The GPP of the established *F. serratus* community showed some seasonal variability, ranging from 580.5 ± 90.6 mgC m⁻² h⁻¹ to 1 089.6 ± 93.7 mgC m⁻² h⁻¹ (Fig. 4.5b).

In the *F. vesiculosus* area, the metabolic balance (i.e. ratio R:GPP) measured on slabs showed a slight increase from 0.103 ± 0.039 in December 2013 (n = 3) to 0.703 ± 0.090 in August 2015 (n = 4), despite large seasonal variability (Fig. 4.6a). During the first year, a metabolic balance higher than 1 was recorded for a few number of slabs (May, July and August 2013, R:GPP > 1 for one slab at each occasion). The metabolic balance of the established *F. vesiculosus* community varied from 0.257 ± 0.036 to 0.478 ± 0.042, showing seasonal variability and being minimum in winter and maximum in summer (Fig. 4.6a).

In the *F. serratus* area, the metabolic balance measured on slabs showed a slight increase from 0.129 ± 0.041 in December 2013 (n = 3) to 0.673 ± 0.180 in May 2016 (n = 5), despite some seasonal variability (Fig. 4.6b). A metabolic balance higher than 1 was recorded at only one occasion (May 2013, 0.821 ± 0.710, n = 2). The metabolic balance of the established *F. serratus* community varied from 0.180 ± 0.007 to 0.377 ± 0.059, showing seasonal variability being minimum in winter and maximum in summer (Fig. 4.6b).

Recovery of metabolism in a *F. serratus* community after harvesting

The *F. serratus* community harvested in February 2013 exhibited a GPP that progressively increased over time, ranging from 131.7 ± 22.7 mgC m⁻² h⁻¹ in March 2013 to 1 229.1 ± 108.7 mgC m⁻² h⁻¹ in April 2014. The metabolic balance showed substantial seasonal variability (Fig. 4.7), reaching its minimal value (0.16 ± 0.03) in January 2014 and its maximal value (0.42 ± 0.03) in September 2014.

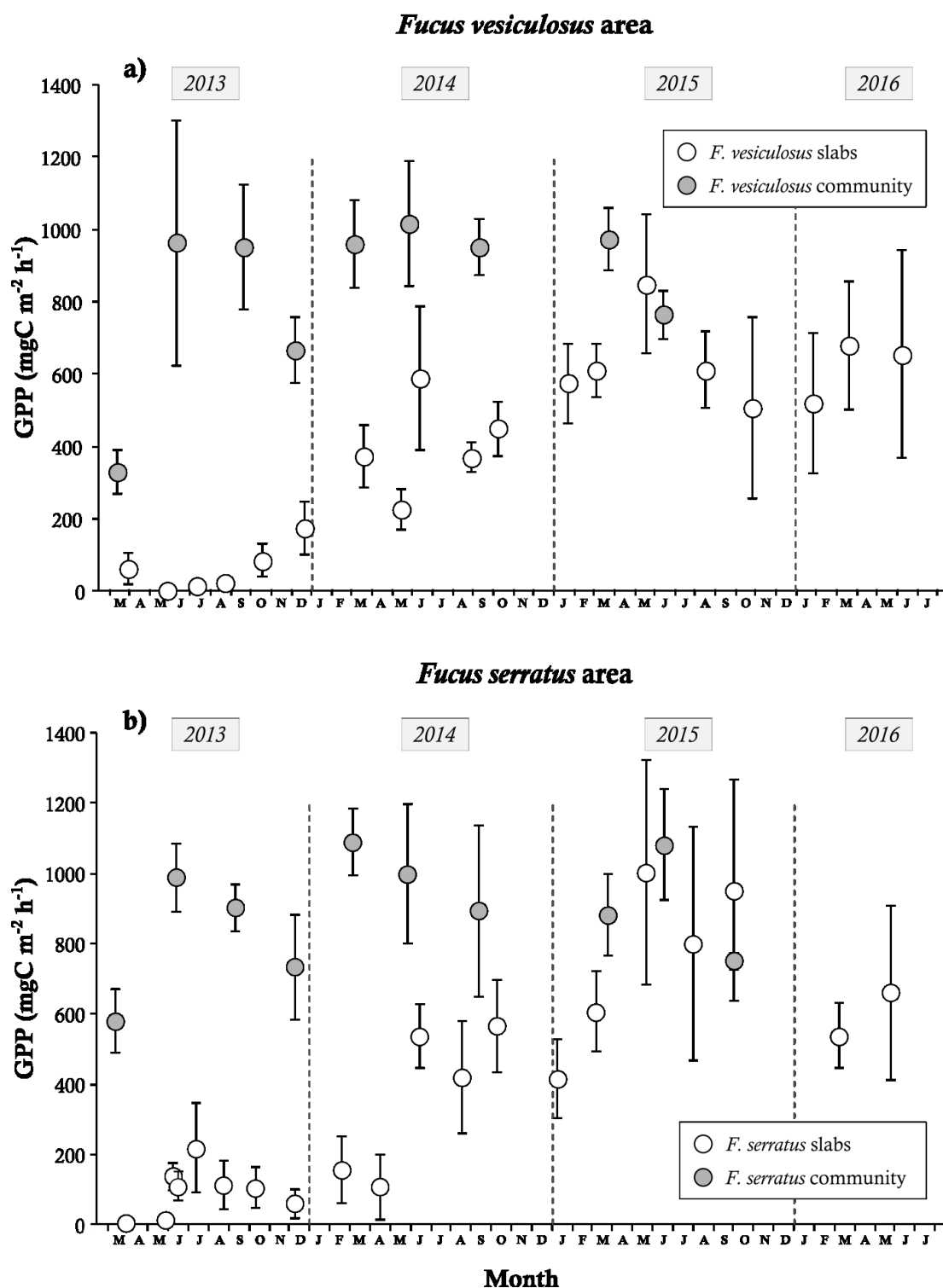


Fig. 4.5 Mean ($\pm$ SE) gross primary production (GPP, in $\text{mgC m}^{-2} \text{h}^{-1}$) over time for **a)** assemblages settled on the slabs of the *F. vesiculosus* area ($1 \leq n \leq 5$, white circles) and for the established *F. vesiculosus* community ($n = 3$, gray circles) and **b)** for assemblages settled on the slabs of the *F. serratus* area ($1 \leq n \leq 6$, white circles) and for the established *F. serratus* community ($n = 3$, gray circles).

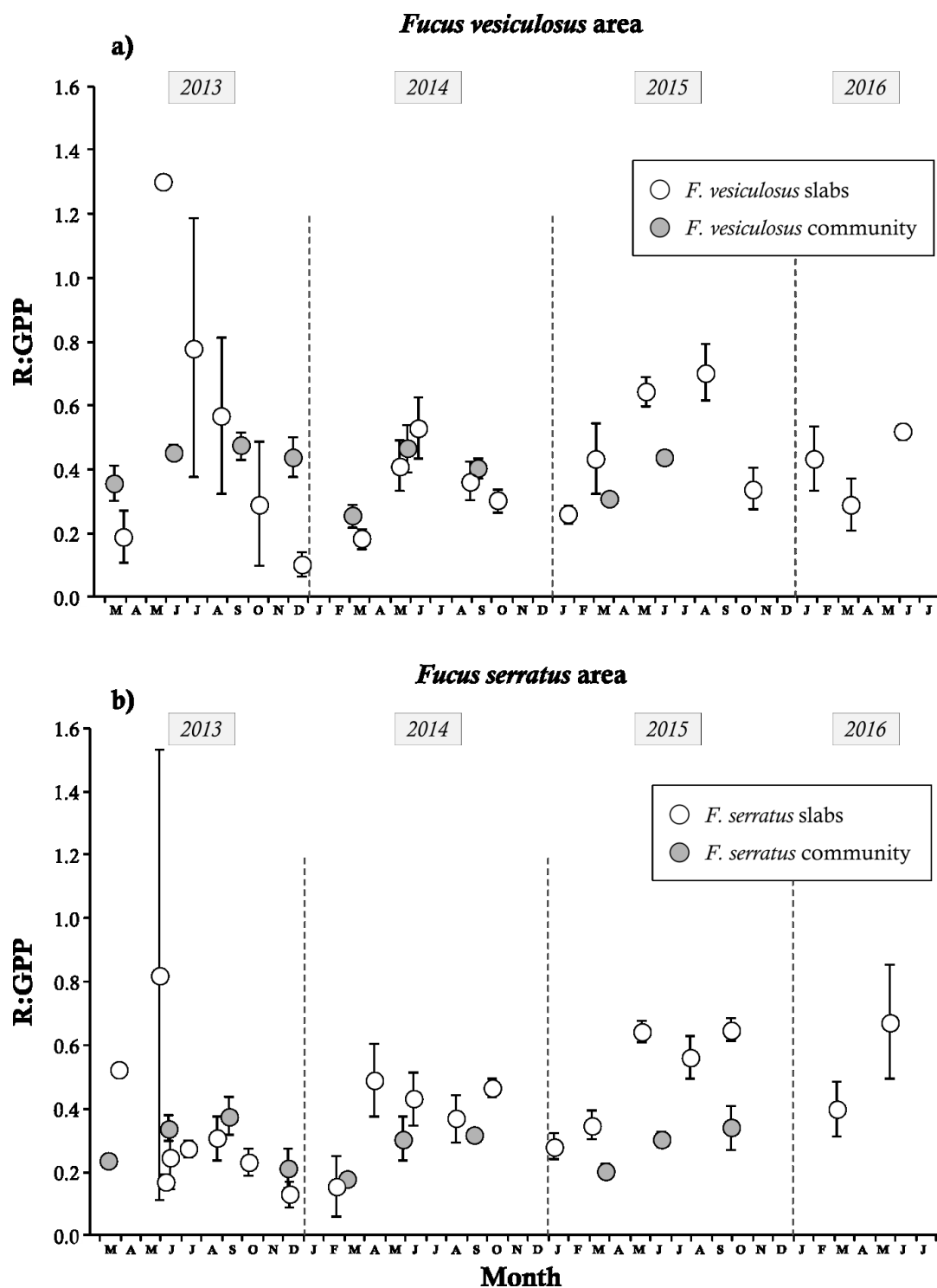


Fig. 4.6 Mean ($\pm$ SE) metabolic balance (R:GPP) over time for **a)** assemblages settled on the slabs of the *F. vesiculosus* area ($1 \leq n \leq 5$, white circles) and for the established *F. vesiculosus* community ($n = 3$, gray circles) and **b)** for assemblages settled on the slabs of the *F. serratus* area ($1 \leq n \leq 6$, white circles) and for the established *F. serratus* community ($n = 3$, gray circles).

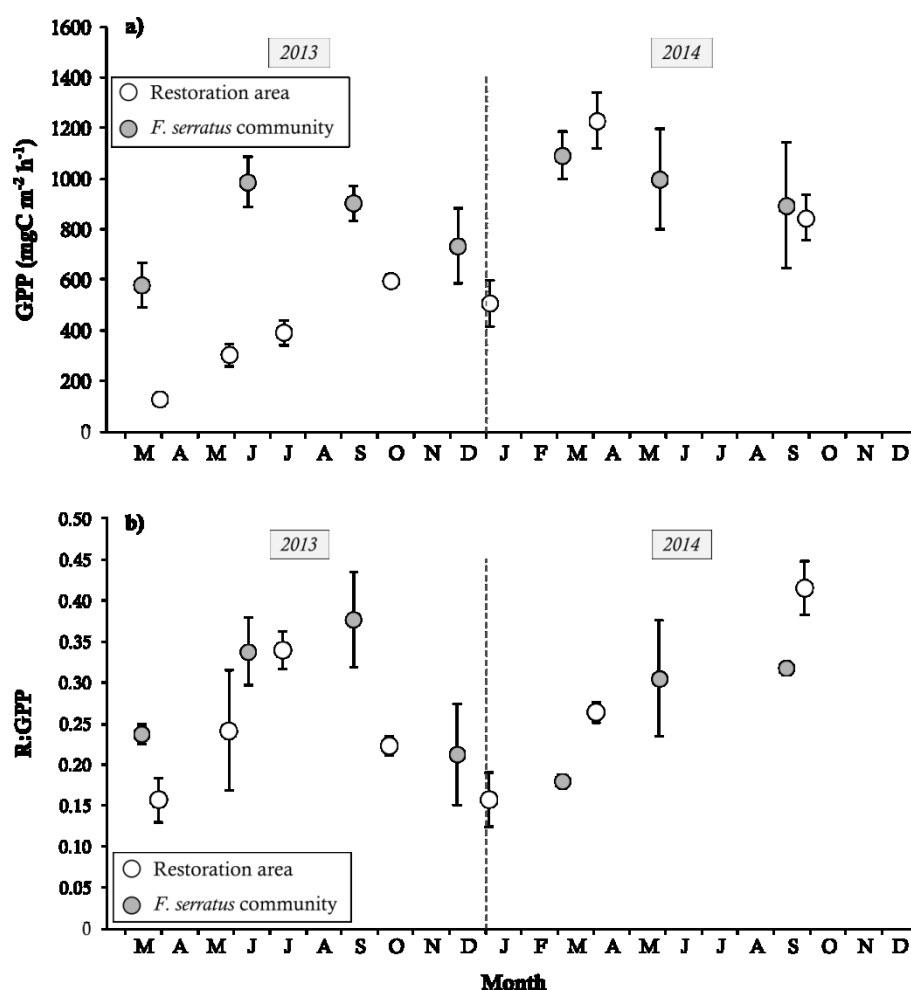


Fig. 4.7 a) Mean ($\pm$ SE) gross primary production (GPP, in $\text{mgC m}^{-2} \text{h}^{-1}$) over time for the restoration area ($3 \leq n \leq 4$, white circles) and the established *F. serratus* community ($n = 3$, gray circles). **b)** Mean ($\pm$ SE) metabolic balance (R:GPP) over time for the restoration area ($3 \leq n \leq 4$, white circles) and the established *F. serratus* community ($n = 3$, gray circles).

Recruitment of *F. serratus* after experimental treatments

In control plots, the *Fucus* sp. juveniles (i.e. < 50 mm) were the most abundant class size and remained constant over the experiment, with a mean abundance index of 2.7 ± 0.1 . The young *F. serratus* (i.e. $50 - 250$ mm) remained also constant, with a mean abundance index of 1.4 ± 0.1 , and the large *F. serratus* (i.e. > 250 mm) were the least abundant class, showing a slight increase with a mean abundance index varying from 0.4 ± 0.2 in March 2015 to 1.4 ± 0.2 in June 2016 (Fig. 4.8a). In the *Fucus* removal treatment, the abundance of *Fucus* juveniles was not significantly different from control plots three weeks after furoid removal (Wilcoxon-Mann-Whitney, $W = 16$, $p > 0.05$) and can be considered as constant throughout the experiment (mean abundance index of 2.2 ± 0.6). The abundance of young *F. serratus* increased during the first three months, reaching

a mean abundance index of 1.0 ± 0.4 in May 2015, and remained constant and not significantly different from control plots hereafter (Wilcoxon-Mann-Whitney, $W = 14$, $p > 0.05$). Large *F. serratus* were absent of these plots during the first 8 months, and then progressively increased in abundance until the end of the experiment when they reached a mean abundance index of 1.0 ± 0.4 . Abundance of large *F. serratus* has recovered, compared to control plots, approximately one year after treatment was applied (February 2016, Wilcoxon-Mann-Whitney, $W = 17.5$, $p > 0.05$) (Fig. 4.8b).

In the scraping treatment, *Fucus* juveniles were observed 6.5 weeks after treatment application, and rapidly recovered, being not significantly different from control plots 11 weeks after treatment (Wilcoxon-Mann-Whitney, $W = 20.5$, $p > 0.05$). Young *F. serratus* were first observed 15.5 months after treatment and had not recovered at the end of the experiment (Wilcoxon-Mann-Whitney, $W = 24$, $p = 0.015$). Large *F. serratus* were never observed (Fig. 4.8c).

Finally, in the scraping and burning treatment, *Fucus* juveniles rapidly recovered to control level (9 weeks, Wilcoxon-Mann-Whitney, $W = 18.5$, $p > 0.05$). Young *F. serratus* were first observed in these plots 6.5 weeks after treatment, but remained in very low abundance during 11 months. Their mean abundance index was not significantly different from control plots 14 months after treatment (Wilcoxon-Mann-Whitney, $W = 16$, $p > 0.05$). In these plots, large *F. serratus* were first observed 17 months after treatment, and had not recovered to control level at the end of the experiment (Wilcoxon-Mann-Whitney, $W = 23.5$, $p = 0.019$) (Fig. 4.8d).

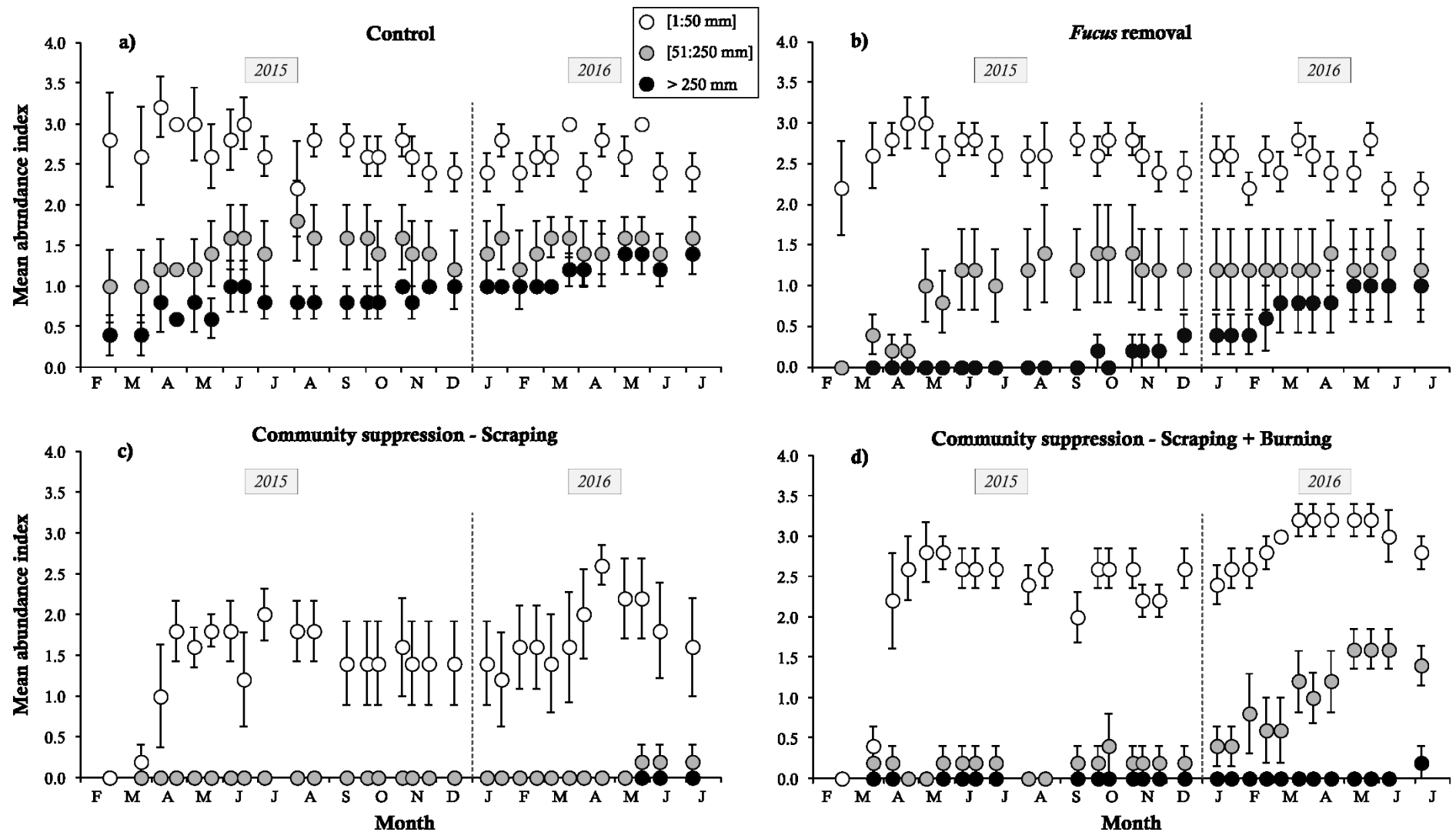


Fig. 4.8 Mean (± SE) abundance index over time for juveniles (white circles), young (gray circle) and large (black circles) *F. serratus*, in control plots (a), *Fucus* removal plots (b), scraping plots (c) and scraping and burning plots (d). (n = 5 for all treatments)

Evaluation of Fucus spp. maturity

Both *F. vesiculosus* and *F. serratus* exhibited a high percentage of individuals able to spawn gametes throughout the year. Thus, this percentage ranged from 75 to 100% for *F. vesiculosus*, with an average of $87.6 \pm 6.4\%$, and from 62.5 to 100% for *F. serratus*, with an average value of $92.4 \pm 9.3\%$ (Fig. 4.9). On average, the maturity of these two species was not significantly different (paired *t*-test, $t = 1.67$, $df = 21$, $p > 0.05$).

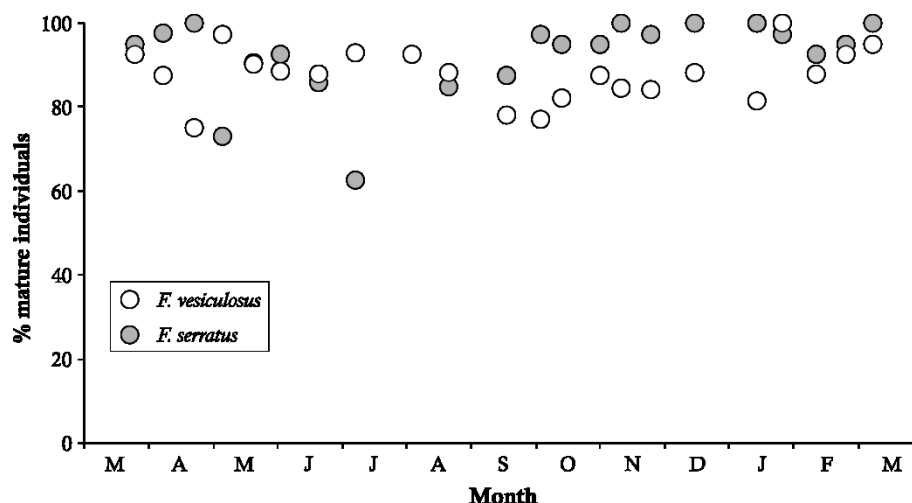


Fig. 4.9 Percentage (%) of mature *F. vesiculosus* (white circles) and *F. serratus* (gray circles) for sampled individuals over time (from March 2015 to March 2016).

Discussion

The successional sequences of two intertidal communities dominated by *Fucus* species were studied on granite slabs during 3 years and a half. Interestingly, on some slabs, the *Fucus* settled during the first months, while on some others, any *Fucus* has been recorded during the entire survey. On the slabs without *Fucus*, a low number of species was usually recorded, which consisted mainly in mobile grazers (e.g. the limpet *Patella vulgata* and the trochid gastropods *Gibbula* spp. and *Phorcus lineatus*). This pattern concerned 43% of the slabs placed in the *F. vesiculosus* area (9 slabs on 21) and 10% of those placed in the *F. serratus* area (2 slabs on 20), highlighting that the successional process in intertidal rocky shores is highly variable over small spatial scales. The absence of settlement or growth of *Fucus* on some slabs should result from numerous reasons acting together (Vadas et al. 1992). The canopy cover in the areas where the slabs have been attached may have played an important role. Indeed, if the canopy can cover the

slabs during low tides, it protects them from severe drying and extreme temperatures for instance. Thus, the important canopy cover in the *F. serratus* area (75 to 100% cover of substratum) may have facilitated algal settlement in a greater extent than in the *F. vesiculosus* area (40 to 60% cover of substratum). As well, grazers have certainly contributed to control algal colonization through consumption of early life stages, as demonstrated by Lubchenco (1983). These early life stages have been proved to be highly vulnerable to grazers as they do not possess protective mechanisms as efficient as adults (Santelices 1990). Even though macroalgal settlement or growth has been prevented on these slabs, some primary production was detected, emphasizing the presence of biofilms comprising autotrophic species. The aerial GPP recorded on these slabs remained low all over the course of the survey (0 to 34.8 mgC m⁻² h⁻¹), being of the same order of magnitude than those obtained for exposed rocky shores (Tagliarolo 2012). The assemblages of these slabs also regularly acted as heterotrophic entities during our measurements, which is consistent with the results of Tagliarolo et al. (2015). These slabs were considered to be not representative of the successional sequences of *Fucus* communities and therefore not included in the analyses. However, their survey should be to carry on, studying more precisely the biotic and abiotic factors likely to constrain the successional process.

Focusing on slabs where *Fucus* have settled, the present study highlights that *F. vesiculosus* settled rapidly (being recorded as soon as September 2013) and dominated in the *F. vesiculosus* area but also in the *F. serratus* area. In the *F. serratus* area, *F. serratus* settled far latter than *F. vesiculosus* (being recorded in June 2014) and exhibited similar density only 3 years after the beginning of the survey. The timing of zygotes arrival in bare space, which is critical for population dynamic of some fucoids (Lamote & Johnson 2008), may explain the dominance of one to several species during succession (Kim & DeWreede 1996). However, the monitoring of *Fucus* maturity in the study site showed that a large proportion of *F. vesiculosus* and *F. serratus* (longer than 20 cm) were fertile all over the year, suggesting that zygotes of these two species should be available to settle in bare space at any time. This was confirmed by the recruitment observed after experimental treatments performed in the *F. serratus* community, as *F. serratus* juveniles (i.e. < 50 mm) were observed in large quantities throughout the year in all treatments. Yet, these experimental treatments also showed that growth of *F. serratus* juveniles depended on the presence of understory community. The abundance of young *F. serratus* (i.e. 50-250 mm) recovered to the

level of control plots faster in the *F. serratus* removal plots than in the scraping and burning plots, while recruits were observed rapidly at the same density in all treatments. The understory community in the *F. serratus* removal plots should have provides shelter against predator, canopy sweeping and/or physiological stresses for young *Fucus*, improving their survivorship as shown for other benthic algae (e.g. Brawley and Johnson 1991; Vadas et al. 1992). Thus, on the slabs placed in the *F. serratus* area, *F. vesiculosus* may have settled first due to its higher tolerance to environmental stresses than *F. serratus*. Then, *F. serratus* may have settled and grown on the slabs, benefitting from the presence of *F. vesiculosus* that mitigated environmental conditions. Such facilitation processes have been reported for intertidal fucoids (Chapman 1995, Choi & Norton 2005) and *F. vesiculosus* has already been observed to replace a dominant fucoid after canopy removal (Dudgeon & Petraitis 2001, Jenkins et al. 2004). The survey should be carry on to check for a shift in *Fucus* dominance in favor of *F. serratus* in the lower zone, and to determine the time needed for *Fucus* settled on the slabs to reach the density observed in the established communities (43 ± 7 *F. vesiculosus* m⁻² of in the *F. vesiculosus* area and 71 ± 16 *F. serratus* m⁻² in the *F. serratus* area).

The mean number of taxa recorded per slab has increased over time in the two areas and was similar to that of established communities after about one year. Some mobile fauna may have migrated from nearby environment (Hartnoll & Hawkins 1985), while for algae and sessile fauna, the local pool of mature individuals was of critical importance for their settlement on the slabs, as demonstrated by Dethier (1984). The dynamic of succession in intertidal assemblages strongly depends on recruitment success, but also on numerous direct and indirect species interactions (van Tamelen 1987, Benedetti-Cecchi 2000, Bertness et al. 2014). Importantly, these interactions can vary in time (Viejo et al. 2008). For instance, *Fucus* species have been described to negatively affect associated species during the first successional stages (e.g. competition for space, nutrients), but to facilitate their establishment and survival in subsequent successional stages, due to mitigation of abiotic conditions (Jenkins et al. 1999, Viejo et al. 2008). Furthermore, when growing fucoid thalli offer new substrata for numerous algal and invertebrate species, as observed during this study (e.g. *Elachista fucicola*, *Electra pilosa*). Ephemeral Ulvophyceae (tubular species) have been recorded during the first months of this survey. However, they do not seem to have inhibitory effect on successional sequences, as evidenced by Lubchenco (1983). In contrast, these

ephemeral species may have protected young fucoids from grazing and severe desiccation during low tide, therefore counterbalancing the reduction in light availability they caused. Finally, even if the number of taxa was about the same, assemblages recorded on the slabs were not similar to those of established communities after 42 months, for any of the two areas. This is consistent with the pattern of succession observed by Murray and Littler (1978) for algal assemblage, which did not completely recover 30 months after experimental denudation. The comparisons performed in the present study have however to be interpreted cautiously as the scale of observation differs between slabs and established communities monitoring (i.e. 8 to 18 slabs of 0.16 m² vs 5 quadrats of 0.1 m²). Thus, the survey should be carry on to determine the time needed for the assemblages on the slabs to be similar to the established communities.

While taxonomic composition of slab's assemblages still differed from established communities after 42 months, gross primary production and metabolic balance were of the same order of magnitude than in established communities approx. 24 months after the beginning of successional sequences in the two areas. This might be a consequence of the rapid growth of *Fucus* which settled during the first months of survey. This growth led rapidly to multilayer assemblages in which self-shading reduced the metabolic balance (Bordeyne et al. 2015). Excepted at very few occasions during the first year of succession, slabs assemblages acted on average as autotrophic entities during our measurements (i.e. GPP > R). Photosynthetic efficiency strongly depends on abiotic conditions during emersion periods and may be drastically reduced in response to desiccation (Quadir et al. 1979), especially in the youngest stages (Lamote et al. 2007, 2012). Intertidal gradient had no detectable influence on the delay needed for slabs assemblages to reach GPP similar to the one of in established communities, but in the lower intertidal level, *F. vesiculosus* has fulfilled the role of *F. serratus*. Understory species could have also contributed to the increase in primary production over the course of succession, especially in a context of complementarity between species, which has been proved to occur for light use in intertidal communities (Tait & Schiel 2011a). The ephemeral Ulvophyceae observed on the slabs at the beginning of the survey (especially from March to August 2013) with a relatively low cover, did not drive the GPP at levels as high as in established communities, contrary to what was observed in rock pools by Martins et al. (2007). This confirms that the role of particular

species in succession is highly variable according to local conditions (emergent substratum vs rock pool, for instance).

By cutting *F. serratus* canopy to mimic harvesting, we strongly altered the metabolism of the community as expected, as canopies have been shown to be responsible for the large majority of primary production and respiration of whole community (Golléty et al. 2008, Migné et al. 2015b, Bordeyne et al. 2015). The time necessary for primary production to recover after harvesting was approximately of one year, in accordance with what was already observed by (Stagnol et al. 2013). Cutting canopies reduced shading on understory species, including young *F. serratus* for which growth is stimulated by the increase in light availability. A bloom of ephemeral Ulvophyceae was observed a few months after harvesting, and might have contributed to the increase in primary production in this area, but not sufficiently to reach production level of the surrounding community, as pointed out by Stagnol et al. (2013).

Overall, this study highlights that the process of colonization was highly variable in intertidal areas, with some slabs where *Fucus* species did not settle. Where *Fucus* settled, slabs assemblages rapidly achieved a metabolism similar to established communities, even though their structure still differed. The rapid acquisition of the essential community function of primary production appeared to be mainly related to the rapid growth of *Fucus* species. This is fundamental for the dynamic of these ecosystems, and especially for transfer of organic matter within food webs. The same pattern was observed in the two areas investigated and the acquisition of high primary production rates was not delayed in the higher shore level. The granite slabs were all installed on the shore at the same period while the timing of creation of bare space can strongly affect the pattern of succession, due to the influence of seasonality on life-history traits of species (e.g. reproductive period, growth) (see Jenkins and Martins 2009, and references therein). Further investigations in that way are thus needed, to test for the influence of seasonality on successional sequence and, therefore, on changes in productivity during succession.

Supplementary material 4.1 List of taxa recorded on the slab of the *Fucus vesiculosus* area, and date of first observation.

Taxa of primary producers		Fucus vesiculosus area	
Taxa of primary producers	Date	Taxa of fauna	Date
<i>Caulacanthus ustulatus</i>	Dec-13	Acarian	Dec-15
<i>Ceramium</i> sp.	Dec-13	<i>Actinia equina</i>	Mar-15
<i>Chondracanthus acicularis</i>	Dec-13	<i>Alcyonidium</i> sp.	Jun-14
<i>Chondrus crispus/Mastocarpus stellatus</i> complex	Dec-13	Amphipod	Sep-13
<i>Cladophora</i> sp.	Jun-15	<i>Anemonia viridis</i>	Feb-14
<i>Elachista fucicola</i>	Jun-14	<i>Asterina gibbosa</i>	Sep-15
<i>Fucus serratus</i>	Mar-16	<i>Austrominius modestus</i>	Dec-13
<i>Fucus vesiculosus</i>	Sep-13	Bryozoa Ctenostomatida stolonifera	Sep-14
Gelidiales	Sep-14	Campanulariidae	Feb-14
Hapalidiaceae	Dec-13	<i>Carcinus maenas</i>	Jun-15
<i>Hildendrandia rubra</i>	Sep-13	<i>Clava multicornis</i>	Mar-15
<i>Lomentaria articulata</i>	Dec-13	<i>Dynamena pumila</i>	Jun-14
Other Ectocarpales	Dec-13	<i>Dynamene bidentata</i>	Feb-14
Other Rhodophyta	Jun-14	<i>Electra pilosa</i>	Sep-14
<i>Palmaria palmata</i>	Jun-15	<i>Flustrellidra hispida</i>	Sep-15
<i>Polysiphonia</i> sp.	Jun-14	<i>Gibbula cineraria</i>	Sep-15
<i>Porphyra</i> sp.	Sep-13	<i>Gibbula pennanti</i>	Sep-13
<i>Pseudolithoderma</i> sp.	Jun-14	<i>Gibbula umbilicalis</i>	Sep-13
<i>Ulva</i> sp. 1 (foliose species)	Sep-14	<i>Idotea</i> sp.	Feb-14
<i>Ulva</i> sp. 2 (tubular species)	Sep-13	<i>Lipophrys pholis</i>	Sep-15
<i>Vertebrata lanosa</i>	Jun-15	<i>Littorina obtusata</i>	Sep-13
		<i>Littorina littorea</i>	Dec-13
		<i>Nucella lapillus</i>	Dec-13
		Other Bryozoa	Jun-15
		Other Decapod	Jun-16
		Other Gastropod	Jun-14
		Other Hydrozoa	Jun-16
		Other Isopod	Sep-13
		Paguridae	Jun-16
		<i>Patella vulgata</i>	Sep-13
		<i>Perforatus perforatus</i>	Dec-13
		<i>Phorcus lineatus</i>	Sep-13
		Plathelminthe	Mar-15
		Polyclinidae	Sep-14
		Pycnogonid	Mar-15
		<i>Schizoporella unicornis</i>	Dec-14
		<i>Spirorbis</i> sp.	Sep-13
		<i>Tricolia pullus</i>	Feb-14
		<i>Trivia</i> sp.	Dec-14

Supplementary material 4.2 List of taxa recorded on the slab of the *Fucus serratus* area, and date of first observation.

Fucus serratus area			
Taxa of primary producer	Date	Taxa of fauna	Date
<i>Ascophyllum nodosum</i>	Jun-14	<i>Alcyonidium</i> sp.	Jun-14
<i>Caulacanthus ustulatus</i>	Dec-13	Amphipod	Sep-13
<i>Ceramium</i> sp.	Feb-14	<i>Anemonia viridis</i>	Feb-14
<i>Chondracanthus acicularis</i>	Dec-13	<i>Anomia ephippium</i>	Sep-14
<i>Chondracanthus teedei</i>	Sep-14	<i>Asterina gibbosa</i>	Jun-15
<i>Chondrus crispus/Mastocarpus stellatus</i> complex	Dec-13	<i>Botrylloides</i> sp.	Dec-13
<i>Cladophora</i> sp.	Jun-15	<i>Botryllus schlosseri</i>	Dec-13
<i>Cryptopleura ramosa</i>	Sep-15	Bryozoa Ctenostomatida stolonifera	Sep-14
<i>Dictyota dichotoma</i>	Sep-14	Bryozoa Cyclostomatida (encrusting)	Sep-14
<i>Elachista fucicola</i>	Jun-14	<i>Calliostoma zizyphinum</i>	Sep-13
<i>Fucus serratus</i>	Jun-14	Campanulariidae	Jun-14
<i>Fucus vesiculosus</i>	Sep-13	<i>Carcinus maenas</i>	Sep-13
<i>Gastroclonium ovatum</i>	Sep-15	<i>Clava multicornis</i>	Sep-14
Gelidiales	Jun-15	<i>Dynamena pumila</i>	Sep-13
Hapalidiaceae	Dec-13	<i>Dynamene bidentata</i>	Feb-14
<i>Hildendrandia rubra</i>	Sep-13	<i>Electra pilosa</i>	Jun-14
<i>Lomentaria articulata</i>	Dec-13	<i>Flustrellidra hispida</i>	Jun-14
<i>Osmundea</i> sp.	Feb-14	<i>Gibbula cineraria</i>	Dec-13
Other Chlorophyceae	Jun-14	<i>Gibbula pennanti</i>	Sep-13
Other Ectocarpales	Jun-14	<i>Gibbula umbilicalis</i>	Sep-13
Other Rhodophyta	Jun-14	<i>Idotea</i> sp.	Sep-14
<i>Palmaria palmata</i>	Sep-14	<i>Littorina littorea</i>	Jun-15
<i>Petrocelis cruenta</i>	Mar-16	<i>Littorina obtusata</i>	Sep-13
<i>Polysiphonia</i> sp.	Jun-14	<i>Nucella lapillus</i>	Sep-13
<i>Porphyra</i> sp.	Sep-13	Other Nudibranch	Sep-15
<i>Pseudolithoderma</i> sp.	Jun-14	<i>Ocenebra erinaceus</i>	Jun-15
<i>Ulva</i> sp. 1 (foliose species)	Dec-13	Other Actiniaria	Dec-13
<i>Ulva</i> sp. 2 (tubular species)	Sep-13	Other Bryozoa	Sep-13
		Other Decapod	Jun-14
		Other Gastropod	Jun-15
		Other Isopod	Sep-14
		Other Polychaete	Sep-14
		Paguridae	Sep-14
		<i>Patella pellucida</i>	Dec-13
		<i>Patella vulgata</i>	Sep-13
		<i>Phorcus lineatus</i>	Feb-14
		Plathelminthe	Sep-14
		Polyclinidae	Sep-13
		Pycnogonid	Mar-15
		<i>Schizoporella unicornis</i>	Dec-13
		<i>Spirobranchus triqueter</i>	Sep-13
		<i>Spirorbis</i> sp.	Sep-13
		<i>Tricolia pullus</i>	Sep-13

PARTIE III - BILANS ANNUELS DE PRODUCTION

PRIMAIRE DES COMMUNAUTES A CANOPEE

DE *FUCUS*



Introduction

Le processus de production primaire constitue un élément clé dans le fonctionnement des milieux côtiers, jouant un rôle primordial dans l'apport d'énergie pour de nombreuses espèces (Raven & Hurd 2012). De nature variable, ce processus a fait l'objet de nombreuses études au cours des dernières décennies, notamment en milieu rocheux, afin de mieux appréhender ses fluctuations à différentes échelles de temps (par ex. King & Schramm 1976, Dring & Brown 1982, Williams & Dethier 2005). A l'échelle annuelle, les algues brunes formant des canopées (Phaeophyceae) se révèlent particulièrement productives (Mann 1973, Cousens 1984, Vadas et al. 2004) et pourraient constituer un puit de carbone non négligeable dans le cadre du bilan planétaire (Smith 1981). Néanmoins, ces études, réalisées à l'échelle populationnelle, ont négligé l'ensemble des interactions se déroulant au sein de communautés multispécifiques. Ces interactions peuvent pourtant avoir des conséquences directes sur la production primaire, en raison de la compétition pour l'accès aux ressources (Sand-Jensen 1977, Rohde et al. 2008), ou de la complémentarité entre espèces pour l'utilisation de la lumière (Tait & Schiel 2011a), par exemple. Il apparaît donc nécessaire d'établir des bilans annuels de production primaire à l'échelle des communautés, de façon à quantifier plus précisément leur rôle dans les flux biogéochimiques des milieux côtiers. L'émergence et le développement de systèmes de mesures *in situ* et à l'échelle de la communauté ont permis, au cours des dernières années, de caractériser la production primaire et la respiration de différents systèmes côtiers de substrat rocheux (par ex. Cheshire et al. 1996, Golléty et al. 2008, Miller et al. 2009). Les communautés intertidales dominées par les algues brunes ont ainsi fait l'objet de plusieurs études visant à préciser leur métabolisme au cours des périodes d'émersion (Golléty et al. 2008, Migné et al. 2015b) ou à l'immersion (Tait & Schiel 2010, South et al. 2016), faisant généralement état d'une forte variabilité saisonnière. Les mesures de métabolisme acquises pour une même communauté lors des périodes d'émersion et d'immersion au cours de différentes saisons constituent une base de données indispensable pour établir de manière fiable et précise son bilan annuel de production primaire.

A notre connaissance, de tels bilans n'ont jamais été réalisés pour des communautés intertidales d'algues brunes. A contrario, Tagliarolo et al. (2015) ont récemment estimé le bilan annuel de carbone pour des communautés intertidales établies en milieu rocheux de mode battu, caractérisés par la dominance d'organismes hétérotrophes. Ce bilan se révèle être une source précieuse d'informations concernant la dynamique et le fonctionnement de cet écosystème. De

telles informations concernant les communautés d'algues brunes permettraient donc d'appréhender de façon plus concrète leur fonctionnement, formant un complément essentiel aux connaissances actuelles sur le rôle et le devenir de cette production primaire, qu'elle soit exportée (Duarte & Cebrian 1996, Crawley et al. 2009, O'Brien et al. 2016) ou non (Golléty et al. 2010) vers d'autres écosystèmes.

L'ensemble des mesures *in situ* de métabolisme acquises au cours de cette thèse sur les communautés de *Fucus vesiculosus* et de *Fucus serratus*, à la fois lors de périodes d'émersion et d'immersion, a généralement permis de mettre en évidence des tendances saisonnières marquées, et similaires d'une année à l'autre, confirmant l'importance des paramètres environnementaux pour le fonctionnement des communautés intertidales. A partir de ces données, couplées aux données environnementales (intensité lumineuse, température par ex.) acquises à haute fréquence, l'objectif de cette étude consiste à établir un bilan annuel de production primaire fiable pour ces deux communautés, à l'aide d'une approche de modélisation réalisée en collaboration avec Martin Plus (Ifremer Plouzané). Ces deux communautés étant caractéristiques de deux niveaux intertidaux distincts (i.e. médiolittoral moyen et médiolittoral inférieur), les résultats de ces bilans sont analysés dans un contexte de zonation intertidale.

Matériel & méthodes

Site d'étude

Le calcul du bilan annuel de production primaire des communautés de *Fucus vesiculosus* et de *F. serratus* repose sur les mesures *in situ* de production primaire et de respiration réalisées tout au long de cette thèse, ainsi que sur des relevés réguliers de paramètres environnementaux caractérisant la zone d'étude. Ces paramètres biologiques et physico-chimiques ont été mesurés au niveau de l'estran rocheux situé devant la Station Biologique de Roscoff (48°44'N, 3°59'W). Sur cet estran, que l'on peut considérer comme semi-abrité, l'étagement vertical des communautés est particulièrement marqué et suit le schéma généralement observé sur les côtes rocheuses européennes (Raffaelli & Hawkins 1999). A ce titre, la communauté à *F. vesiculosus* est représentative de l'étage médiolittoral moyen (3,5 à 4,5 m au-dessus du niveau zéro des cartes marines), alors que celle à *F. serratus* est représentative de l'étage médiolittoral inférieur (2,5 à 3,5 m au-dessus du niveau zéro des cartes marines). Sur ce site d'étude, le cycle de marée est semi-diurne avec un marnage qui varie de 2,5 à 9 m, en fonction du jour de l'année. Ce cycle de marée

a un rôle prépondérant pour les communautés intertidales, puisque l’alternance des périodes d’émersion et d’immersion détermine en partie les conditions environnementales (en particulier lumière et température) auxquelles elles sont soumises.

Paramètres environnementaux

***** Alternance émersion-immersion et hauteur d’eau *****

L’alternance des périodes d’émersion et d’immersion constitue donc un facteur important à prendre en compte pour obtenir un bilan annuel de production primaire précis et réaliste. Afin de déterminer ces périodes, et de connaître la hauteur de la colonne d’eau présente au-dessus de ces communautés lorsque celles-ci sont immergées, nous avons considéré qu’en moyenne, la communauté à *F. vesiculosus* est établie à une hauteur de 4,0 m par rapport au zéro des cartes marines (h_{fves}) et que celle à *F. serratus* est établie à une hauteur de 3,0 m par rapport au zéro des cartes marines (h_{fser}). A l’immersion, la hauteur de la colonne d’eau au-dessus des deux communautés (z_{fves} et z_{fser}) a été calculée toutes les 15 minutes, du 1^{er} juin 2014 au 31 mai 2015, à partir du niveau de marée (correspondant à la hauteur d’eau mesurée au-dessus du zéro des cartes marines h_e , données du marégraphe de Roscoff, <http://data.shom.fr/#donnees/refmar/54>), selon l’équation suivante (5.1) :

$$z = h_e - h \quad (5.1)$$

***** Intensité lumineuse dans l’air *****

L’intensité lumineuse est généralement considérée comme le paramètre environnemental le plus important pour la régulation de l’activité photosynthétique des communautés considérées (cf. Chapitres 1 & 3). Cette intensité lumineuse est filtrée de façon plus ou moins prononcée par la couche nuageuse, rendant ce paramètre extrêmement variable. De ce fait, le bilan de production primaire de ces deux communautés a été calculé en utilisant d’une part l’irradiance disponible pour la photosynthèse (PAR en $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, 400-700 nm) mesurée I_m (i.e. avec nébulosité), et d’autre part l’irradiance théorique I_{th} (i.e. sans nébulosité).

I_m a été mesurée toutes les 15 minutes à l’aide d’un capteur plan (Quantum sensor SKP215, Skye Instruments LTD.) fixé sur le toit de la Station Biologique de Roscoff (données de l’Observatoire de la Station Biologique de Roscoff), alors que l’irradiance théorique a été calculée pour chaque

pas de temps t , à partir de l'équation (5.2), dépendant de l'élévation solaire sur le site d'étude (Kirk 1994).

$$I_{th}(d, t) = I_o(d) \times \sin\left(\frac{\pi t}{DL(d)}\right) \quad (5.2)$$

Où $I_{o(d)}$ est l'irradiance théorique maximale (au zénith) du jour d (variant de 1 au 1^{er} janvier à 365 au 31 décembre), et $DL_{(d)}$ est la durée de ce jour d (i.e. période pendant laquelle le soleil est au-dessus de l'horizon, Monteith & Unsworth 2013).

A l'échelle annuelle, I_o varie de façon cyclique, en lien avec la trajectoire elliptique de notre planète autour du soleil (Monteith & Unsworth 2013). La valeur maximale de I_o est atteinte au solstice d'été et a été fixée à $2\,200 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. La valeur minimale de I_o est atteinte au solstice d'hiver, et a été fixée à $700 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. I_o au jour d a été calculée selon l'équation sinusoïdale (5.3) ajustée à ces deux points.

$$I_o(d) = 1450 + 750 \times \sin\left(\frac{2\pi}{365} d + 4,667\right) \quad (5.3)$$

La durée du jour DL varie également en fonction du jour de l'année considéré (d) et a été calculée à partir de l'angle d'incidence de la lumière au zénith du jour d (δ) et de la latitude ϕ du site d'étude ($48^\circ 44' \text{N}$), selon l'équation (5.4).

$$DL = 0,133 \times \cos^{-1}(-\tan \phi \tan \delta) \quad (5.4)$$

$$\begin{aligned} \text{Où } \delta = & 0,39637 - 22,9133 \cos\left(360 \times \frac{d}{365}\right) + 4,02543 \sin\left(360 \times \frac{d}{365}\right) \\ & - 0,3872 \cos\left(2 \times 360 \times \frac{d}{365}\right) + 0,052 \cos\left(2 \times 360 \times \frac{d}{365}\right) \end{aligned} \quad (5.5)$$

***** Intensité lumineuse dans l'eau *****

Les conditions de lumière auxquelles sont soumises les communautés à l'immersion sont très différentes des conditions aériennes. Ces différences proviennent majoritairement de deux mécanismes distincts, entraînant une atténuation plus ou moins prononcée de la lumière disponible pour la photosynthèse au fond de l'eau. Le premier mécanisme se situe à l'interface air-eau et consiste en la réflexion d'une partie de la lumière incidente, en raison de la différence de vitesse de propagation de la lumière dans l'air et dans l'eau. Le second mécanisme se situe

dans la colonne d'eau, où les molécules d'eau elles-mêmes, les particules et les organismes en suspension vont jouer un rôle important dans l'absorption et la diffusion de la lumière (Kirk 1994). L'intensité lumineuse mesurée au fond de l'eau est donc fonction de l'intensité lumineuse juste sous la surface (I_s , résultant de la réflexion), de la hauteur de la colonne d'eau (z) et du coefficient d'atténuation de la lumière dans l'eau de mer (k). L'intensité lumineuse au niveau du substrat rocheux a été calculée à partir de ces paramètres, pour chaque pas de temps t et pour chaque communauté (à partir de la lumière mesurée, puis de la lumière théorique), selon la relation de Beer-Lambert (5.6).

$$I(t) = I_s(t) e^{-(k(t) z(t))} \quad (5.6)$$

$$\text{Où } I_s(t) = I_{th}(t) \times (1 - r) \quad (5.7)$$

I_s est calculé à partir d'un coefficient de réflexion r à l'interface air-eau, considérant l'eau comme une surface plane et un rapport entre la vitesse de propagation de la lumière dans l'eau et dans l'air de 1,33 (Kirk 1994). Ce coefficient de réflexion a été calculé, pour chaque pas de temps t , à partir de la position du soleil dans le ciel et de l'équation de Fresnel (Kirk 1994) (5.8).

$$r = \frac{1}{2} \frac{\sin^2(\theta_a - \theta_w)}{\sin^2(\theta_a + \theta_w)} + \frac{1}{2} \frac{\tan^2(\theta_a - \theta_w)}{\tan^2(\theta_a + \theta_w)} \quad (5.8)$$

Où θ_a correspond à l'angle d'incidence de la lumière dans l'air, et θ_w correspond à l'angle de transmission de la lumière dans l'eau.

Le coefficient d'atténuation de la lumière dans l'eau de mer (k) a été déterminé à partir de mesures simultanées d'intensité lumineuse dans l'air et dans l'eau. Pour ces mesures, des capteurs (UA-002-64 HOBO Waterproof Temperature/Light Pendant Data Logger, HOBO®) mesurant l'intensité lumineuse des longueurs d'onde comprises entre 150 et 1 200 nm, ont été déployés sur le terrain, à raison d'un capteur placé sur le toit de la Station Biologique de Roscoff pour la mesure dans l'air et de deux autres capteurs fixés sur l'estran, à une hauteur connue, pour les mesures dans l'eau. Les capteurs placés sur l'estran ont été fixés à des rochers suffisamment surélevés par rapport aux communautés de *Fucus* pour éviter toute ombre indésirable. Le coefficient d'atténuation de la lumière a été calculé à partir des données obtenues entre 10:00 et 16:00 (TU), pour une hauteur d'eau de 1m. Dans ces conditions proches du zénith, la réflexion de la lumière incidente est négligeable (i.e. $I_s \approx I$), permettant au coefficient d'atténuation de la lumière de refléter au mieux l'absorption de la lumière par la colonne d'eau. Afin de limiter la

variabilité liée aux artefacts de mesures, un coefficient d'atténuation moyen a été calculé par semaine (3 à 10 valeurs par semaine), puis interpolé linéairement de façon à obtenir une valeur de k pour chaque pas de temps (Fig. 5.1).

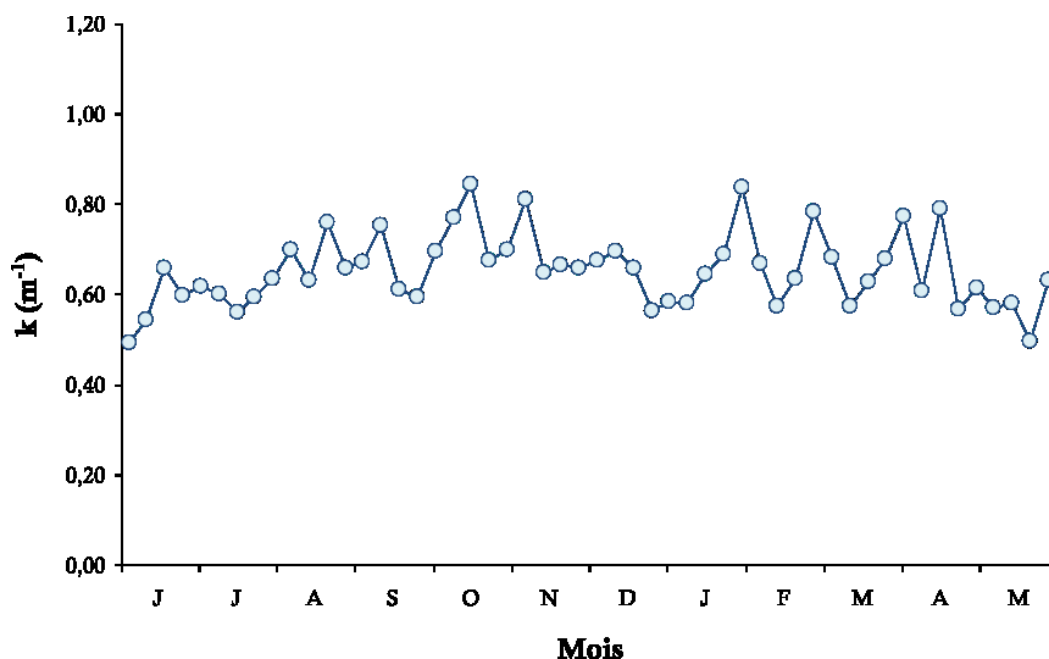


Fig. 5.1 Variation du coefficient d'atténuation de la lumière dans l'eau (k , en m^{-1}), du 1^{er} juin 2014 au 31 mai 2015.

**** Température ****

La température constitue également un paramètre environnemental fondamental pour le métabolisme des organismes intertidaux, intervenant notamment de façon importante dans la régulation des taux de respiration (cf. Chapitres 1 & 3). La température de l'air (Fig. 5.2) a été mesurée pour chaque pas de temps à l'aide du capteur HOBO placé sur le toit de la station. La température de l'eau (Fig. 5.2) a quant à elle été calculée chaque jour, en ajustant une courbe sinusoïdale (5.9) aux données SOMLIT ($n = 24$, $R^2 = 0,966$, $p < 0,001$, point d'échantillonnage Estacade de Roscoff, <http://somlit-db.epoc.u-bordeaux1.fr/bdd.php>).

$$T_{\text{eau}} = 13,42 - 3,07 \times \sin\left(\frac{2\pi}{365}d + 0,59\right) \quad (5.9)$$

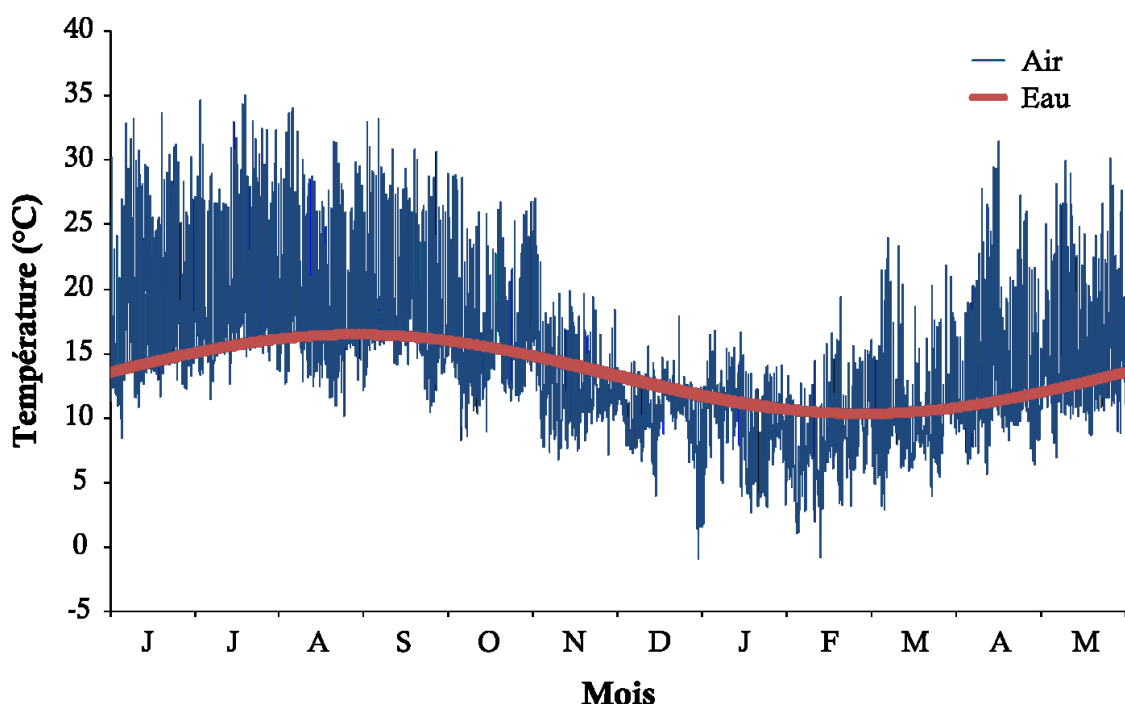


Fig. 5.2 Variation de la température de l'air (°C, en bleu) et de l'eau (°C, en rouge), du 1^{er} juin 2014 au 31 mai 2015.

Métabolisme des communautés de Fucus

Dans la mesure où une part plus importante de mesures *in situ* a été réalisée sur la communauté à *F. serratus* (en particulier les mesures comparatives entre l'émersion et l'immersion, cf. Chapitre 3), les données biologiques utilisées pour le calcul du bilan seront détaillées dans un premier temps pour cette communauté, puis dans un second pour la communauté à *F. vesiculosus*.

**** Production primaire ****

La production primaire brute (PPB) de chaque communauté a été calculée pour chaque pas de temps t , à partir du modèle théorique de Webb et al. (1974), décrivant la relation entre production primaire et irradiance (5.10) (Encart 1).

$$PPB_t = PPB_{max,d} \times (1 - e^{-\frac{I_t}{I_{k,d}}}) \quad (5.10)$$

Où $PPB_{max,d}$ correspond à la production primaire brute maximale réalisable au jour d , I_t correspond à l'irradiance à l'instant t (mesurée ou théorique, selon le cas) et $I_{k,d}$ correspond à l'irradiance de début de saturation au jour d .

La PPB_{max} de la communauté à *F. serratus* (en $mgC\ m^{-2}\ 15min^{-1}$) a été caractérisée à partir des données obtenues à l'émersion, lors des mesures comparatives entre l'émersion et l'immersion (cf. Chapitre 3). Ce paramètre a été calculé pour chaque jour d , à l'aide de l'ajustement sinusoïdal (5.11) effectué sur ces données ($n = 13$, $R^2 = 0,637$, $p = 0,014$).

$$PPB_{max\ Fser,d} = 1000,5/4 - 307,7/4 \times \sin\left(\frac{2\pi}{365}d + 4,5/4\right) \quad (5.11)$$

La PPB_{max} de la communauté à *F. vesiculosus* (en $mgC\ m^{-2}\ 15min^{-1}$) a quant à elle été caractérisée à partir des données obtenues lors du suivi saisonnier à l'émersion (cf. Chapitre 1), et a été calculée pour chaque jour d , à l'aide de l'ajustement sinusoïdal (5.12) effectué sur ces données ($n = 14$, $R^2 = 0,555$, $p = 0,023$).

$$PPB_{max\ Fves,d} = 618,9/4 - 214,9/4 \times \sin\left(\frac{2\pi}{365}d + 7,3/4\right) \quad (5.12)$$

Le paramètre I_k a été estimé à l'aide de courbes production-irradiance (courbe P-I, Encart 1) réalisées au cours de différents mois de l'année, pour chaque communauté. A chaque occasion, une série de courtes incubations successives (i.e. 5-10 min) a permis de déterminer la relation entre PPB et irradiance. Au cours de ces courtes incubations, réalisées *in situ* et à l'émersion, la PPB a été évaluée via les changements de concentrations en CO_2 au sein des chambres benthiques. L'intensité lumineuse a été contrôlée au moyen d'un jeu de filtres gris neutre (Fig. 5.3), de façon à l'atténuer progressivement depuis l'intensité maximale du jour de mesure, jusqu'à l'obscurité complète. Afin de palier à l'absence de réplicat pour chaque période de mesure, les I_k obtenus pour chacune des deux communautés ont été regroupés par saison et moyennés. Le bilan de production a été calculé à partir de ces I_k moyens (Fig. 5.4 & 5.5, Table 5.1).

L'exposition à de longues périodes d'émersion peut entraîner d'importantes pertes en eau pour les organismes intertidaux, conduisant à terme à une possible réduction du métabolisme des communautés (cf. Chapitre 3). La PPB a donc été corrigée de façon à tenir compte de la durée d'émersion (t_e), selon l'équation suivante (5.13) :

$$PBB_{cor} = PPB \times [(a_1 + a_2 \times t_e + a_3 \times t_e^2)/100] \quad (5.13)$$

Où a_1 , a_2 et a_3 sont des coefficients (sans unité) issus, pour chaque communauté, des régressions polynomiales ajustées aux données obtenues lors de mesures *in situ* réalisées à différentes périodes de l'année afin d'évaluer l'influence de la durée de l'émersion sur la production primaire (Fig. 5.6). Chaque régression polynomiale a été testée à l'aide d'un test de Fisher (Table 5.2).

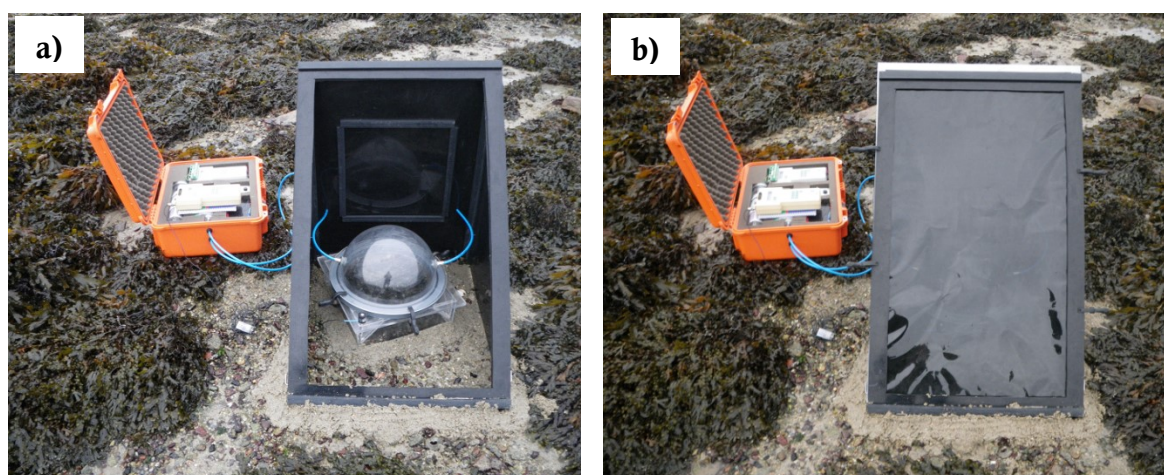
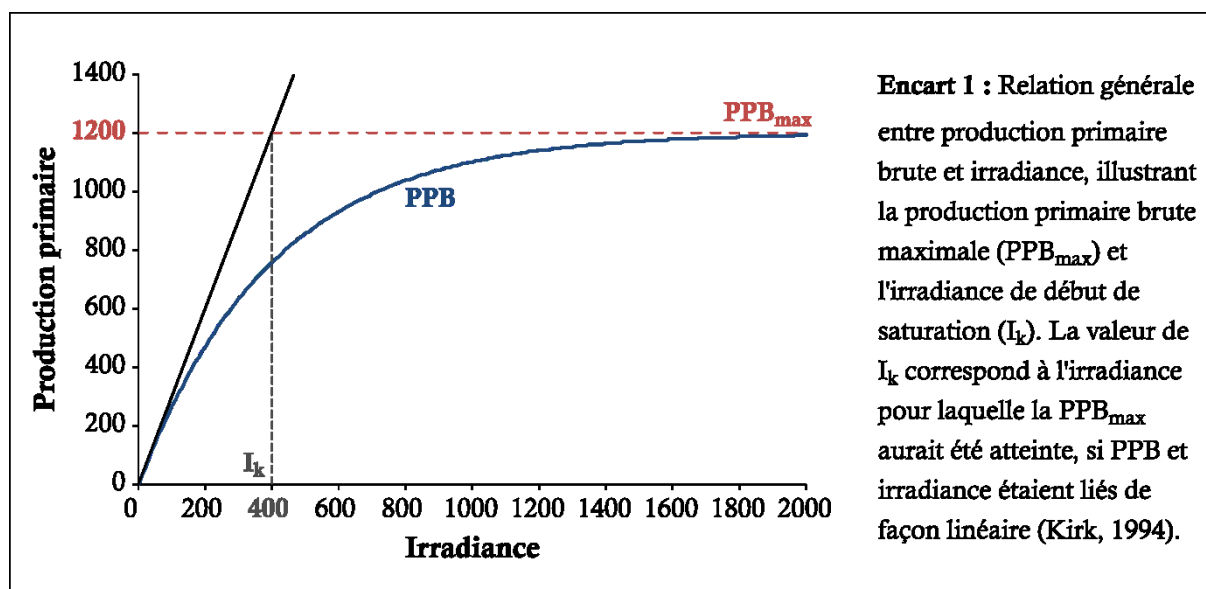


Fig. 5.3 Système expérimental utilisé à l'émersion pour l'obtention de courbes production-irradiance, sans filtre (a), puis avec (b).

**** Respiration ****

La respiration de chacune des deux communautés a été calculée sur la base de relations linéaires entre respiration et température (5.14), déterminées au cours de cette thèse.

$$R = r_1 \times \text{Température} + r_2 \quad (5.14)$$

Ainsi, pour la communauté à *F. serratus*, ces relations linéaires ont été déterminées séparément pour les périodes d'émersion et d'immersion, à partir des mesures comparatives entre l'émersion et l'immersion (cf. Chapitre 3). Pour la communauté à *F. vesiculosus*, une relation a également été déterminée à partir de mesures à l'émersion. Une correction de cette relation a été appliquée pour l'immersion, conformément aux résultats observés pour la communauté à *F. serratus* (i.e. à température égale, une respiration plus élevée à l'émersion).

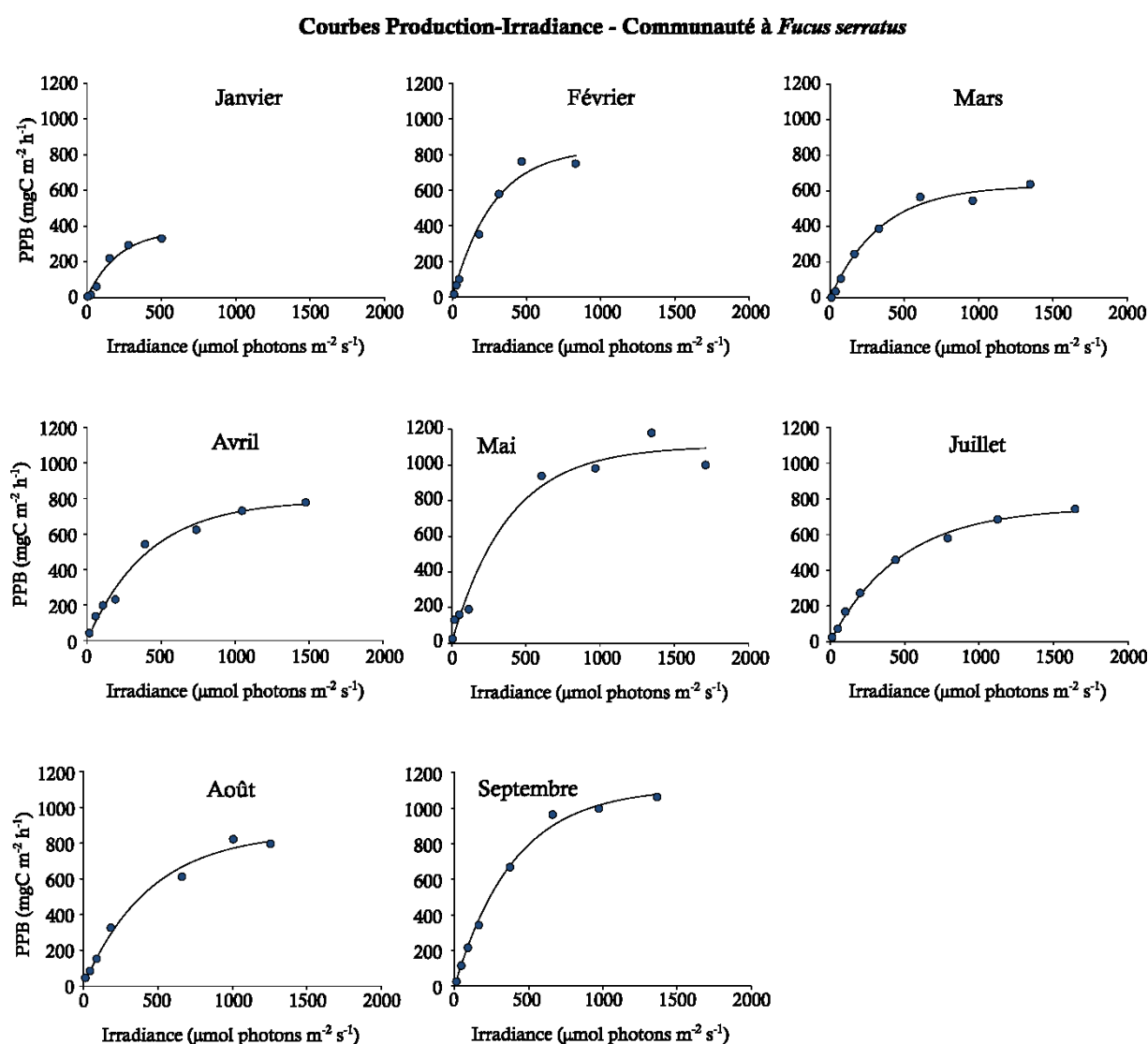


Fig. 5.4 Relations entre production primaire brute (PPB, en $\text{mgC m}^{-2} \text{h}^{-1}$) et irradiance (en $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) déterminées à l'émersion pour la communauté à *F. serratus*, au cours de différents mois de l'année.

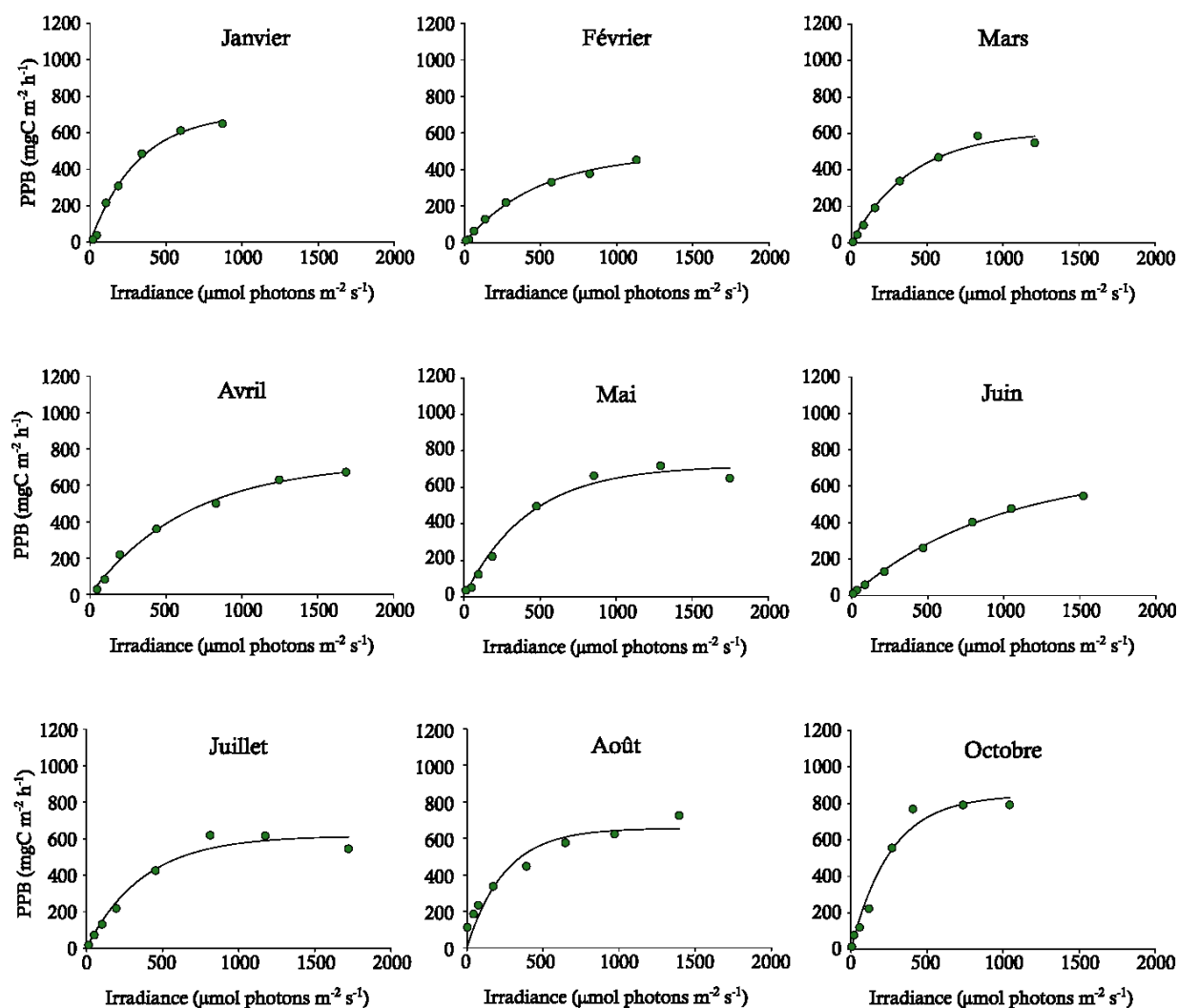
Courbes Production-Irradiance - Communauté à *Fucus vesiculosus*


Fig. 5.5 Relations entre production primaire brute (PPB, en mgC m⁻² h⁻¹) et irradiance (en μmol photons m⁻² s⁻¹) déterminées à l'émersion pour la communauté à *F. vesiculosus*, au cours de différents mois de l'année.

Table 5.1 I_k moyens (± SE, en μmol photons m⁻² s⁻¹) utilisés pour chaque saison, dans chacune des communautés et déterminés à partir des courbes P-I présentées en Fig. 4 & 5.

Saison	Communauté à <i>F. serratus</i>	Communauté à <i>F. vesiculosus</i>
Printemps	396 ± 15	492 ± 81
Été	459 ± 14	522 ± 302
Automne	399	260
Hiver	278 ± 36	399 ± 83

Enfin, de façon similaire à la production primaire, la durée des périodes d'émersion (t_e) peut affecter la respiration des communautés, qui a donc été corrigée en conséquence, selon l'équation suivante (5.15) :

$$R_{cor} = R \times [(b_1 + b_2 \times t_e)/100] \quad (5.15)$$

Où b_1 et b_2 sont des coefficients (sans unité) issus, pour chaque communauté, des régressions linéaires ajustées aux données obtenues lors de mesures *in situ* réalisées à différentes périodes de l'année afin d'évaluer l'influence de la durée de l'émersion sur la respiration (Fig. 5.6). Chaque régression linéaire a été testée à l'aide d'un test de Fisher (Table 5.2). Les coefficients b_1 et b_2 ont été déterminés au cours des mêmes séries de mesures que celles utilisées pour déterminer les coefficients a_1 , a_2 et a_3 .

Table 5.2 Résultats des tests de Fisher pour chacune des régressions ajustées aux données concernant l'évolution de la production primaire (PPB) et de la respiration (R) au cours du temps, durant l'émersion.

Communauté	Paramètre métabolique	R ²	n	F	p
<i>F. serratus</i>	PPB	0,327	117	18,5	< 0,001
	R	0,296	117	48,4	< 0,001
<i>F. vesiculosus</i>	PPB	0,502	114	37,2	< 0,001
	R	0,439	114	87,6	< 0,001

Sorties des modèles

Pour les deux communautés, en conditions de lumière mesurée ou théorique, la PPB, la R et la production primaire nette (PPN = PPB - R) ont été calculées pour chaque jour de l'année et exprimées en gC m⁻² j⁻¹. La PPN journalière a également été déterminée séparément pour les périodes d'immersion (PPN_{imm}) et d'émersion (PPN_{em}). Enfin, pour chaque communauté, la production primaire brute, la respiration et la production primaire nette annuelles (PPB_{tot}, R_{tot}, PPN_{tot}) ont été déterminées et exprimées en gC m⁻² an⁻¹. La contribution des périodes d'immersion et d'émersion à la PPN_{tot} a été déterminée, afin d'estimer leur rôle respectif dans l'apport de carbone organique au sein des communautés. En conditions de lumière mesurée, la proportion de la production primaire respirée par les organismes vivant au sein des communautés a été calculée comme le ratio entre R_{tot} et PPB_{tot}. L'ensemble de ces calculs a été réalisé à l'aide du logiciel libre R v3.2.2 (R Core Team 2015).

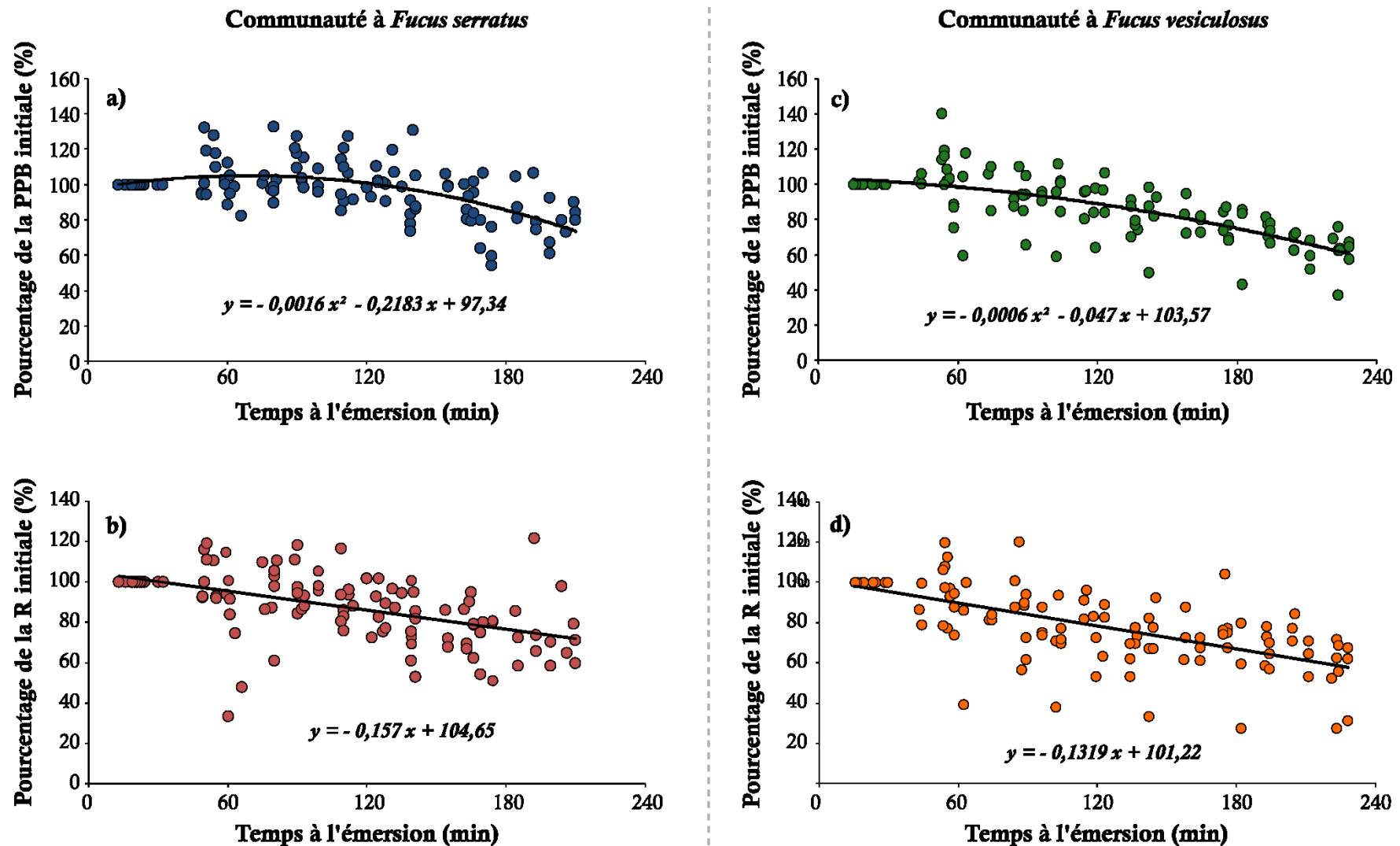


Fig. 5.6 Evolution de la production primaire brute (PPB) et de la respiration (R) en fonction du temps (en minutes) depuis le début de l'émergence, pour la communauté à *Fucus serratus* (a) et (b)) et pour celle à *Fucus vesiculosus* (c) et d)).

Résultats

Pour faciliter la lecture des résultats, ceux-ci sont présentés sur une année théorique, allant du 1^{er} janvier au 31 décembre.

Pour la communauté à *F. vesiculosus*, la PPB calculée à partir de la lumière mesurée est minimale en janvier ($0,12 \text{ gC m}^{-2} \text{ j}^{-1}$) et maximale en juin ($6,67 \text{ gC m}^{-2} \text{ j}^{-1}$) alors que R est minimale en février ($0,60 \text{ gC m}^{-2} \text{ j}^{-1}$) et maximale en juillet ($2,59 \text{ gC m}^{-2} \text{ j}^{-1}$) (Fig. 5.7a). La PPB et R montrent donc des tendances saisonnières marquées avec un léger décalage dans le temps. La PPN totale est minimale en novembre ($-1,34 \text{ gC m}^{-2} \text{ j}^{-1}$) et maximale en juin ($4,69 \text{ gC m}^{-2} \text{ j}^{-1}$) (Fig. 5.7b). Au total, cette PPN est positive (i.e. $\text{PPB} > \text{R}$) au cours de 248 jours, soit environ les deux tiers de l'année (68,0 %). La majorité des jours pendant laquelle la PPN est négative se situent entre la fin de l'automne et l'hiver. En séparant la PPN en fonction des périodes d'immersion et d'émersion, nous observons qu'elle varie de $-1,10$ à $3,12 \text{ gC m}^{-2} \text{ j}^{-1}$ à l'immersion, étant positive 176 jours de l'année (48,2 %) (Fig. 5.7c) et de $-0,52$ à $2,15 \text{ gC m}^{-2} \text{ j}^{-1}$ à l'émersion, étant positive 281 jours par an (77,0 %) (Fig. 5.7d). L'amplitude annuelle de la PPN_{imm} est donc plus prononcée que pour la PPN_{em} . Sur l'année, la PPN_{tot} s'élève à $305,7 \text{ gC m}^{-2}$, dont 78,6 % réalisés en période d'émersion. Au total, l'équivalent des deux tiers (65,3 %) de la PPB_{tot} ($898,4 \text{ gC m}^{-2} \text{ an}^{-1}$) sont respirés par les organismes vivant au sein de cette communauté ($\text{R}_{\text{tot}} = 586,6 \text{ gC m}^{-2} \text{ an}^{-1}$).

En lumière théorique, la variabilité de la production primaire d'un jour à l'autre est fortement réduite pour la communauté à *F. vesiculosus* (Fig. 5.8), et l'alternance des cycles de marée de morte-eau et de vive-eau est plus marquée, en particulier lorsque la PPN est représentée pour les périodes d'immersion (Fig. 5.8c) ou d'émersion (Fig. 5.8d) uniquement. A l'échelle annuelle, la PPB_{tot} s'élève à $1\,327,3 \text{ gC m}^{-2}$ et la PPN_{tot} à $740,7 \text{ gC m}^{-2}$. Les périodes d'émersion contribuent à la PPN_{tot} annuelle à hauteur 55,8 %.

Communauté à *Fucus vesiculosus* - Lumière mesurée

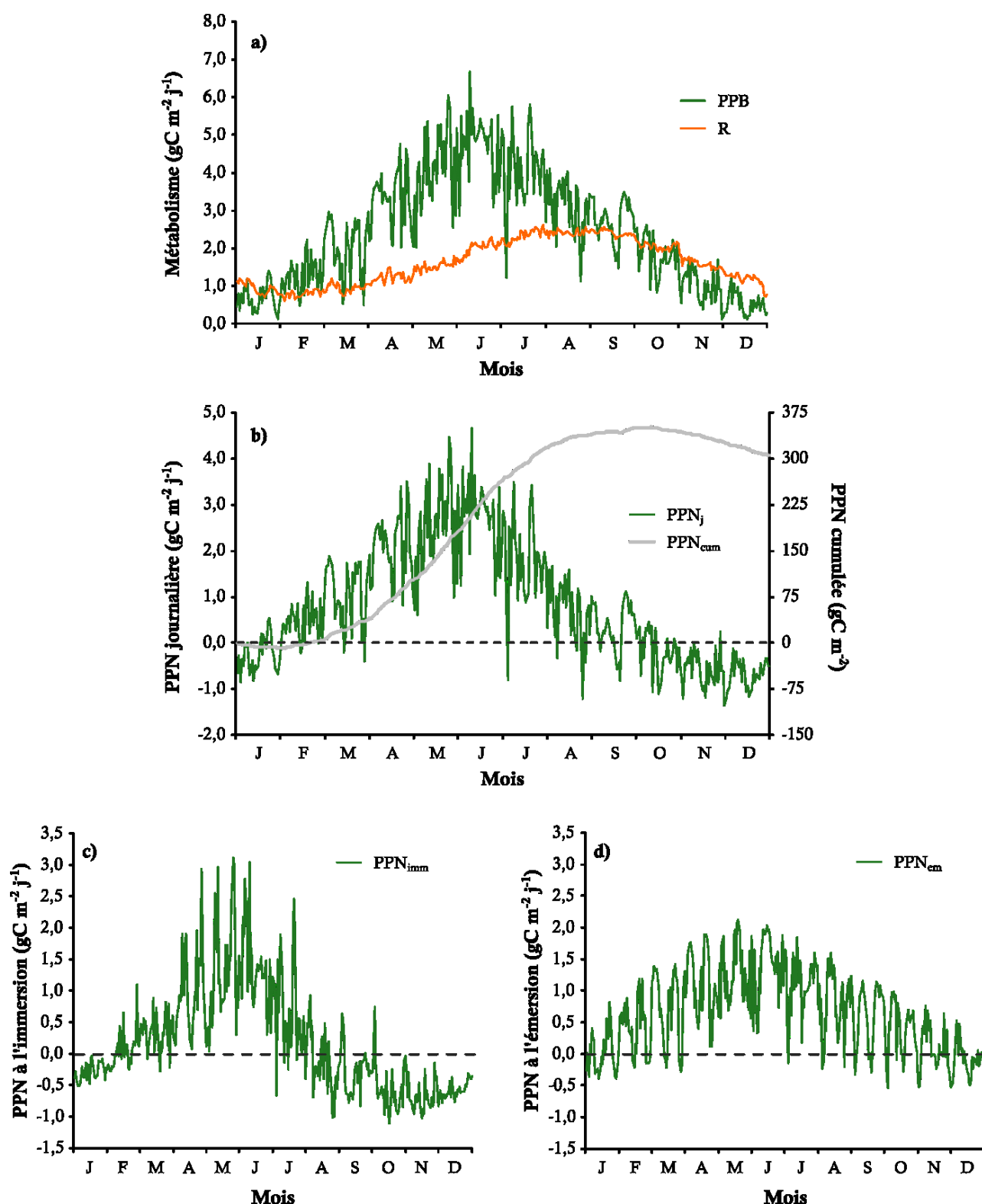


Fig. 5.7 Variations en fonction du temps de a) la production primaire brute (PPB, en vert) et de la respiration (R, en orange) journalières, b) de la production primaire nette journalière (PPN_j, en vert) et de la production primaire nette cumulée (PPN_{cum}, ligne grise), c) de la production primaire nette journalière à l'immersion (PPN_{imm}) et d) de la production primaire nette journalière à l'émersion (PPN_{em}), pour la communauté à *Fucus vesiculosus* en conditions de lumière mesurée.

Communauté à *Fucus vesiculosus* - Lumière théorique

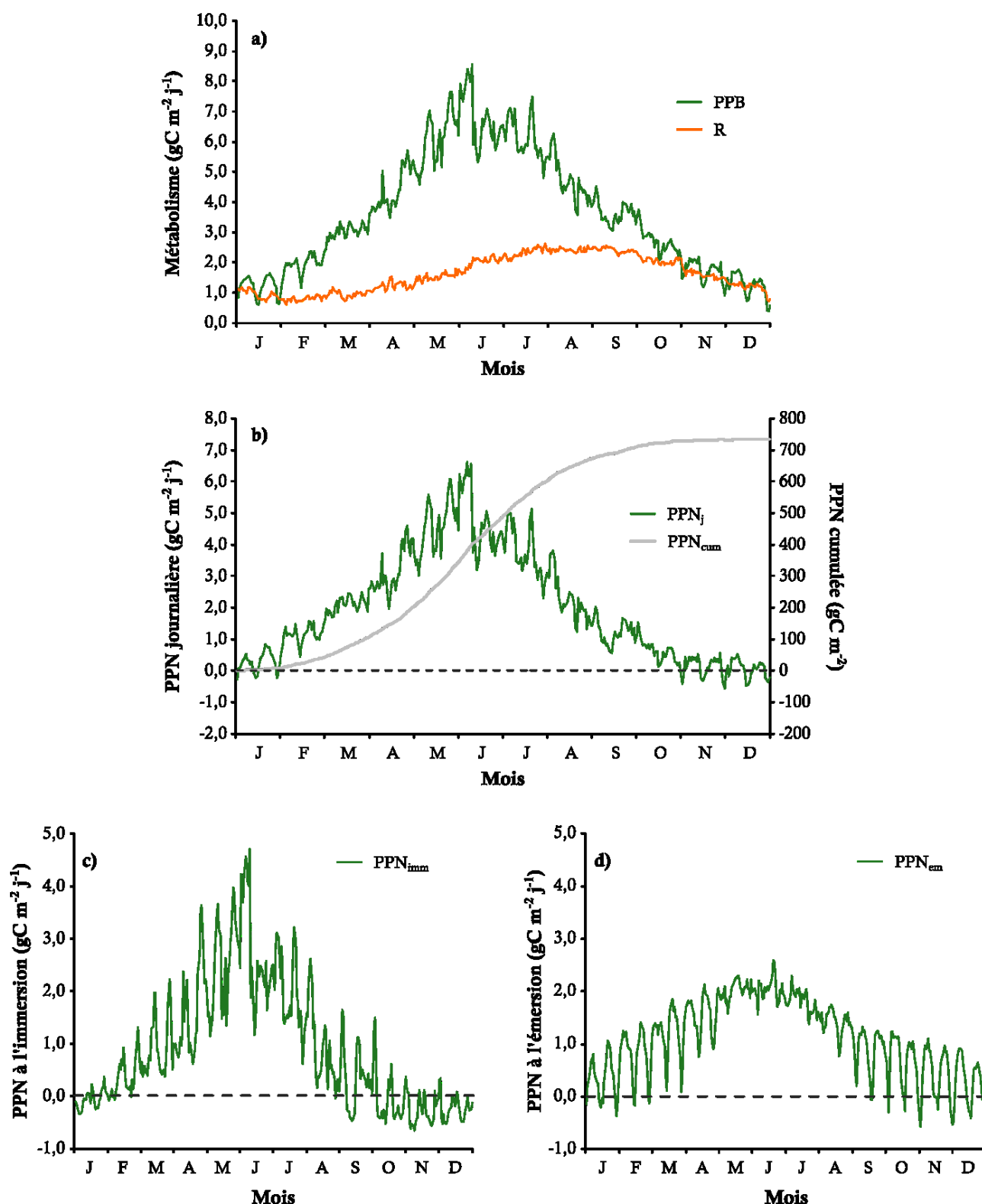


Fig. 5.8 Variations en fonction du temps de a) la production primaire brute (PPB, en vert) et de la respiration (R, en orange) journalières, b) de la production primaire nette journalière (PPN_j, en vert) et de la production primaire nette cumulée (PPN_{cum}, ligne grise), c) de la production primaire nette journalière à l'immersion (PPN_{imm}) et d) de la production primaire nette journalière à l'émersion (PPN_{em}), pour la communauté à *Fucus vesiculosus* en conditions de lumière théorique.

Pour la communauté à *F. serratus*, la PPB calculée à partir de la lumière mesurée est minimale en novembre ($0,07 \text{ gC m}^{-2} \text{ j}^{-1}$) et maximale en juin ($11,19 \text{ gC m}^{-2} \text{ j}^{-1}$) alors que R est minimale en février ($0,63 \text{ gC m}^{-2} \text{ j}^{-1}$) et maximale en septembre ($4,47 \text{ gC m}^{-2} \text{ j}^{-1}$) (Fig. 5.9a). La PPB et R montrent donc également des tendances saisonnières marquées, dont les maximums sont décalés dans le temps (respectivement en début et en fin d'été). La PPN varie également de façon saisonnière, minimale en octobre ($-2,55 \text{ gC m}^{-2} \text{ j}^{-1}$) et maximale en juin ($8,10 \text{ gC m}^{-2} \text{ j}^{-1}$) (Fig. 5.9b). Au total, cette PPN est positive pendant 230 jours, soit environ les deux tiers de l'année (63,0 %). La PPN est majoritairement négative à la fin de l'automne et pendant l'hiver. En ne considérant que les périodes d'immersion, la PPN_{imm} fluctue de $-2,55$ à $6,77 \text{ gC m}^{-2} \text{ j}^{-1}$, étant positive durant la moitié de l'année (191 jours, soit 52,3 % de l'année, Fig. 5.9c). A l'inverse, à l'émersion, la PPN_{em} fluctue de $-0,40$ à $3,30 \text{ gC m}^{-2} \text{ j}^{-1}$, étant positive durant les deux tiers de l'année (238 jours, soit 65,2 % de l'année, Fig. 5.9d). Sur l'année, la PPN_{tot} s'élève à $450,6 \text{ gC m}^{-2}$, dont 68,4 % sont issus de périodes d'émersion. Au total, l'équivalent des deux tiers (66,0 %) de la PPB_{tot} ($1\,324,8 \text{ gC m}^{-2} \text{ an}^{-1}$) sont respirés par les organismes vivant au sein de cette communauté ($\text{R}_{\text{tot}} = 874,2 \text{ gC m}^{-2} \text{ an}^{-1}$).

Comme pour la communauté à *F. vesiculosus*, l'absence de couverture nuageuse réduit fortement la variabilité de la production primaire d'un jour à l'autre (Fig. 5.10), mettant en évidence l'alternance des cycles de marée de morte-eau et de vive-eau pour la PPN (Fig. 5.10c & 5.10d). A l'échelle annuelle, la PPB_{tot} s'élève à $1\,937,7 \text{ gC m}^{-2}$ et la PPN_{tot} à $1\,063,6 \text{ gC m}^{-2}$, dont 41,9 % pendant les périodes d'émersion.

Communauté à *Fucus serratus* - Lumière mesurée

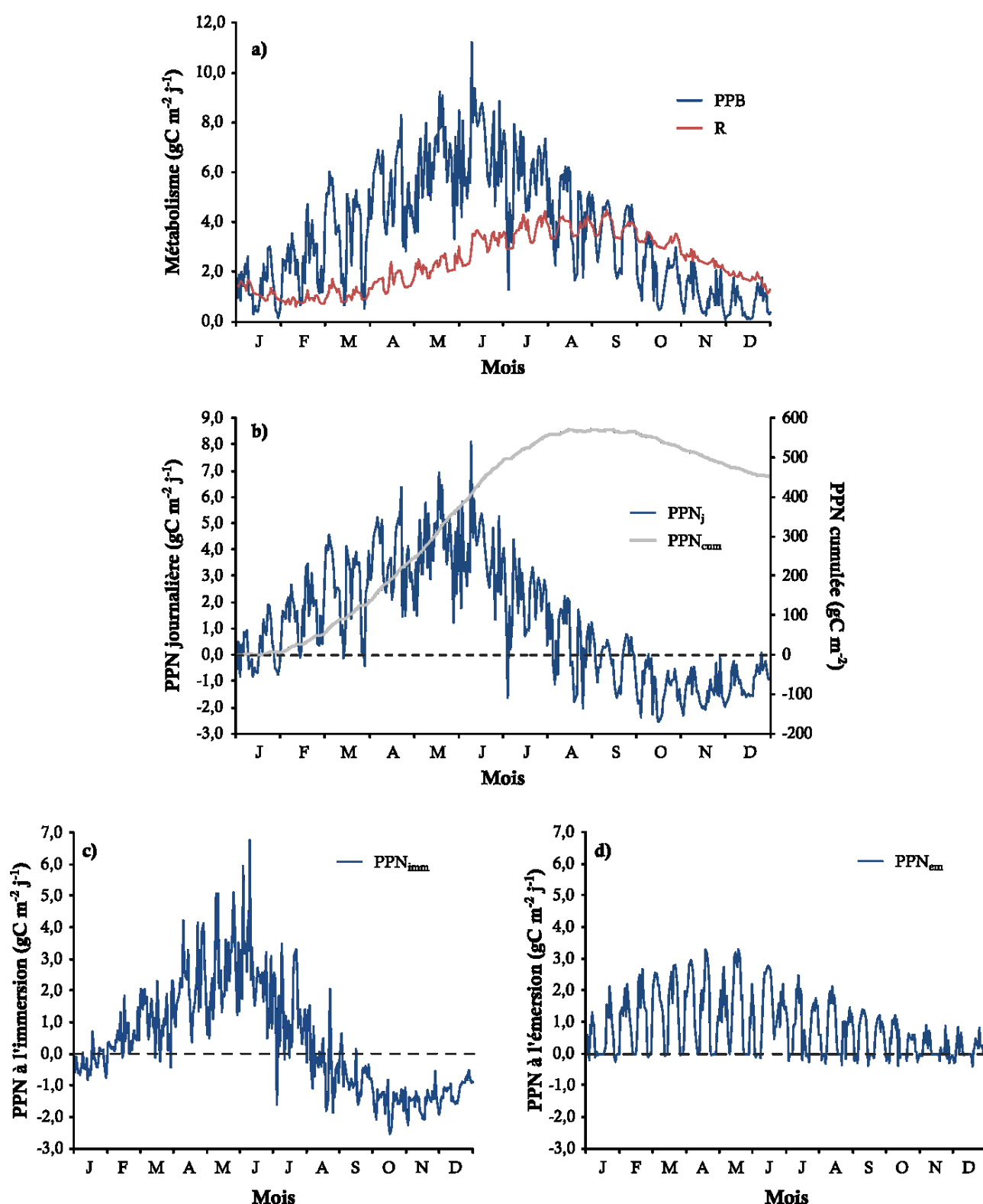


Fig. 5.9 Variations en fonction du temps de a) la production primaire brute (PPB, en bleu) et de la respiration (R, en rouge) journalières, b) de la production primaire nette journalière (PPN_j, en bleu) et de la production primaire nette cumulée (PPN_{cum}, ligne grise), c) de la production primaire nette journalière à l'immersion (PPN_{imm}) et d) de la production primaire nette journalière à l'émersion (PPN_{em}), pour la communauté à *Fucus serratus* en conditions de lumière mesurée.

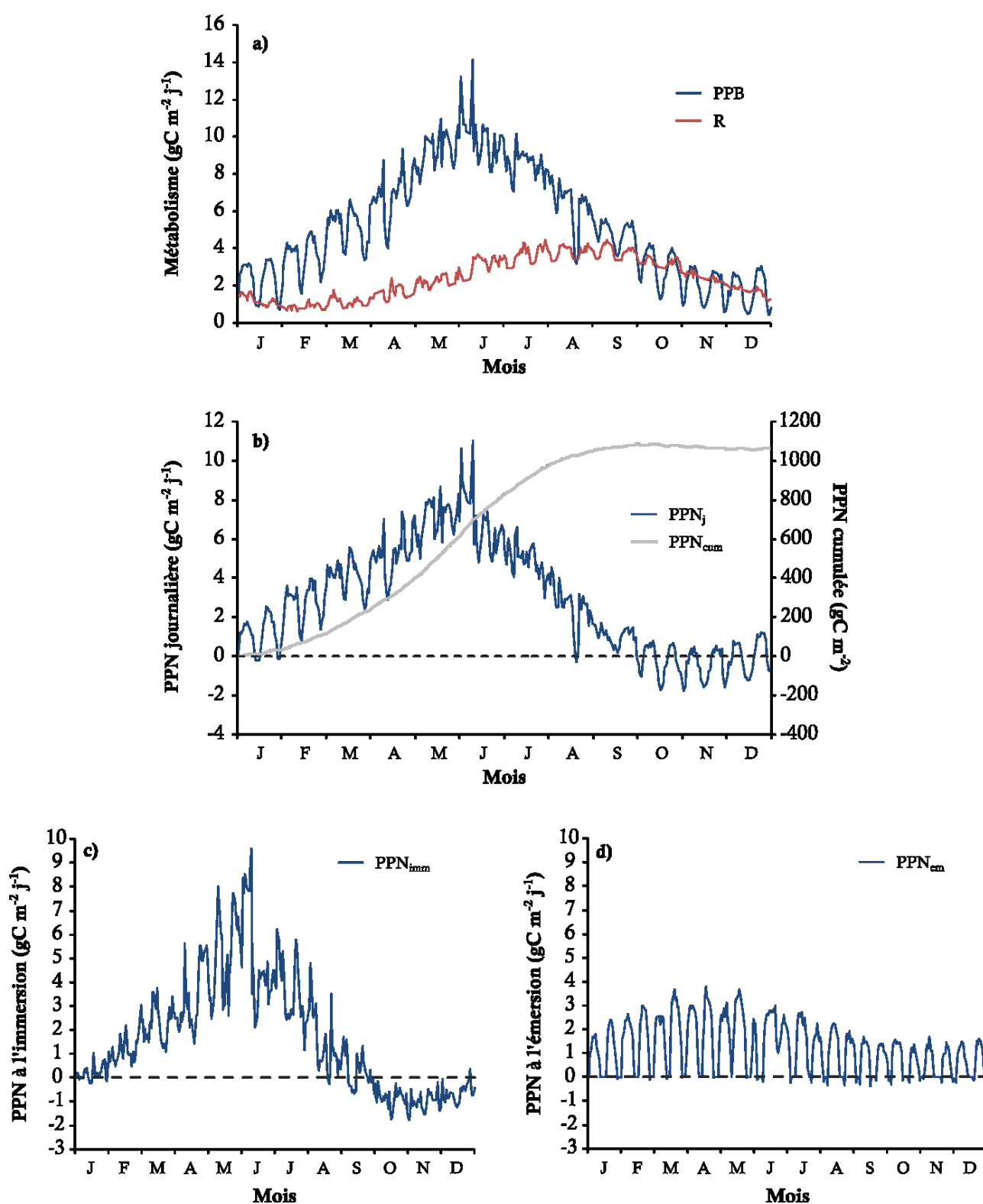
Communauté à *Fucus serratus* - Lumière théorique


Fig. 5.10 Variations en fonction du temps de a) la production primaire brute (PPB, en bleu) et de la respiration (R, en rouge) journalières, b) de la production primaire nette journalière (PPN_j, en bleu) et de la production primaire nette cumulée (PPN_{cum}, ligne grise), c) de la production primaire nette journalière à l'immersion (PPN_{imm}) et d) de la production primaire nette journalière à l'émersion (PPN_{em}), pour la communauté à *Fucus serratus* en conditions de lumière théorique.

Discussion

Les résultats obtenus par cette approche de modélisation numérique traduisent le rôle déterminant de la variabilité des conditions environnementales dans la régulation du métabolisme des communautés de *Fucus*. En particulier, les larges différences de PPB et de PPN résultants des modèles réalisés en conditions de lumière mesurée et de lumière théorique confirment le caractère primordial de la lumière pour la production primaire. En effet, l'atténuation de l'intensité lumineuse par la couche nuageuse a réduit de façon considérable le bilan de production primaire nette ($\approx 60\%$) de ces deux communautés. Ces résultats sont du même ordre de grandeur que ceux obtenus précédemment pour l'herbier de *Zostera marina* ($\approx 50\%$ de réduction) à proximité de notre site d'étude et pour lequel une approche de modélisation similaire a été employée (Ouisse 2010). Malgré de profondes différences du point de vue de leur structure et du milieu dans lequel ces systèmes évoluent (i.e. substrat rocheux vs sédimentaire), ces concordances sont particulièrement intéressantes et démontrent le caractère déterminant de la couche nuageuse sur le métabolisme des communautés intertidales. De la même façon, l'alternance des cycles de morte-eau et de vive-eau a des conséquences importantes sur l'activité photosynthétique des deux communautés de *Fucus*, mêmes si elles sont légèrement atténuées en conditions de lumière mesurée. Ces fluctuations s'expliquent en partie par les larges variations des conditions environnementales auxquelles sont soumises les communautés au cours de ces cycles. En effet, en milieu de journée lorsque l'intensité lumineuse et la température sont maximales, les communautés de ce site d'étude sont généralement immergées en période de morte-eau et émergées en période de vive-eau, ce qui conduit à d'importantes disparités.

La PPN journalière de ces deux communautés varie de façon importante au cours de l'année, suggérant que le statut métabolique d'une communauté ne peut pas être déterminé à partir de mesures ponctuelles réalisées sur une courte période de l'année. Ces mesures doivent au contraire être intégrées sur différentes saisons afin de tenir compte du mieux possible de cette forte variabilité (Rheuban et al. 2014). De façon intéressante, pour les deux communautés de *Fucus*, un tiers des jours de l'année (principalement à la fin de l'automne et durant l'hiver) se sont achevés avec une PPN journalière négative, indiquant que les besoins énergétiques dépassent régulièrement les apports liés à l'activité photosynthétique. Des tendances similaires ont été observées sur l'herbier de *Zostera marina* avec une PPN journalière généralement négative en fin d'automne et en hiver, et positive le reste de l'année (Ouisse 2010). Les résultats de ces modèles

montrent que la PPN journalière de ces communautés peut aussi être négative en été, en raison d'une importante couche nuageuse (cf. résultats lumière mesurée vs lumière théorique) et/ou de conditions de marée défavorables.

A l'échelle annuelle, ces deux communautés de *Fucus* présentent un bilan largement autotrophe, s'élevant à 305,7 gC m⁻² pour la communauté à *F. vesiculosus* et à 450,6 gC m⁻² pour la communauté à *F. serratus*. Ces taux annuels de PPN sont supérieurs à ceux de certaines forêts boréales (Goulden et al. 2011) ou de plantations de conifères en milieu tempéré (Arain & Restrepo-Coupe 2005 et références incluses). Ils sont du même ordre de grandeur que ceux de certaines forêts tempérées (Arain & Restrepo-Coupe 2005 et références incluses), de communautés planctoniques de milieu côtier (Oviatt et al. 2002) ou encore d'herbiers de phanérogames marines (Mateo et al. 2006, Ouisse 2010). Cependant, ils sont inférieurs à ceux de forêts tropicales, qui pourraient dépasser 1 000 gC m⁻² (Aragão et al. 2009). De même, nos estimations sont inférieures à celles calculées par Tait et al. (2015) pour deux communautés intertidales de bas niveaux (i.e. communautés à *Cystophora torulosa* et à *Durvillaea antarctica*, PPN estimée à 2 500 et 4 000 gC m⁻² an⁻¹ respectivement), même si ces dernières reposent sur des mesures ponctuelles réalisées uniquement à l'immersion et sur une courte période (de mi-septembre à fin novembre), puis extrapolées sur l'année. Bien que ces comparaisons soient loin d'être exhaustives, elles confirment que les communautés de Phaeophyceae constituent des systèmes fortement productifs. Néanmoins, il semble qu'une très faible partie du carbone fixé par ces communautés ne soit stockée de façon pérenne (i.e. sans dégradation) (Duarte & Cebrian 1996) contrairement aux herbiers de phanérogames marines par exemple (Duarte et al. 2005), conférant donc aux systèmes dominés par les *Fucus* un statut mineur dans le bilan carbone à l'échelle planétaire.

Sur l'année, la part de la PPB directement respirée par l'ensemble des organismes composant ces systèmes (i.e. autotrophes + hétérotrophes) est similaire pour les deux communautés de *Fucus*, et s'élève à environ 66 % de la PPB. Cela apparaît inférieur aux estimations fournies par Gattuso et al. (1998) pour les écosystèmes dominés par les macrophytes ($\approx$ 90 % de la PPB respirée), qui ne reposent pas uniquement sur des bilans de production primaire précis (taux de métabolisme annuels parfois obtenus en extrapolant des taux journaliers). Cette part apparaît par contre supérieure à ce qui a été estimé suivant la même approche de modélisation pour l'herbier de *Z. marina* (environ 55 %, Ouisse 2010). Cette différence peut, en partie, résulter d'une densité de

producteur primaire plus importante pour les communautés de *Fucus*, entraînant de ce fait une augmentation de l'auto-ombrage.

A l'immersion, la part de PPB respirée est quasiment similaire pour les deux communautés de *Fucus* (83,9 % et 81,7 %, respectivement), alors qu'une différence plus importante est notée à l'émersion (49,4 % pour la communauté à *F. vesiculosus* contre 43,6 % pour celle à *F. serratus*). La communauté à *F. vesiculosus* se montre donc légèrement moins efficace que la communauté à *F. serratus* dans l'air, confirmant les résultats obtenus lors du chapitre 1 (i.e. ratio R:PPB à l'émersion), mais bénéficie d'un temps d'émersion plus long. La position sur l'estran semble donc contribuer à l'équilibre observé pour ces deux communautés. Il serait intéressant d'approfondir ces résultats en réalisant notamment des mesures complémentaires sur d'autres communautés intertidales dominées par les Fucales, de façon à voir si cette tendance est généralisable.

Les résultats de ces modèles montrent que la communauté à *F. vesiculosus* est moins compétitive que celle à *F. serratus* d'un point de vue de la fixation de carbone, que l'on considère la PPB ou la PPN annuelles, ainsi que la part de la PPB respirée lors des périodes d'émersion et d'immersion (dans une moindre mesure). Placés dans un contexte de zonation verticale le long d'un gradient d'émersion, ces résultats sont en accord avec Raffaelli & Hawkins (1999), suggérant que des notions de compétition entre communautés déterminent en partie les patrons de zonation observés. Il est en effet généralement admis que la limite haute de répartition d'une communauté dépend principalement de ses limites de tolérances aux conditions environnementales, alors que sa limite basse est plutôt déterminée par des facteurs d'origine biologiques, et en particulier par la compétition avec la communauté située au niveau inférieur. Dans le cas des communautés de *Fucus*, les différences de métabolisme observées (et en particulier la part de la PPB respirée à l'émersion) suggèrent que la communauté située le plus haut sur l'estran supporte un « coût physiologique » supérieur, lié à la mise en place et au maintien de mécanismes de protection efficaces vis-à-vis des conditions environnementales (Somero 2002, Tomanek & Helmuth 2002). Ce gradient d'émersion semble également influencer sur l'assimilation des nutriments par les producteurs primaires, qui ne bénéficient d'un accès à ces nutriments que lors des périodes d'immersion (Phillips & Hurd 2003, Raven & Hurd 2012). Bien que les organismes autotrophes mettent en œuvre différentes stratégies afin d'éviter une limitation de l'activité physiologique par les nutriments (Phillips & Hurd 2003), ceux établis aux bas niveaux de l'estran profitent d'un accès plus important à ces ressources essentielles pour la photosynthèse, pouvant entraîner des

différences en termes de métabolisme, notamment en été lorsque les concentrations en nutriments sont au plus faibles.

Quoi qu'il en soit, la PPN annuelle de ces deux communautés est fortement liée aux périodes d'émersion, alors que ces dernières sont généralement considérées comme les moins favorables pour l'activité photosynthétique (par ex. Quadir et al. 1979, Lamote et al. 2012). Ainsi, la PPN annuelle de la communauté à *F. vesiculosus* provient à 78 % des périodes d'émersion et à 68 % pour la communauté à *F. serratus*. Ces résultats sont particulièrement intéressants compte tenu du temps d'émersion de ces deux communautés, qui s'élève à 25 à 40 % du temps pour la communauté à *F. vesiculosus* et à 15 à 25 % pour la communauté à *F. serratus*. Ces résultats soulignent donc l'importance capitale des périodes d'émersion pour le métabolisme des communautés de *Fucus*, en particulier en automne et en hiver, lorsque la luminosité et la durée du jour déclinent. A ces périodes, l'activité photosynthétique est généralement limitée à l'immersion par la faible intensité lumineuse reçue par les communautés (cf. Chapitre 3) et la PPN journalière à l'immersion est alors plus ou moins fortement négative. La production primaire sous l'eau s'avère donc insuffisante pour compenser les besoins énergétiques de ces communautés en fin d'automne et en hiver. Les périodes d'émersion ont donc probablement un rôle essentiel dans la pérennité de ces communautés à cette occasion, leur fournissant une partie non négligeable des ressources utiles à leur fonctionnement. Il est intéressant de noter que des résultats similaires ont été observés pour l'herbier de *Zostera noltei* en baie de Morlaix (3,30 m au-dessus du zéro marégraphique, Ouisse 2010). Ces résultats remettent donc en question la vision que nous avons jusqu'à présent des périodes d'émersion, les considérant comme des périodes fortement stressantes du fait de l'exposition à des températures extrêmes et à la dessiccation. Bien que ces contraintes puissent se révéler déterminantes pour les communautés de hauts niveaux marégraphiques, l'atténuation de l'intensité lumineuse dans l'eau semble contraindre davantage les communautés établies à des niveaux marégraphiques inférieurs, particulièrement en fin d'automne et en hiver.

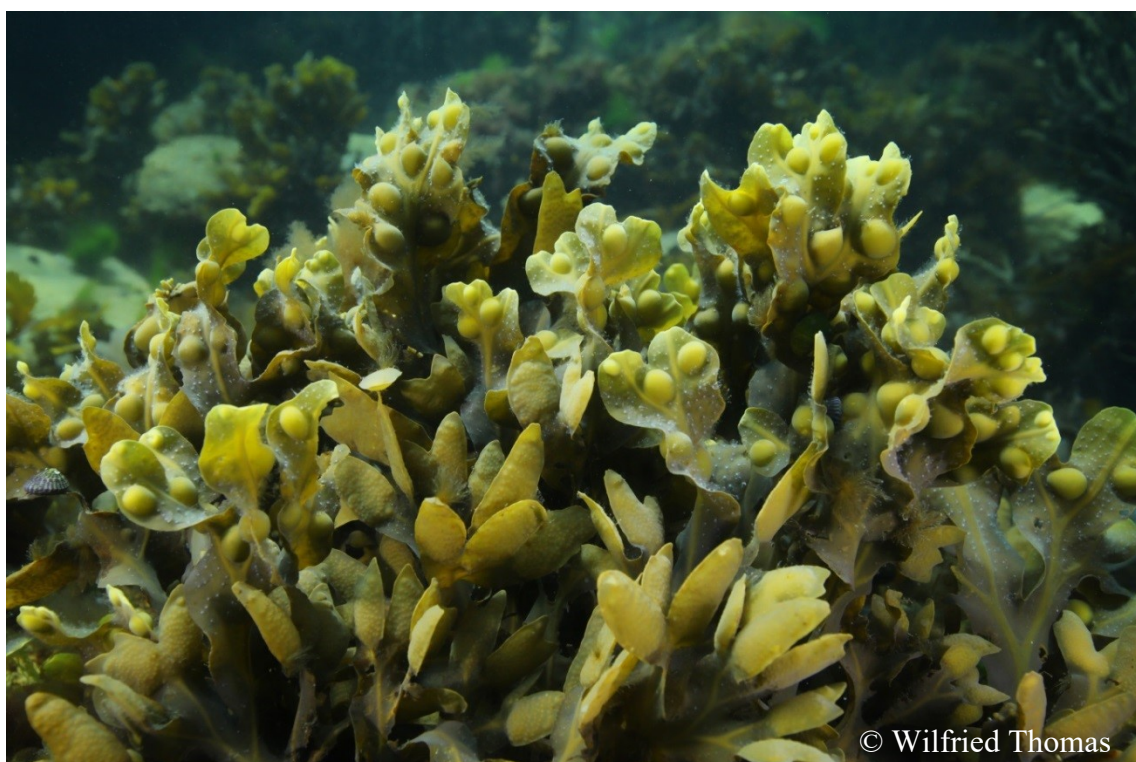
Synthèse et perspectives

Les résultats obtenus au cours de cette étude suggèrent que les communautés de *Fucus vesiculosus* et *F. serratus* constituent des systèmes autotrophes à l'échelle d'une année. La modélisation du bilan annuel de production de ces deux communautés dans des conditions de lumière théorique

sans nébulosité a confirmé le caractère fondamental de l'intensité lumineuse dans la régulation de l'activité photosynthétique de ces communautés, et mis en évidence l'importance de la couche nuageuse dans la variabilité des flux de carbone observés à l'échelle annuelle. Globalement, ces communautés s'avèrent fortement productives, démontrant un métabolisme fluctuant au gré de l'alternance des cycles de morte-eau et de vive-eau. Les périodes d'émersion s'avèrent finalement particulièrement importantes, notamment lors des mois d'automne et d'hiver.

Cette approche de modélisation a donc apporté de précieuses informations concernant le fonctionnement des communautés intertidales dominées par les *Fucus*, via l'usage de données environnementales à une fine échelle de temps. Néanmoins, les modèles développés ici demeurent moins complexes que les communautés que nous avons étudiées, bien que les hypothèses formulées reposent sur l'acquisition de nombreuses mesures *in situ* réalisées à l'échelle communautaire. Il convient donc de tester les résultats obtenus lors de cette étude à l'aide d'analyses de sensibilité, qui nous permettront d'examiner et de quantifier les effets de biais potentiels dans les paramètres des modèles (Loucks et al. 2005). Ainsi, en identifiant la façon dont le modèle réagit aux variations des paramètres entrants, les analyses de sensibilité apporteront des informations précieuses sur la fidélité et la fiabilité des résultats. Elles permettront également de mettre en évidence les paramètres les plus influents sur les résultats observés, et ceux ayant au contraire un moindre rôle. Finalement, il pourrait également être intéressant d'inclure dans ces modèles des informations concernant une limitation potentielle de la production primaire par les nutriments, de façon à tenir compte de leurs fluctuations à l'échelle annuelle (cf. Chapitre 1).

DISCUSSION GENERALE & SYNTHÈSE



Discussion générale

Au cours de cette thèse, je me suis attaché à évaluer différents processus ayant trait au fonctionnement de deux communautés de *Fucus* à des échelles de temps variées, avec pour objectif d'approfondir les connaissances à leur sujet.

Les résultats présentés ici confirment l'importance de la température et de la lumière dans la régulation du métabolisme des communautés à canopée de macroalgues, aux différentes échelles de temps considérées, dans l'air comme dans l'eau. La température régule la respiration des deux communautés de *Fucus*, alors que l'intensité lumineuse est fortement impliquée dans la régulation de la production primaire. A l'échelle saisonnière, la production primaire fluctue au gré des variations de lumière inhérentes à la rotation de notre planète autour du soleil, même si d'autres facteurs abiotiques, tels que la température ou la disponibilité en nutriments sont susceptibles de l'influencer. A l'échelle du cycle de marée, la production primaire semble être régulièrement limitée par les faibles intensités lumineuses à l'immersion. Les communautés de *Fucus* s'avèrent ainsi être plus productives lors des périodes d'émersion qu'à l'immersion et une large part de leur production nette annuelle provient de ces périodes. Les périodes d'émersion seraient donc fondamentales pour le fonctionnement des communautés à canopée de *Fucus*, alors qu'elles sont généralement considérées comme des périodes de fort stress pour les organismes intertidaux. Cependant, nous n'avons pas pu réaliser des séries de mesures *in situ* à différentes intensités lumineuses de façon à établir des courbes production-irradiance lors des périodes d'immersion, alors que l'utilisation de la lumière est susceptible de différer des périodes d'émersion, en particulier pour les intensités lumineuses les plus faibles. La structure tridimensionnelle des communautés à canopée de macroalgues, qui conduit à une distribution inégale et variable de la lumière, est depuis longtemps considérée comme un facteur important dans la régulation du métabolisme (par ex. Binzer & Sand-Jensen 2002b, Middelboe & Binzer 2004) et pourrait être à l'origine de cette différence. En effet, à l'immersion, les canopées sont mises en mouvement par l'hydrodynamisme et les conditions lumineuses changent en permanence (Tait 2010). Au contraire, à l'émersion, elles s'étalent littéralement sur le substrat, formant un ensemble multicouches, plaçant les sous-couches à l'ombre (Fig. 6.1).

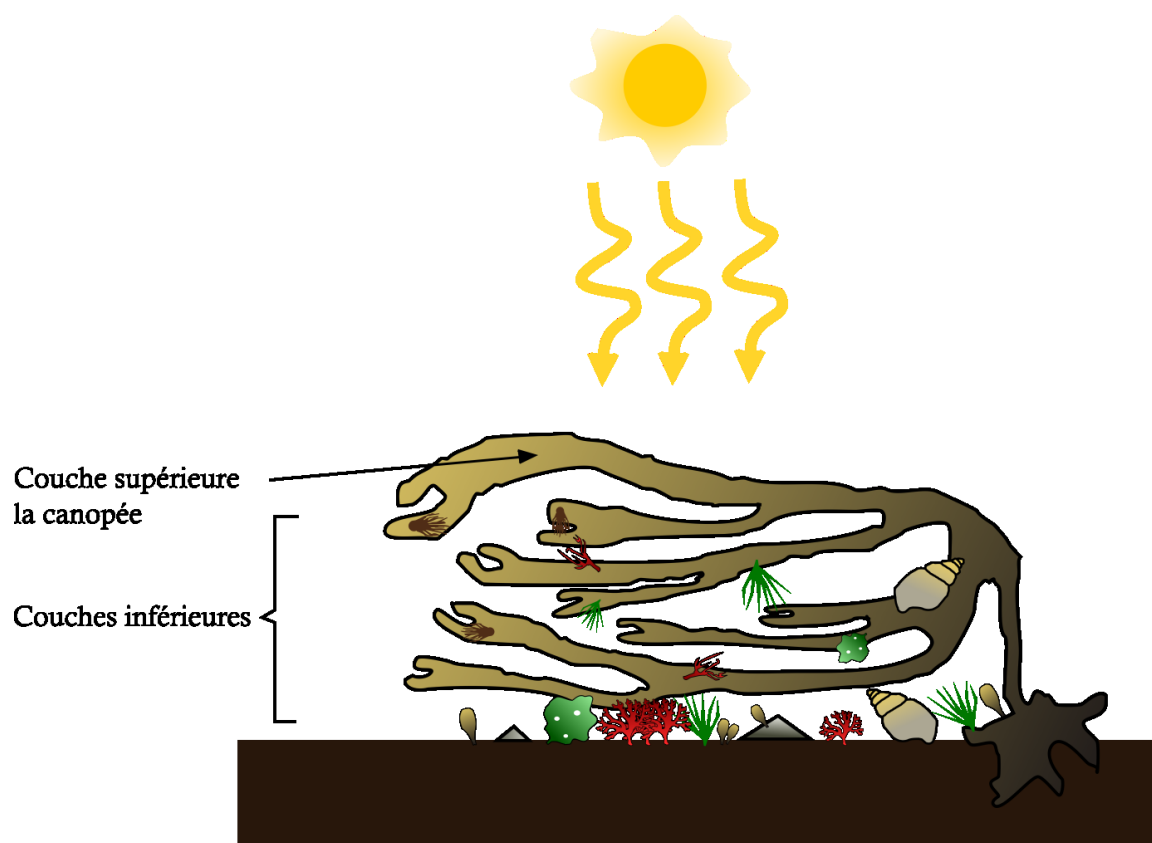


Fig. 6.1 Représentation schématique de la structure des communautés de *Fucus* lors des périodes d'émersion.

Cet ensemble multi-couches permet aussi une protection contre les conditions environnementales contraignantes de l'émersion, en limitant la dessiccation et en atténuant les variations de températures. Cela apparaît clairement dans les mesures d'intensité lumineuse et de température (UA-002-64 HOBO Waterproof Temperature/Light Pendant Data Logger, HOBO®) obtenues simultanément au-dessus et en-dessous des canopées de *Fucus* (Fig. 6.2). En particulier, il peut être supposé que ce rôle de protection est assuré en grande partie par la couche supérieure de la canopée. Ainsi, compte-tenu des fortes productions primaires observées à l'émersion, il serait intéressant d'étudier la dynamique de l'activité photosynthétique à différents endroits de la canopée durant des périodes complètes d'émersion. Cette étude pourrait s'appuyer sur des mesures de fluorescence par PAM (pulse amplitude modulated fluorescence) qui ont le grand avantage d'être non-intrusives. En réalisant ce type de mesures sur la couche supérieure de la canopée à *Ascophyllum nodosum*, Golléty (2008) a mis en évidence une diminution conséquente de sa capacité photosynthétique au cours de l'émersion, suivi d'une récupération lors de l'immersion, révélant la mise en place de mécanismes de photo-protection réversibles durant l'émersion (Häder & Figueroa 1997). Des mesures sur différentes couches de la canopée (la

couche supérieure et la couche la plus près du substrat par ex.) permettraient de vérifier que ces mécanismes de photo-protection se mettent en place essentiellement au niveau de la couche supérieure, permettant aux autres couches de maintenir un taux de production primaire élevé.

La protection assurée par les canopées à l'émersion permet aussi la survie et le développement de nombreuses espèces (Bertness et al. 1999, Dijkstra et al. 2012). Si les canopées jouent un rôle prépondérant dans les flux de carbone de ces deux communautés (i.e. 83 à 95 % de la production primaire brute à l'émersion), les autres espèces de producteurs primaires sont généralement complémentaires et permettent de maximiser l'utilisation de la lumière (Tait & Schiel 2011a, Tait et al. 2014). Cela confirme l'importance de réaliser des études à l'échelle de la communauté et *in situ*, en particulier lorsque l'objectif consiste à évaluer les performances physiologiques et écologiques des producteurs primaires dans leur milieu (Binzer & Middelboe 2005, Migné et al. 2015a).

Ces communautés se révèlent donc relativement diversifiées, ce qui donne lieu à des réseaux trophiques complexes, composés de nombreuses sources et de différentes voies de transfert de la matière. Au sein de ces réseaux trophiques, il s'avère que la plupart des herbivores sont généralistes (i.e. consomment une grande partie des sources disponibles), que les filtreurs sont opportunistes (i.e. tirent profit des macroalgues via la voie détritique durant les saisons où le plancton est en faible concentration) et que certains prédateurs (les crabes par ex.) sont également opportunistes. La présence de nombreuses espèces généralistes/opportunistes semblent caractéristiques des communautés littorales à canopée de macroalgues (Golléty et al. 2010, Leclerc et al. 2013), et pourrait contribuer à maintenir une structure trophique peu variable au cours des différentes saisons malgré les fluctuations importantes de l'abondance des producteurs primaires (Golléty 2008).

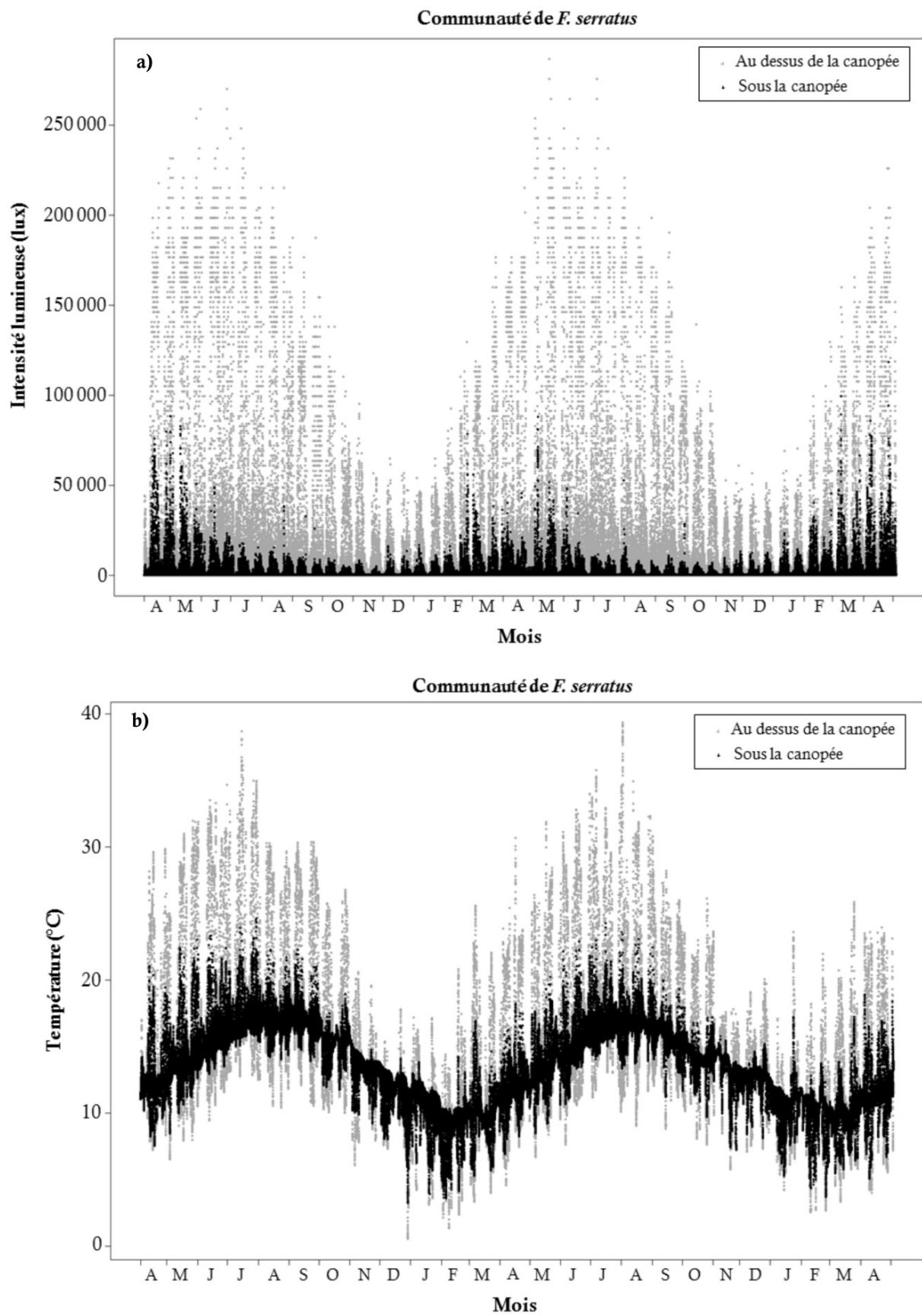


Fig. 6.2 Fluctuations de a) l'intensité lumineuse (en lux) et de b) la température (en °C) d'avril 2014 à mai 2016, sous la canopée de *Fucus serratus* (points noirs) et au-dessus (points gris).

Les canopées de *Fucus*, qui constituent justement la grande majorité de la biomasse algale au sein de ces communautés, ne constituent pas la source dominante de matière organique pour les herbivores associés. Ces canopées semblent en revanche avoir une fonction déterminante pour de nombreux systèmes adjacents, puisqu'une large part de la production primaire de ces communautés est exportée (Duarte & Cebrian 1996, Krumhansl & Scheibling 2012, Gómez et al. 2013). Cette exportation se fait principalement sous forme de carbone organique dissous et de détritits, contribuant ainsi à la connectivité entre habitats côtiers. L'exportation de matière organique sous forme de détritits joue par exemple un rôle primordial au niveau des zones d'échouage. En effet, les lasses de mer contribuent significativement à l'apport de nourriture pour les organismes vivant dans ces milieux (Crawley et al. 2009, Spiller et al. 2010). De plus, de nombreuses espèces terrestres se nourrissent d'organismes vivant au milieu des lasses de mer (Fig. 6.3) ou profitent des nutriments issus de la dégradation des algues (Spiller et al. 2010). Ces détritits participent ainsi au couplage entre le milieu marin et le milieu terrestre. Une estimation précise du devenir de la production primaire des communautés à canopée de macroalgues pourrait donc apporter des informations précieuses concernant l'influence qu'ont ces systèmes dans le fonctionnement de la zone côtière.



Fig. 6.3 Pipit sur épaves de *Fucus serratus* à Roscoff.

La communauté de *F. vesiculosus*, qui est située le plus haut sur l'estran, s'est révélée moins productive que la communauté de *F. serratus*. Elle est également moins diversifiée en raison du gradient d'émersion, qui la soumet à des contraintes environnementales plus importantes (Raffaelli & Hawkins 1999). Malgré ces différences, le réseau trophique des deux communautés s'est avéré similaire, suggérant d'une part que le gradient environnemental ne modifie pas le fonctionnement trophique de communautés semblables (i.e. formée d'une canopée fortement dominante à laquelle sont associées de nombreuses espèces autotrophes et hétérotrophes) et d'autre part que les organismes composant ces communautés partagent généralement des fonctions trophiques identiques.

Au cours de la succession, *F. vesiculosus* s'est installé et s'est développé de façon inattendue sur les plaques disposées dans la zone de *F. serratus*. Ces observations sont vraisemblablement liées aux capacités de tolérance différentes dont font preuve les juvéniles des deux espèces de *Fucus* envers les conditions environnementales. Dans la zone intertidale la plus basse, *F. vesiculosus* a ainsi rempli temporairement les fonctions de *F. serratus*, en facilitant la survie et le développement de nombreuses espèces (dont *F. serratus*), mais aussi en générant une production primaire élevée, assurant une ressource trophique pour les consommateurs. Ceci implique donc que l'identité de l'espèce de canopée a un rôle mineur dans la mise en place de la communauté du moment que les fonctions qu'elles assurent sont remplies de façon similaire.

Conclusions générales

L'ensemble des travaux réalisés au cours de cette thèse a permis de démontrer que les deux communautés à canopée de *Fucus* considérées ont globalement un fonctionnement et une dynamique similaires, basés en particulier sur un métabolisme élevé et fluctuant au cours de l'année et sur un réseau trophique complexe mais stable dans le temps. Les quelques différences observées peuvent être associées à leur niveau marégraphique divergent, les exposant à des contraintes environnementales différentes. Les bilans annuels de production nette de ces deux communautés sont particulièrement élevés, confirmant que ces systèmes sont parmi les plus productifs par unité de surface. Néanmoins, ces systèmes semblent n'avoir qu'un rôle mineur dans le bilan carbone, puisque seule une faible part de la production primaire serait stockée de façon pérenne (i.e. sans dégradation, comme l'enfouissement par exemple, Duarte & Cebrian

1996). Cette production primaire semble plutôt bénéficier à de nombreux organismes, vivants au sein de ces communautés ou non (export vers d'autres écosystèmes).

Cette étude a également souligné le rôle fondamental de la canopée pour ces communautés. Les modifications climatiques en cours, couplées aux autres menaces qui pèsent sur les communautés à canopée de macroalgues, sont donc de nature à modifier de façons profondes leur fonctionnement et leur dynamique (Wahl et al. 2015, Duarte et al. 2015), aussi bien en terme de métabolisme (Tait 2010, Stagnol et al. 2013), que de fonctionnement trophique (Duarte et al. 2015). Il est donc fondamental de continuer à étudier ces communautés intertidales, afin de mieux comprendre leur fonctionnement, leurs rôles au sein de la zone côtière et l'influence des changements à venir sur ces communautés.

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Annexe

Liste des publications et des communications scientifiques

Publications

Bordeyne F., Migné A., Davoult D. (2015) Metabolic activity of intertidal *Fucus* spp. communities: evidence for high aerial carbon fluxes displaying seasonal variability. Marine Biology doi: 10.1007/s00227-015-2741-6

Communications

Bordeyne F., Migné A., Davoult D. (Oral) Variability of carbon fluxes over tidal and seasonal cycles in an intertidal fucoid community. 11th International Temperate Reef Symposium, Juin 2016, Pise, Italie

Bordeyne F., Bertaud du Chazaud E., Leroux C., Migné A., Davoult D., Riera P. (Oral) Seasonal variability in food webs of two mid-intertidal *Fucus* spp. communities using a $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ approach. 21st Aquatic Biodiversity and Ecosystems, Septembre 2015, Liverpool, Angleterre

Bordeyne F., Migné A., Davoult D. (Oral) Métabolisme *in situ* d'une communauté à *Fucus serratus* : variabilité des flux de carbone aux échelles tidale et saisonnière. Colloque annuel de la Société Phycologique de France, Septembre 2015, Vannes, France

Bordeyne F., Migné A., Davoult D. (Oral) *In situ* metabolism of *Fucus serratus* community: carbon fluxes variability over a tidal cycle. 6^{ème} édition de la Journée des Jeunes Chercheurs, Décembre 2014, Roscoff, France

Bordeyne F., Migné A., Davoult D. (Oral) A year of primary production and respiration monitoring on the *Fucus vesiculosus* and *Fucus serratus* communities, during low tide. Colloque annuel de la Société Phycologique de France, Novembre 2014, Paris, France

Bordeyne F., Bertaud du Chazaud E., Leroux C., Migné A., Davoult D., Riera P. (Poster) Food web structure of two intertidal *Fucus* spp. communities: complexity and temporal variability evidenced by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ approach. 21st Benelux Congress of Zoology, Décembre 2015, Liège, Belgique

Bordeyne F., Migné A., Davoult D. (Poster) Seasonal variations of primary production and respiration of two rocky-shore communities dominated by canopy-forming algae, *Fucus vesiculosus* and *Fucus serratus*. 10th International Temperate Reef Symposium, Janvier 2014, Perth, Australie

RESUME : En milieu intertidal rocheux, les communautés dominées par des canopées d'algues brunes (Phaeophyceae) sont particulièrement répandues. Malgré leur accessibilité, leur fonctionnement reste encore largement méconnu. En particulier, l'influence de la saisonnalité et du gradient d'émersion sur le métabolisme, le réseau trophique ou encore le processus de succession a été peu étudiée. Ce travail de thèse a donc eu pour objectif d'analyser le fonctionnement de deux communautés de *Fucus* établies à des niveaux marégraphiques différents, en portant une attention particulière aux conditions environnementales. Sur les côtes bretonnes (France), les communautés de *Fucus vesiculosus* Linnaeus et de *Fucus serratus* Linnaeus sont respectivement caractéristiques des étages médiolittoral moyen et inférieur. Des mesures de métabolisme (production primaire et respiration) réalisées *in situ* à différentes périodes de l'année ont mis en évidence une forte influence de la saisonnalité et le rôle primordial de la canopée dans les flux de carbone. Le métabolisme s'est avéré être plus élevé à l'émersion qu'à l'immersion, où l'intensité lumineuse constitue régulièrement un facteur limitant pour la production primaire. Par une approche de modélisation basée sur ces mesures et sur des données environnementales acquises à haute fréquence, un bilan annuel de production primaire a été calculé pour chaque communauté. Ces bilans confirment que ces systèmes sont fortement productifs et permettent de préciser leur régulation à l'échelle des cycles de marées. Le réseau trophique de ces communautés, analysé via les isotopes stables du carbone et de l'azote, apparaît basé sur l'utilisation de nombreuses sources de matière organique par les consommateurs et varie peu d'une saison à l'autre. Le suivi de la colonisation de substrats vierges montre que les *Fucus* favorisent l'installation de nombreuses espèces et conduisent rapidement à une production primaire élevée. Finalement, bien que des différences attribuables à leur localisation sur l'estran aient été détectées au niveau du métabolisme et du processus de succession, ces communautés présentent un fonctionnement similaire en raison de la présence d'une canopée qui modifie les conditions environnementales.

Mots-clés : Communautés intertidales ; *Fucus serratus* ; *Fucus vesiculosus* ; Production primaire ; Réseau trophique ; Respiration ; Succession ; Zonation.

ABSTRACT: Along intertidal rocky shores, communities dominated by canopy-forming brown algae (Phaeophyceae) are particularly widespread. Their functioning is however largely understudied, especially concerning the influence of seasonality and shore height on primary production and respiration, on food webs or on successional process. The aim of this study was to investigate the functioning of two intertidal *Fucus* communities which are established at different tidal levels. During this study, a special consideration was given to the effects of environmental conditions. On the coasts of Brittany (France), communities dominated by *Fucus vesiculosus* Linnaeus and *Fucus serratus* Linnaeus are characteristic of mid-intertidal and low mid-intertidal levels, respectively. *In situ* measurements of metabolism (primary production and respiration) carried out at different periods of a year highlighted a strong seasonal influence on carbon fluxes and emphasized the importance of canopies in the metabolism of whole communities. Metabolism was higher during emersion than during immersion periods, for which light intensity regularly limits the primary production. Based on these measurements and on high-frequency measurements of environmental parameters, an annual primary production was calculated by modelling for both communities. These annual estimations confirmed that these communities are among the most productive systems of coastal region and specify their regulation at the tidal cycles scale. Food webs, which were analysed through carbon and nitrogen stable isotopes, are based on the use of almost all available sources of organic matter by consumers, and revealed a strong conservation of food webs across seasons. The colonisation survey of bare substrates shows that *Fucus* species improve the settlement success of numerous species and increase rapidly primary production of whole assemblages. Overall, despite some differences in metabolism and successional sequences according to the shore height at which they are located, these communities exhibited similar functioning due to the canopy which damns the environmental conditions.

Keywords: Food web; *Fucus serratus*; *Fucus vesiculosus*; Intertidal communities; Primary production; Respiration; Succession; Zonation.