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Pasquale Paoli

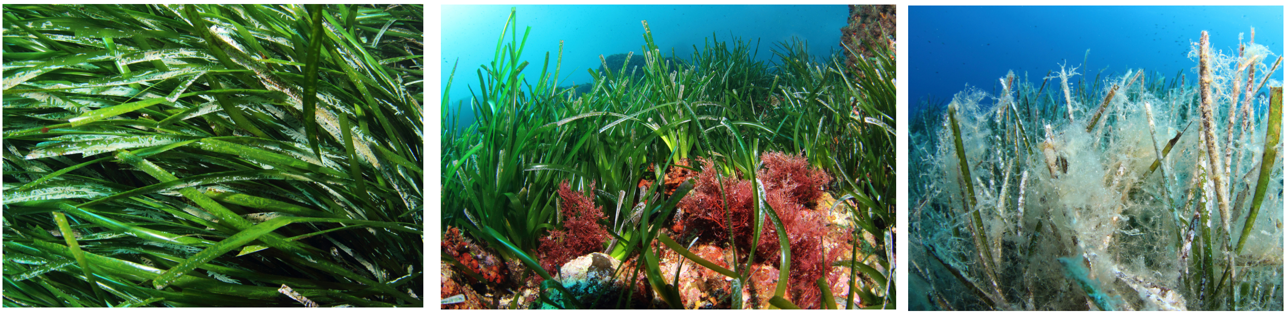
Université de Liège

Etude des intermattes des herbiers à *Posidonia oceanica*

Analyse à différentes échelles spatiales de la structure des paysages sous-marins

Thèse de doctorat en cotutelle internationale
France/Belgique

Arnaud Abadie



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Etude des intermattes des herbiers à *Posidonia oceanica*

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A mon grand-père Bernard et à mon oncle Philippe,
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Note : quatre références bizarres se sont glissées dans ce manuscrit. Le premier à les découvrir obtiendra une surprise. Envoyez-moi ces références complètes à arnaudabadie@aol.fr. Attention c'est pas (trop) évident et il faut tout lire !

Résumé

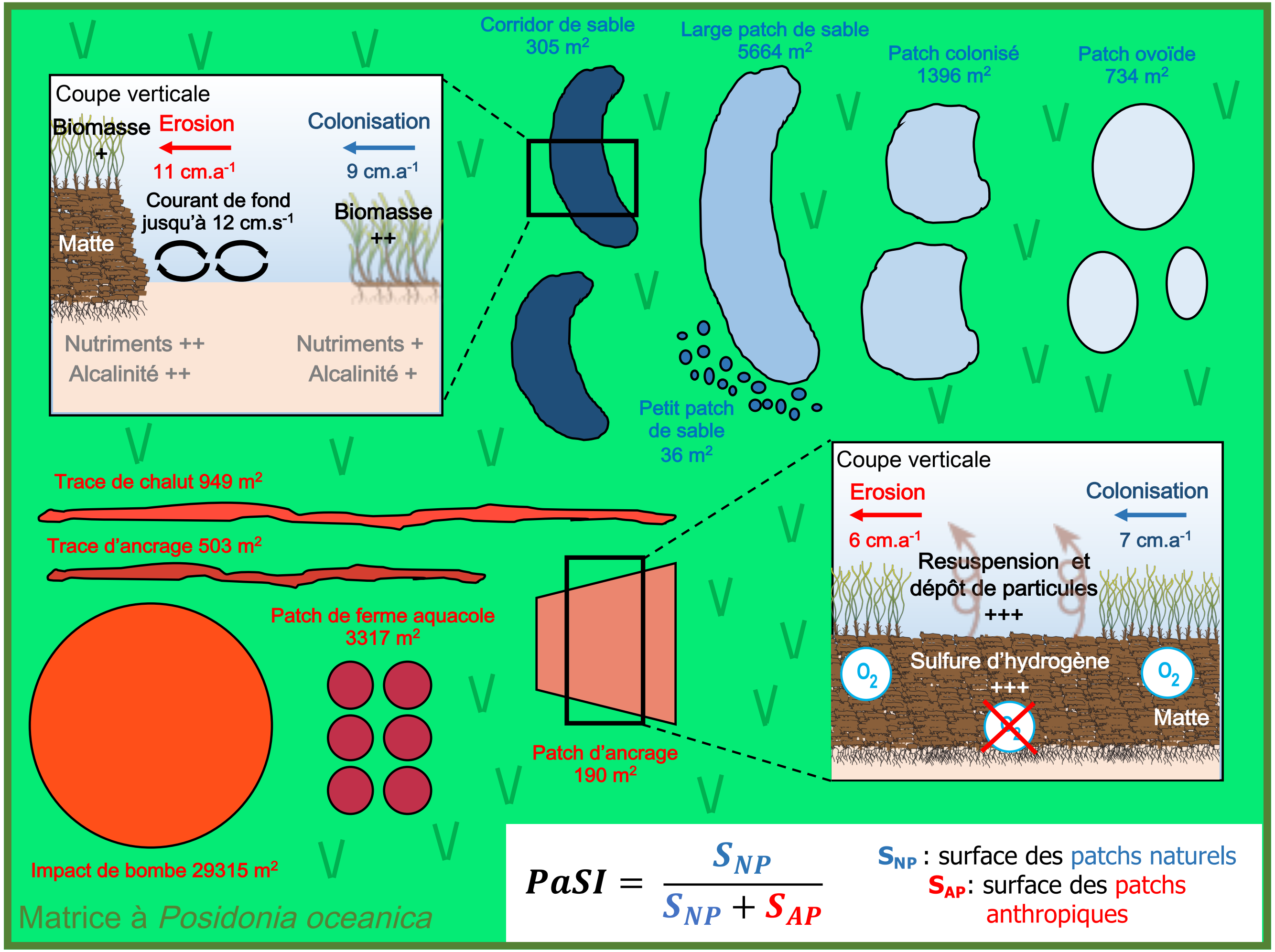
Parmi les écosystèmes marins de Méditerranée, les herbiers à *Posidonia oceanica* (L.) Delile représentent un habitat jouant une rôle écologique et économique majeur. Ils forment des paysages hétérogènes influencés par l'impact de phénomènes naturels et anthropiques, dont l'ancrage des navires de plaisance. Ces impacts se traduisent par la formation de patchs de sable ou de matte morte appelés 'intermattes'.

En décrivant et en utilisant les caractéristiques des intermattes observées en Baie de Calvi et plus largement autour de la Corse, ces travaux de doctorat ont décrit de manière précise la dynamique des intermattes et du paysage sous-marin formé par les herbiers à *P. oceanica* pour créer de nouvelles méthodes d'analyse.

Les intermattes naturelles sableuses créées, par les courants de fond, présentent deux types de bordures distincts : un tombant de matte érodé et une recolonisation par l'herbier. Chacun présente des caractéristiques propres au niveau de la biogéochimie du sédiment. Les intermattes anthropiques issues de l'ancrage (matte morte) ont une taille et une forme différente découlant d'une dynamique particulière. Elles ne sont pas recolonisées lorsque la pression d'ancrage est toujours présente. Une détérioration de la qualité chimique du substrat se met en place après la destruction mécanique.

En utilisant les caractéristiques surfaciques et la nature des intermattes, un indice paysager cartographique, le Patchiness Source Index, a été créé. En comparant les méthodes d'étude des intermattes, deux nouveaux indices (le Map Anchoring Index et le Anchoring Index) à destination des gestionnaires du milieu côtier ont été mis au point pour évaluer l'impact de l'ancrage dans les herbiers à *P. oceanica*.

Mots clés : paysage sous-marin, plante sous-marine, *Posidonia oceanica*, intermatte, ancrage, gestion, indices



$$PaSI = \frac{S_{NP}}{S_{NP} + S_{AP}}$$

Study of intermattes in *Posidonia oceanica* meadows

Summary

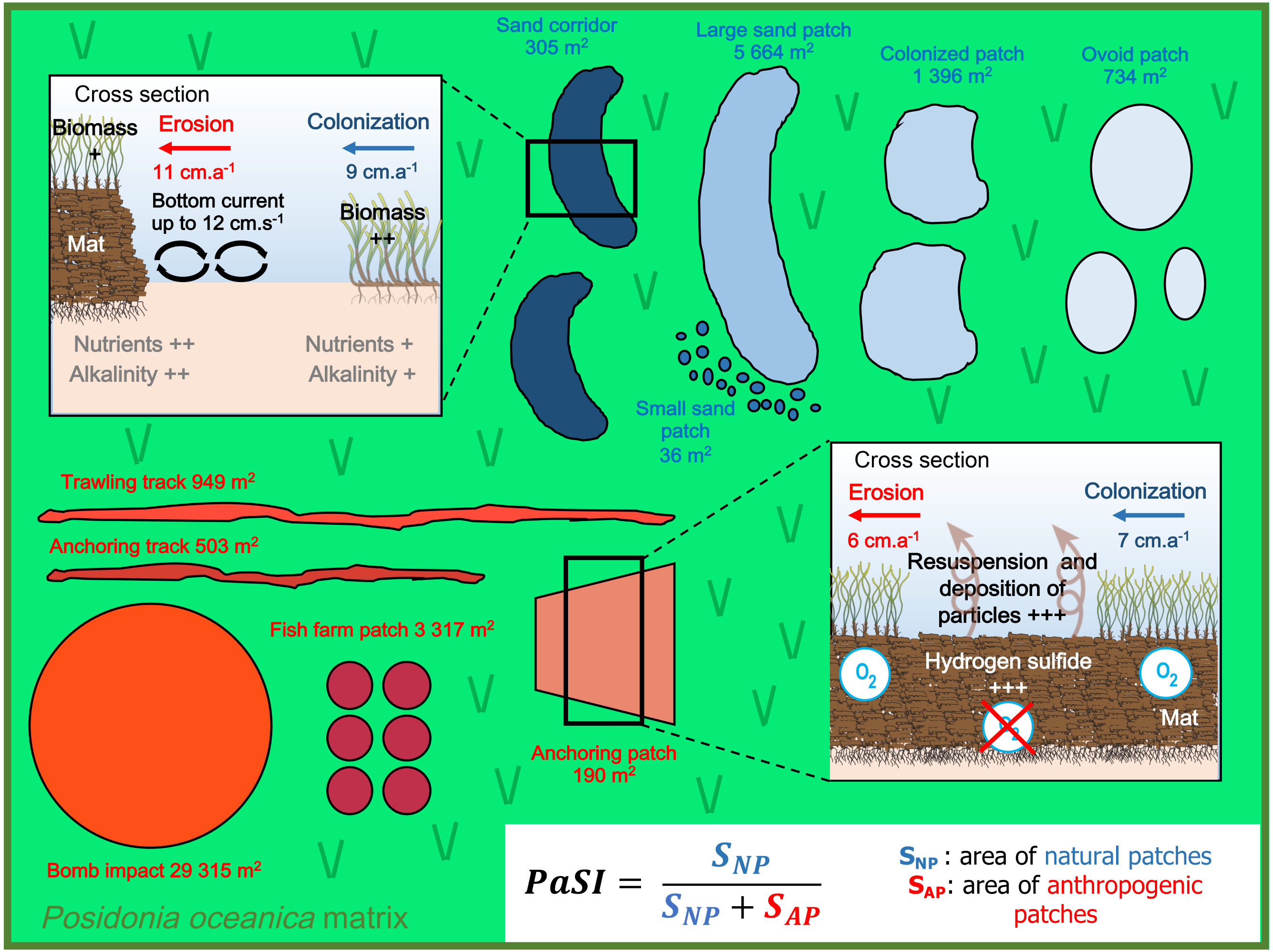
Among Mediterranean marine ecosystems, *Posidonia oceanica* (L.) Delile seagrass meadows form a habitat playing an important ecological and economical role. They form heterogeneous seascapes influenced by the impact of natural and anthropogenic phenomenon (of which the anchoring of leisure ships). These impacts lead to the formation of sand and bare mat patches called 'intermattes'.

By describing and using intermatte characteristics observed in Calvi Bay and more widely around Corsica, these PhD works precisely described intermatte and *P. oceanica* seascape dynamics in order to develop new methods of analysis.

On the one hand, natural sandy intermattes formed by bottom currents show two types of border. Each has its own characteristics at the level of the sediments biogeochemistry. On the other hand, anthropogenic intermattes generated by anchoring (bare mat) present different sizes and shapes resulting from specific dynamics. They are not recolonized when the anchoring pressure remains high. A depletion of the substrate chemical quality occurs after the mechanical destruction.

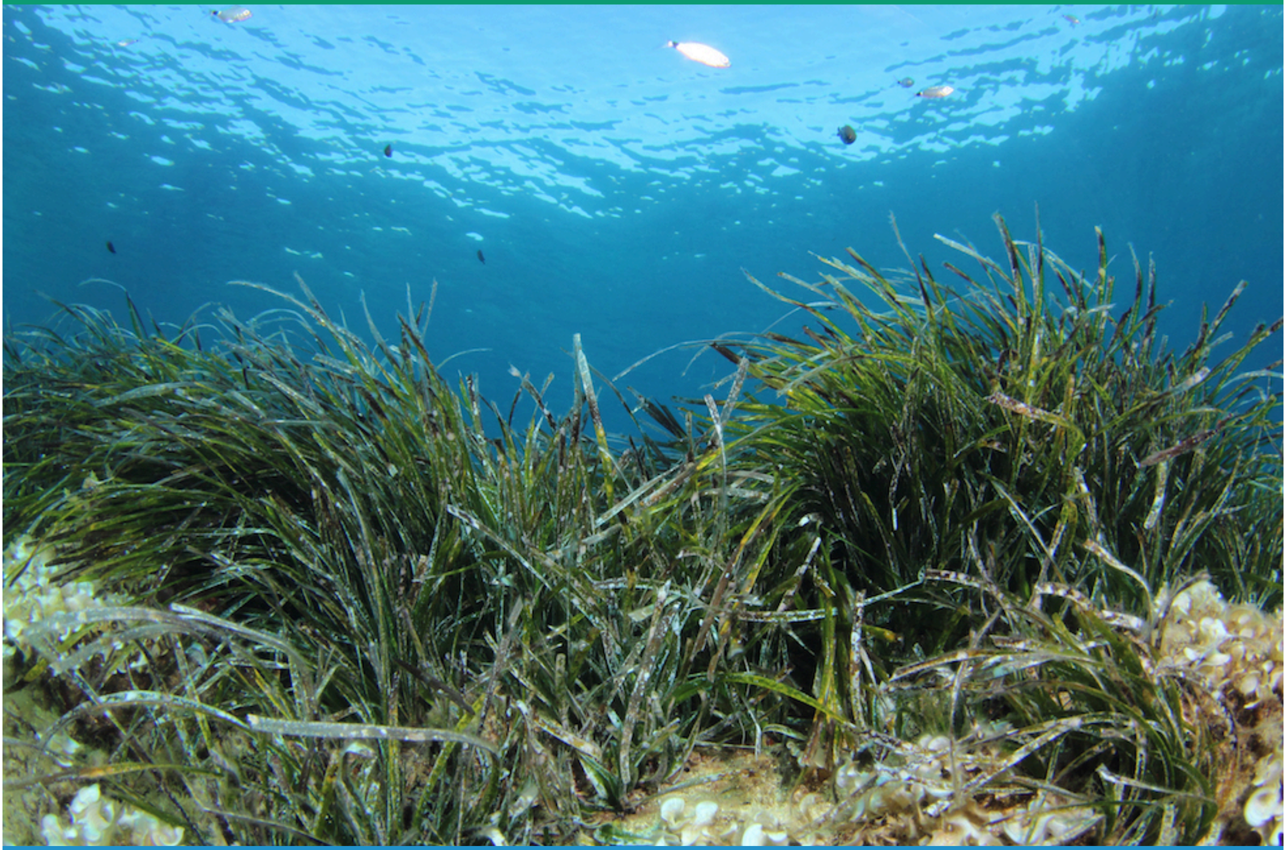
A new cartographic seascape index, the Patchiness Source Index, was created using the size and the nature of intermattes at large spatial scale. After a comparison of methods used for the study of intermattes, two new indices (Map Anchoring Index and Anchoring Index) for managers of coastal areas were developed to evaluate the impact of anchoring within *P. oceanica* meadows.

Keywords : seascape, seagrass, *Posidonia oceanica*, patch, anchoring, management, indices


Sand corridor 305 m^2
Large sand patch 5 664 m^2
Colonized patch 1 396 m^2
Ovoid patch 734 m^2
Small sand patch 36 m^2
Cross section
Biomass +
Erosion
11 cm.a^{-1}
Colonization
9 cm.a^{-1}
Bottom current up to 12 cm.s^{-1}
Biomass ++
Mat
Nutrients ++
Alkalinity ++
Nutrients +
Alkalinity +
Trawling track 949 m^2
Anchoring track 503 m^2
Fish farm patch 3 317 m^2
Bomb impact 29 315 m^2
Anchoring patch 190 m^2
Cross section
Erosion
6 cm.a^{-1}
Colonization
7 cm.a^{-1}
Resuspension and deposition of particles +++
Hydrogen sulfide +++
O_2
O_2
O_2
Mat
Posidonia oceanica matrix
$PaSI = \frac{S_{NP}}{S_{NP} + S_{AP}}$
S_{NP} : area of natural patches
S_{AP}: area of anthropogenic patches

Sommaire

CHAPITRE 1



INTRODUCTION : Les intermattes, unités fondamentales d'un paysage sous-marin dynamique

1. Une plante, des paysages

1.1. Des plantes à fleurs sous-marines

Les Magnoliophytes marines (*seagrass* en anglais) sont des plantes à fleurs (Fig. 1) regroupant un ensemble d'environ soixante espèces, i.e. 65 selon les derniers travaux (den Hartog & Kuo 2006, Guiry & Guiry 2016), d'origine polyphylétique (Fig. 2) au sein du taxon monophylétique des Alismatidae (Chen *et al.* 2004, Waycott *et al.* 2006). Après avoir conquis dans un premier temps le milieu terrestre, elles se sont adaptées à l'environnement marin il y a environ 100 Ma depuis les zones tropicales, probablement grâce à des moyens de polonisation hydrophiles (den Hartog 1970, Brasier 1975).

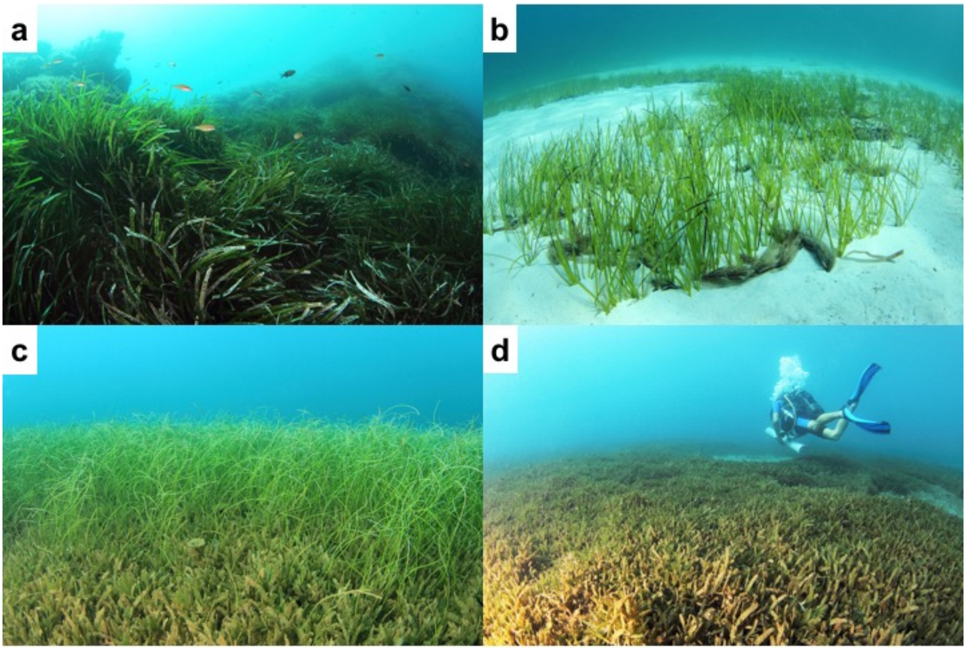


***Figure 1** : Exemples de Magnoliophytes marines a)* Posidonia oceanica *(L.) Delile (Corse, France) ; b)* Cymodocea nodosa *(Corse, France) ; c)* Syringodium filiforme *Kützing et* Halophila stipulacea *(Forsskål) Ascherson (Martinique, Caraïbes) ; d)* Halophila stipulacea *(Martinique, Caraïbes).*

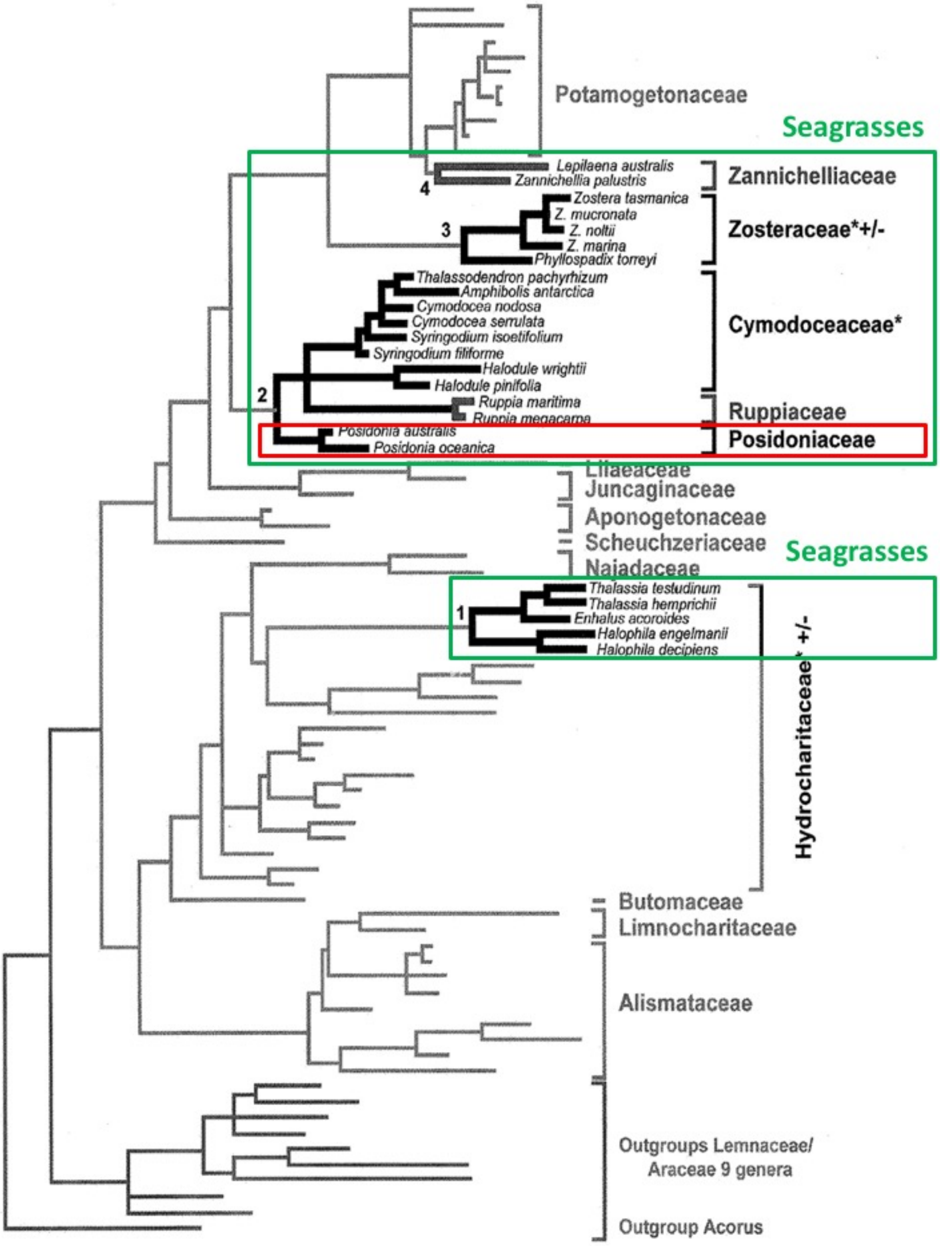


Figure 2 : *Classification phylogénétique de la sous-classe des Alismatidae basée sur des données ADN de l'enzyme RuBisCO, comprenant les différents taxons des Magnoliophytes marines en vert et* P. oceanica *en rouge [modifié d'après Waycott et al. (2006)].*

Les Magnoliophytes marines sont réparties sur l'ensemble des mers du globe (Fig. 3) et forment de vastes herbiers couvrant une surface allant jusqu'à 500 000 km² (Green & Short 2003, Short *et al.* 2007).

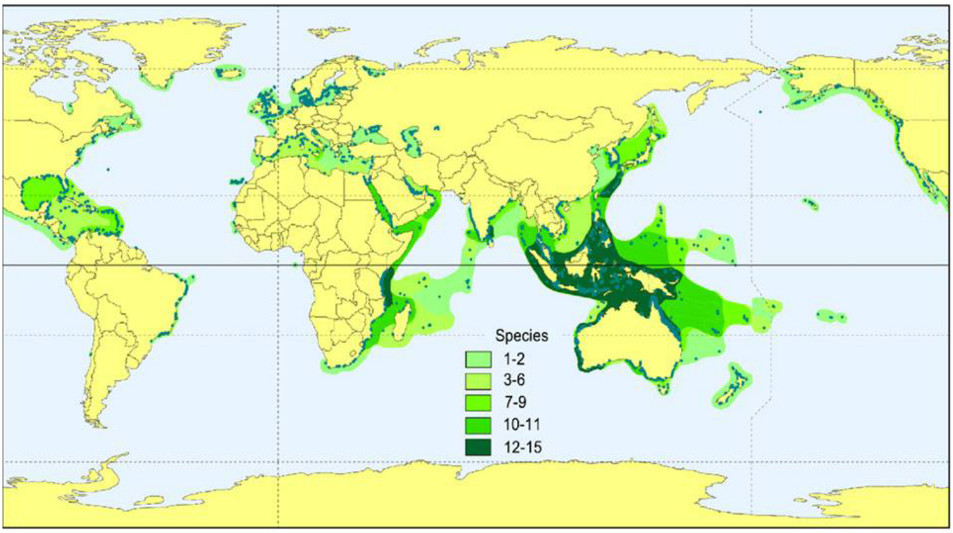


Figure 3 : *Diversité spécifique des Magnoliophytes marines dans le monde (Short et al. 2007).*

Les Magnoliophytes marines jouent à l'échelle mondiale plusieurs rôles d'une importance cruciale pour le fonctionnement de nombreux écosystèmes (Costanza *et al.* 1997, Cullen-Unsworth & Unsworth 2013). Elles, constituent notamment un abri et une nurserie pour de nombreuses espèces et produiraient plus de 30 % des individus adultes (Beck *et al.* 2001), procurant un réservoir important pour de nombreuses activités halieutiques. De plus, à une époque où la séquestration des gaz à effet de serre (dont le CO_2) occupe une place prépondérante dans les stratégies politiques et environnementales, les Magnoliophytes marines seraient capables de stocker de 4.2 à 8.4 Pg (4.2 à 8.4 x 10^{12} kg) de carbone sous forme organique. Cette quantité représente environ 10 % du carbone stocké par les océans (Duplantier *et al.* 2006, Fourqurean *et al.* 2012). Ce system de stockage est ainsi appelé ‘carbone bleu’ (McLeod *et al.* 2011). Enfin, les herbiers sous-marins fournissent une protection contre l'érosion du littoral. Ils réduisent la vitesse des courants en atténuant la force des vagues (jusqu'à 50 % dans des conditions de houle de faible amplitude), et stabilisent le sédiment (Infantes *et al.* 2012, Ondiviela *et al.* 2014).

Au sein des Magnoliophytes marines, certaines profitent d'un effort d'étude plus important du fait de leur situation géographique et par extension, des intérêts économiques qui y sont liés (zones touristiques, urbanisation du littoral, ressources naturelles). Parmi elles, *Posidonia oceanica* (*Linnaeus*) Delile est l'une des plus étudiée (Telesca *et al.* 2015).

1.2. *Posidonia oceanica*

Posidonia oceanica (Fig. 4), est une Magnoliophyte marine endémique de Méditerranée (Boudouresque & Meinesz 1982, Gobert *et al.* 2006a). Elle se développe dans les eaux côtières entre la surface et une quarantaine de mètres de profondeur sur une grande partie du pourtour méditerranéen (Fig. 5). *P. oceanica* couvrirait ainsi une surface comprise entre 25 000 et 45 000 km², 12 247 km² ayant déjà été cartographiés (Pasqualini *et al.* 1998, Telesca *et al.* 2015).

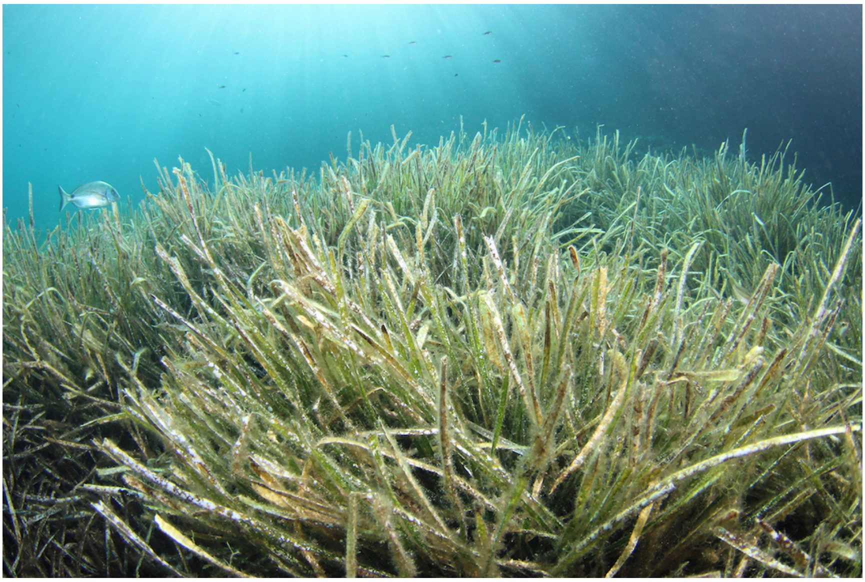


Figure 4 *: Herbier à* P. oceanica *dans la baie de Calvi (Corse, France).*

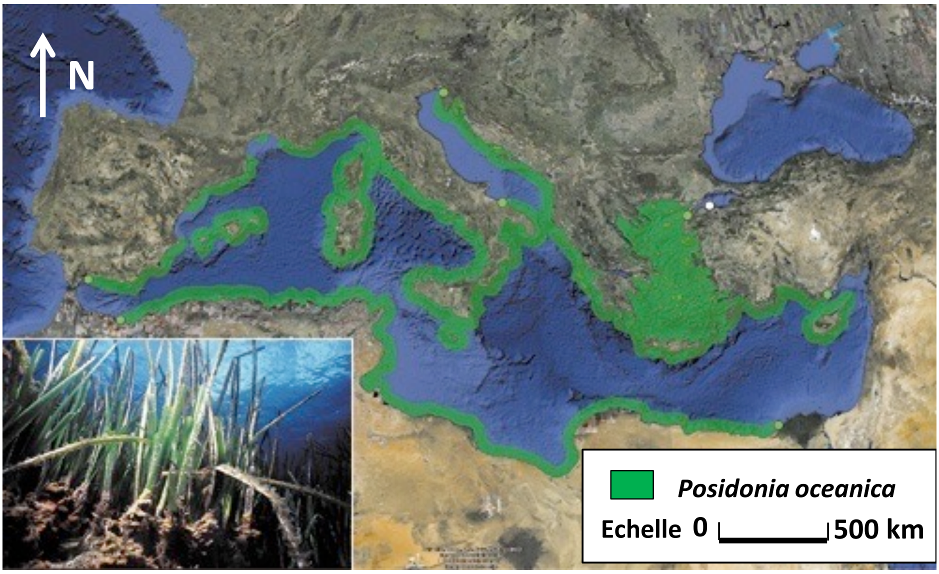


Figure 5 *: Répartition de* P. oceanica *dans le bassin Méditerranéen [modifié d'après Pergent et al. (2012)].*

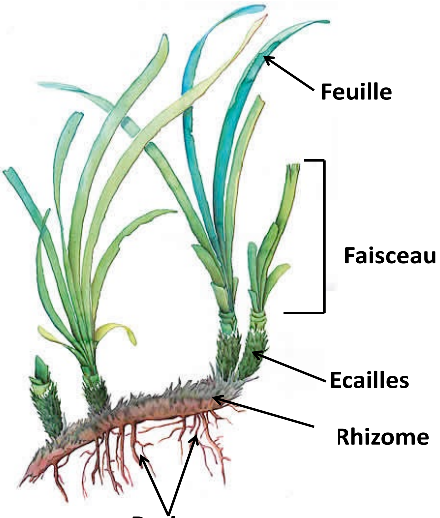


Figure 6 *: Détails morphologiques de* P. oceanica.

Ses rhizomes (Fig. 6), axes cylindriques fixés par des racines, portent les faisceaux de feuilles sénescentes assemblées par groupes dont la base forme des écailles lorsque le limbe tombe (Giraud 1979, Boudouresque *et al.* 2012). Tout comme les Magnoliophytes terrestres, *P. oceanica* peut se reproduire de façon sexuée en produisant des fleurs (Fig. 7a) puis des fruits (Gobert *et al.* 2006a). Ce phénomène ne se produit pas de façon annuelle (Pergent *et al.* 1989a), l'activité solaire étant l'un des facteurs potentiels influençant la floraison (Montefalcone *et al.* 2013a). De par la relative rareté de ces événements, *P. oceanica* assure sa reproduction principalement de façon végétative afin de maintenir les effectifs de population des herbiers (Procaccini & Mazzella 1998).

La croissance des rhizomes de *P. oceanica* peut se dérouler de deux façons réversibles :

- Verticalement, afin de compenser son enfouissement par le dépôt de particules piégées par sa canopée. Les rhizomes, dits "orthotropes", s'allongent ainsi de 5 à 7 mm par an (Boudouresque & Jeudy De Grissac 1983), cette structuration verticale formant la "matte" de *P. oceanica* (Fig. 7d et 7e), c'est-à-dire un complexe comprenant les rhizomes, les racines, leur nécromasse et le sédiment (Boudouresque & Meinesz 1982).
- Horizontalement, afin de coloniser de nouveaux espaces. Leur croissance annuelle est alors de 10 à 60 mm (Marbà & Duarte 1998). Les rhizomes de ce type sont dits "plagiotropes".

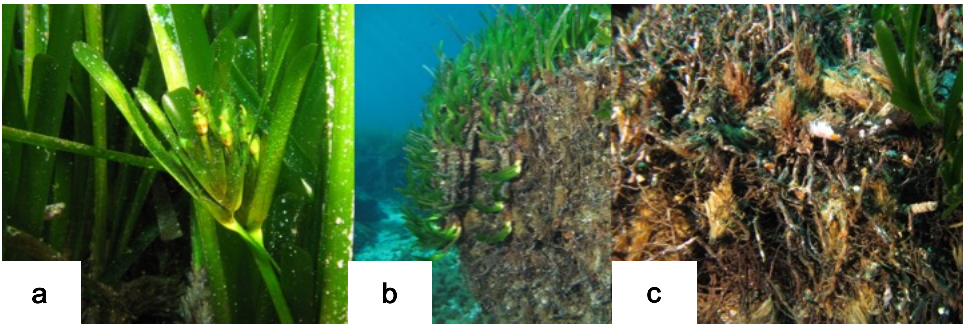


***Figure 7** : a) fleur de* P. oceanica*, floraison de 2015 (Corse, France) ; b) tombant de matte ; c) détail des racines et des rhizomes composant la structure de la matte.*

Comme toutes les plantes à fleur, *P. oceanica* pratique la photosynthèse afin d'obtenir des nutriments et de l'énergie indispensables à son développement (Alcoverro *et al.* 2001, Zimmerman 2006), son activité photosynthétique diminuant avec l'atténuation de l'intensité lumineuse liée à l'augmentation de la profondeur (Elkalay *et al.* 2003). Il en résulte des herbiers hautement productifs et communément considérés autotrophes nets (Champenois & Borges 2012), cette dernière assertion étant cependant remise en question par l'approche de Velimirov *et al.* (2016). De plus, afin de soutenir la croissance de ses rhizomes plagiotropes et orthotropes ainsi que sont importante production de biomasse, *P. oceanica* est capable de puiser des nutriments (Fig. 8), selon la saison, piégés dans sa canopée ou bien dans le sédiment (Gobert *et al.* 2002, Lepoint *et al.* 2002, Romero *et al.* 2006). Il en résulte de nombreuses interactions entre la plante et le sédiment (Fig. 8) qui en modifie les paramètres physico-chimiques (Marbà *et al.* 2006). *P. oceanica* joue ainsi un rôle d'espèce ingénieure d'écosystème autogène[1] (Jones *et al.* 1994, Wright & Jones 2006, Boudouresque 2010).

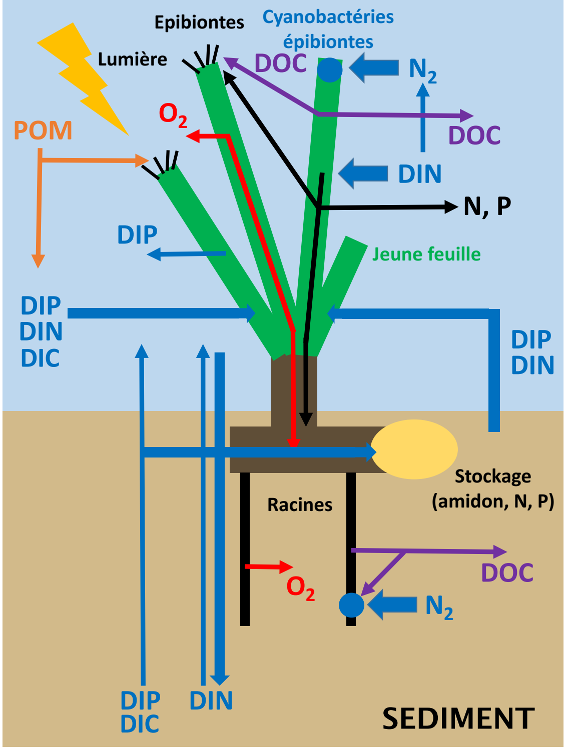


Figure 8 *: Flux de carbone, de nutriments et d'oxygène entre* P. oceanica, *la colonne d'eau et le sédiment. DOC : Dissolved Organic Carbon; DIN : Dissolved Inorganic Nitrate; DIP : Dissolved Inorganic Phosphorus; POM : Particulate Organic Matter;* N_2 *: diazote;* O_2 *: oxygène [redessiné d'après Boudouresque et al. (2006)].*

Parmi les interactions chimiques plante/sédiment, le cycle du soufre (Fig. 9) occupe une importance primordiale dans le développement de la plante (Santschi *et al.* 1990). La forme soufrée utilisée par les plantes dans la formations de certain de leurs acides aminés est le sulfate ou SO_4^{2-} (Leustek & Saito 1999). Le sédiment marin au sein duquel se

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[1] Une espèce ingénieur d'écosystème autogène est un organisme changeant son environnement au travers de sa structure physique, *i. e.* ses tissues vivants et morts [Lawton JH (1994) What do species do in ecosystems? Oikos 71:367-374]

développe *P. oceanica* est de nature anoxique (Holmer *et al.* 2003), le soufre est donc majoritairement disponible sous forme de sulfure d'hydrogène (H_2S). Ce composé toxique est capable de limiter le développement des Magnoliophytes marines en s'introduisant par les racines et en s'exportant ensuite vers les rhizomes et les feuilles (Calleja *et al.* 2007, Holmer & Hasler-Sheetal 2014). *P. oceanica*, à l'instar d'autres Magnoliophytes marines, serait ainsi capable d'oxyder ce composé réduit nocif en créant un "sphère oxique" de quelques micromètres au niveau de l'extrémité de ses racines (Fig. 9) (Pedersen *et al.* 2004, Borum *et al.* 2006). A ces composés soufrés classiques s'ajoute le dimethylsulfoniopropionate (DMSP), un élément agissant comme antioxidant contre d'autres espèces chimiques oxidantes, présent notamment dans les feuilles de *P. oceanica* (Borges & Champenois 2015).

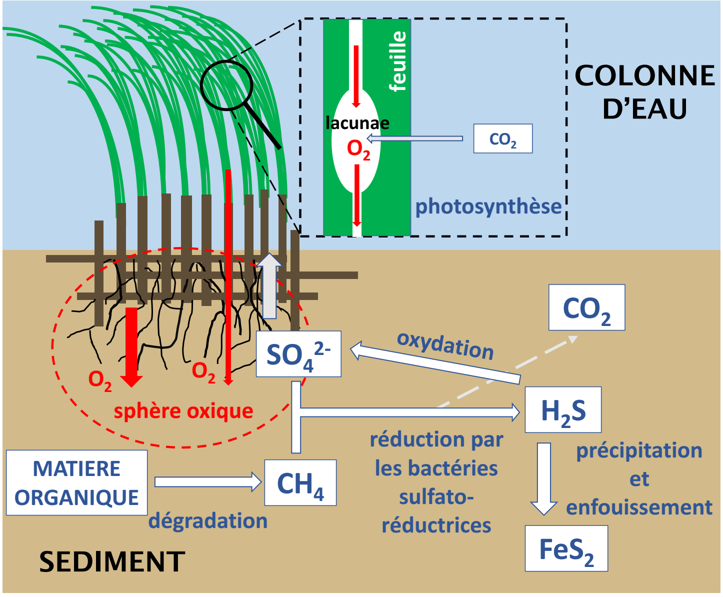

Figure 9 *: Vue simplifiée du cycle du soufre dans le sédiment et son interaction avec les herbiers à* P. oceanica*.*

L'ensemble des paramètres physico-chimiques tant biotiques que abiotiques au sein de la colonne d'eau et du sédiment induiront ainsi une dynamique variable au développement de *P. oceanica* (Bay 1978, 1984, Alcoverro *et al.* 1995, Dauby *et al.* 1995, Di Maida *et al.* 2013). La somme de ces variations rencontrées à l'échelle de l'individu conduit à la formation d'herbiers de tailles très variables avec une structure qui leur est propre.

1.3. Des herbiers formant des paysages à la structure complexe

La formation d'herbiers de *P. oceanica* débute par la génération de patchs qui ensuite vont s'agréger, leur persistance augmentant avec la taille des patchs (Almela *et al.* 2008). Ce processus a lieu sur un substrat correspondant à une matrice dont la nature aura une influence sur la dynamique de l'herbier. Ainsi, l'herbier se développant sur roche a un taux croissance (-42 %) ainsi qu'une longueur (-23 %) et une surface de feuille (-32 %) moindre que celui se formant sur du sable ou de la matte (Di Maida *et al.* 2013). Le processus d'assemblage de ces patchs conduisant à la formation d'herbiers se déroule sur une grande échelle de temps. Par exemple, en 600 ans, une surface de 0.3 ha sera colonisée aux deux tiers par *P. oceanica* (Kendrick *et al.* 2005b). La colonisation peut dans certains être plus rapide sur certains types de substrat, comme dans le cas des larges zones de matte morte produites par l'explosion de bombes militaires (Meinesz & Lefèvre 1984). Tout au long de cette période des facteurs externes naturels et anthropiques influenceront la morphologie de l'herbier. Parmi les influences naturelles, la vitesse des courants de fond induit par l'énergie des vagues joue un rôle majeur sur la répartition de *P. oceanica* à toutes les profondeurs où elle est susceptible de se développer (Infantes *et al.* 2009, Vacchi *et al.* 2012). Les activités humaines quant à elles peuvent agir de façon directe (e.g. ancrage, chalutage) ou indirecte (e.g. turbidité, hyper-sédimentation) sur la structure de l'herbier à des échelles spatiales et temporelles variées (Balestri *et al.* 2004, Boudouresque *et al.* 2009, Giakoumi *et al.* 2015b).

Le résultat de la fusion des patchs est toujours fortement hétérogène à toutes les échelles spatiales de considération (Fig. 10), de l'individu (génétique, morphologie) à des herbiers de plusieurs kilomètres carrés (Gobert 2002, Borg *et al.* 2005, Zupo *et al.* 2006a, Abadie *et al.* 2015a). Aux échelles spatiales les plus grandes, i.e. de plusieurs centaines de mètres carrés à plusieurs centaines de kilomètres carrés, l'unité d'étude devient alors le "patch" appelé aussi "intermatte". La mosaïque créée par les intermattes à l'intérieur d'une matrice d'herbier forme ainsi des paysages sous-marins très variés (Robbins & Bell 1994).

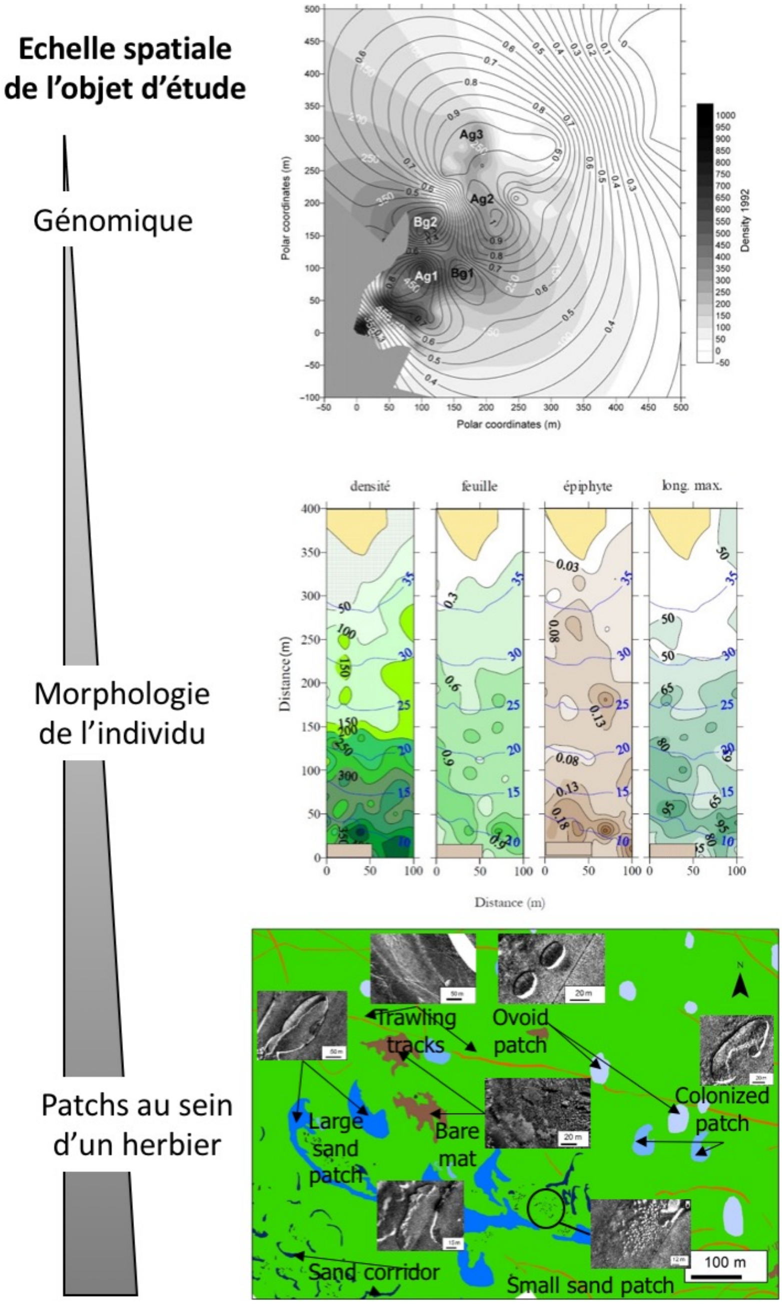

Figure 10 *: Exemples de variabilité spatiale au sein d'un herbier : au niveau de la génétique (Zupo et al. 2006), de la morphologie de la plante (Gobert 2002) et de la diversité des patchs (Abadie et al. 2015a).*

2. La nécessité de gérer l'écosystème

2.1. Estimer les services fournis par les herbiers de *P. oceanica*

A l'instar des autres Magnoliophytes marines, *P. oceanica* joue un rôle écosystémique majeur de par sa fonction d'ingénieur d'écosystèmes (Boudouresque *et al.* 2012). De cette importance fonctionnelle résulte des services économiques (Fig. 11) délivrés aux usagers des zones littorales de la Méditerranée.

L'une des premières estimations spécifique aux herbiers à *P. oceanica* propose une valeur de 2 243 € $m^{-2}.a^{-1}$ pour l'ensemble de ses services (Blasi 2009). Une étude plus récente les estime à 172 € $m^{-2}.a^{-1}$ en utilisant une méthode de calcul de l'émergie[2] du système, la majeure partie de cette valeur provenant du service de rétention des sédiments par la plante (Vassallo *et al.* 2013). En utilisant des données bibliographiques couplées à des méthodes des transferts, Campagne *et al.* (2015) estiment que la valeur économique des services varie entre 0.284 et 0.514 € $m^{-2}.a^{-1}$. A ces mesures très variables et dépendantes de la méthode d'évaluation sont couplées des données de régression des herbiers qui elles aussi sont fortement sujettes à discussion. De plus, la plupart de ces évaluations ne prennent pas en compte le rôle tampon des herbiers face aux changements climatiques globaux avec notamment la séquestration d'une partie du carbone atmosphérique (Pergent *et al.* 2014).

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[2] Émergie (*EMergy* en anglais) : quantité totale d'énergie sous une forme donnée qui a été directement et indirectement utilisée pour créer une autre forme d'énergie [Odum HT (1996) Environmental Accounting: Emergy and environmental decision making. John Wiley, New York, USA]

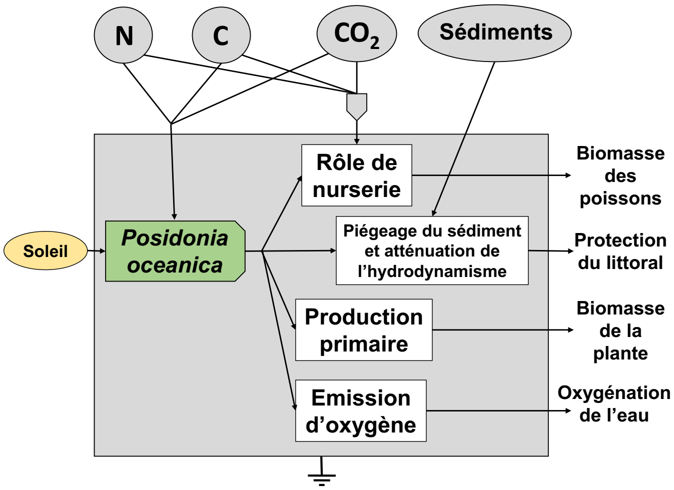

Figure 1-11 *: Lien entre le rôle écosystémique de* P. oceanica *et ses services économiques [traduit et redessiné d'après Vassallo et al. (2013)].*

Même s'il est difficile, d'estimer la valeur monétaire de ces services, ces données sont primordiales afin de fournir une base de décision pour les gestionnaires du milieu côtier. Ces valeurs permettent également de sensibiliser un large public souvent peu informé de l'importance des herbiers à *P. oceanica*.

2.2. Quelle régression des herbiers à *P. oceanica* ?

L'ensemble des impacts anthropiques mentionnés précédemment entraînent une régression globale à l'échelle de la Méditerranée des herbiers à *P. oceanica* (Boudouresque *et al.* 2009). Les régressions estimées les plus importantes sont de l'ordre de 5 à 8 % par an et ont été observées en Espagne (Marbà *et al.* 1996). Cependant ces estimations ne semblent pas réalistes à l'échelle de l'ensemble des herbiers. D'autres déclins conséquents de la surface couverte par les herbiers à *P. oceanica* ont été observés mais correspondent plus certainement à des phénomènes locaux (Montefalcone *et al.* 2007, Lasagna *et al.* 2011). A l'opposé, un déclin beaucoup plus modéré de 13 % en 85 ans a été observé en région Provence Alpes Côte d'Azur (France), une zone pourtant fortement soumise aux pressions anthropiques côtières (Holon *et al.* 2015a).

L'estimation la plus récente réalisée sur la totalité de la Méditerranée par Telesca *et al.* (2015), en utilisant des données cartographiques, fait état d'une diminution d'environ 34 % au cours des 50 dernières années. Ce chiffre est cependant basé sur une faible portion de la couverture totale de l'herbier et des méthodes de calcul différentes. Ces estimations sont ainsi, dans leur large majorité, réalisées à l'aide de cartographies. L'évolution des techniques de cartographie aux cours des dernières décennies, et par extension leur précision, est très certainement le principal facteur à l'origine des différences observées (Fig. 12) entre 1960 et la première moitié des années 2000s (Bonacorsi *et al.* 2013, Abadie *et al.* 2015c).

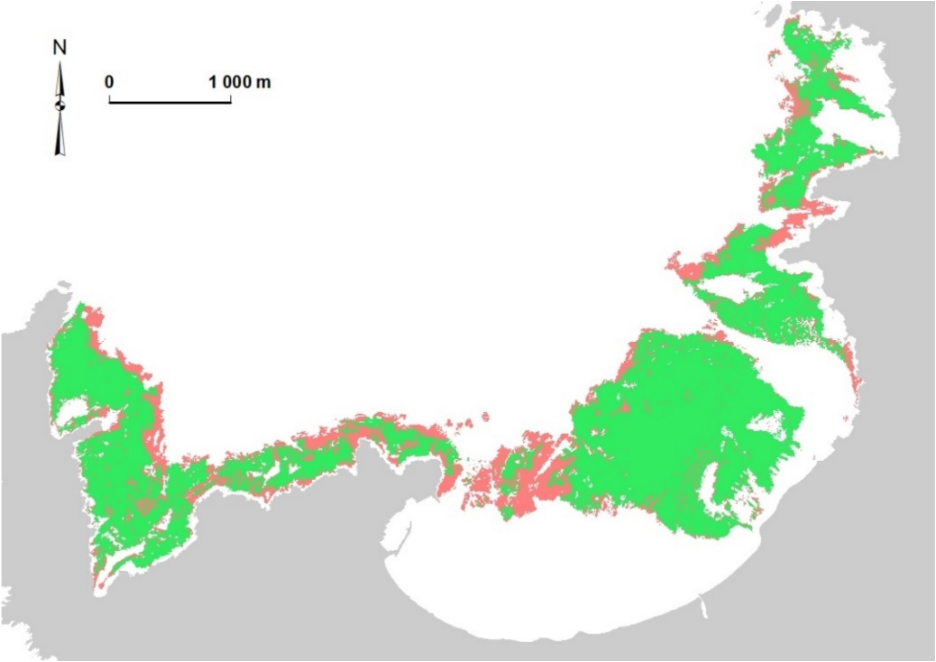

***Figure 12** : Exemple de surestimation de la régression (environ 17 %, en rouge) des herbiers à* P. oceanica *(en vert) en baie de Calvi (Corse, France) entre 2002 et 2010 dû à l'augmentation de la résolution des données sonars et aériennes (Abadie 2012).*

Si le fait qu'une réelle régression existe fait largement consensus, l'amplitude de cette régression est très largement discutée. Face à ce constat, qu'il soit global ou local, il incombe aux gestionnaires de prendre des mesures de conservation pour évaluer l'état des herbiers et de mettre en place des règles de protection.

2.3. Vers une approche écosystémique de la conservation

Les régressions ainsi provoquées par l'impact des activités humaines sur cette espèce de grande importance écologique et économique sont sources de mesures de gestion spécifiques. En France, *P. oceanica* est une espèce protégée depuis 1988 (JO du 9 août 1988, p. 10 à 128) par décret d'application de la loi sur la protection de la nature de 1976. Il est ainsi interdit de prélever et colporter toute partie de la plante vivante ou morte sans autorisation spécifique. A l'échelle de l'Union Européenne, elle apparaît notamment dans la Convention de Berne en 1982 (Convention relative à la conservation de la vie sauvage et du milieu naturel de l'Europe, transcription dans le droit français en 1999), Directive Habitats de 1992 (92/43 CEE/Habitats Naturels) et la Directive Cadre Eau (2000/60 CE/Cadre Eau, DCE).

Dans le cadre de la DCE, *P. oceanica* est ainsi utilisée en tant que bioindicateur de la bonne qualité de l'eau en étudiant sa physiologie et la structure des herbiers tout en les reliant aux pressions anthropiques de la zone d'étude (Montefalcone 2009). A cette fin, plusieurs indices synthétiques ont été développés pour réaliser le monitoring nécessaire au maintien ou à l'amélioration de la qualité des eaux côtières (Romero *et al.* 2007, Gobert *et al.* 2009, Lopez y Royo *et al.* 2010). Ces indices visent à estimer le ratio de qualité écologique (Ecological Quality Ratio, EQR) d'un site en fournissant un résultat chiffré interprété à l'aide d'un code couleur (Tabl. 1) facilement utilisable par les gestionnaires du milieu côtier.

Tableau 1 *: Interprétation du statut écologique en fonction de la valeur du ratio de qualité écologique (Ecological Quality Ratio, EQR) [traduit d'après Gobert et al. (2009)].*

EQR	Statut écologique	Code couleur
1-0.775	Elevé	Bleu
0.774-0.550	Bon	Vert
0.549-0.325	Modéré	Jaune
0.324-0.100	Pauvre	Orange
<0.100-0	Mauvais	Rouge

Suite à l'analyse des premiers résultats de la DCE, l'action de l'Union Européenne pour la préservation de la bonne qualité de l'environnement marin évolue en 2008. La Directive Cadre Stratégie pour le Milieu Marin (2008/56/CE, DCSMM) est ainsi mise en place avec comme but d'atteindre un bon état écologique des habitats marin d'ici 2020. Ce ne sont plus seulement les compartiments fonctionnels de la plante qui sont étudiés, mais l'ensemble de ceux composant l'écosystème supporté par les herbiers à *P. oceanica* (Fig. 13). Ce ne sont donc plus seulement les impacts anthropiques affectant la qualité de l'eau qui sont évalués, mais la totalité des activités humaines ayant une influence sur l'écosystème (Boudouresque *et al.* 2015b). Ainsi, un indice de qualité basé sur l'écosystème (Ecosystem Based Quality Index, EBQI) est calculé en estimant l'état de conservation de chaque compartiment fonctionnel en tenant compte du degré de fiabilité des données disponibles (bibliographiques ou acquises sur le terrain) (Personnic *et al.* 2014). Un code couleur similaire à celui de l'EQR est utilisé pour une utilisation aisée par les gestionnaires.

A l'évaluation globale de la conservation de l'écosystème s'ajoute la possibilité d'étudier l'impact des activités humaines sur chaque compartiment fonctionnel (Giakoumi *et al.* 2015b) afin d'adapter les mesures de gestion à l'échelle locale.

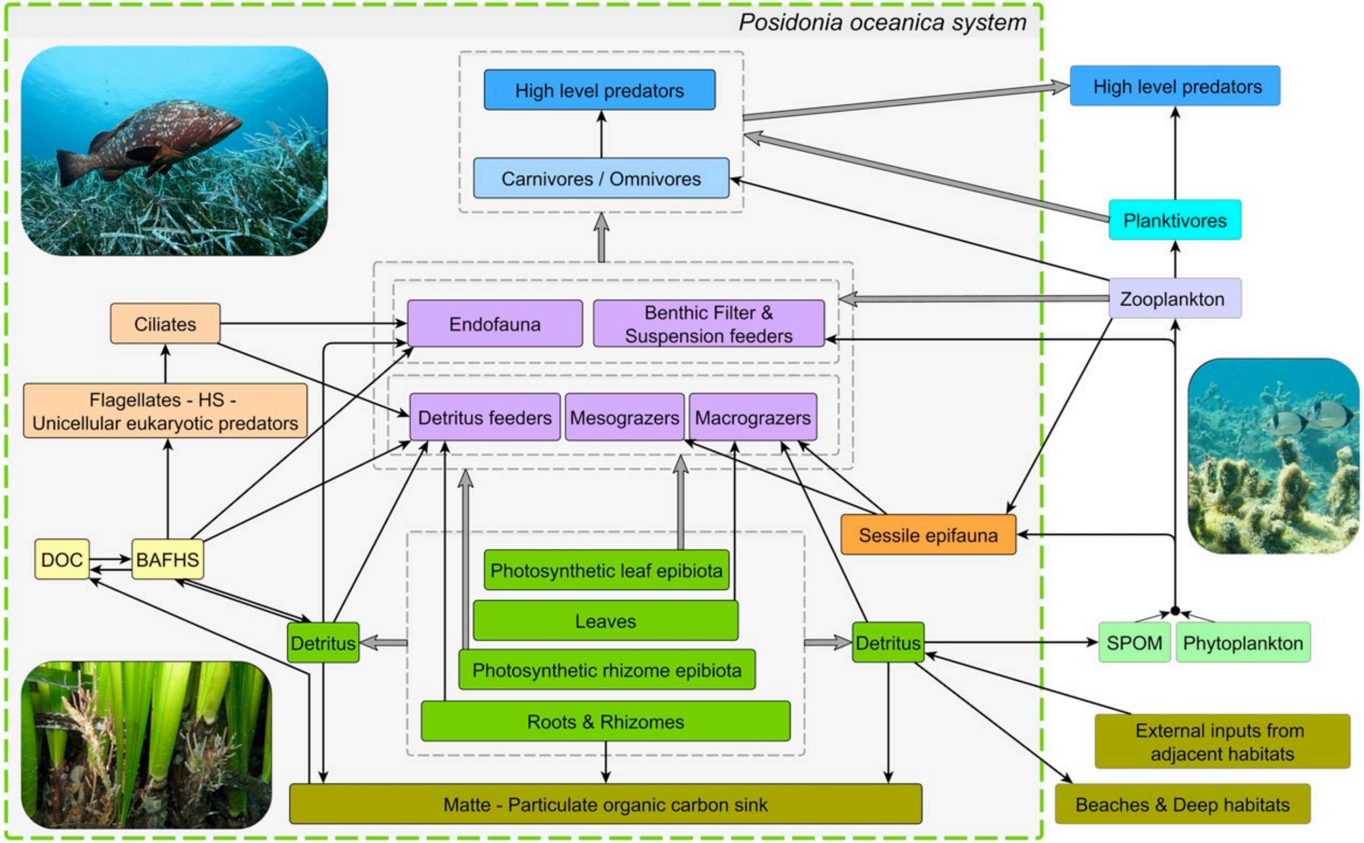

***Figure 13** : Modèle conceptuel du fonctionnement de l'écosystème supporté par les herbiers à* P. oceanica *composé de compartiments fonctionnels (Giakoumi et al. 2015b).*

3. Les intermattes : des structures variées et dynamiques

L'intermatte est définie comme un patch de sable ou de matte morte au sein d'un herbier (Boudouresque *et al.* 2012). Plusieurs processus naturels et anthropiques sont à l'origine de ces structures si particulières, source d'hétérogénéité pour un habitat marin souvent perçu, à tort, comme continu et homogène (Fig. 14).

***Figure 14** : Alternance d'intermattes naturelles au sein d'un herbier à* P. oceanica *(Aleria, Corse).*

3.1. L'érosion naturelle de l'herbier, source de création d'intermattes

Le principal moteur naturel de création d'intermattes est l'hydrodynamisme (Boudouresque & Meinesz 1982, Boudouresque *et al.* 2012). Cette force érode ainsi l'herbier en créant des courants de fonds orbitaux qui entraînent dans un premier temps le transport du sédiment (Fig. 15b), puis sa remise en suspension (Fig. 15c et 15d) dans la canopée (Blanc & Jeudy De Grissac 1984). La puissance de ces courants peut mener à l'arrachage de *P. oceanica* lorsque son intensité augmente (lors de tempêtes, par exemple) et au creusement du substrat (Fig. 15e). Un tombant de matte se forme ainsi et continue à être érodé à sa base par le courant (Fig. 15f). Des portions entières peuvent s'effondrer lors de brefs épisodes d'intensification de l'hydrodynamisme (Fig. 15g) (Boudouresque *et al.* 1980b).

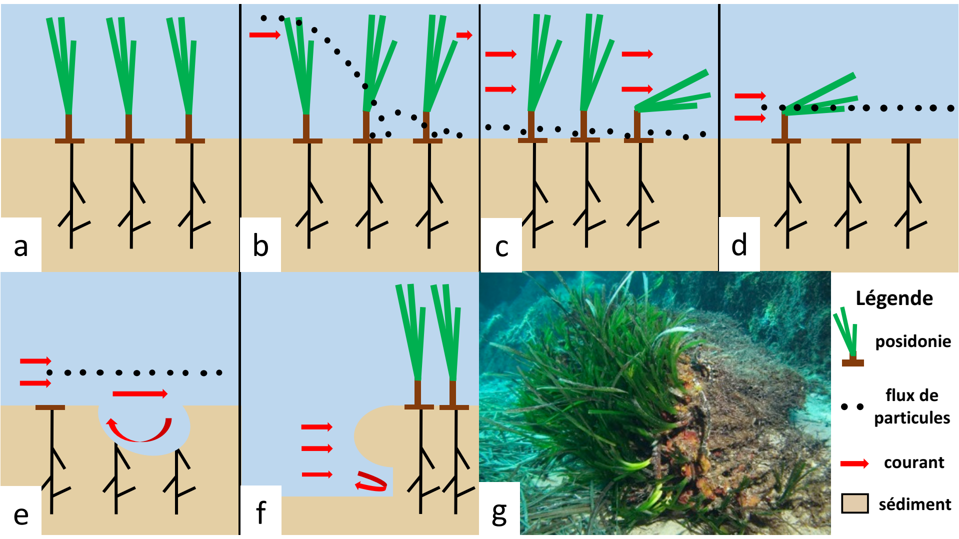

***Figure 15** : Processus de création des intermattes au sein de l'herbier à* P. oceanica *; a) sédimentation en équilibre avec la croissance de la plante ; b) piégeage du sédiment dans la canopée ; c) mise en suspension du sédiment de surface ; d) les rhizomes se déchaussent et sont cassés par la force du courant ; e) creusement du substrat et création d'une intermatte ; f) formation d'un tombant de matte qui s'érode à sa base ; g) lors d'événements extrêmes de larges portions de matte peuvent s'effondrer [redessiné et modifié d'après Blanc and Jeudy De Grissac (1984)].*

Faisant face au tombant de matte érodée (Fig. 16a et 16b), l'herbier recolonise l'espace sableux en favorisant le développement de ses rhizomes plagiotropes (Fig. 15c). La dynamique de ces intermattes les conduirait donc à se déplacer vers la côte à vitesse annuelle relativement constante (Boudouresque *et al.* 1980b).

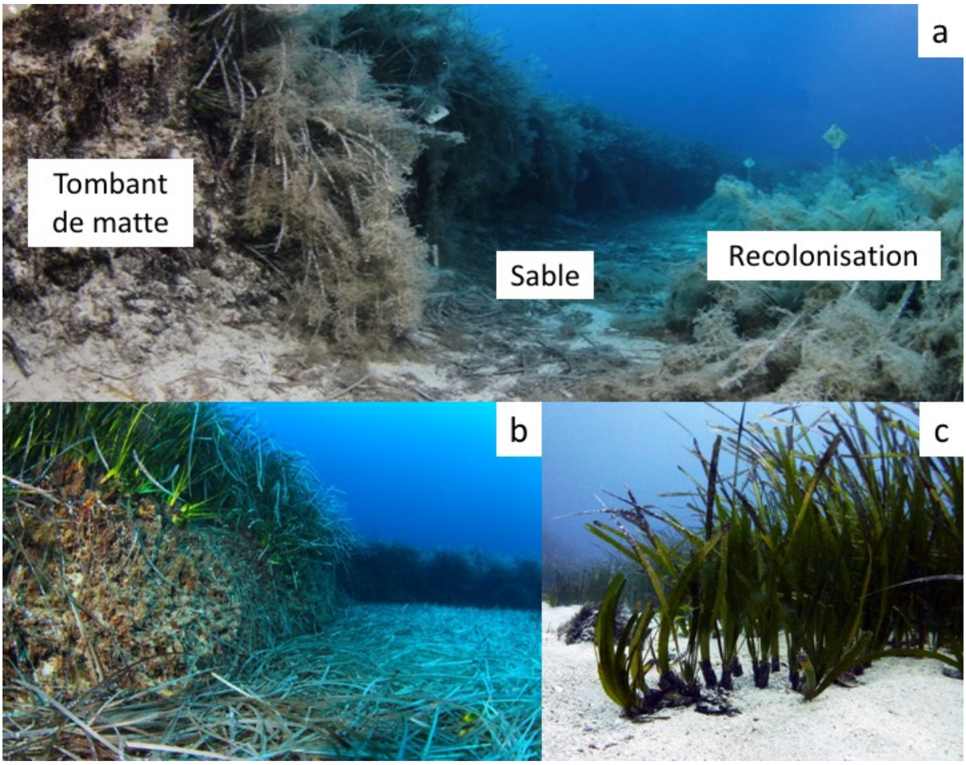

Figure 16 *: Intermattes naturelles en Baie de Calvi (Corse, France) à 15 m de profondeur a) intermatte naturelle sableuse ; b) tombant de matte érodée par les courants ; c) rhizomes plagiotropes dans la partie recolonisée de l'intermatte.*

3.2. La génération anthropique d'intermattes

En parallèle des intermattes générées par le mouvement de l'eau, des structures d'origine anthropique sont générées par l'impact physique de certaines activités humaines, i.e. des perturbations[3], responsables de la régression des herbiers de *P. oceanica* (Boudouresque *et al.* 2009, Montefalcone *et al.* 2010b). Certaines activités continues, i.e. stress[4], mènent à la création de patchs à moyen et long terme. D'autres entraînent une destruction mécanique directe de la strate foliaire créant immédiatement des intermattes de matte nue au sein du paysage sous-marin (Fig. 17).

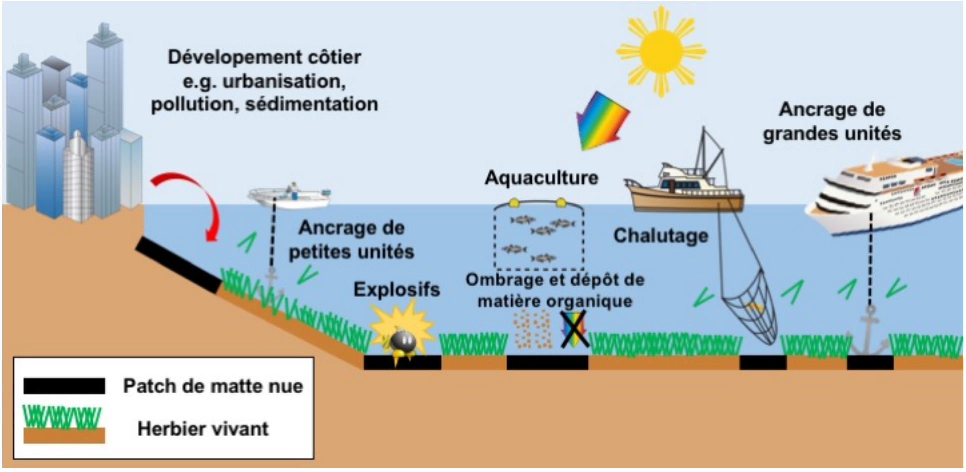

Figure 17 : Impact des activités anthropiques générant des intermattes au sein des paysages sous-marins à P. oceanica*.*

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[3] Perturbation : dans un écosystème donné, une perturbation est le résultat d'une déviation imprédictible et de courte durée d'un paramètre physico-chimique, éventuellement chimique, d'une amplitude telle qu'elle est supérieure à l'inertie d'une ou plusieurs espèces-clé, ou d'une guilde, ou d'un compartiment fonctionnel [Boudouresque CF, Bernard G, Pergent G, Shili A, Verlaque M (2009) Regression of Mediterranean seagrasses caused by natural processes and anthropogenic disturbances and stress: a critical review. Botanica Marina 52:395-418]

[4] Stress : perturbation s'installant dans la durée [Connell JH, Sousa WP (1983) On the evidence needed to judge ecological stability or persistence. The American Naturalist 121:789-824]

Le développement côtier est l'une des principales causes de la régression de la strate foliaire des herbiers à *P. oceanica* (Giakoumi *et al.* 2015b). Il est ainsi source de pollution notamment par le déversement d'eaux usées (matière en suspension et éléments traces, Fig. 18) qui entraînent une diminution de la croissance des rhizomes et un changement dans la structure foliaire (Balestri *et al.* 2004).

Figure 18 *: Canalisation de rejet d'eaux usées en baie de Calvi (Corse, France).*

L'expansion des zones urbaines littorales peut également provoquer d'importantes modifications du paysage sous-marin. La construction de ports et le rechargement en sable des plages provoquent une atténuation de la lumière et une sédimentation de matière en suspension supérieure à la vitesse de croissance verticale de la plante, menant ainsi à la régression de la plante sur de larges zones (Ruiz & Romero 2003, Montefalcone *et al.* 2007). Les effluents d'aquacultures sont, au même titre, responsables de la disparition de larges portions de l'herbier. De cette façon, en diminuant la pénétration des rayons solaires et en rejetant de grandes quantités de matière organique, les cages d'aquaculture provoquent l'anoxie du sédiment dans lequel se développe *P. oceanica* (Pergent-Martini *et al.* 2006). Ces conditions favorisent l'apparition de composés toxiques tel que le sulfure d'hydrogène et la régression de l'herbier à *P. oceanica* (Holmer & Frederiksen 2007).

En parallèle des impacts mentionnés précédemment, certaines activités provoquent des dommages mécaniques immédiats générant instantanément des intermattes anthropiques (Abadie *et al.* 2013). Parmi ces impacts directs, le chalutage (illégal ou non selon le pays) est l'une des activités provoquant les dégâts les plus importants (Pergent *et al.* 2013). Leurs panneaux créent de longues "cicatrices" de matte nue (Fig. 19), substrat propice pour l'installation d'espèces invasives comme la Chlorobionte *Caulerpa cylindracea* Sonder (Kiparissis *et al.* 2011). Une modification de la structure des communautés d'invertébrés benthiques est également observée au niveau des familles d'amphipodes et d'isopodes (Sánchez-Jerez & Ramos Esplá 1996).

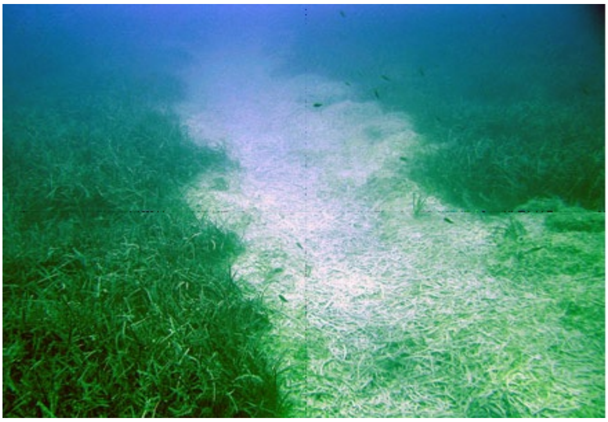


***Figure 19** : Chenal créé par les panneaux du chalut lors de son action de pêche dans les herbiers à* P. oceanica *[photo : G. Tryphonopoulos].*

D'autres activités humaines moins actuelles, telles que les bombardements de la Seconde Guerre Mondiale, ont généré des intermattes de très grandes tailles encore visibles actuellement (Meinesz & Lefèvre 1984). D'autres traces de déflagration sont visibles dans l'herbier, certainement le résultat d'une ancienne activité de pêche à l'aide d'explosifs (Pasqualini *et al.* 2000).

D'une façon similaire aux dommages causés par le chalutage dans les herbiers à *P. oceanica*, l'ancrage est une source de création d'intermattes de matte nue (Montefalcone *et al.* 2006b). Cependant, à la différence du chalutage, l'intensité de destruction dépend de la taille et du type d'ancre, et par extension de la taille de l'embarcation (Milazzo *et al.* 2004). Ainsi le mouillage forain répété des petites unités (<10 m, Fig.

20a) engendre une diminution de la densité de l'herbier (Francour *et al.* 1999, Ceccherelli *et al.* 2007) sans création d'un nombre significatif d'intermattes (Ganteaume *et al.* 2005a). Cette destruction mécanique de la strate foliaire augmente avec la taille des embarcations, menant à la génération de zones de matte nue (Fig. 20b) caractérisée par des sillons d'ancrage (Ganteaume *et al.* 2005b, Okudan *et al.* 2011).

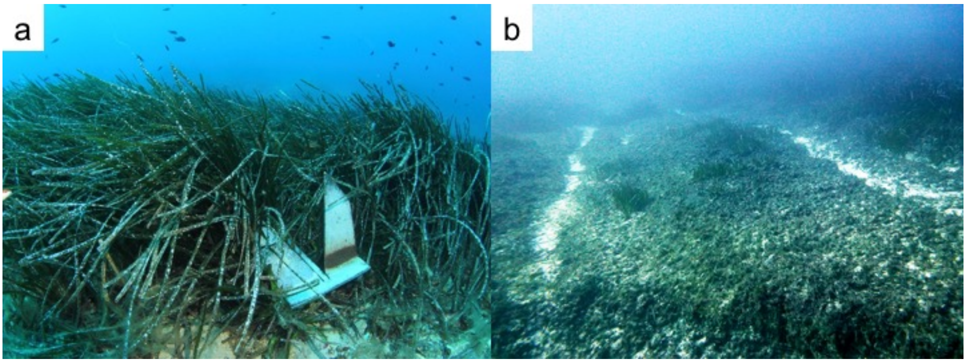


***Figure 20** : a) Ancre d'une embarcation de petite taille (environ 10 m) dans un herbier près de l'ilot de la Vacca (Corse, France) ; b) matte nue générée par le mouillage de grandes unités présentant des sillons d'ancre dans la baie de l'Alga (Corse, France).*

4. Objectifs et cheminement

En tant qu'élément structurant dynamique des paysages sous-marins, les intermattes (naturelles et anthropogéniques) semblent posséder un fort potentiel d'utilisation pour l'évaluation de l'évolution des herbiers à *P. oceanica*. Cependant, avant de les inclure dans des programmes de gestion ou de développer des outils appliqués spécifiques, il est impératif d'en étudier précisément la dynamique. Les travaux de recherches présentés ici ayant été menés en entreprise, leur préparation ainsi que leur réalisation ont été effectuées en se focalisant sur l'application concrète des résultats obtenus.

Les travaux réalisés durant cette thèse de doctorat ont été effectués dans l'optique de répondre aux questions suivantes :

1) **Les intermattes naturelles et anthropiques ainsi que l'herbier qui les entoure ont-ils des caractéristiques biologiques et physico-chimiques spécifiques ?**
2) **Comment ces structures si particulières s'insèrent-elles dans le paysage sous-marin ? Quelle est leur influence sur sa structure ?**
3) **Est-il possible d'utiliser les intermattes pour évaluer l'état de conservation des herbiers à *P. oceanica* ? Si oui, de quelle façon ?**

Ce document s'articule autour de ces trois interrogations, chaque chapitre tentant d'apporter des éléments de réponse à plusieurs d'entre elles. Il compile ainsi l'analyse des résultats de l'ensemble de ces travaux sous la forme d'articles scientifiques. La structure globale suit le schéma suivant (Fig. 21) :

- **Chapitre 1 – Introduction** : Les intermattes, unité fondamentale d'un paysage sous-marin dynamique

- **Chapitre 2** : Dynamique des intermattes naturelles : variabilité des paramètres physico-chimiques et biologiques

  L'évolution temporelle des facteurs biotiques et abiotiques structurant les intermattes naturelles sableuses est étudiée afin d'examiner leur influence sur l'ensemble du paysage sous-marin.

- **Chapitre 3** : D'un impact mécanique à chimique de l'ancrage dans les plantes sous-marines : prémices de la génération de patchs anthropiques dans les herbiers à *Posidonia oceanica*

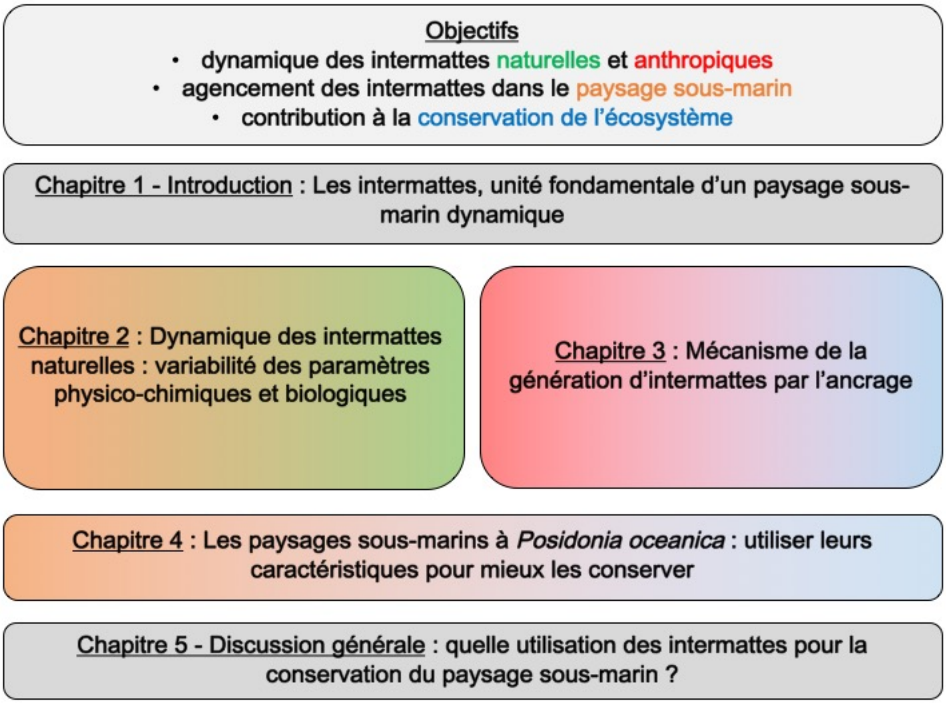
  Les phénomènes indirects émanant d'un impact anthropique mécanique (ici l'ancrage) et leur lien avec la recolonisation des intermattes générées sont explorés pour proposer de nouvelles perspectives de gestion du milieu littoral.

- **Chapitre 4** : Les paysages sous-marins à *P. oceanica* : utiliser leurs caractéristiques pour évaluer leur état de conservation

  Les spécificités structurelles des paysages sous-marins formés par *P. oceanica* ainsi que leur fonction sont mises en évidence afin de cerner l'impact des activités humaines sur leur morphologie et proposer un nouvel outil de conservation.

- **Chapitre 5 - Discussion générale** : utiliser les intermattes pour la conservation du paysage sous-marin

  Ce chapitre final compile les résultats de travaux de recherche réalisés durant ce doctorat (directement ou par supervisions de travaux de fin d'étude) ainsi que durant des collaborations plus ponctuelles à d'autres programmes. A travers cette synthèse, plusieurs méthodes de mesure et outils de gestion sont proposés pour étudier les paysages à *P. oceanica* grâce aux intermattes.



Objectifs
- dynamique des intermattes naturelles et anthropiques
- agencement des intermattes dans le paysage sous-marin
- contribution à la conservation de l'écosystème

Chapitre 1 - Introduction : Les intermattes, unité fondamentale d'un paysage sous-marin dynamique

Chapitre 2 : Dynamique des intermattes naturelles : variabilité des paramètres physico-chimiques et biologiques

Chapitre 3 : Mécanisme de la génération d'intermattes par l'ancrage

Chapitre 4 : Les paysages sous-marins à *Posidonia oceanica* : utiliser leurs caractéristiques pour mieux les conserver

Chapitre 5 - Discussion générale : quelle utilisation des intermattes pour la conservation du paysage sous-marin ?

Figure 21 *: Objectifs et structuration de la synthèse des recherches. Les thèmes abordés dans chaque chapitre sont indiqués par la couleur des cadres : vert = intermattes naturelles ; rouge = intermattes anthropiques ; orange = paysages sous-marins ; bleu = conservation.*

CHAPITRE 2

Dynamique des intermattes naturelles Variabilité des paramètres physico-chimiques et biologiques

Ce chapitre est composé de deux articles :

Article 1 : Sylvie Gobert, Gilles Lepoint, Corinne Pelaprat, François Remy, Pierre Lejeune, Jonathan Richir, Arnaud Abadie (accepté) Temporal evolution of sand corridors in a *Posidonia oceanica* seascape: a 15-years study. Mediterranean Marine Science

Article 2 : Arnaud Abadie, Alberto V. Borges, Willy Champenois, Sylvie Gobert (soumis) Sediment biogeochemistry in two edge types of *Posidonia oceanica* seagrass meadows and its influence on colonization processes. Estuaries and Coasts

Les justificatifs de l’acceptation et de la soumission de ces articles sont disponibles en Annexe 1.

Les données utilisées dans l’articles 2 sont disponible dans les Annexes 2, 3 et 4.

Article 1: Temporal evolution of sand corridors in a *Posidonia oceanica* seascape: a 15-years study

Abstract

The spatial dynamic of *Posidonia oceanica* meadows is a process extending over centuries. This paper shows evidence of the natural dynamics of *P. oceanica* “shifting intermattes” or “sand corridors” (hereafter SCs): unvegetated patches within a dense meadow. We studied features and temporal evolution (2001-2015) of 5 SCs in the Calvi Bay (Corsica) at 15 m depth and followed the characteristics the *P. oceanica* meadow lining the edge of patches. All SCs show a similar morphology. The eroded side is a vertical edge where roots, rhizomes and sediments are visible, when on the opposite colonized side, the sand is at the same level as the continuous meadow. The vertical edge reaches a maximum height of 160 cm and is eroded by orbital bottom currents with a maximum speed of 12 $cm.s^{-1}$, the erosion speed ranging from 0.6 to 15 $cm.a^{-1}$. SCs progress toward the coastline with a mean speed of 10 $cm.a^{-1}$, the rate of colonization by *P. oceanica* shoots ranging from 1.5 to 21 $cm.a^{-1}$. We calculated that the studied SCs would reach the coastline within 500 to 600 years. We finally discuss the implication of such dynamic in the framework of meadows’ colonization assessment and the seascape dynamic.

Keywords : seagrass colonization; *Posidonia oceanica* dynamic; intermatte; Mediterranean Sea; seascape

1. Introduction

The endemic species *Posidonia oceanica* (L.) Delile is the main seagrass of the Mediterranean Sea. This plant forms extensive meadows from the surface to 40 m depth considered as “climax” habitats (Boudouresque *et al.* 2012, Pergent *et al.* 2012). Over the last three decades the interest in landscape ecology has grown and spread from land to marine ecosystems (Bell *et al.* 2006) and *P. oceanica* meadows (Montefalcone *et al.* 2013b) to assess conservation state of coastal areas. Presently, meadows’ morphology such as the presence and arrangement of bare patches (*e.g.* natural or anthropogenic bare matte and intermattes) are used as characteristic imprints of environmental conditions (Pergent *et al.* 1995, Montefalcone 2009, Montefalcone *et al.* 2010b, Abadie *et al.* 2015b). The use of landscape tools in the study of seagrass meadows (seascapes) begins to be widely spread but still require the establishment of several bases. More precisely, patch descriptions and their temporal evolution must be investigated to sort out natural from anthropogenic erosion of *P. oceanica* meadows.

Among patches, a special focus has been made on a particular structure called “shifting intermattes” or “sand corridors” (SCs), *i.e.* a sand patch within a *P. oceanica* meadow, described sixty years ago by Molinier and Picard (1952). This patch type displays an interesting structural particularity for the study of erosive and colonization processes of the meadows. On one side, bottom currents erode the meadow creating a vertical edge of matte when on the other side *P. oceanica* colonizes the bare sandy bottom (Boudouresque *et al.* 1980b).

In order to follow the spatial evolution of *P. oceanica* meadows and patch generation at small scale, several non-destructive methods have been developed, *e.g.* the permanent square (Noël *et al.* 2012) and the acoustic telemetry (Descamp *et al.* 2011). Another way to assess *P. oceanica* ability to colonize bare substrates consist in measuring rhizome elongation using lepidochronology, *i.e.* the annual cycles of scales’ thickness (Pergent *et al.* 1989b). However, these methods remain time consuming, expensive or destructive. Thus, the present work aims, through the long term study of SCs particularities, (1) to propose a non-destructive and cost effective method to assess their spatial evolution, (2) to describe the dynamic of natural patches inside *P. oceanica* meadows and (3) to discuss its implication for the whole *P. oceanica* seascape.

2. Materials and Methods

This study took place in the Calvi Bay, located in the Mediterranean Sea on the northwest coast of Corsica (42°35’ N, 8°45’E; Fig. 22), a nutrient-poor (ultra-oligotrophic) and pristine area. *P. oceanica* is the dominant macrophyte bottom species of that bay and covers sandy and rocky substrata. Its lower limit reaches 38 m depth (Bay 1984). Despite these very low nutrient concentrations, the meadow displays both high biomass and productivity (more than 500 $g_{DW}.m^{-2}.y^{-1}$); *P. oceanica* beds are thus considered as Low Nutrient-High Chlorophyll (LNHC) systems (Gobert *et al.* 2002). The meadow in the studied bay is qualified as healthy (Gobert *et al.* 2009) and no significant changes of its vitality have been registered since 1975 (Jousseaume *et al.* 2014).

The study was carried out from July 2001 to June 2015 on SCs (Fig. 22) located in front of the research station of STARESO (STAtion de REcherches Sous marines et Océanographiques) between 13 m and 16 m depth, resulting in a fifteen-years temporal survey. In July 2001, the borders of five patches were marked out with labelled pegs anchored 50 cm deep in the sediments. A map was then obtained using triangulation measurements between pegs. This first delimitation was left in place and a same marking process was performed in June 2002 and in June 2003. The distance between each peg was recorded in June 2002 (evolution from 2001 to 2002) and in June 2003 (evolution from 2002 to 2003). In June 2010 and 2015, the relative position of the pegs was again measured on patch 2 (Fig. 22).

In September 2001, four sediment cores (diameter of 5 cm) were sampled in the middle of patch 5 and in the adjacent continuous *P. oceanica* meadow. The mean length of sediment cores was approximately 10 cm. Grain size (fine silt to coarse sand) was measured using sieves of 0.8, 0.4, 0.2, 0.1, 0.05, 0.025 and 0.0125 mm. Each fraction was dried during 48 h at 60 °C and was weighed before and after drying. Sediments were classified according to their grain size using the scale of Wentworth (1922).

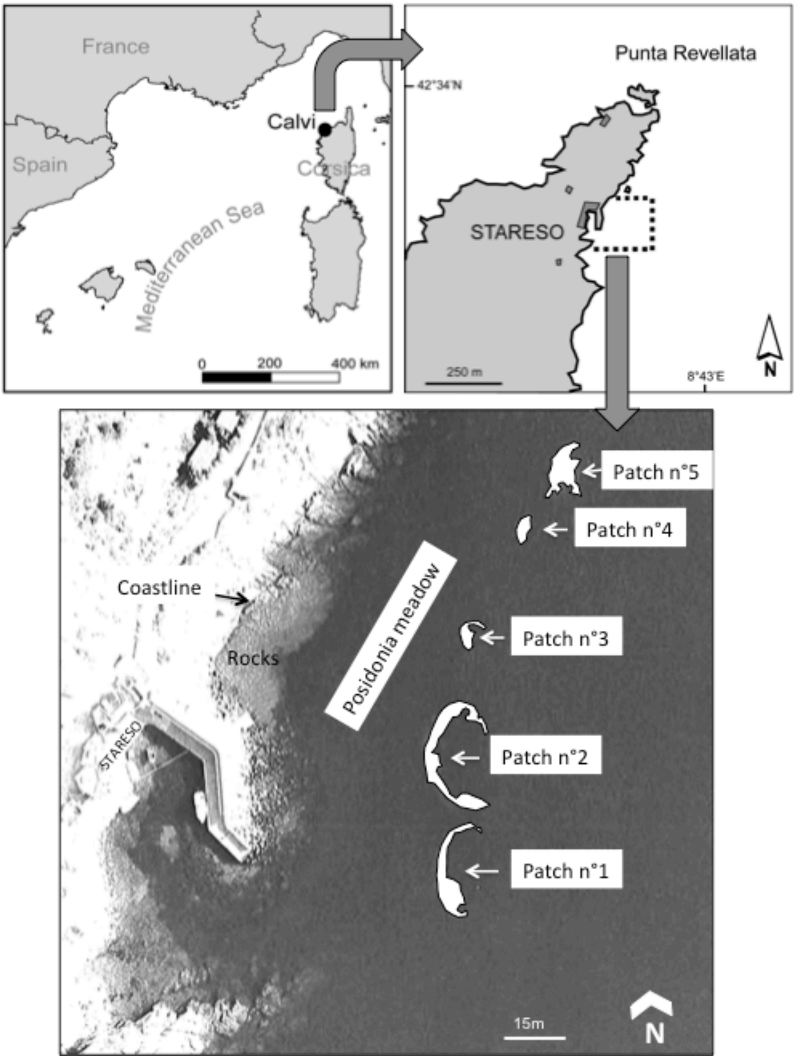


***Figure 22**: Study site in front of STARESO in the Calvi Bay (Corsica): sand corridors forming a row of five sand patches in the P. oceanica meadow.*

The speed and direction of bottom currents were measured from November 2001 to October 2002 using an Aanderaa™ RCM7 current meter placed within patch 1 close to the eroded side. The current speed and its direction were measured every 20 minutes and data were retrieved each month.

Morphologic transects of patches were performed in from 2001 to 2003 (description and measurement). Within the same period, shoot density and the number of creeping (plagiotropic) and erect (orthotropic) shoots were counted in the surrounding meadow near patches (on both eroded and colonized sides) by using a square of 40 cm x 40 cm (n = 16) (Soullard *et al.* 1994). Furthermore, one plagiotropic rhizome from each patch's colonized side was sampled in July 2015 to measure the mean annual growth thanks to lepidochronology (Pergent *et al.* 1989b).

3. Results

The five SCs are aligned one after the other parallel to the coast. The shape of patches 1 and 2 can be compared to a banana; patches 3 and 4 display a reduced area in comparison to the other three, and the outline of patch 5 is more serrated (Fig. 22). All patches show a similar morphology. The eroded side (landward) is a vertical edge facing west in which roots, rhizomes and sediments forming the matte are visible (Fig. 23a). The edge maximum height, *i.e.* up to 160 cm (patch 2), is at the mid length of the eroded side and decreases toward patch extremities. It can be described as a sheer vertical matte or a beetling scarp (Fig. 23). At the colonized side (seaward), the sand is at the same level as the continuous meadow and presents and the matte less thick with plagiotropic rhizomes (Fig. 23b).

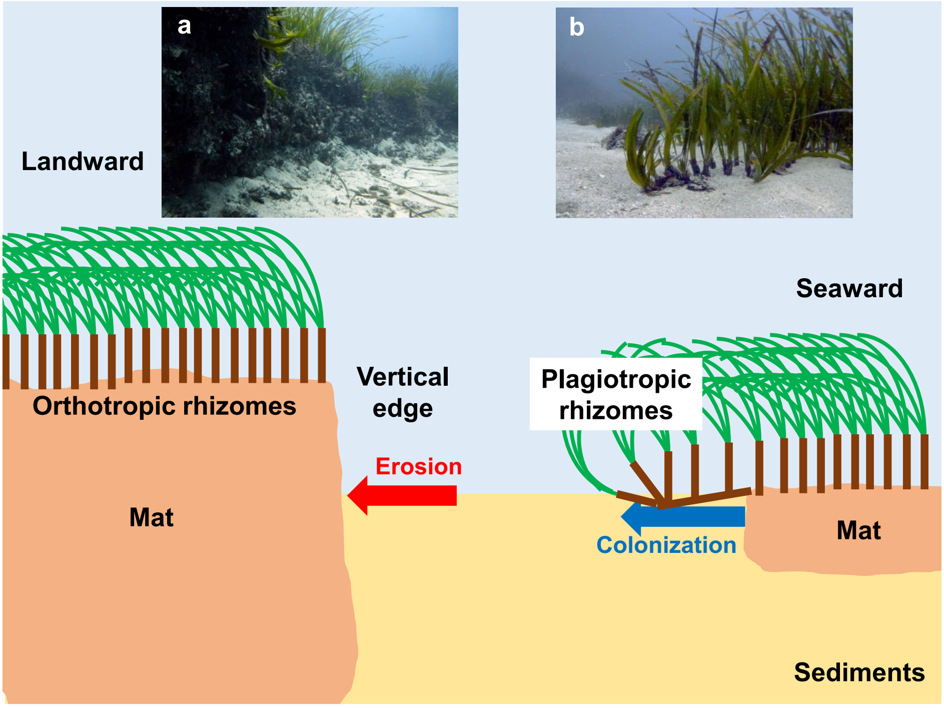


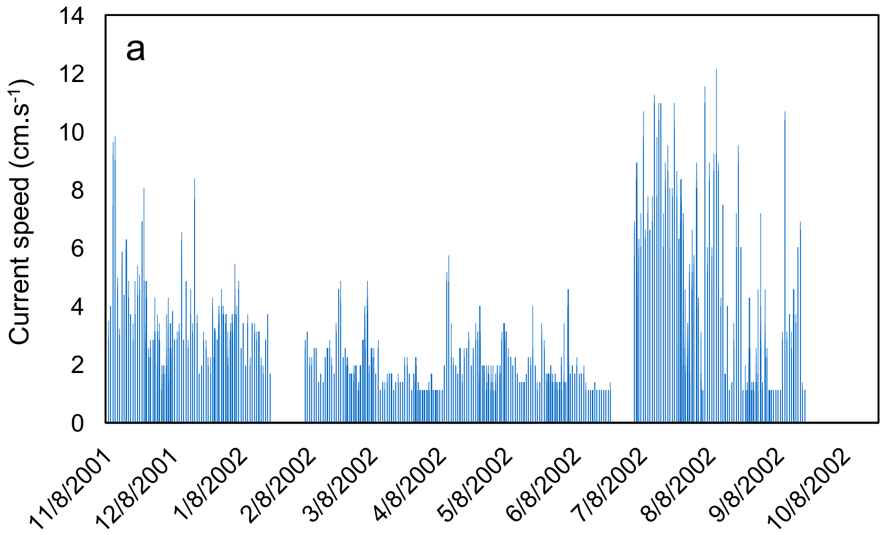
***Figure 23**: Schematic representation of a sand corridor with pictures of a) the eroded side; b) the colonized side (photos a and b: A. Abadie).*

In *P. oceanica* meadow around 75 % of the sediments below 0.8 mm grain-size are constituted by grains smaller than 0.1 mm, *i.e.* silts, while in the SC this proportion is only 60 % (Tab. 2). On the eroded side sediments are fine (Fig. 23a) while at the colonized side sediments are coarse-grained and composed of organic material and shell fragments (Fig. 23b).

***Table 2**: Percentage of each granulometric fraction according the sieve meshing and the classification of Wentworth (1922).*

	Sand				Silt			
Granulometry	Coarse	Medium	Fine	Very fine	Coarse	Medium	Fine	
Sieve size (mm)	**0.8**	**0.4**	**0.2**	**0.1**	**0.05**	**0.025**	**0.0125**	**< 0.0125**
SC sample 1	0.6	2.0	9.8	28.2	39.3	17.0	2.6	0.5
SC sample 2	0.6	4.3	6.6	23.5	40.2	17.6	4.9	2.4
Meadow sample 1	0.5	0.5	4.8	18.3	34.2	30.7	8.3	2.9
Meadow sample 2	0.7	1.1	6.0	18.8	41.4	22.5	6.6	3.0

Currents speed varies from 1.00 to 12.14 cm.s^{-1} at the eroded side with a mean value of 1.72 ± 0.69 cm.s^{-1} (Fig. 24a). Currents mainly come from the south-east (39 %) and more seldom from east (17 %) and north-west (15 %) (Fig. 24b).



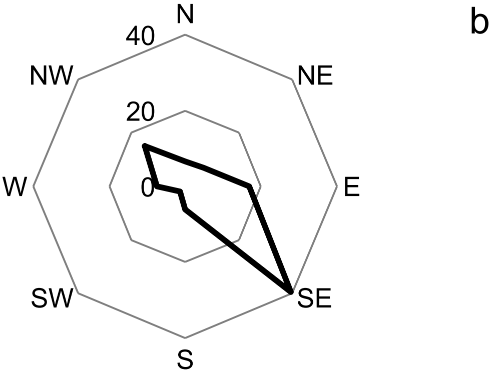


***Figure 24**: a) Current speed (cm.s-1) from November 2001 to October 2002 at patch 1 near the vertical edge; b) current frequency (%) according to their cardinal source.*

The temporal survey of the five patches performed in 2002 and 2003 reveals that the mean erosion of the vertical edge does not differ from one patch to another, *i.e.* between 19.5 ± 13.9 and 24.4 ± 12.2 cm.a^{-1} from 2001 to 2002, and between 5.4 ± 3.3 and 11.8 ± 7.0 cm.a^{-1} from 2002 to 2003 (Tab. 3). However, the mean erosion is significantly higher from 2001 to 2002 (22.8 cm.a^{-1}) in comparison with the 2002-2003 period (9.0 cm.y^{-1}). The long-term survey of patch 2 spatial dynamic between 2001 and 2015 shows erosion of its vertical edge ranging between 50 and 135 cm for the 15 years' time interval and a colonization ranging from 14 to 190 cm (Tab. 3). Rhizomes length lepidochronological analysis revealed past growth back to 2007 for patch 4, back to 2008 for patches 2 and 3, back to 2009 for patch 1 and back to 2011 for patch 5. Plagiotropic rhizomes show relatively homogeneous mean annual growth rates between the five patches ranging from 3.2 to 4.5 cm.a^{-1}. Strong knotworks of roots were observed at the extremities of plagiotropic rhizomes (Fig. 25). At the top of the vertical edge in patch 2 (13 m depth), mean density of the *P. oceanica* meadow is 403 ± 203 shoots.m^{-2} (with 9% of plagiotropic rhizomes). On the colonized side (15 m depth), the mean density reaches 229 ± 58 shoots.m^{-2} (with 21% of plagiotropic rhizomes).

***Table 3**: Surface area (m^2), vertical edge erosion and colonization speed by* P. oceanica *($cm.y^{-1}$) at the five SCs. Erosion and colonization data are given as mean ± SD, minimum and maximum values and number of measurements. The mean growth ($cm.y^{-1}$) of plagiotropic rhizomes for each patch are given as mean ± SD for their respective time interval.*

Patch	**1**	**2**	**3**	**4**	**5**
Surface area (m²)	104	135	28	24	99
Yearly mean erosion ($cm.a^{-1}$)					
2001-2002	24.2 ± 12.0	24.4 ± 12.2	22.4 ± 7.7	23.3 ± 3.2	19.5 ± 13.9
	0-46	11-45	10-35	19-26	0-56
	18	26	9	7	14
2002-2003	11.8 ± 7.0	9,4 ± 4.1	9.0 ± 5.3	5.4 ± 3.3	9.7 ± 7.4
	3-31	3-18	7-20	0-8	0-27
	18	26	9	7	14
2001-2010		77.0 ± 29.4			
		50-135			
		23			
2014-2015	10.3 ± 8.5				
	0-19.5				
	17				
Yearly mean colonization ($cm.a^{-1}$)					
2001-2010		98.6 ± 58.1			
		14-190			
		14			
2014-2015	11.1 ± 6.6				
	1-23.5				
	29				
Yearly mean plagiotropic	4.1 ± 1.4	3.2 ± 1.2	4.3 ± 0.6	4.5 ± 1.4	3.5 ± 0.8
rhizomes growth ($cm.a^{-1}$)	2009-2014	2008-2014	2008-2014	2007-2014	2011-2014

***Figure 25**: Plagiotropic rhizome sampled for lepidochronology at the colonized side of patch 4 showing a knotwork of roots at its extremity (photo: S. Gobert).*

4. Discussion

The SCs studied here are natural structures eroded by water movements (Boudouresque & Meinesz 1982, Blanc & Jeudy De Grissac 1984), embedded in a whole *P. oceanica* seascape structured by waves energy at shallow depth (Infantes *et al.* 2009, Vacchi *et al.* 2010). Our work aimed to characterize SCs' dynamic with a temporal approach to provide a new insight to the colonization evaluation in the framework of seascape studies.

On the one hand, the mean colonization speed of patches measured thanks to lepidochronology (rhizome growth of 3.9 cm.a^{-1}) is consistent with previous data. An average speed of rhizome growth of 3 to 4 cm.a^{-1} was measured by Meinesz and Lefèvre (1984); between 1.0 and 7.0 cm.a^{-1} by Caye (1982) ; between 0.4 and 1.1 cm.y^{-1} and between 0.4 et

7.4 cm.a^{-1} for orthotropic and plagiotropic rhizomes respectively by Molenaar and Meinesz (1995). On the other hand, the colonization of the patches by the *P. oceanica* shoots based on our long-term census (2001-2015) using labelled pegs ranged between 1.0 and 23.5 cm.a^{-1}. The average recolonization speed value (11.0 cm.a^{-1}) is higher than those obtained with lepidochronology. The present study therefore suggests that plagiotropic rhizome elongation as determined by lepidochronology does not correspond to the observed longitudinal spreading capacity of the meadow using anchored fixed marks. Our observations (Figs. 25 and 26) show that leaves, through their horizontal growth pattern with a production of primary roots close to their insertion rank basis (Fig. 25), could initiated the colonization process. This colonization rate measured with pegs further match with the progression rate assessed by acoustic telemetry along the French coast (Descamp *et al.* 2011). For colonization assessment of *P. oceanica* meadows, it is primordial to take into account the advance of the entire meadow, *i.e.* plagiotropic rhizomes as well as their leaves and scales (Fig. 26) and not only rhizome elongation. Consequently, the use of beacons appears well suited for such monitoring studies. Moreover, the meadow progression measured with this method corresponds to the one assessed with remote sensing, *e.g.* side scan sonar, satellite images (Descamp *et al.* 2011, Clabaut *et al.* 2014).

Looking at the opposite eroding side of SCs, the temporal evolution of vertical edges leads to seascape features similar to beach banquette dynamic of *P. oceanica* leaves as described by Mateo *et al.* (2003). The process occurs through the removal of sediments from the matte edge and the modification of the deposal rate of particles (Folkard 2005). A diagram of the successional stages of erosion is proposed in Figure 27. The base of the vertical edge is eroded leading the *P. oceanica* meadow to hang over the notch. The notch increases and the overhang meadow then collapses. Debris from the meadow - pieces of matte with living *P. oceanica* - are finally removed or else possibly start to grow again.

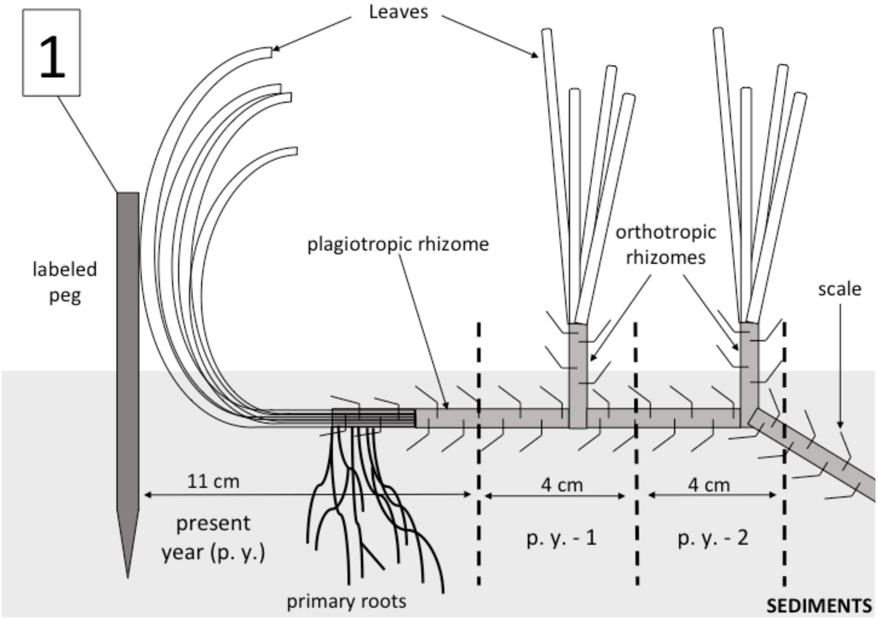


***Figure 26**: Schematic representation of the* P. oceanica *meadow progression encompassing the present year (p. y.) colonization assessed by the labeled peg, and past rhizomes elongation (p. y. -1 and p. y. -2) measured according to lepidochronology.*

According to Blanc and Jeudy De Grissac (1984), SCs parallel to the coast depend on drift currents but the effects of intense storms, even those short in duration, are preponderant. The two main wind sectors in the Calvi Bay are the north-east (Tramontane) and south-west (Libeccio) winds (Skliris & Djenidi 2006), both being powerful enough to generate waves and thus bottom currents derived from wave energy. In the present study, SCs are subjected to low currents with a maximum recorded speed of 12 cm.s^{-1} (Fig. 24). This maximum current speed is far from the one considered to prevent *P. oceanica* meadows development (about 40 cm.s^{-1} (Infantes *et al.* 2009). However, at the mean depth of the present study (15 m) wave remain capable of generating dead matte areas (Vacchi *et al.* 2016), their constant erosion activity on the seagrass meadow possibly leading to SCs.

The mechanic influence of current speed results in part from the granulometric characteristics of sediment grains. Sediments of sand patches originate mainly from the erosion of the vertical edge (Cinelli *et al.* 1995) as well as from the pieces of collapsed living matte (De Falco *et al.* 2000). At the colonized side of SCs, more plagiotropic shoots are found in this zone of sediments accretion. From the eroded side to the colonized one, the grain size is increasing causing appearance of coarse sediments between plagiotropic shoots (Fig. 23a-b). Within the surrounding *P. oceanica* meadow, the canopy acts as a sink of particles and reduces flow velocity (Gacia *et al.* 1999). Under the relatively low bottom water motion of the studied area, the surrounding meadow has a stabilization influence on nearby SCs' sediments (Stratigaki *et al.* 2011, Manca *et al.* 2012).

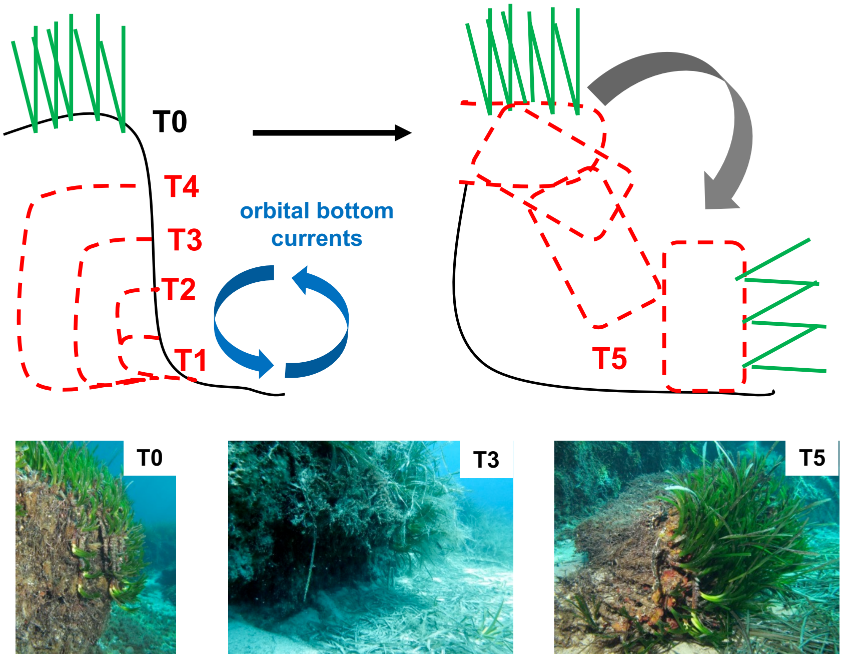


***Figure 27**: Temporal evolution of the vertical edge on the eroded side. T0: sheer edge, T1 to T4: erosion of edge bottom, T5: collapsing of the meadow overhang (photos: A. Abadie).*

Finally, due to the parallel and equivalent dynamic of their eroded and colonized sides, the five studied SCs progress simultaneously toward the coastline. Their speed progression probably depends of the weather conditions (storms, wind direction and speed that force currents) but may also be influenced by the meadow structure (*e.g.* density, matte compactness on the cliff edge, sediment retention). Considering a mean speed movement of 10 $cm.a^{-1}$ and their landward distance, we predict that the studied SCs will reach the coast within 500-600 years.

Conclusion

The spatial dynamic of *P. oceanica* is a process extending over centuries (Meinesz & Lefèvre 1984, Boudouresque *et al.* 2009, Vermaat 2009). But the exceedingly slowness of this process complicates the direct measurement of the progression of sand patches and seagrass meadow. Nevertheless, this study has shown evidence of recolonization of natural sand patches by *P. oceanica* shoots. We have described for the first time the progression of SCs toward the coastline, highlighting an enhanced shoot recruitment and rhizome growth rate on their colonized side. At the opposite regressive side, a high shoot removal rate balances colonization process, creating vertical edges. This kind of structures have also been observed in other places around Corsica and the Mediterranean Sea from the upper to the lower limit of the meadow (Borg *et al.* 2009, Pedersen *et al.* 2011). Results obtained with a simple and cost-effective method proved to be able to provide precise data on the spatial evolution of natural patches within *P. oceanica* seascapes.

Article 2: Sediment biogeochemistry in two edge types of *Posidonia oceanica* seagrass meadows and its influence on colonization processes

Abstract

Seagrass meadows can be assimilated to seascape matrixes encompassing a mosaic of natural and anthropogenic patches. Natural patches within the Mediterranean *Posidonia oceanica* meadows show a structural particularity which consist in a duality of their edge types. One edge is eroded by bottom currents while the adjacent meadow colonizes the bare sediments. This study aims to investigate the dynamic of these two edges through the investigation of the biogeochemistry (pH, total alkalinity, dissolved inorganic carbon, CO_2, CH_4, N_2O, H_2S, dissolved inorganic nitrogen, PO_4^{3-}) within vegetated and unvegetated sediments. These observations are compared with the adjacent meadow in order to have a better understanding of colonization processes and their influence on patch characteristics. Our results show that the *P. oceanica* matrix show strong differences with the vegetated edges of sand patches especially with regards to nutrients availability. A clear disparity also occurs between the eroded and colonized edge with both a seasonal and bathymetrical variation of leaf biomass. Most important contrasts during this study were assessed in June, suggesting that the warmest period of the year is the more suitable for sampling to highlight disparate characteristics in temperate seagrass meadows. At the scale of the seascape, these findings put into light the importance of biogeochemical processes in the dynamic of natural patch edges and thus of their size and shape.

Keywords: edge effect; seascape; colonization; biogeochemistry; patchiness; seagrass meadows; sediments

1. Introduction

Among marine ecosystems, seagrass meadows are described (den Hartog 1970) and recognized as playing a dominant role by acting as a carbon sink (Fourqurean *et al.* 2012), creating a nursery for many commercial species (Beck *et al.* 2001) and sheltering coasts against erosion (Ondiviela *et al.* 2014). Over the last three decades, a new kind of approach, deriving from the terrestrial field, has emerged to investigate the functioning and evolution of seagrass ecosystems: the “seascape ecology” also called “marine space ecology” (Robbins & Bell 1994, Li & Mander 2009). The basis of this scientific discipline consists in studying the structure of the seascape, linking it with its function, *i.e.* its influence on the distribution of other organisms (Turner 1989). The structure of a seascape can be defined as the varying arrangements of biotic structures, with the resulting mosaic of marine habitat patches encompassed within a matrix (Robbins & Bell 1994).

The extensive meadows formed by the Mediterranean seagrass *Posidonia oceanica* (L.) Delile are particularly suitable for seascape studies due to the capacity of the plant to build complex structures. They provide a highly heterogeneous habitat sheltering many important functional species, such as the sea urchin *Paracentrotus lividus* and the salema *Sarpa salpa* (Borg *et al.* 2006, Prado *et al.* 2009, Gera *et al.* 2013). In this way, a *P. oceanica* seascape corresponds to a set of the different habitats, *i.e.* types of patch, of natural and anthropogenic origin included in a meadow matrix (Abadie *et al.* 2015b). Natural patch types encompass a particular structure called “intermatte” or “sand corridor” (Fig. 28) generated by bottom currents stemming from wave energy, its boundaries being referred as “edges” (Molinier & Picard 1952, Vacchi *et al.* 2016). Edges (or ecotones) in seascapes, and in a wider viewpoint in landscapes, are considered as interface location of two types of habitats (Forman 1995, Boström *et al.* 2006a). They play an important functional role, their structural characteristics conditioning organisms’ distribution (Angelstam 1992).

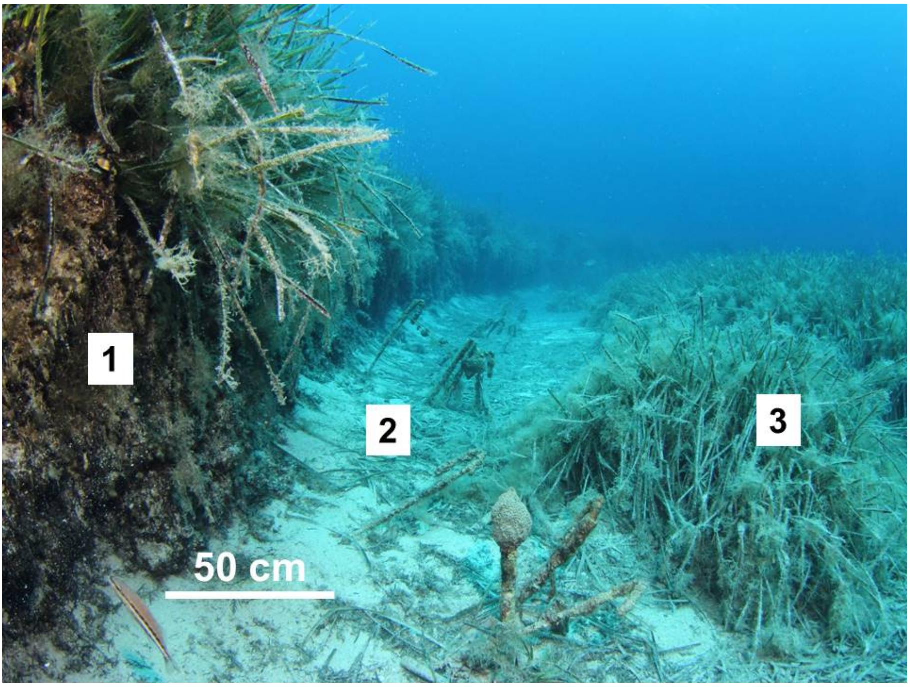


***Figure 28**: Underwater photograph of a sand corridor within a* Posidonia oceanica *meadow in Calvi Bay (42° 34.823' N 8° 43.433' E, Corsica, France) at 15 m depth. 1) eroded vertical edge; 2) Sandy bottom; 3) colonized edge (photo: A. Abadie).*

When observing *P. oceanica* meadows surrounding sand corridors, two edges with contrasted dynamics are clearly observed (Fig. 28). On the one hand, a side is eroded by bottom currents forming a vertical edge (sediments, rhizomes and roots), when on the other hand the meadow recolonizes the bare sandy bottom with plagiotropic (horizontal) rhizomes (Gobert *et al.* accepted). Current speeds up to 13 cm.s^{-1} and 8 cm.s^{-1} were respectively observed at 15 and 20 m depth on this kind of patch (Gobert *et al.* accepted), far under 40 cm.s^{-1}, the speed at which *P. oceanica* survival is compromised in shallow areas (Infantes *et al.* 2009).

Our working hypothesis is that from this apparent structural duality between the two edges, a contrast of the sediment biogeochemistry should ensue. Indeed, *P. oceanica* is an autogenic ecosystemic engineer (Lawton 1994) able to modify the substrate through the release and uptake of chemical compounds (Marbà *et al.* 2006). In this way, *P. oceanica* meadows influence the carbonate balance by dissolving or producing $CaCO_3$, thus modifying the uptake or release of CO_2 (Barrón *et al.* 2006). $CaCO_3$ dissolution in *P. oceanica* meadows could be driven by H_2S oxidation with O_2 (Barrón *et al.* 2006) related to sulfate reduction that occurs within the anoxic layer of the sediment (Holmer *et al.* 2003, Holmer *et al.* 2004), and diffusion of O_2 or the hypothetical release of O_2 by the roots (Ku *et al.* 1999, Burdige & Zimmerman 2002). Although these processes have been studied within continuous *P. oceanica* beds and compared with unvegetated sediments (Holmer *et al.* 2003, Barrón *et al.* 2006, Holmer & Frederiksen 2007), no investigation taking into account their edge particularities exists to date.

Moreover, natural sandy patches are found all along the extent of *P. oceanica* meadows, *i.e.* from their lower limit (down to 40 m depth) to depths closer to the upper limit (10 m) (Clabaut *et al.* 2014). The same duality between eroded vertical edge and recolonization process occurs at all depth however patches display different sizes and shapes (Abadie *et al.* 2015b). This structural difference of the seascape is expected to derive from chemical processes (associated with the plant dynamic) linked with light availability and water temperature (Elkalay *et al.* 2003, Díaz-Almela *et al.* 2009, Pedersen *et al.* 2011). Furthermore, *P. oceanica* seascapes morphology is influenced by water movement even at the level of the lower limit, although their speed, and thus influence, decreases with the depth (Vacchi *et al.* 2012, Vacchi *et al.* 2016).

On the basis of the structural disparities observed on natural sandy patches, we aimed to study the potential contrast of chemical processes that occur at the edge of seagrass meadows at different depths (10, 15 and 20 m). More specifically, we aim to answer four questions:

- Is there a distinct sediment biogeochemical signature between a continuous *P. oceanica* meadow (the matrix) and its edges surrounding natural sandy patches?
- Do the two types of edge differ in term of sediment biogeochemistry and plant biomass (eroded vertical edge *versus* colonized edge)?
- Is there seasonality in differences in (1) and (2)?
- Do chemical processes in sediments differ with depth, and by extension the patch type?

On the basis of these four questions, this work intends to prospect the potential influence of the sediments biogeochemistry dynamic on the structural evolution of *P. oceanica* seascapes.

2. Material and methods

2.1. Study site and *in situ* sampling

The study took place in Calvi Bay (Corsica, France) near the STARESO research station along the Punta Revellata (42° 34.823' N 8° 43.433' E; Fig. 29a). Six sites in three areas at 10, 15 and 20 m depth encompassing a natural sandy patch (P10, 15, 20) and a continuous meadow (C10, 15, 20) were considered (Fig. 29b). At each site, sediment pore water was sampled by scuba diving during the year 2015 in February, June and October. The sampling was carried out at 5 and 10 cm using 60 ml syringes according to the method of Gobert *et al.* (2006b). On sandy patches, sampling was carried out at both eroded and colonized edges, with a special focus on the closest collection to the meadow/bare sediment interface (Fig. 29c). Water samples were directly stored or treated according to the chemical analyses required. Seawater temperature was measured during the sampling in February, and then every 10 minutes from April to December 2015 (Onset® HOBO® Data Loggers UA-002-64 placed at 10, 15 and 20 m depth).

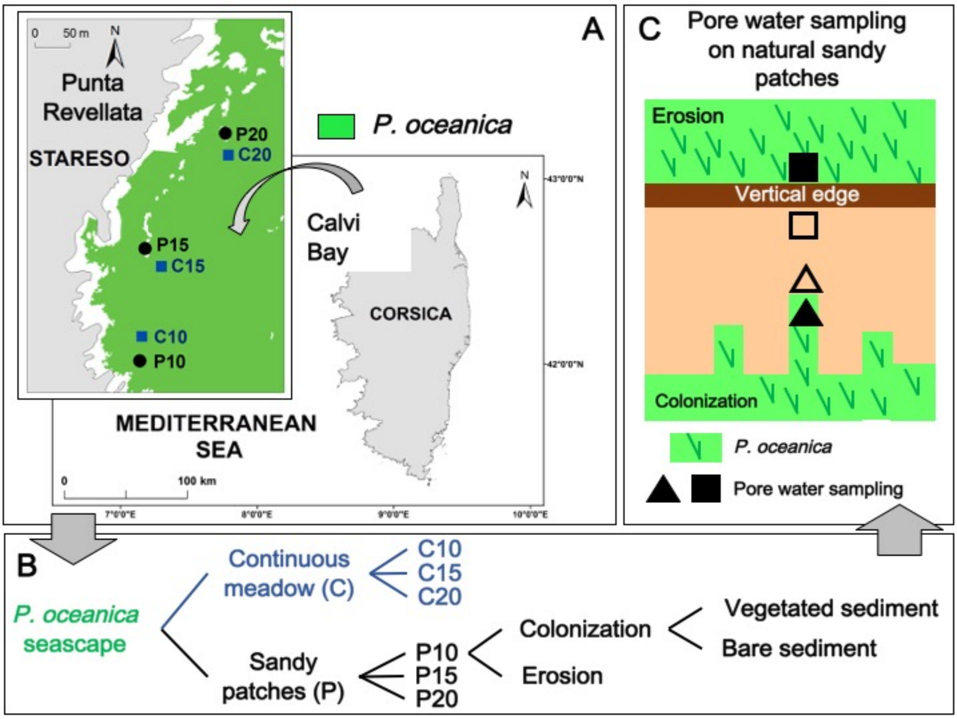


***Figure 29**: a) Map of the study site in Calvi Bay at Punta Revellata (Corsica, France); b) sampling strategy; c) vertical schematic representation of the pore water sampling on natural sandy patches. PX = Sandy patch at depth X; CX = Continuous meadow at depth X.*

2.2. Chemical analyses

Sediment pore water chemistry was investigated through measurements of pH, total alkalinity (TA), carbon dioxide partial pressure (pCO_2), hydrogen sulfur (H_2S), oxygen (O_2), methane (CH_4), nitrous oxide (N_2O) and inorganic nutrients (NO_2^-, NO_3^-, NH_4^+ and PO_4^{3-}). After sampling, syringes were stored in shadow and kept in an icebox at a low temperature for O_2 and H_2S assessment. 30 ml of their content was placed in serum bottles with 50 µl of mercury chloride ($HgCl_2$) to stop biochemical processes for later pCO_2, Ch_4 and N_2O analyses and hermetically crimped with butyl stoppers and aluminium caps.

At the laboratory, pH was immediately measured using a Metrohm™ 6.0202.100 electrode connected to a Metrohm™ 713 pH Meter and temperature probe Metrohm™ Pt 100. The pH electrode was calibrated on the total hydrogen ion concentration scale, using 2-amino- 2-hydroxymethyl-1,3-propanediol (TRIS) and 2-amino-pyridine (AMP) buffers prepared at a salinity of 38 (Dickson 1993). pH was re-calculated at in-situ temperature with TA data and seawater temperature using the CO2sys software developed by Lewis and Wallace (1998). TA (eq. 1) was measured with the open-cell titration technic, *i.e.* HCl 0.1M on 100 mL filtered (PES syringe filter 0.2 µm) seawater samples (Gran 1952). DIC (eq. 2) was computed from pCO_2 (see hereafter) and TA with CO2sys using the carbonic acid dissociation constants of Mehrbach *et al.* (1973) refitted by Dickson and Millero (1987).

$$TA = [HCO_3^-]+2[CO_3^{2-}]+[B(OH)_4^-]+[\text{minor ions}]+[OH^-]-[H^+] \quad \text{(equation 1)}$$

$$DIC = [CO_2] + [HCO_3^-] + [CO_3^{2-}] \quad \text{(equation 2)}$$

O_2 presence/absence was checked using a iodine titration with thiosulfate according to the method of Winkler (1888) with an automatized system for small sampling volumes (Carpenter 1965, Strickland & Parsons 1972) adapted by R. Biondo (Laboratory of Oceanology - University of Liège). H_2S concentration was measured with a silver/sulfide ISM-146 FTH 25-XS electrode, coupled with a Sulfide Anti-Oxydant Buffer (SAOB) solution given the protocol of Abadie *et al.* (2016) adapted from Brooks (2001).

pCO_2, CH_4, and N_2O concentrations were measured by headspace equilibration method and gas chromatography (GC) (Weiss 1981) based on protocols described by Borges *et al.* (2015), using a flame ionization detector with a methanizer and electron capture detector (SRI 8610C) calibrated with mixtures of CH_4:CO_2:N_2O:N_2 (Air Liquide Belgium) of 404, 1018 and 3961 ppm CO_2, 1, 10 and 30 ppm CH_4 and 0.2, 2.0 and 6.0 ppm N_2O.

Phosphate (PO_4^{3-}), ammonium (NH_4^+) and Nitrite (NO_2^-)/Nitrate (NO_3^-) concentrations were measured by using a SKALAR auto-analyzer following the method of Aminot and Kérouel (2007) adapted for oligotrophic samples (Laboratory of Oceanology-University of Liège).

2.3. Leaf biomass assessment

Meadow density was measured at each station by scuba diving with a 25 cm x 40 cm quadrat (n=10). In parallel, leaves were sampled (n = 20) for biometry and biomass assessment according to the non-destructive method (de los Santos *et al.* 2016). In laboratory, leaf biometry was performed (Giraud 1979) and epiphytes were stripped from the leaves with a razor blade (Dauby & Poulicek 1995). Leaves were dried in an oven at 60 °C during four days and then weighted.

2.4. Statistical analysis

Statistical analyses were performed under the R 3.0.2 software using the FactoMineR package. Normality of leaf biomass values was checked using a Shapiro-Wilk test. Stations were then statically tested two by two (continuous *vs* colonization *vs* erosion) for each depth (10 m, 15 m and 20 m) with one-way ANOVA (after checking their homoscedasticity with a Fisher test) for Gaussian data, and with a Kruskal Wallis test for non-parametric ones. One-way ANOVAs were followed by a Tukey post-hoc test and Kruskal Wallis tests by a Dunns test.

At each depth, a Principal Component Analysis (PCA) was realized by computing pH, TA, DIC, pCO_2, leaf biomass as well as concentrations of CH_4, N_2O, H_2S, NO_2^-, NO_3^-, NH_4^+ and PO_4^{3-}. The analysis was performed using a covariance matrix. Stations (individuals) were separated according to the sampling month.

3. Results

3.1. Physico-chemical features of natural sand corridors

The seawater temperature ranged from 13.9 °C in April at 20 m to 28.1 in July at 10 m depth. Temperature showed clear seasonal variations (Fig. 30) and thermal stratification occurred between May and October as shown by differences in temperature between 10 and 20 m.

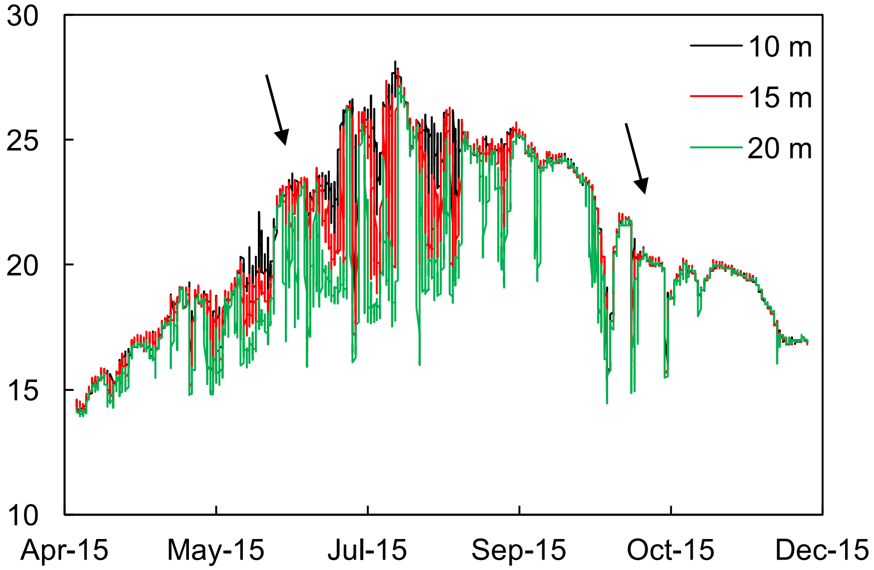


***Figure 30**: Seawater temperature at 10 (black), 15 (red) and 20 m (green) at sampling sites from April to December 2015. Black arrows indicate the in situ sampling date.*

Taking into account the theoretical evolution to attain the highest TA and DIC values according to the biogeochemical processes that can control these variables: aerobic respiration (aerobic resp.), sulfate reduction (SO_4 red.) and calcium carbonate dissolution ($CaCO_3$ dissol.), TA and DIC were mainly driven by the process of sulfato reduction in February, June and October at all station and at 15 et 20m depth (Fig. 31b, c). At 10 m depth (Fig. 31a) this observation differed at the level of the colonized edge where in June and October aerobic respiration and $CaCO_3$ dissolution had also an influence on TA and DIC concentrations.

H_2S concentrations were the lowest in February (Fig. 31d, e, f). In June, high concentrations were found within the continuous meadow at 10 and 20 m depth (respectively 10.3 and 10.0 µM), as well as at the colonized edge at 20 m depth both inside the bare sediments and within the meadow (respectively 28.8 and 68.8 µM). In October, highest concentrations were found within the continuous meadow (Fig. 31d, e) at 10 and 15 m depth (respectively 43.8 and 27.0 µM).

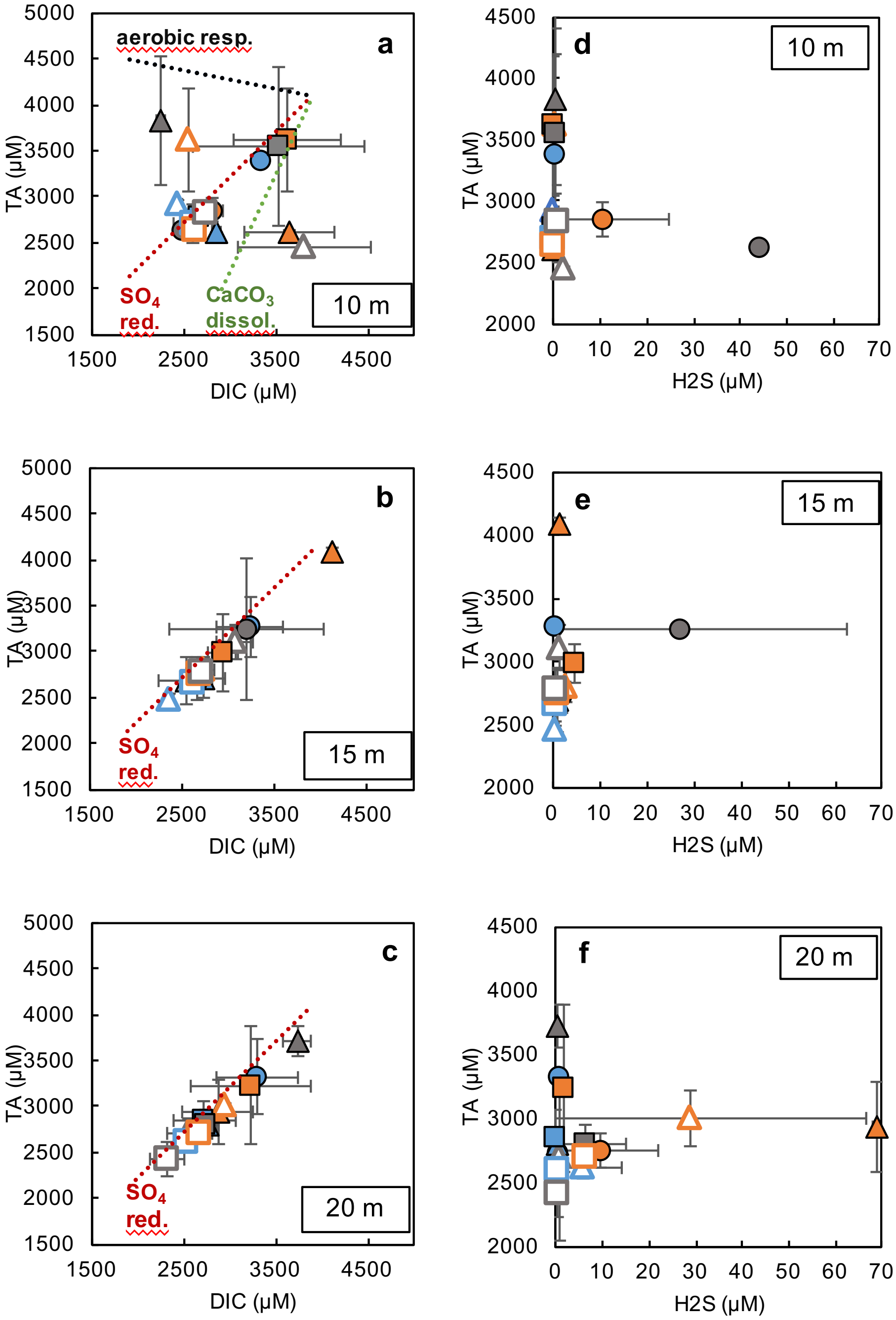

a
aerobic resp.
SO_4 red.
$CaCO_3$ dissol.
10 m
TA (µM)
DIC (µM)
5000
4500
4000
3500
3000
2500
2000
1500
1500
2500
3500
4500
b
SO_4 red.
15 m
c
SO_4 red.
20 m
d
10 m
e
15 m
f
20 m
H2S (µM)
0
10
20
30
40
50
60
70

Figure 31*: Total alkalinity (TA) as function of the dissolved inorganic carbon (DIC) and the hydrogen sulfur (H_2S) at 10, 15 and 20 m depth. Dotted lines indicate the theoretical evolution to attain the highest TA and DIC values according to the biogeochemical processes that can control these variables: aerobic respiration (aerobic resp.), sulfate reduction (SO_4 red.) and calcium carbonate dissolution ($CaCO_3$ dissol.). Vertical and horizontal bars indicate SD. Blue: February; orange: June; grey: October. Circle: continuous meadow; triangle: colonization vegetated, empty triangle: colonization bare sediments; square: erosion vegetated, empty square: erosion unvegetated.*

Values of pCO_2 were low (around 2,000 ppm) all along the three months sampled (Fig. 32). A different pattern was observed at the vegetated eroded edge and at the vegetated colonized one. Within the vegetated eroded edge, pCO_2 increased in June (3,852 ppm) and remained high in October (3,369 ppm) at 10 m depth (Fig. 32). On the vegetated colonized edge, pCO_2 increased in June at 10 and 15 m depth (respectively 4,093 and 4,462 ppm) and then decreased in October. A reverse pattern was observed at this edge at 20 m (Fig. 32) with a highest value in October (4,030 ppm). CH_4 concentrations were low (under 500 nM, Fig. 2-11), except at 10 m depth at the vegetated colonized edge (691 nM) as well as at 20 m at the colonized and eroded unvegetated edge (respectively 1,487 and 506 nM). N_2O values were found to be low at each depth and all sampling stations (Fig. 32), and unlike CO2 and CH4, the N2O were below saturation (maximum 8.88 nM in February). Concentrations of inorganic nutrients increased with depth, generally with higher values in June (Table 2-3). NO_2^- + NO_3^- concentrations were low (under 1 µM) at each station all along the year, except at the unvegetated colonized edge at 10 m depth in February and June (respectively 8.52 and 8.80 µM). Ammonium (NH_4^+) showed a different pattern with highest concentrations at 20 m depth in June at both vegetated and unvegetated colonized side (respectively 65.39 and 68.06 µM). This outline also occurred at 15 m depth in October for the same stations (Tab. 4). High NH_4^+ concentrations were also found in February at all depths at the unvegetated eroded edge. PO_4^{3-} concentrations were low (Tab. 4) with maximum values at 20 m at the vegetated colonized edge in February and June (respectively 3.49 and 4.61 µM).

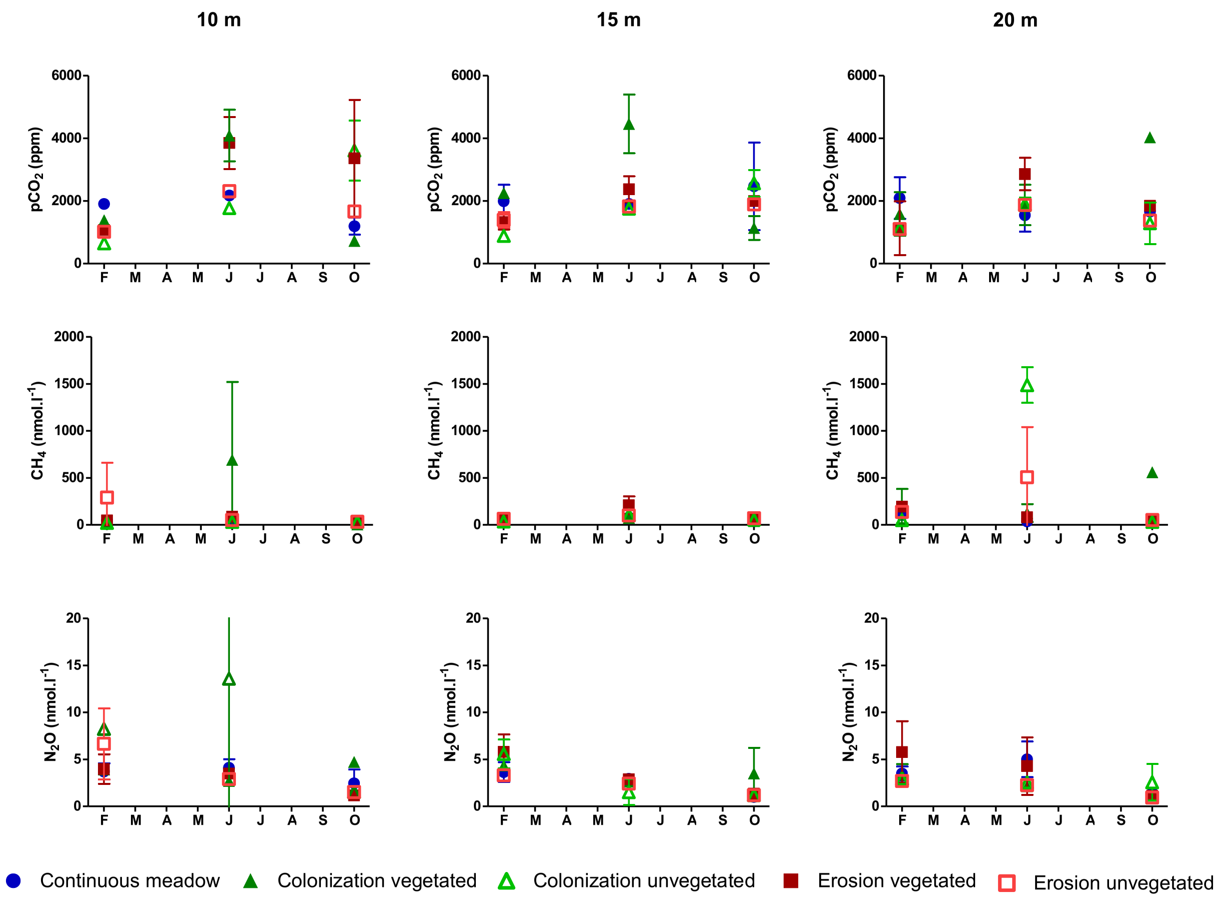


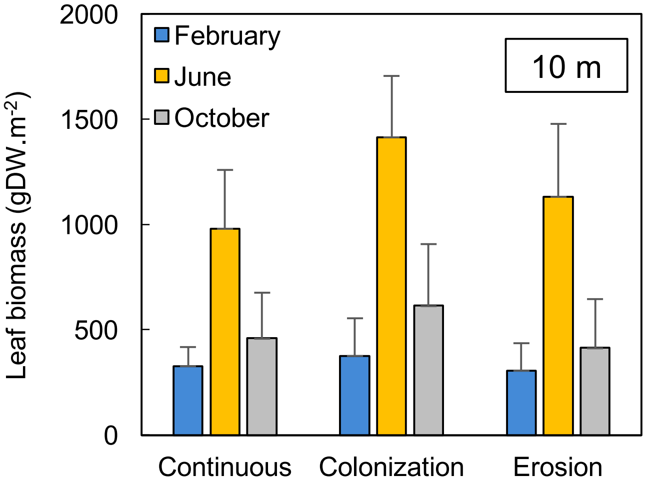
Figure 32: mean values of pCO_2, CH_4 and N_2O concentration at 10, 15, 20 m depth in sediments pore water. Vertical bars indicate SD.

Table 4: *Mean nutrients concentration ± SD at each station in February, June and October 2015. Cont.: continuous; Colo.: colonized edge; Ero: eroded edge.*

	$[NO_2^-] + [NO_3^-]$			$[NH_4^+]$			$[PO_4^{3-}]$		
	February	June	October	February	June	October	February	June	October
10 m									
Cont. meadow	0.86 ± 0.86	0.64 ± 0.62	0.08 ± 0.07	1.63 ± 0.63	1.70 ± 1.53	2.64 ± 3.04	0.69 ± 0.08	0.57 ± 0.39	1.94 ± 2.06
Colo. vegetated	2.91 ± 0.04	0.90 ± 0.21	2.25 ± 2.04	1.85 ± 0.49	2.22 ± 0.98	1.33 ± 0.62	0.29 ± 0.08	0.94 ± 0.06	0.20 ± 0.03
Colo. unvegetated	8.52 ± 0.62	8.80 ± 0.42	0.19 ± 0.04	0.32 ± 0.1	0.79 ± 0.35	1.61 ± 0.11	0.15 ± 0.01	0.36 ± 0.05	0.45 ± 0.13
Ero. vegetated	0.98 ± 0.46	0.67 ± 0.06	0.25 ± 0.12	1.21 ± 0.95	4.45 ± 0.46	1.38 ± 1.17	0.46 ± 0.06	0.78 ± 0.37	0.27 ± 0.14
Ero. unvegetated	0.44 ± 0.15	0.09 ± 0.01	0.36 ± 0.26	20.78 ± 9.4	1.39 ± 0.78	4.74 ± 2.77	0.22 ± 0.04	0.26 ± 0.02	0.31 ± 0.04
15 m									
Cont. meadow	0.17 ± 0.08	0.30 ± 0.04	0.36 ± 0.06	0.72 ± 0.28	8.61 ± 7.67	8.91 ± 9.58	0.8 ± 0.04	0.74 ± 0.52	1.23 ± 0.76
Colo. vegetated	0.35 ± 0.32	0.19 ± 0.17	0.10 ± 0.02	20.04 ± 20.62	2.45 ± 1.29	10.62 ± 0.34	0.95 ± 0.13	1.52 ± 1.48	0.67 ± 0.19
Colo. unvegetated	0.91 ± 1.12	0.40 ± 0.13	0.49 ± 0.66	1.94 ± 1.8	1.78 ± 1.06	10.06 ± 4.59	0.62 ± 0.55	0.56 ± 0.18	1.89 ± 0.99
Ero. vegetated	1.27 ± 0.02	0.36 ± 0.26	0.78 ± 0.49	1.03 ± 0.4	9.13 ± 7.98	2.19 ± 2.59	0.45 ± 0.08	0.86 ± 0.62	0.27 ± 0.21
Ero. unvegetated	0.66 ± 0.68	0.34 ± 0.33	0.18 ± 0.06	7.64 ± 0.98	7.35 ± 0.81	14.19 ± 0.44	1.10 ± 0.84	0.73 ± 0.18	0.65 ± 0.1
20 m									
Cont. meadow	1.22 ± 1.12	0.58 ± 0.61	0.47 ± 0.21	3.25 ± 0.5	10.28 ± 6.26	16.74 ± 7.61	0.61 ± 0.22	1.59 ± 0.11	2.09 ± 0.49
Colo. vegetated	0.32 ± 0.2	0.13 ± 0.11	0.27 ± 0.21	10.7 ± 8.57	65.39 ± 21.71	11.76 ± 9.07	3.49 ± 1.17	4.61 ± 1.22	1.54 ± 0.63
Colo. unvegetated	0.62 ± 0.48	0.19 ± 0.07	0.24 ± 0.17	9.20 ± 12.26	68.06 ± 44.28	5.17 ± 5.81	1.31 ± 1.65	3.02 ± 2.44	1.39 ± 0.71
Ero. vegetated	0.21 ± 0.06	0.41 ± 0.08	0.25 ± 0.06	6.77 ± 1.99	21.91 ± 6.95	5.38 ± 1.51	1.53 ± 0.01	2.22 ± 0.63	0.94 ± 0.07
Ero. unvegetated	0.13 ± 0.01	0.08 ± 0.05	0.29 ± 0.23	15.45 ± 4.3	7.01 ± 1.48	4.29 ± 2.49	1.56 ± 0.26	1.58 ± 0.04	0.97 ± 0.3

3.2. Leaf biomass

Leaf biomass reached its highest value (1 415 $gDW.m^{-2}$) in June at 10 m at the colonized edge, and its lowest value (79 $gDW.m^{-2}$) in February at the eroded edge (Fig. 33). At 10 m depth, significant differences were found between the colonized edge and both the continuous meadow and the eroded edge in June (Kruskal Wallis: $p = 0.0279$; KW-statistic = 18.67), and between colonized and eroded edge in October (Kruskal Wallis: $p < 0.0001$; KW-statistic = 7.16). At 15 m a single significant difference was observed between colonized and eroded edge in February (One-way ANOVA: $p = 0.0013$; $F = 7.52$). Finally, at 20 m depth, significant differences were found between the eroded edge and both the continuous meadow and the colonized edge in February (One-way ANOVA: $p = 0.0002$; $F = 10.09$), and in June (Kruskal Wallis: $p < 0.0001$; KW-statistic = 24.81).



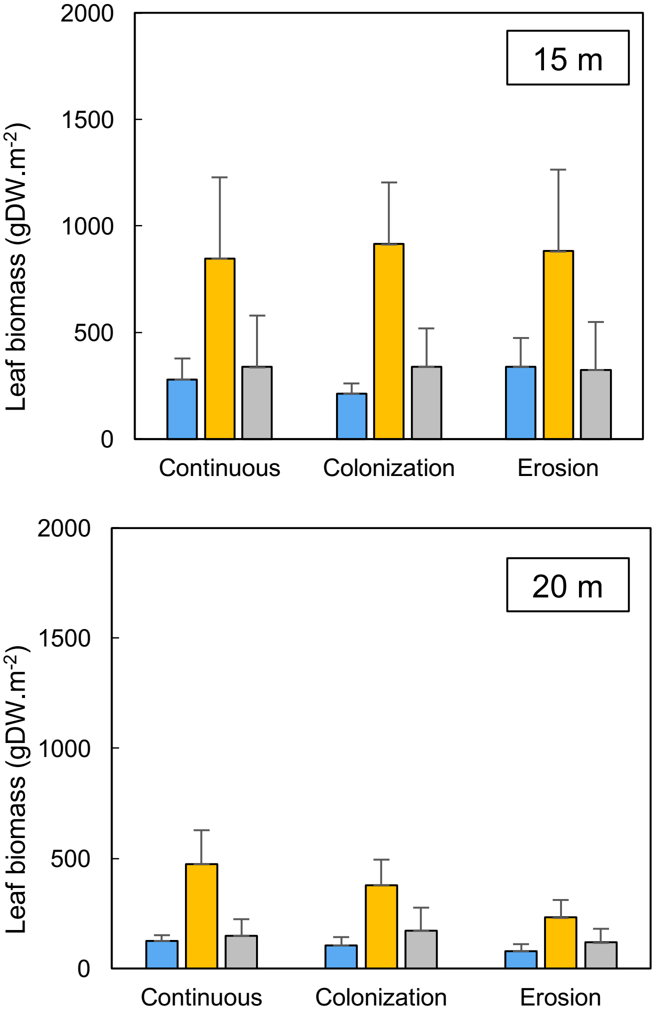


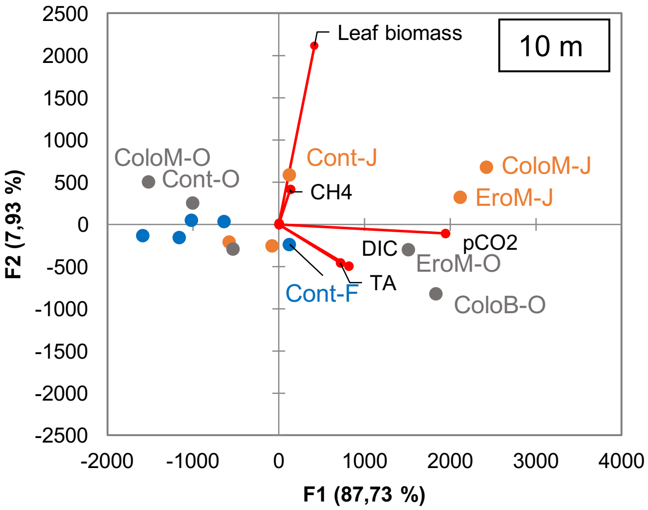
***Figure 33**: Leaf biomass at 10, 15 and 20 m depth in the continuous meadow, the colonized border and the eroded edge in February (blue), June (orange) and October (grey).*

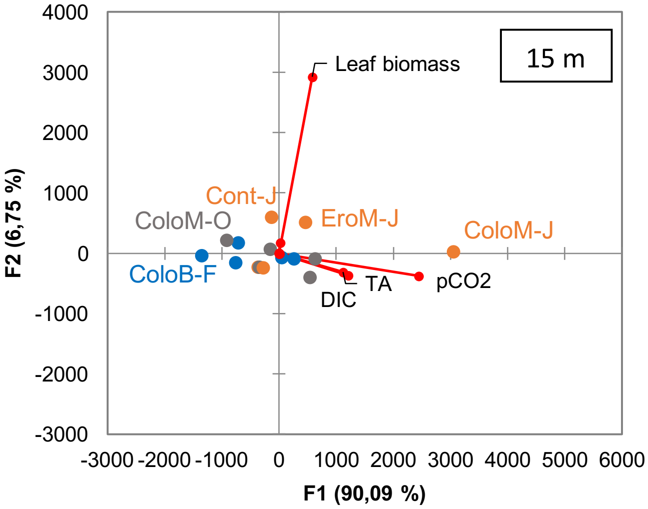
3.3. Edge characteristics

The percentage of variation expressed by the axis of the bi-dimensional representation for each PCA is around 95 % with a major contribution to the distribution of individuals of pCO_2 at each depth ranging from 66 to

73 % (Fig. 34). At 10 and 15 m depth, leaf biomass contributed up to 95 % and at 20 m CH_4 contributes in the same range.

At all depths no segregation pattern is found in February. At 10 m depth in June, edge meadows (ColoM-J and EroM-J) were separated from the unvegetated and continuous stations (Fig. 34). This pattern is also observed in October except for the continuous meadow (Cont-O) which is grouped with the vegetated colonized edge (ColoM-O). A different arrangement was visible at 15 m depth with a single station segregated in June at the vegetated colonized edge (ColoM-J, Fig. 34). Finally, at 20 m depth edge meadows (ColoM-J and EroM-J) were separated from the unvegetated and continuous stations in June, while in October the vegetated colonized edge (ColoM-O) alone is segregated (Fig. 34).





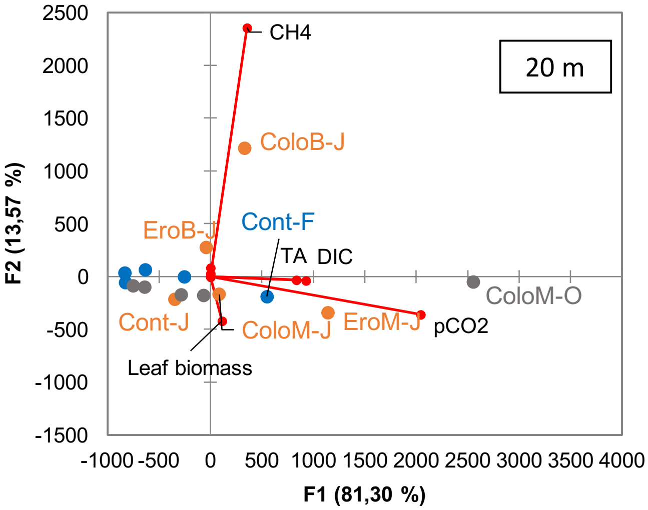


Figure 34*: Biplot of the PCA analysis at 10, 15 and 20 m for each station in February (F, blue), June (J, orange) and October (O, grey). The percentage reflects the proportion of variance expressed by each axe. Cont: continuous meadow; ColoM: colonization meadow; ColoB: colonization bare sediment; EroM: erosion meadow; EroB: erosion bare sediment. Red lines represent variables contributions. Only variables with high percentage of contribution are labeled.*

4. Discussion

By investigating biogeochemical features of natural sandy patches within *Posidonia oceanica* seascapes, our study highlights the seasonal and bathymetrical variability of their dynamic, as well as a contrast between the two edge types. These results allow us to provide some response elements to our four interrogations on patch chemistry dynamic.

4.1. *P. oceanica* matrix *versus* patch edges

Our results show that sediment characteristics of continuous *P. oceanica* meadows adjacent to natural sandy patches, *i.e.* the matrix, differed from those of unvegetated sediments of sand corridors (Fig. 34). This phenomenon was previously assessed in *P. oceanica* meadows at 7 m depth by Barrón *et al.* (2006), where a higher production and dissolution of $CaCO_3$ within vegetated sediments was assessed. In the present work, this report depends of the type of edge considered, eroded unvegetated edges showing less contrast with the continuous meadow than colonized ones. In this way, at a comparable depth (10 m), TA was found to have seasonally higher values within the continuous meadow than within unvegetated colonized sediments, revealing an enhanced $CaCO_3$ dissolution (Fig. 31). This contrast was not observed at the eroded unvegetated edge which showed a pattern similar with the continuous meadow. A stronger contrast between the matrix and the two unvegetated edges is observed when looking at the nutrients results with higher concentrations of NH_4^+ within unvegetated sediments than in continuous meadow (Tab. 4). These higher concentrations in inorganic nutrients suggest that the degradation of litter (Mateo & Romero 1997, Gacia *et al.* 2002) and collapsed meadow overhangs from the vertical edge (Pedersen *et al.* 2011) can be incorporated within sediments through the process of ammonification (López *et al.* 1998, Romero *et al.* 2006). This recycled nutrient pool provides suitable conditions for the development and beginning of the colonization process of *P. oceanica*.

The *P. oceanica* matrix also showed heterogeneous biogeochemical differences with the two different vegetated patch edges. Once again, differences observed on vegetated sediments were more visible between the continuous meadow and the colonized edge. Moreover, the vegetated colonized edge showed contrasted biogeochemical characteristics with regard to the eroded one (Fig. 34). Like mentioned above for unvegetated edges, this difference was mainly highlighted by the distribution of inorganic nutrients. Through an increase of the dead leaf trapping and other organic debris, the canopy at the colonized edge allows the recycling of nutrients (de Boer 2007) and thus colonization by the meadow of the sand corridor. This dual assessment is supported by the leaf biomass which is always equal or higher at the colonized edge than at the eroded edge (Fig. 33). This pattern, linked with a similar or higher DIC (Fig. 31) and pCO_2 (Fig. 32), suggests better conditions within the sediments that enhance photosynthetic efficiency for colonization processes of the bare sand (Invers *et al.* 1997). Conversely, by colonizing bare substrates, *P. oceanica* also modifies biogeochemical characteristics of the sediments (Marbà *et al.* 2006).

4.2. Influence of seasonality

Although several general disparities between eroded and colonized edge are outlined, the biogeochemical dynamic within temperate seagrass sediments must be seasonally investigated (Marba *et al.* 1996, Barrón *et al.* 2006). Results of the present work, in agreement with Canals and Ballesteros (1997) and Barrón *et al.* (2006), suggest that in February $CaCO_3$ dissolution was mainly responsible of TA increasing (Fig. 31) through the temperature decreasing (Fig. 30) which reduces $CaCO_3$ saturation and enhance its dissolution. In June, the increase of TA (Fig. 31) was mainly driven by sulfato-reduction (Holmer *et al.* 2003, Holmer *et al.* 2004). From February to October a general trend in the diminution of N_2O was observed at all stations reflecting an increasing of denitrification from the inorganic nutrient pool through the year (Fig. 32). This process is classically found to be higher in seagrass meadows than in unvegetated sediments (Caffrey & Kemp 1990, Romero *et al.* 2006, Eyre *et al.* 2011).

When analyzing seasonally several variables of the sediment chemistry, it appears that main contrasts between continuous meadow, vegetated eroded and colonized edges were greater in June, especially for the colonized stations (Fig. 34). Our results thus highlight the potential of the summer period for sampling and assessment of chemical processes within a seagrass under colonization processes (Fig. 35). This statement is particularly observed for H_2S measurements (Fig. 31) with higher concentrations recorded during the seasonal warm period (Calleja *et al.* 2007, García-Martínez *et al.* 2009, García *et al.* 2012).

4.3. Bathymetrical display of chemical characteristics

In parallel with seasonal variations, strong bathymetrical disparities were also observed when looking at the duality between eroded and colonized vegetated edges. Higher differences were found at the lowest depth of this study (10 m) and decrease while depth increases (Fig. 8). These disparate features were mainly driven by the leaf biomass and the carbonate system properties. A depth gradient was clearly observable concerning the leaf biomass (Bay 1984, Buia *et al.* 1992) which was the highest at 10 m depth at the colonized edge, shows less variations between the continuous meadow and the two edges at 15 m, and finally is higher within the continuous adjacent meadow than the colonized and eroded edges at 20 m (Fig. 33). These results are not consistent with pore water nutrient concentrations measured in this study that increased with depth (Fig. 35). It is thus more probable that this difference in leaf biomass is ascribable to the diminution of light intensity and the photosynthetic activity of the plant at increasing depths (Alcoverro *et al.* 2001, Elkalay *et al.* 2003). These distinct physico-chemical and biotic particularities suggest that the different shapes of natural sand patches within *P. oceanica* seascapes, observed along a bathymetric gradient by Abadie *et al.* (2015b), were largely derived from biogeochemical characteristics of their vegetated edges. This statement seems particularly true for the colonized edge which appears to modify sediments chemical characteristics to enhance its development.

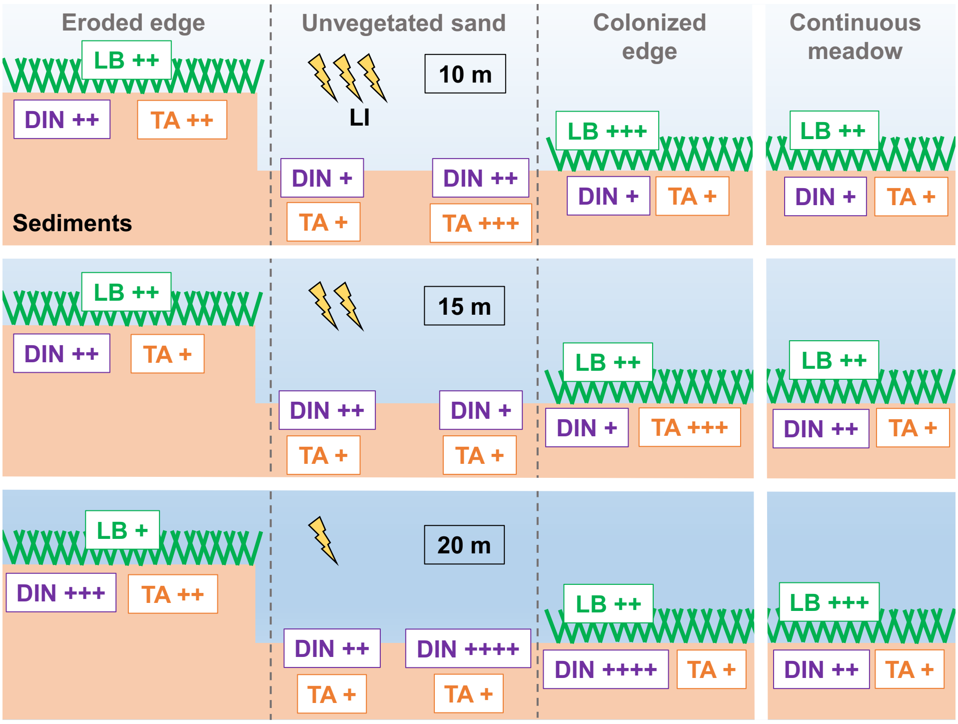


Figure 35*: Summary of leaf biomass (LB, green), dissolved inorganic nitrogen (DIN, purple) and total alkalinity (TA, orange) in June at 10, 15 and 20 m depth for each compartment investigated. LI: light intensity.*

Conclusion

Natural sand patches within *Posidonia oceanica* seascapes show contrasted biogeochemical features at different spatial and temporal scales. We are now able to answer to the four questions asked at the beginning of this paper:

1. Chemical and biotic features within the *P. oceanica* matrix are generally separated from those of the sand patch edges, particularly with the colonized one.
2. The two types of edges (eroded vertical edge *versus* colonized edge) are clearly distinct from one to another in biogeochemical viewpoint.
3. Seasonality plays an important role through temperature variations and their influence on $CaCO_3$ dissolution and the sulfato-reduction in sediments.
4. A depth gradient is observed at the level of the leaf biomass ascribable to the decrease of light intensity and presence of a thermocline during the warm period.

These particularities lead to bathymetrical variations in shapes and areas of the natural sand patches, due to seasonal variations of biogeochemical features within sediments that modify colonization dynamic. At a wide spatial scale, such processes drive the whole seascape patchiness and its long term evolution.

CHAPITRE 3

Mécanisme de la génération d’intermattes par l’ancrage

Article 3: From mechanical to chemical impact of anchoring in seagrasses: the premises of anthropogenic patch generation in *Posidonia oceanica* meadows[5]

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[5] Arnaud Abadie, Pierre Lejeune, Gérard Pergent, Sylvie Gobert (2016) From mechanical to chemical impact of anchoring in seagrasses: the premises of anthropogenic patch generation in Posidonia oceanica meadows. Marine Pollution Bulletin 109: 61-71

Abstract

Intensive anchoring of leisure boats in seagrass meadows leads to mechanical damages. This anthropogenic impact creates bare mat patches that are not easily recolonized by the plant. Several tools are used to study human impacts on the structure of seagrass meadows but they are not able to assess the indirect and long term implication of mechanical destruction. We chose to investigate the possible changes in the substrate chemistry given contrasted boat impacts. Our observations show that hydrogen sulfide concentrations remain high at 15 and 20 m depth (42.6 µM and 18.8 µM) several months after the highest period of anchoring during the summer. Moreover, our multidisciplinary study reveals that anchoring impacts of large boats at 15 and 20 m depth can potentially change the seascape structure. By taking into account both structural and chemical assessments, different managing strategies must be applied for coastal areas under anthropogenic pressures.

Keywords: Anchoring; Conservation; Seagrass; Seascape; Patch

1. Introduction

Over the last decades, marine ecosystems all around the world have been facing impacts of human activities at various extents (Halpern *et al.* 2008, Jorda *et al.* 2012). This statement is particularly observed in the Mediterranean Sea at the level of the coastal habitat formed by seagrass meadows (Grech *et al.* 2012, Giakoumi *et al.* 2013). Seagrasses play a major ecological and economical role at the level of the global ocean, covering an area reaching up to 500 000 km² (Costanza *et al.* 1997, Short *et al.* 2007, Cullen-Unsworth & Unsworth 2013). Thus, they constitute a nursery (Beck *et al.* 2001), a large carbon sink (Fourqurean *et al.* 2012), as well as a protection against coastal erosion by attenuating waves and currents (Ondiviela *et al.* 2014). Among Mediterranean seagrasses, *Posidonia oceanica* (L.) Delile is the most studied due to its major ecological and economical role (Ruíz *et al.* 2009, Vassallo *et al.* 2013). The meadows it forms are observed from the surface to 40 m depth and are subject to the impact of human activities like coastal development, eutrophication, trawling, fish farms and anchoring (Boudouresque *et al.* 2009, Giakoumi *et al.* 2015b).

Along the French Mediterranean coasts, the main substrate affected by boat anchoring appear to be *Posidonia oceanica* (Holon *et al.* 2015b). Anchoring inside *P. oceanica* meadows seems to have various degrees of impact according to its density, frequency, the type of anchor and the depth as well as the size of boats (Boudouresque *et al.* 2012). Thus, repeated anchoring of cruise ships, at depths greater than 15 m, causes large-scale degradations of the meadows (Ganteaume *et al.* 2005b, Abadie *et al.* 2015b). In the same way small units, less than 10 m long, can have an important impact at a local scale (Francour *et al.* 1999, Milazzo *et al.* 2004, Ceccherelli *et al.* 2007).

At the present day, studies mainly targeted the degradation of small boats at shallow depths *i.e.* less than 10 m. Few works treat the effects of larger pleasure ships anchoring which can measure more than 80 m long and have an important impact in confined areas (Abadie 2012). In order to assess their impact, several parameters are classically measured: the meadow density, the mat structure and the bottom cover (Boudouresque *et al.* 1995, Francour *et al.* 1999, Pergent-Martini *et al.* 2005). However, some of these metrics seem not relevant enough to assess the damages observed on *P. oceanica* meadows. More specifically, classical indicators can indicate a good state of conservation of the meadow with no anthropogenic impact when tracks of bare mat (Fig.36a) are clearly observed (Milazzo *et al.* 2004, Ganteaume *et al.* 2005a).

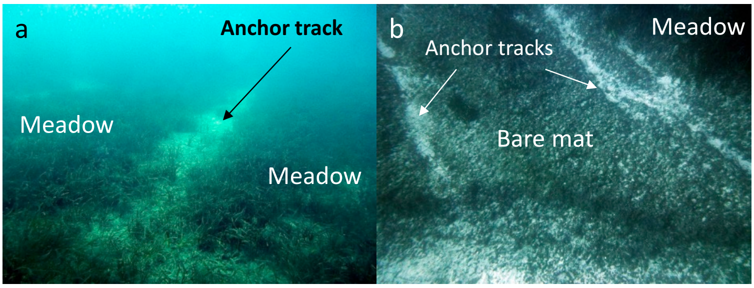


***Figure 36**: a) Anchoring track inside a* P. oceanica *meadow at 30 m depth in Calvi Bay (Corsica, France); b) Bare mat of* P. oceanica *generated by intensive anchoring at 18 m depth in Calvi Bay (Corsica, France) with furrows dug by large ships (photos: Arnaud Abadie).*

Intensive anchoring can lead to modifications of substrate qualities, passing from meadows to large bare mat areas in which anchoring tracks are visible (Fig. 36b). This phenomenon also induces a change in sediments nature going from carbonate sediments possibly oxygenized by the living plant to fine particles filling crevices inside decomposing organic tissues forming an anoxic bare mat (Mateo & Romero 1997). Such evolution of the substrate qualities can lead to the hydrogen sulfide (H_2S) intrusion in healthy meadows of the area, limiting the plant development (Holmer *et al.* 2003, Marbà *et al.* 2006). Thus, it has been observed that in carbonate sediments H_2S concentrations higher than 10 µM can cause a limitation of *P. oceanica* growth (Calleja *et al.* 2007).

This study aims to trigger a new way to approach the study of the anchoring impact on seagrass meadows by (1) testing the relevance of the classical structural tools (*e.g.* meadow density and cover, mat compactness); (2) exploring the relevance of chemical properties of the sediment as a new tool; and by extension, (3) assessing the impact of large leisure ships in a confined area; at last, (4) investigating the possible consequences for management and conservation of the areas concerned correlated with anchoring pressure.

2. Material and methods

This study was conducted in Alga Bay (8°43'52" E; 42°34'20" N), an area of 1 km² of intensive anchoring in Calvi Bay (Corsica, France), colonized by a *P. oceanica* meadow covering 0.78 km² (Fig. 37). This site encompasses a particular structure called "return river", a large sand patch where no seagrass meadow can grow, possibly due to strong bottom currents deriving from the surface ones reflected by the coast as described by Boudouresque and Meinesz (1982).

Six stations on two different sites in Calvi Bay were studied at three different depths, *i.e.* 10 m, 15 m and 20 m. Three stations were chosen as control in a continuous meadow with no traces of impact from human activities near the research facility of STARESO (C10, C15 and C20). Three stations were sampled at Alga Bay in areas of intensive anchoring (A10, A15 and A20) where it can generate anthropogenic patches.

2.1. Anchoring pressure assessment

A boat counting in Alga Bay was daily performed in the afternoon from May to October 2014 (the touristic period in Corsica) where anchoring frequency is the higher. Ships sizes were classified in three categories according to their length: <10 m; 10-20 m; and >20 m. In parallel, the substrate of anchoring (meadow, rock or sand) was assessed. Moreover, the spatial distribution of boats anchored in the area was investigated by using AIS positioning system of leisure boats (www.marinetraffic.com) from 2012 to 2014 as well as direct catches obtained between 2012 and 2014. These observations were inserted in the GIS software ArcGis® 10 coupled with a map of *P. oceanica* meadows in the area from previous studies (Michel *et al.* 2012, Jousseaume *et al.* 2013, Richir *et al.* 2015).

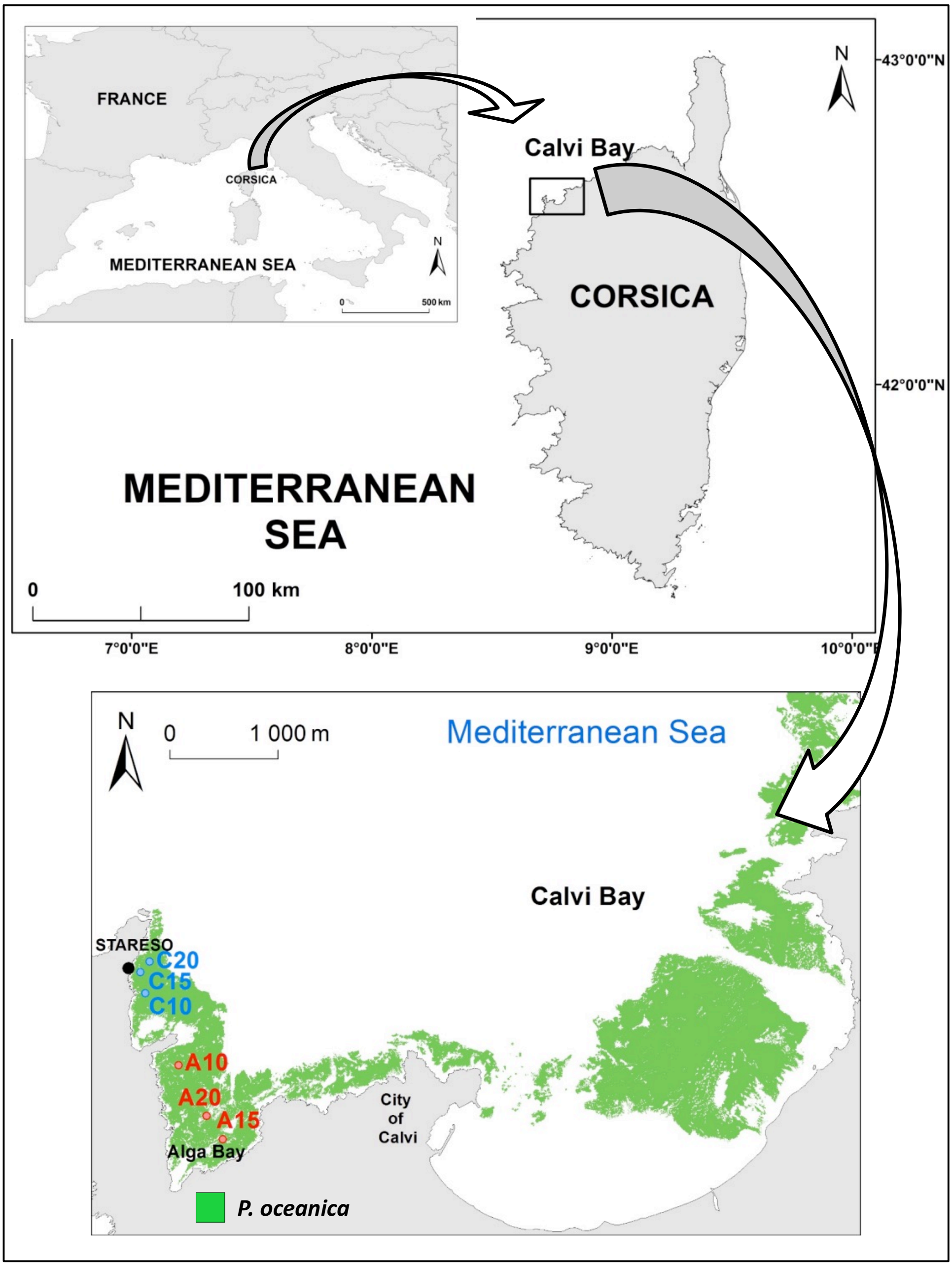


Figure 37*: Map of the study site. Green polygons in Calvi represent the mapping of* P. oceanica *meadows realized with data of 2010 (Abadie 2012).*

2.2. Meadow structure

The impact of anchoring on the *P. oceanica* meadows was assessed using six metrics commonly used in the study of its impact on seagrass meadows, *i.e.* the density, the proportion of orthotropic/plagiotropic rhizomes, the mat compactness, and the rhizomes baring. Ten replicates of the meadow density were randomly counted using quadrats of 25 cm x 40 cm and classified according to the grid of UNEP-MAP-RAC/SPA (2011). Assessment of the proportion of orthotropic/plagiotropic rhizomes was performed during density measures and interpreted thanks to the classes made by Charbonnel *et al.* (2000) (Tab. 5). Mat compactness was investigate given the method and classification of Francour *et al.* (1999) using a 1 m long rod and a 5 kg weight, repeating ten times the measure for each station (Tab. 5). Twenty replicates per station of the rhizomes baring, i.e. the distance between rhizome and substrate, were measured and classified according the protocol of Boudouresque *et al.* (1980a). Meadow cover was measured using a 30 cm x 30 cm quadrat hold at arm-length 3 m above the meadow (Gravez *et al.* 1995). Thirty replicates were performed for this measure and results were interpreted given the scale of Charbonnel *et al.* (2000) (Tab. 5). This measured was standardized by keeping the same observer for all measures and placing a depth gauge on the quadrat in order to avoid a distance variation from the vegetation. Finally, 20 longest standing leaves per station (corresponding to the canopy height) were measured in September after the touristic period).

2.3. Conservation Index (CI)

The Conservation Index (CI) was used as a reflection of damages in *P. oceanica* meadows visually observed by scuba diving. Triplicate transects were made to calculate the CI for each station according to the process of Moreno *et al.* (2001):

$$CI = L / (L + D)$$

where L (%) corresponds to the proportion of living *P. oceanica* and D (%) the percentage of bare mat. For intervals were calculated to assess the meadow's state of conservation on each station:

1. CI < (x_{mean} - 1/2 s)
2. CI from (x_{mean} – 1/2 s) to x_{mean}
3. CI from x_{mean} to (x_{mean} + 1/2 s)
4. CI > (x_{mean} + 1/2 s)

where mean (x_{mean}) and standard deviation (s) were calculated from all CI values of the study.

***Table 5**: Meadow structure parameters interpretation according to their value*

Parameter	Unit	Range	Interpretation	Classification reference
Meadow density	shoots.m^{-2}	Depends of depth	High Good Normal Moderate Bad	UNEP-MAP-RAC/SPA 2011
Proportion of orthotrophic/plagiotropic rhizomes	%	< 30 %	Stable meadow	Charbonnel et al 2000
		30 to 70 %	Slight trend to progress	
		> 70 %	Net trend to progress	
Mat compactness	cm	< 50 cm	Strong compactness	Francour et al 1999
		50 to 100 cm	Medium compactness	
		> 100 cm	Weak compactness	
Rhizomes baring	cm	< 5 cm	Low baring	Boudouresque et al 1980
		5 to 15 cm	Medium baring	
		> 15 cm	High baring	
Meadow cover	%	> 80 %	Very high covering	Charbonnel et al 2000
		60-80 %	High covering	
		40-60 %	Medium covering	
		20-40 %	Low covering	
		< 20 %	Very low covering	

2.4. Sediment chemistry and nutrients

Sediment chemistry was studied by sampling pore water in the control (C) and anchoring (Am) meadow, as well as in anchoring bare mat patches' sediments (Ap) given the method of Gobert *et al.* (2006b). Collection was performed in September after the warmest period of the year and in November when seawater temperature starts to decrease. Thus, the concentration of several essential components was studied in the substrate: dissolved dioxygen (O_2), free hydrogen sulfides (H_2S) and nutrients.

The pore water sampling for O_2 measurements was made within the oxygenic layer at a maximum depth of 1 cm in the sediments. O_2 concentration was obtained using a iodine titration with thiosulfate according to the method of Winkler (1888) with an automatized system for small sampling volumes (Carpenter 1965, Strickland & Parsons 1972) adapted by R. Biondo, (Laboratory of Oceanology-University of Liège).

The sample collection for H_2S and nutrient analysis was performed in triplicates inside the layer encompassing the plant living parts at 10 cm depth in the substrate. H_2S concentration was measured with a silver/sulfide ISM-146 FTH 25-XS electrode, coupled with a Sulfide Anti-Oxydant Buffer (SAOB) solution given the protocol of Brooks (2001). For detailed protocols of the measure of O_2 and H_2S, see Annex 5 and 6. Ammonium (NH_4^+) and Nitrite (NO_2^-)/Nitrate (NO_3^-) concentrations were measured by using a SKALAR auto-analyzer following the method of Aminot and Kérouel (2007) adapted for oligotrophic samples (Laboratory of Oceanology-University of Liège).

2.5. Statistical analyses

Statistical analyses were performed under the R 3.0.2 software using the FactoMineR package. Normality of structural parameters values was checked using a Shapiro-Wilk test. Stations were then statically tested two by two (control *vs* anchoring) for each depth (10 m, 15 m and 20 m) with an unpaired t-test (after checking their homoscedasticity with a Fisher test) for Gaussian data, and with a Mann Whitney test for non-parametric ones. T-tests were followed by a Tukey post-hoc test and Mann Whitney tests by a Dunns test.

Relations between the structural (i.e. meadow density, mat compactness, rhizomes baring, meadow cover, plagiotropic/orthotropic rhizomes proportion, Conservation Index and canopy height) and chemical (*i.e.* O_2, H_2S and NH_4^+ concentrations) parameters were investigated with a Pearson matrix of correlation.

Finally, a cluster analysis was performed using the Ward method of aggregation and Euclidean distances between individuals for testing dissimilarity. Clusters were thus defined by minimizing the loss of inertia (*i.e.* the Euclidean distance) between several individuals (*i.e.* stations) when grouping them. Prior to the analyses, data were standardized to take into account the difference of units. First, structural parameters alone were considered. Then only chemical features were used. Finally, both structural and chemical parameters were computed in order to study the impact of chemical parameters on the evaluation of the meadows' state of conservation.

3. Results

3.1. Ships: spatial distribution and frequenting

The spatial ship distribution in Alga Bay follows a bathymetrical zonation according to data from 2012 to 2014 (Fig. 38). Small boats (length < 10 m) appear to anchor at shallow depths (< 5 m, Fig. 3-3). The majority of ships measuring between 10 and 20 m prefers to anchor outside the meadow in the main part of the return river at depths shallower than 15 m, when bigger ships choose to lay their anchors in the meadow from 10 to 30 m depth (Fig. 38).

Anchoring substrates vary widely according to ship sizes in Alga Bay (Fig. 38). Sand appears to be the preferred anchoring substrate for small boats (53 %, Fig. 38) while those of medium and large size chose *P. oceanica* meadows (respectively 55 % and 84 %, Fig. 38). In general, ships anchor equally in sand (45 %) and meadow (47 %), few anchoring on rock (8 %, Fig. 38).

A total of 1 768 ships anchoring in Alga Bay were observed from May to October 2014, encompassing 43 % (754 ships) of small boats (length < 10 m), 53 % (935 ships) of medium size (length 10-20 m) and 7 % (79 ships) of large size (length > 20 m) (Fig. 39). Period of most intense anchoring occurs from mid-July to mid-August, reaching a frequenting peak of 74 ships the 7th of August (Fig. 39).

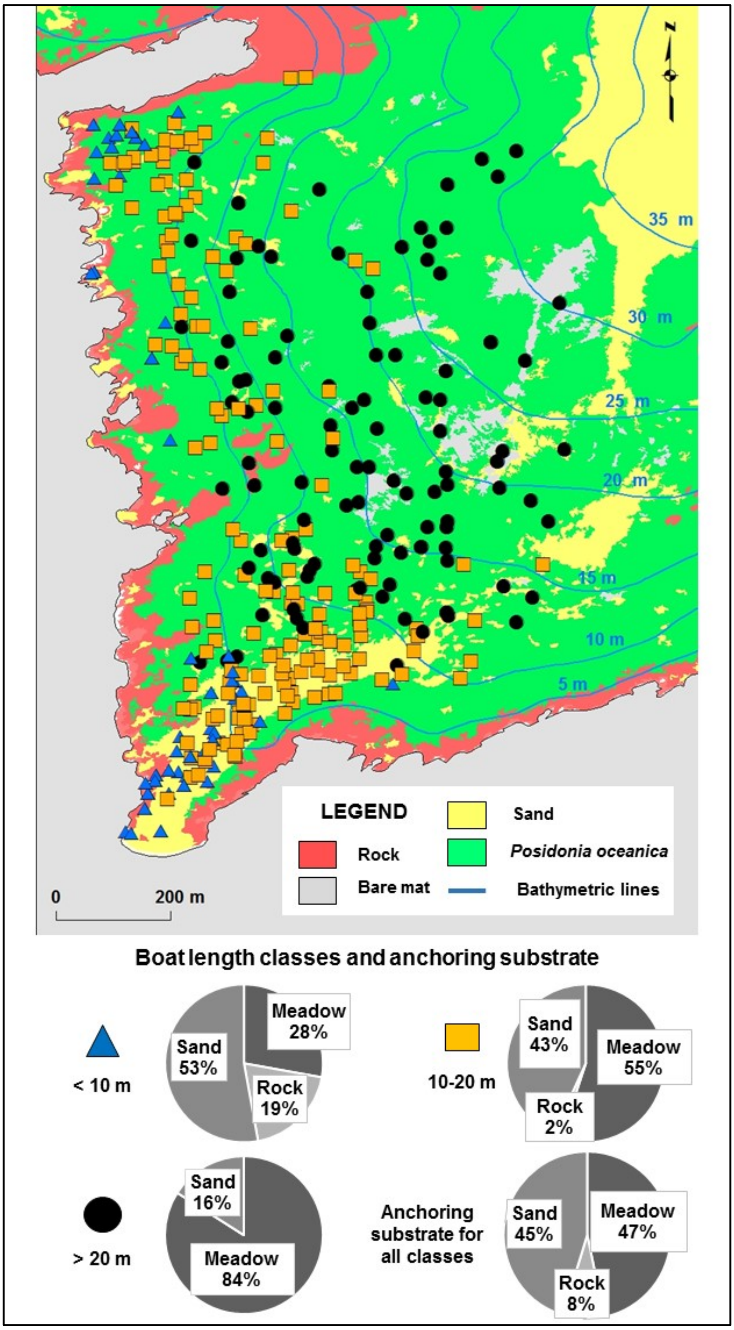


Figure 38: *Ships positioning using AIS and direct catches from 2012 to 2014 at Alga Bay coupled with a map of marine habitats and proportion of anchoring on the three different substrates in 2014 for ships with a length lower than 10 m; between 10 and 20 m, upper than 20 m and for all classes.*

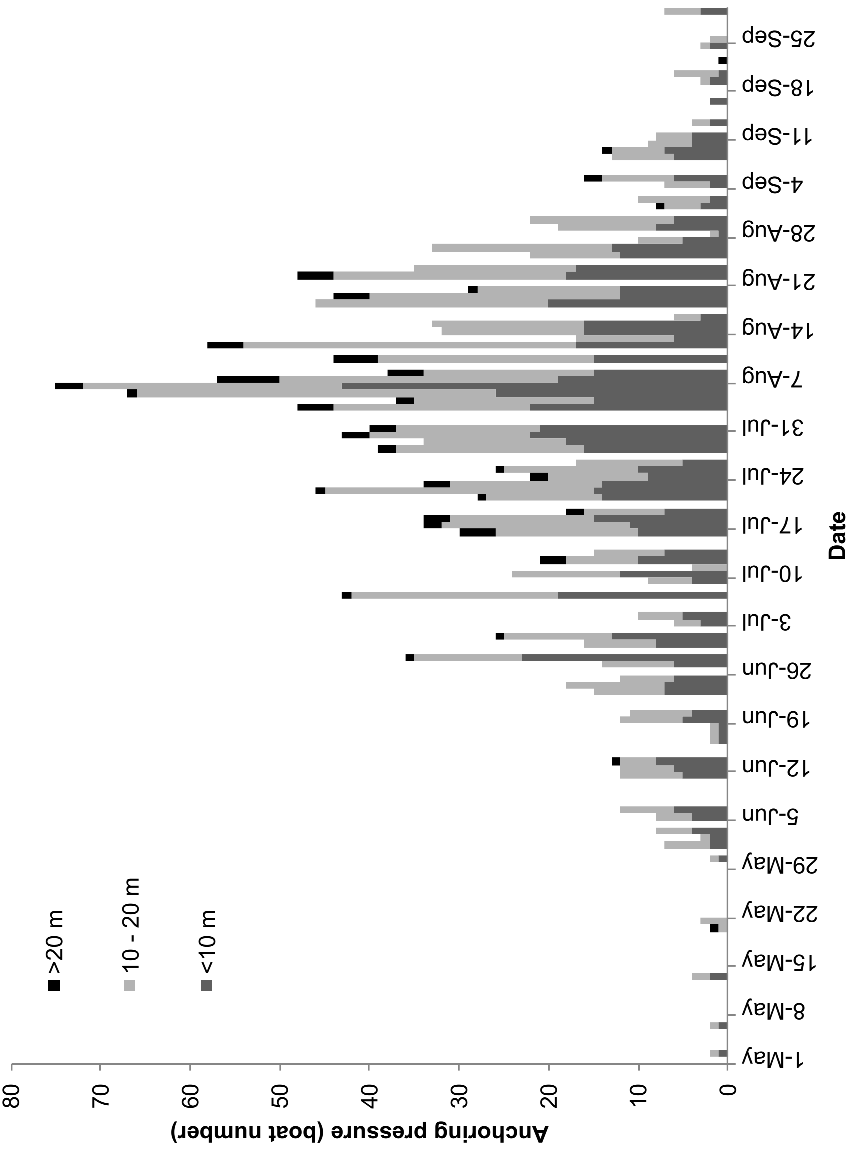


***Figure 39**: daily boat counting and size classes from June to September 2014 in Alga Bay.*

3.2. Meadow structure and conservation

Meadow densities are classified as "normal" according to their depths for two control (C) stations (C10 and C20) and all anchoring (A) stations A10, A15 and A20 (Fig. 40a). The control station at 15 m depth appears as "good" (437 ± 112 shoots.m^{-1}). Mean values of meadow density obtained at 15 m depth are significantly different (t-test: t = 892; p = 0.0097; df = 18). The same statement is made concerning the proportion of orthotropic/plagiotropic rhizomes which correspond to a stable meadow for all stations (Fig. 40e) except for the station A20 which is considered to have a "slight trend to progress" (70/30 ± 25 %). Mat compactness is characterized as "strong" for all stations sampled (Fig. 40b) with the exception of A20 with a "medium" mat compactness revealed by a relatively high penetration length of the rode (51 ± 9 cm). A significant difference (t-test: t = 6.172; p < 0.0001; df = 18) of the compactness was observed at 20 m between the control station and the anchoring one. Rhizomes baring is "medium" for all stations except for C10 (3.6 ± 1.9 cm) and A20 (2.0 ± 1.1 cm) where it is "weak" (Fig. 3-5c), these differences at 10 m (t-test: t = 4.493; p = 0.0001; df = 28) and 20 m (Mann Whitney test: p = 0.0002; U = 24) being confirmed by the statistical analysis. Meadow cover varies from "very high" (C10, C15, and A10) to "high" (C20, A15 and A20) (Fig. 40d), thus highlighting a difference of the mean meadow cover between the control station and the anchoring one at 15 m depth (Mann Whitney test: p < 0.0001; U = 182.5). At last, canopy height shows no significant differences between control and anchoring stations, its value decreasing from June to September at all depths (Fig. 40f).

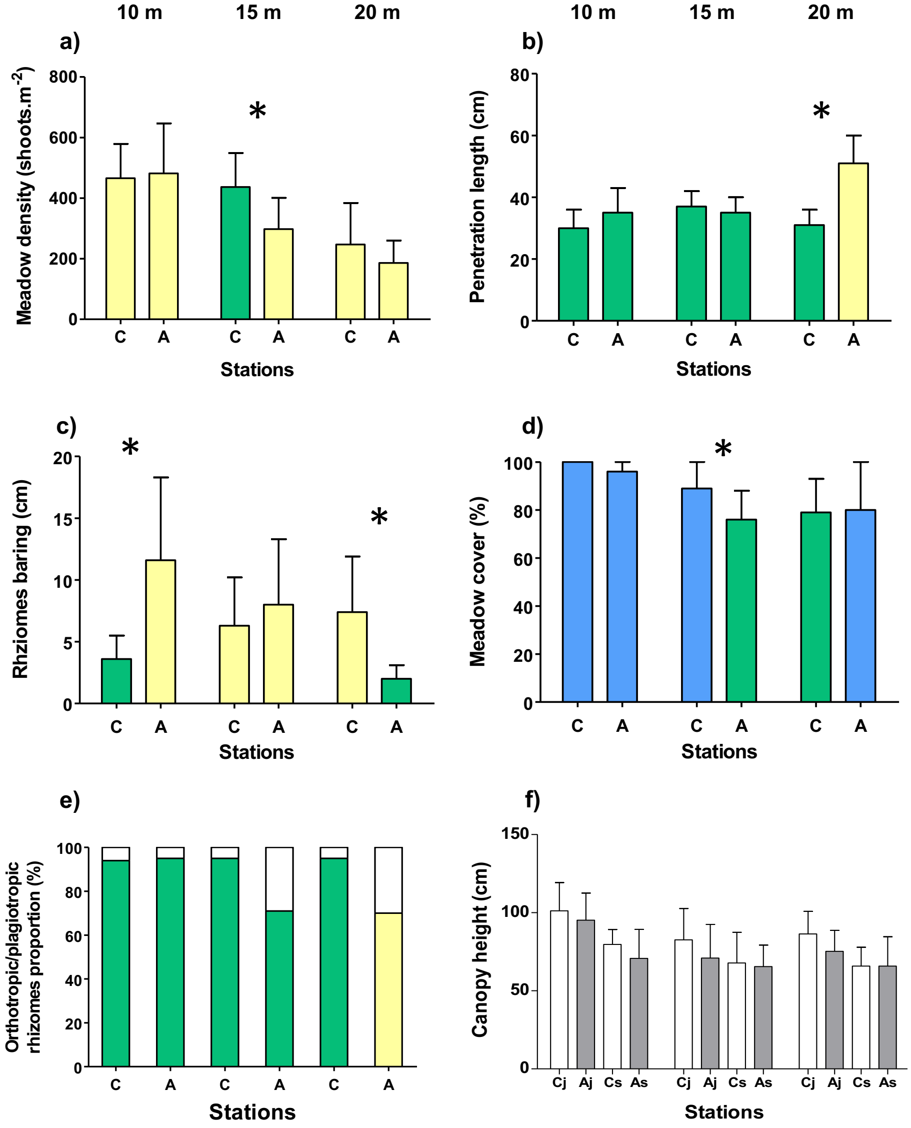


Figure 40: *Mean value (± SE) at 10, 15 and 20 m depth of a) meadow density (green: good; yellow: normal); b) penetration length (green: high compactness; yellow: medium compactness); c) rhizomes baring (green: weak; yellow: medium); d) meadow cover (blue: very high covering; green: high covering); e) orthotropic/plagiotropic rhizomes proportion, colored bar: orthotropic, white bar: plagiotropic (green: stable meadow; yellow: slight trend to progress); f) mean canopy height. * above a pair of bars indicates a significant difference between the two mean values. C = control; A = anchoring; j = June; s = September.*

The state of conservation of each control station, expressed by the Conservation index (CI), is the higher for C10 and C15 (1 ± 0.00 for each station), and decreases (0.98 ± 0.03) for C20 (Tab. 6). At Alga Bay, the anchoring site, the station at 10 m depth (A10) appears to have a state of conservation (CI = 0.97 ± 0.03) similar to C20 while the deeper stations (A15 and A20) have a lowest one (with a CI of respectively 0.85 ± 0.11 and 0.79 ± 0.15; Table 3-2).

Table 6*: Interpretation scale of the Conservation Index (CI) and its mean value (± SE). C: control; A: anchoring. 10, 15 and 20 m depth.*

CI classes	Color
CI > 0,99	Green
0,93 < CI ≤ 0,99	Yellow
0,88 < CI ≤ 0,93	Orange
CI <0,88	Red

Station	CI	CI class
C10	1.00 (± 0.00)	Green
A10	0.97 (± 0.03)	Yellow
C15	1.00 (± 0.00)	Green
A15	0.85 (± 0.11)	Red
C20	0.98 (± 0.03)	Yellow
A20	0.79 (± 0.15)	Red

3.3. Patches and meadows chemistry

In September, lowest concentrations of O_2 were found inside the patch at -10 m (Ap10: 102.7 µM) while a decrease with the depth in control meadows is observed (Tab. 7). The same pattern is observed in November with concentrations similar in both control (C) and anchoring (Am) meadows. Low concentrations in O_2 are related with high concentration in H_2S inside the patches at the three depths in September (20.5 µM at 10 m; 9.9 µM at 15 m; 12.8 µM at 20 m). High sulfide concentrations are also found in control meadows in September, except at 15 m (Tab. 7). In November, H_2S concentrations are relatively low at 10 m for all stations when they remain high at 15 and 20 m (except for C15).

NO_2^- and NO_3^- show very low concentrations in both September and November. NH_4^+ shows in September an increase of its concentration along with the depth (Tab. 7), as well as higher values inside anchoring patches (except for Ap15). The same pattern is observed in November with the exception that lower values are found in anchoring patches at 10 m instead of 15 m (Tab. 7).

Tab. 7*: Concentration of dissolved oxygen (O_2) within the first centimeter of substrate and mean concentration of free hydrogen sulfides (H_2S), nitrite (NO_2^-), nitrate (NO_3^-) and ammonium (NH_4^+) in the first ten centimeters of substrates (± SE) in September (Sep.) and November (Nov.) at control (C), anchoring meadow (Am) and anchoring patch (Ap) stations.*

Station	O_2 (µM)		H_2S (µM)		NO_2^- (µM)		NO_3^- (µM)		NH_4^+ (µM)	
	Sep.	Nov.	Sep.	Nov.	Sep.	Nov.	Sep.	Nov.	Sep.	Nov.
C10	206.0	226.8	39.1 (± 37.7)	4.0 (± 1.1)	0.06 (± 0.00)	0.20 (± 0.12)	0.22 (± 0.09)	1.92 (± 1.54)	4.68 (± 2.44)	4.40 (± 1.56)
Am10	232.7	213.4	12.0 (± 12.4)	4.2 (± 0.8)	0.08 (± 0.03)	0.06 (± 0.00)	0.22 (± 0.09)	0.30 (± 0.21)	4.74 (± 1.78)	4.44 (± 0.87)
Ap10	102.7	143.6	20.5 (± 30.2)	9.3 (± 4.7)	0.06 (± 0.00)	0.06 (± 0.00)	0.14 (± 0.03)	0.24 (± 0.00)	10.18 (± 8.13)	2.76 (± 0.22)
C15	195.1	199.6	0.4 (± 0.5)	8.0 (± 5.3)	0.06 (± 0.00)	0.08 (± 0.03)	0.42 (± 0.31)	0.38 (± 0.18)	10.34 (± 6.21)	6.32 (± 3.81)
Am15	145.2	189.3	8.1 (± 8.4)	33.4 (± 44.7)	0.12 (± 0.00)	0.08 (± 0.03)	0.76 (± 0.70)	0.42 (± 0.33)	10.76 (± 5.38)	12.38 (± 8.65)
Ap15	116.9	122.0	9.9 (± 7.2)	42.6 (± 56.2)	0.08 (± 0.03)	0.06 (± 0.00)	0.16 (± 0.03)	0.22 (± 0.12)	6.70 (± 3.47)	16.82 (± 7.69)
C20	191.8	210.8	16.5 (± 21.9)	20.9 (± 19.4)	0.08 (± 0.03)	0.08 (± 0.03)	0.30 (± 0.16)	0.34 (± 0.19)	14.38 (± 7.99)	7.44 (± 3.31)
Am20	177.7	211.5	0.9 (± 0.8)	13.2 (± 16.1)	0.08 (± 0.03)	0.08 (± 0.03)	0.40 (± 0.34)	0.26 (± 0.09)	13.82 (± 9.51)	7.70 (± 5.77)
Ap20	155.5	183.6	12.8 (± 21.0)	18.8 (± 8.3)	0.06 (± 0.00)	0.10 (± 0.07)	0.16 (± 0.07)	0.50 (± 0.45)	20.74 (± 26.40)	13.14 (± 15.02)

3.4. Computation of structural and chemical parameters

Among the structural parameters, rhizome baring (Rhiz. Bar.) appears to have weak correlation with all the other one (Tab. 8). Mat compactness (Compact.) appears to be less correlated with meadow cover (Cover) and the canopy height in June (ch_j), this last parameter having also few links with the proportion of orthotropic/plagiotropic rhizomes (Ortho. Prop.; Tab. 8). Between chemical parameters, H_2S concentrations in November (h2s_n) show a strong correlation with O_2 (o2_n) and NH_4^+ (nh4_n) ones at the same period (Tab. 8). This link is not found in September where only H_2S and NH_4^+ concentrations are correlated. Through the two different periods, oxygen in September (o2_s) is strongly correlated with the hydrogen sulfide in November (h2s_n) and ammonium (nh4_n). Looking at both structural and chemical parameters, all chemical parameters appear correlated with meadow cover (Cover) and canopy height (ch_j and ch_s) and to a lesser extent with meadow density (Density; Tab. 8). In contrary, both mat compactness (Compact.) and rhizome baring (Rhiz. Bar.) are not linked. These observations are more contrasted concerning the proportion of orthotropic/plagiotropic rhizomes (Ortho. Prop.) and the Conservation Index (CI) where correlations are only found in November for H_2S and NH_4.

The cluster analysis computing the structural parameters alone shows three classes linking anchoring stations at 15 and 20 depths (A15 and A20), when the two control meadows corresponding (C15 and C20) are grouped with the anchoring station at 10 m (A10), leaving the control one (C10) within a single class (Fig. 41a). When using only chemical features the cluster result changes, aggregating the stations A10 and C10 together and grouping C15, C20 and A20, leaving A15 alone (Fig. 41b). Adding the chemical parameters to the structural ones, three classes, encompassing each two stations, are found linking A15 and A20 but aggregating C10 with A10 and C15 with C20 (Fig. 41c). Few variables being too highly correlated, *i.e.* with a correlation greater than 0.900 (Tab. 8), they are not overrepresented in the clustering analysis.

Table 8: *Pearson's matrix of correlation comparing both structural and chemical parameters of the control and anchoring meadow at a depth of 10, 15 and 20 m. Density: meadow density; Compact.: mat compactness; Rhiz.*

Variables	**Density**	**Compact**	**Rhiz. Bar.**	**Cover**	**Ortho. prop.**	**CI**	**ch_j**	**ch_s**	**o2_s**	**o2_n**	**h2s_s**	**h2s_n**	**nh4_s**	**nh4_n**
Density	1	-0.556	0.463	0.876	0.703	0.740	0.720	0.696	0.660	0.282	0.410	-0.635	-0.900	-0.618
Compact.		1	-0.478	-0.369	-0.669	-0.787	-0.570	-0.462	-0.259	-0.146	-0.667	-0.004	0.452	0.180
Rhiz. Bar.			1	0.159	0.367	0.354	0.204	-0.096	0.360	-0.251	-0.063	0.052	-0.405	-0.041
Cover				1	0.681	0.652	0.896	0.881	0.812	0.689	0.588	-0.872	-0.889	-0.864
Ortho. prop.					1	0.972	0.807	0.492	0.794	0.464	0.430	-0.626	-0.470	-0.760
CI						1	0.763	0.530	0.658	0.364	0.496	-0.509	-0.492	-0.639
ch_j							1	0.848	0.852	0.826	0.767	-0.761	-0.744	-0.875
ch_s								1	0.533	0.752	0.857	-0.648	-0.814	-0.668
o2_s									1	0.687	0.329	-0.871	-0.612	-0.941
o2_n										1	0.710	-0.731	-0.438	-0.818
h2s_s											1	-0.289	-0.569	-0.427
h2s_n												1	0.594	0.961
nh4_s													1	0.574
nh4_n														1

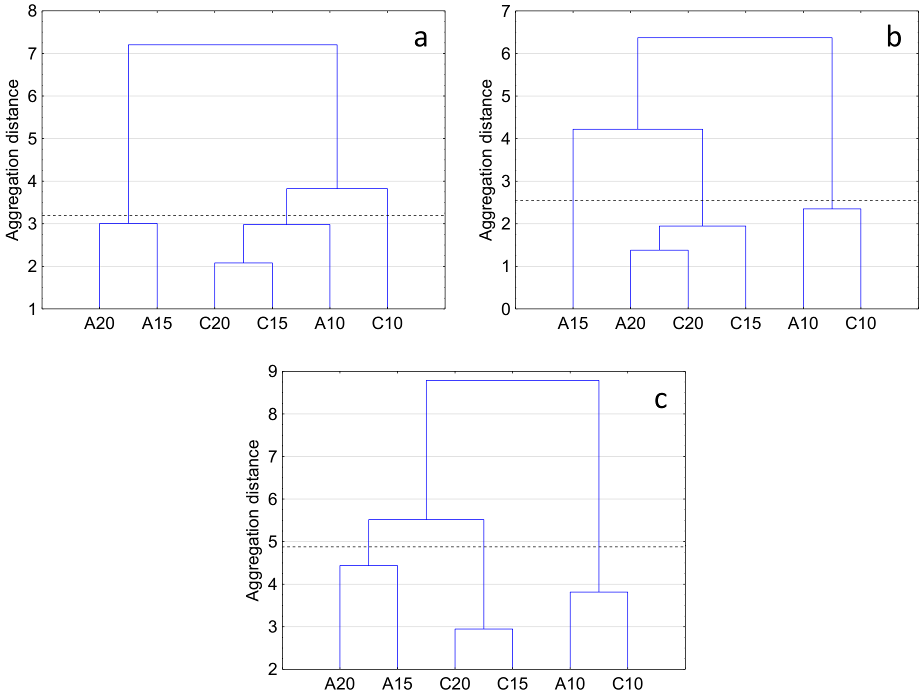


Figure 41*: Cluster analysis of the stations described by a) structural parameters alone; b) chemical parameters alone and c) both structural and chemical parameters of the control (C) and anchoring (A) meadow at a depth of 10, 15 and 20 m. The dotted line materializes classes’ separation according to their dissimilarity.*

4. Discussion

By studying both structural and chemical parameters of two seagrass meadows, one facing intensive anchoring and the other being under no known human pressure, this study highlights the influence of large boats anchoring on the chemistry of *Posidonia oceanica* meadows' substrate and thus, on the seascape structure too.

4.1. An intensive anchoring for a small area?

The first step in a study of anchoring impact on seagrasses should be the analysis and characterization of its frequency according to the size and bathymetry of the area. In the present work, the anchoring pressure at Alga Bay, reaching 0.8 boats.ha^{-1}.d^{-1} during the peak period, appears moderate compared to previous works in Corsica (Jousseaume *et al.* 2013) or in Port-Cros, France witnessing up to 8.8 boats.ha^{-1}.d^{-1} (Ganteaume *et al.* 2005a). However, anchoring pressure cannot be described by boats density alone but requires in complement the proportion of boats size and their favorite substrate. In this case, although being less numerous than small and medium boats, big ships (length >20 m) largely favors meadows for anchoring (84 %) to sandy and rocky bottoms, leading to more important mechanical damages at higher depths (Ganteaume *et al.* 2005b). It is mainly due to the fact that these ships need deep water to anchor and that *P. oceanica* meadows are more present at these depths. Conversely, small boats anchor on shallow sites where rocky and sandy substrates are dominant. Thus, taking into account all these aspects, anchoring appears to be intensive in Alga Bay with a high probability of an impact visible on the meadow structure.

4.2. From structural to chemical impact of anchoring

In this study, the analysis of the classical parameters referring to the structure of the *Posidonia oceanica* meadow are not clearly able to depict the direct observation made by scuba diving (*i.e.* large patches of bare mat crossed by anchoring tracks, Fig. 36). Here rhizomes baring and mat compactness appear not relevant for the study of anchoring, anchors impacting the superficial part of the mat while mat compactness investigate the whole mat thickness. These statement has already been made for mat compactness by Milazzo *et al.* (2004) and Ganteaume *et al.* (2005a) for meadow cover and density. Unlike these works, this case encompasses the study of big boats damages and not only the one of small to medium ships. Thus, large ships anchoring will directly pull out whole portions of the meadow and lead to the creation of anthropogenic patches (Fig. 42), revealed by the Conservation Index, the meadow density, and the proportion of orthotropic/plagiotropic rhizomes. In contrast rhizomes will not be partially uprooted and no effect will be witnessed by the rhizomes baring and mat compactness. Thus, large ships' anchoring causes a mechanical destruction similar to the trawling one (Boudouresque *et al.* 2009, Kiparissis *et al.* 2011, Pergent *et al.* 2013).

Another limit of the structural parameters is their incapacity to assess the impact of the substrate change (from leafy to bare mat). Seagrasses are known to be able to release oxygen in the sediments through their roots to create a small oxic zone (Pedersen *et al.* 1998, Greve *et al.* 2003), this function being suppressed by the destruction of the canopy by anchoring and thus of the photosynthesis process. These modifications are particularly observable by studying the impact of fish farms, their action leading to large areas of bare mats where an increase of the organic matter in decomposition leads to a decrease of the oxygen available and the intrusion of hydrogen sulfide (Pergent-Martini *et al.* 2006, Holmer & Frederiksen 2007, Apostolaki *et al.* 2010). Although no input of organic matter - at least not in the same range as fish farms - are involved in anchoring, the same process is observed here with a decrease of oxygen concentration at the surface of the sediments at all depths and an intrusion of hydrogen sulfide (H_2S) inside anchoring patches. High temperatures enhancing high concentrations of H_2S in *Posidonia oceanica* meadows (García *et al.* 2012), a decrease along with the temperature should be observed in this case in November. In contrary, an increase in both meadows and patches is observed at the stations where the biggest boats anchor (A15 and A20), no thermocline being observed during the two sampling periods with an homogeneous water column of a temperature of 23.5 °C in September and 20.8 °C in November (Richir *et al.* 2015).

The higher concentrations of pore water inorganic nitrate found in Alga Bay at 15 and 20 m depth inside anchoring patches and the surrounding meadow, are another consequence of the change in substrate. Here, the higher concentrations in ammonium (NH_4^+) could be the result of the particulate organic nitrate's ammonification (Romero *et al.* 2006). These values constitute a sufficient nutrient enrichment for *P. oceanica* development although recolonization does not occur (López *et al.* 1998, Gobert *et al.* 2002).

These unsuitable conditions for a recolonization by the meadow (Marbà *et al.* 2006), coupled with the continuation of the high anchoring rate in the area, will thus favor the expansion of anthropogenic patches and modify the whole sediment chemistry (Pergent-Martini *et al.* 2006). In this way, a new arrangement of anthropogenic patches, possibly combined with natural ones, leads to a new seascape (Abadie *et al.* 2015b). The new areas of bare mat thus created are a suitable substrate for the settlement of the alien species *Caulerpa cylindracea* Sonder (Katsanevakis *et al.* 2010, Kiparissis *et al.* 2011) which is able to release H_2S inside sediments (Garcias-Bonet *et al.* 2008) (Fig. 42). The so new-generated small patches may lead to a long-term larger fragmentation of the meadow through aggregation process. Such phenomenon has been studied in *Zostera noltii* Hornemann meadows on the Portuguese coast by Cunha *et al.* (2005). In a wider viewpoint, vegetation systems, and thus seagrass seascapes, are theoretically subject to aggregation models (Irvine *et al.* 2016).

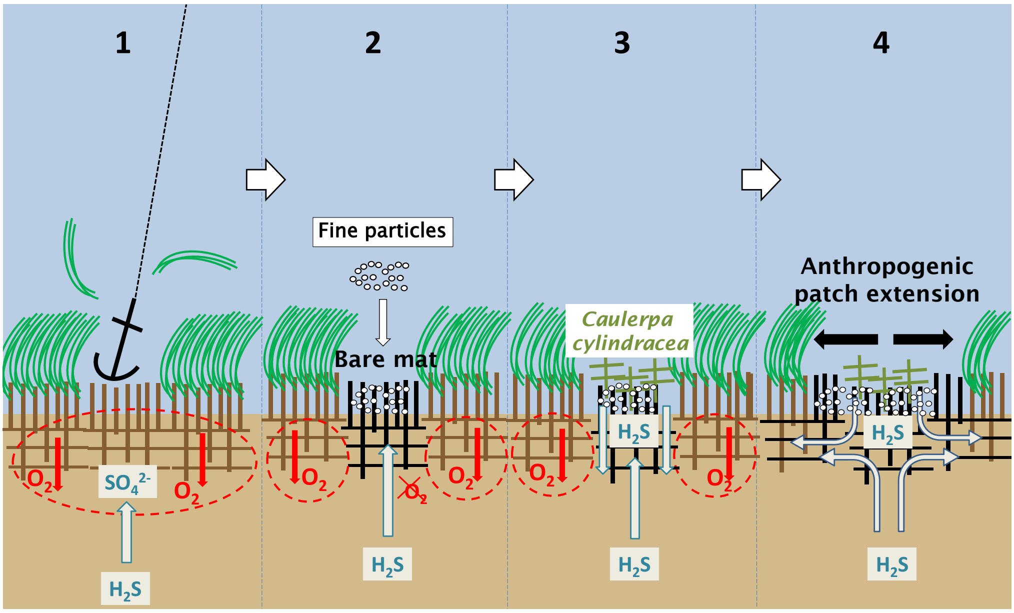


***Figure 42**: Hypothesis on the succession of processes from mechanical damages to the expansion of anthropogenic patches; 1) destruction of the canopy by anchoring 2) fine particles deposit leading to an increase of the organic matter and its degradation; 3) settlement of the alien species* Caulerpa cylindracea*; 4) expansion of the anchoring patch with intrusion of hydrogen sulfide (H_2S).*

4.3. The contribution of chemical parameters in seagrass meadows conservation's assessment

This study highlights the fact that using structural tools alone to assess anchoring in seagrass meadows can lead to a misevaluation of their state of conservation. In the present work, control stations at 15 and 20 m, meaning meadows with no traces of impact from human activities, form a cluster, *i.e.* they have the same characteristics than the anchoring station at 10 m depth. It reflects no significant anchoring impact on the meadow at this depth. Similarly, chemical features alone aggregate a station visibly impacted by anchoring (A20) with meadows (C15 and C20) under no anthropogenic pressures. When adding chemical parameters to the structural ones, this station is classified in the same group than the control site at the same depth, reveling that no impact is observable. In the same way stations A15 and A20 are grouped, stating the impact of anchoring at these depths. Considering the long term process induced by a change in sediments chemistry, the measure of several chemical parameters can provide information about the possible recovery of a meadow under an intensive human pressure (Holmer *et al.* 2008). We suspect that it will be difficult for the meadow in Alga Bay at 15 and 20 m depth to recover given the continuation of anchoring while the meadow at 10 m seems to have the same state of conservation than the control one.

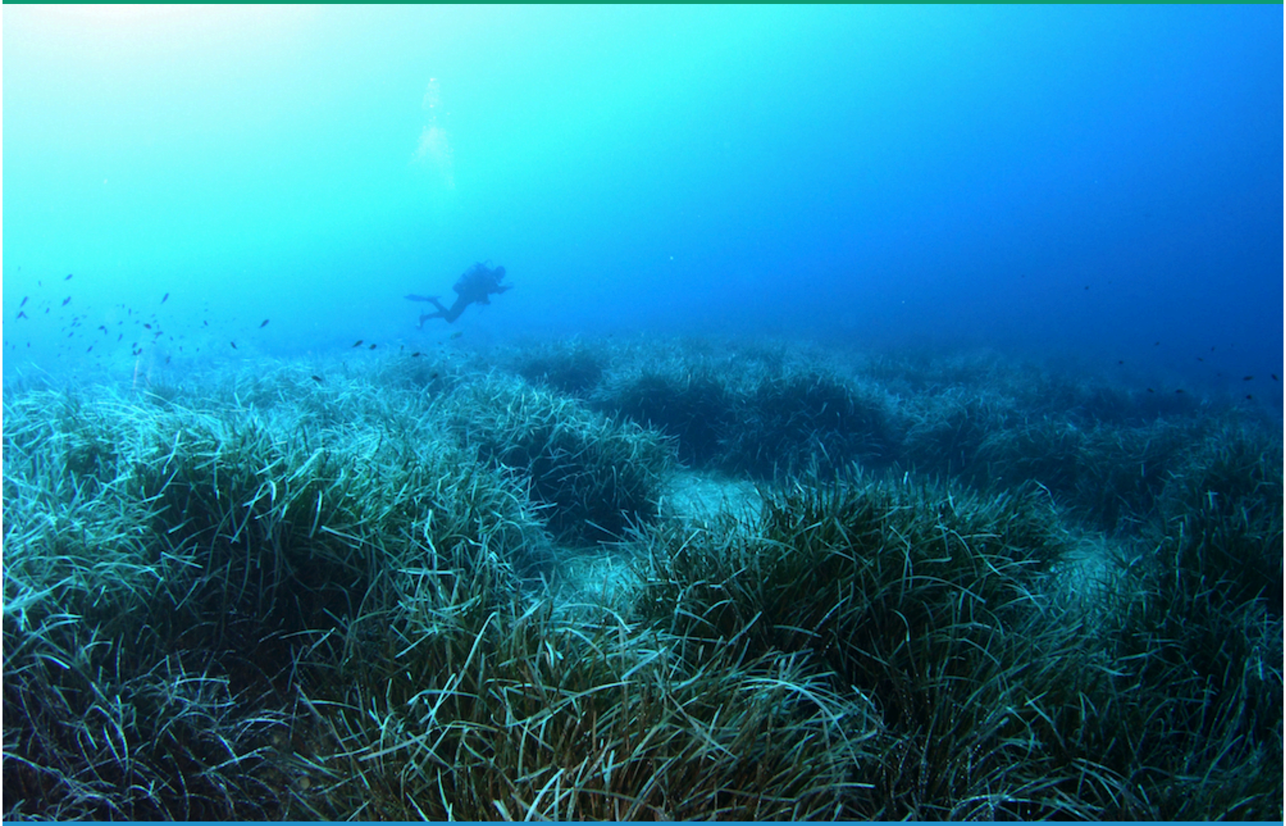
Observation of chemical modifications within seagrass meadows linked with anthropogenic impacts has already been highlighted by Jones and Unsworth (2016) in *Zostera marina* Linnaeus across the British Coast. This study thus reveals an excess of nitrogen within *Z. marina* leaves, associating this observation with the poor water quality and the disturbance of boat-based activities, of which anchoring. Chemical response of the plant to anthropogenic pressures was also stated within *Cymodocea nodosa* (Ucria) Ascherson meadows in Greece by Papathanasiou *et al.* (2016). These accounts indicate that physiological and chemical changes observed within the meadows are not confined to *P. oceanica* and the Mediterranean Sea. They are also observed in other seagrass species with contrasted morphology and seasonal response to environmental changes, supporting the importance of multidisciplinary approaches for conservation assessment.

Measurement of chemical features remains however time consuming and requires specific equipment for each element studied. In this way, new simplified protocols should be developed. Nevertheless, like structural parameters who have already proved their utility to assess seagrasses meadow state of conservation (Montefalcone *et al.* 2006a, Gobert *et al.* 2009, Lopez y Royo *et al.* 2010), chemical measures are non-destructive, have a good capacity of replication and a great potential to provide a deeper insight (Romero *et al.* 2007). Moreover, these tools can be integrated in the future conservation indices based on an ecosystemic approach in the framework of the European Marine Strategy Framework Directive (MSFD) (Personnic *et al.* 2014). They also can be used in the development of descriptors specific to anchoring, built for an easy comprehension by stakeholders and managers.

Conclusion

Mechanical damages of intensive anchoring in *P. oceanica* meadows induce a change in the substrate nature leading to the generation of bare mat areas (anthropogenic patches) at 15 and 20 m depth where the bigger ships are observed. Modifications in chemical processes, and more precisely the intrusion of hydrogen sulfide, decrease the possibility of a recolonization by the meadow leading to the expansion of patches. The development of non-destructive chemical indicators easy to perform, coupled with structural tools, will provide precious information for assisting decisions in conservation issues about mechanical impacts in seagrass meadows which, in some cases, are stoppable when effectively assessed (Giakoumi *et al.* 2015a).

CHAPITRE 4



Les paysages sous-marins à *Posidonia oceanica* : utiliser leurs caractéristiques pour évaluer l'état de conservation

Ce chapitre s'articule autour de deux articles :

- Article 4 : Arnaud Abadie, Sylvie Gobert, Marina Bonacorsi, Pierre Lejeune, Gérard Pergent, Christine Pergent-Martini (2015) Marine space ecology and seagrasses. Does patch type matter in Posidonia oceanica seascapes? Ecological Indicators 57: 435-446

- Article 5 : Arnaud Abadie, Matthew Pace, Sylvie Gobert, Joseph A. Borg (en préparation) Seascape ecology, a gateway for the management of seagrass meadows

Les justificatifs de la publication de ces articles sont disponibles en Annexe 1.

Article 4: Marine space ecology and seagrasses. Does patch type matter in *Posidonia oceanica* seascapes?

Abstract

The use of landscape tools in the study of seagrass meadows (seascapes) begins to be widely spread but still require the establishment of several bases, i.e. a patch type classification based on numerical characteristics. Thanks to the complex seascapes created by the *Posidonia oceanica* meadows, they appear to be suitable for a study at a patch type level (class), which brings a new insight of their arrangement at the whole seascape scale. By interpreting side scan sonar images from the Corsican coast (France) through a GIS software, it was possible to describe 11 types of patches and to evaluate their natural or anthropogenic origin. Comparison of different landscape metrics and wave exposure (Relative wave Exposure Index, REI) at the seascape and the patch level showed that the particularity of *P. oceanica* seascapes are mainly characterized by certain types of patches often of anthropogenic origin. Furthermore, the REI seems not to be a relevant index for a study at a class scale. A bathymetrical succession of natural patches was outlined from the lower to the upper limit of the meadow, with a long-term dynamic opposed to a shorter one concerning anthropogenic patches. In order to assess the origin (natural or induced by human activities) of the patches in *P. oceanica* meadows, as well as in any other seagrass, a Patchiness Source Index (PaSI), ranging from 0 to 1, was defined.

Keywords: seagrass, seascape, patchiness, side scan sonar, human impact

1. Introduction

Over the last three decades the interest in landscape ecology has grown and spread from land to marine ecosystems (Sousa 1984, Li & Mander 2009). A seascape can be defined as the varying arrangements of biotic structures with the resulting mosaic of marine habitat patches (Robbins & Bell 1994). Thus, the study of their function and heterogeneity, including fragmentation and patchiness, should be called the Marine Space Ecology (Li & Mander 2009). Fragmentation refers to a dynamic process which cannot be studied given a single temporal set of data (Boström *et al.* 2011). This term is often used in an erroneous way in place of patchiness which refers to a static state of a landscape.

The Mediterranean meadows of the seagrass *Posidonia oceanica* (Linnaeus) Delile play an important ecological and economic role *e.g.*, fish nursery, carbon sink, and protection from coastal erosion (Costanza *et al.* 1997, Ruíz *et al.* 2009, Boudouresque *et al.* 2012, Vassallo *et al.* 2013). Generally dense and continuous in the coastal zone from the surface to 45 m depth (Molinier & Picard 1952), they are nevertheless subject to fragmentation due to natural phenomena and human activities (e.g. coastal development, pollution, anchoring) (Ardizzone *et al.* 2006, Boudouresque *et al.* 2009). In order to assess the role played by the heterogeneity of seagrass meadows, a landscape approach should be used (Bell & Hicks 1991, Robbins & Bell 1994, Gobert *et al.* 2014).

Heterogeneity in the physical structure of a seagrass meadow plays a major role in its functioning (*e.g.* juvenile survival, species-lined settlement, colonization, predator movements) thanks to the size and the shape of the patches (Micheli & Peterson 1999, Bell *et al.* 2001, Borg *et al.* 2006, Boström *et al.* 2006a, Connolly & Hindell 2006). The habitats created by a natural fragmentation are essential for several key species (Prado *et al.* 2009).

Between 1950 and 1990 many types of *P. oceanica* seascapes have been described (Molinier & Picard 1952, 1954, Clairefond & Jeudy De Grissac 1979, Boudouresque *et al.* 1980a, Boudouresque *et al.* 1980b, Boudouresque *et al.* 1985a, Boudouresque *et al.* 1990a, Pergent *et al.* 2007, Boudouresque *et al.* 2012). These descriptions (Tab. 9) only refer to a visual aspect of the structures that forms *P. oceanica* and do not take into account those induced by human activities. Moreover, each of these structures was described by using scuba diving observations, large-scale tools with enough accuracy (*e.g.* side scan sonar) being not available at that time.

Table 9*: Characteristics of the different types of* Posidonia oceanica *meadows described in the past and their designation.*

Designation	Description	Reference
Barrier reef	Formation of a barrier due to the vertical growth of *P. oceanica* rhizomes at shallow depth. Creation of a lagoon on the shore side of the barrier	Molinier and Picard (1952)
Erosive intermatte	Sand holes with an ellipsoid shape in a continuous meadow	Molinier and Picard (1952)
Hill meadow	Top erosion by hydrodynamism of a group of *P. oceanica* cuttings surrounded by sand	Boudouresque *et al.* (1985a)
Macro-atolls	Circular patches (>20 m in diameter) of *P. oceanica* at a shallow depth separated by sand	Pergent *et al.* (2007)
Micro-atolls	Circular patches of *P. oceanica* (flew meters in diameter) at a shallow depth separated by sand	Boudouresque *et al.* (1990a)
Plain meadow	Continuous, horizontal or gently sloping meadow, broken by erosive structures	Boudouresque *et al.* (1980a), Boudouresque *et al.* (1980b)
Return river	Under a particular orientation of the wind to the coast, channels perpendicular to the shore line can be generated in a continuous meadow	Boudouresque and Meinesz (1982)
Shifting intermatte	Long and narrow corridors parallel to the shore	Boudouresque *et al.* (1980b)
Striped meadow	Strips of *P. oceanica* separated by bare mat	Boudouresque *et al.* (1990a)
Structural intermatte	Small (several dozens of centimeters long) natural patches of bare mat in a continuous meadow	Boudouresque *et al.* (2012)
Sugar loaf meadow	Mounts of mat with living *P. oceanica* on the top	Molinier and Picard (1954)
Tiered meadow	Steps-like patches of *P. oceanica* separated by bare mat following a soft bottom slope	Boudouresque *et al.* (2012)
Undulating meadow	Repeated sequences of patches of bare mat in a continuous meadow	Clairefond and Jeudy De Grissac (1979)

P. oceanica meadows show natural forms of heterogeneity in their structure under the shape of sandy patches as well as "bare mat" (or "dead matte") areas. The term "matte" (or "mat") was originally used by French Mediterranean fishermen to refer to the complex structure formed by *P. oceanica* rhizomes, roots and sediments (Molinier & Picard 1952). Sandy patches seem to be generated by the water movement as well as depend of the slope and the substrate of seagrass beds (Blanc & Jeudy De Grissac 1984). These gaps are traditionally named "intermattes", literally translated "space between the matte". The designation "inter-matte" has been used for every type of sandy or bare mat patches while there are no discontinuities in the mat in the case of the latter. For this reason, we will use hereafter the designation "patch" to refer to any type of discontinuity in a meadow. Moreover, this term is the one commonly used in landscape ecology. Other endings corresponding to "patch elements of one habitat within a matrix of another" (Boström *et al.* 2006a) can be applied to seagrass seascapes like "sand holes" (Ginsburg 1956), "blowouts" (Patriquin 1975), "spaces" “spaces” (Sousa 1984), “halos” (Fonseca & Bell 1998), “gaps” (Bell *et al.* 1999) or “corridors” (Micheli & Peterson 1999).

Bare mat areas can be natural or induced by human activities like the organic matter loads of fish farms (Pergent-Martini *et al.* 2006), trawling (Kiparissis *et al.* 2011, Pergent *et al.* 2013), explosives (Meinesz & Lefèvre 1984), pollution (Pergent-Martini *et al.* 1995) or damages of boat anchoring (Montefalcone *et al.* 2006b). Several of these seascape parts of *P. oceanica* meadows are assumed as “dynamic” and appear to modify their shape and surface through time. Hereafter we define a “*Posidonia oceanica* seascape” as the set of the different habitats (*i.e.* types of patch) of natural and anthropogenic origin included in a meadow matrix.

In the present study we focused on the spatial relationships among distinct elements (patches, matrix), an approach that is still seldom used. The major advances and steps in the study of seagrass seascapes through time are summarized in figure 43. Due to the complexity (Boudouresque *et al.* 2012) and the various types of habitats (Borg *et al.* 2006) encompass by *P. oceanica* meadows it appears to be possible to study their seascapes characteristics at the class patch type level (class). All the patches mentioned above can be identified with the use of side scan sonar (Pasqualini *et al.* 1999, Leriche *et al.* 2006, Bonacorsi *et al.* 2013)) and from the resulting mapping many landscape indices may be computed by using software programs (Sleeman *et al.* 2005, Bell *et al.* 2006, McGarigal *et al.* 2014). Thus we (1) described natural and anthropogenic patches in several *P. oceanica* meadows; (2) established a nomenclature of these structures based on their origin, shape and surface; (3) investigated the relation between various types of patches and the P. oceanica seascapes observed using landscape metrics and we attempt to link it with the local water movement (Murphey & Fonseca 1995); (4) finally we explored the possibility of using patches in seagrass meadows to assess the source of patchiness of *P. oceanica* seascapes.

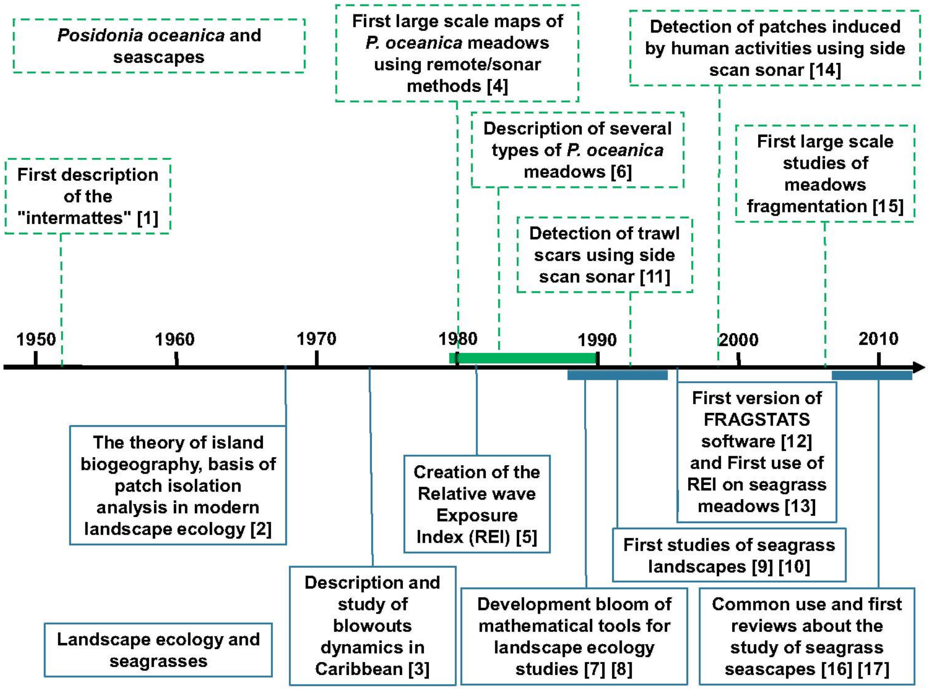


Figure 43: *Major steps in the study of seagrasses and P. oceanica seascapes from 1950 to present days. [1] Molinier and Picard (1952); [2] Losos and Ricklefs (2010); [3] Patriquin (1975); [4] Cristiani (1980); [5] Keddy (1982); [6] synthesis in Boudouresque et al. (2012); [7] Forman and Godron (1986); [8] Turner (1989); [9] Bell and Hicks (1991); [10] Robbins and Bell (1994); [11] Paillard et al. (1993); [12] McGarigal and Marks (1995); [13] Murphey and Fonseca (1995); [14] Pasqualini et al. (1999); [15] Ardizzone et al. (2006); [16] Bell et al. (2006); [17] Boström et al. (2011).*

2. Material and methods

2.1. Sites and data acquisition

Data on *P. oceanica* meadows were acquired in Corsica (France) during the Cartham program in summer 2010 on the West coast, and CoralCorse program in summer 2013 on the East coast (Fig. 44). Sonograms were obtained using a side scan sonar Klein 3000® and the SonarPro® software. This device sends a high frequency acoustic signal (500 kHz) reflected by the sea floor and received by the ship. The intensity of the signal sent back allows the determination of the bottom nature. The data acquired were processed with the Caraibes 3.8® software program (georeferencing, optimization of the quality of sonograms). A mosaic of merged sonar images (resolution of 0.5 m) was developed.

From these georeferenced sonograms, five sites within continuous *P. oceanica* meadows and corresponding to as many types of *P. oceanica* seascapes as possible were selected along the coastline. Furthermore, one of the main selection criterions was the presence of possible traces of human impacts. Three sites were chosen on the East coast (South of Macinaggio, the open sea in front of Biguglia and Urbinu lagoons) and two on the West coast (Calvi Bay and the Gulf of Ajaccio) (Fig. 44).

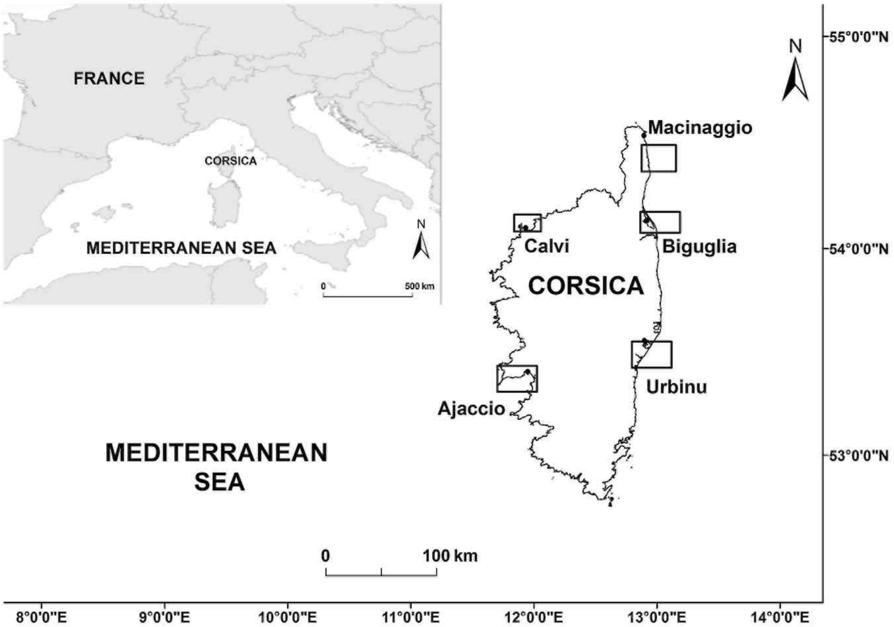


Figure 44: *Location along the Corsican coast of the sites considered in this study.*

2.2. GIS processes

When clearly identified, the limits of sandy and bare mat patches in *P. oceanica* meadows were drawn in the GIS software. Their origin was estimated by looking for the presence of human activities in the neighborhood of the patches. Only patches detectable and recognizable with the sonar resolution are taken into account, that is to say those having an area greater than 1 m². Thanks to this resolution it is thus possible to take into account the smallest patches. The GIS files were finally transformed into rasters (GeoTIFF grid) and analyzed through the computer program FRAGSTATS version 4.2 to obtain landscape indices.

2.3. FRAGSTATS analysis

The FRAGSTATS software, first developed by McGarigal and Marks (1995), allows the calculation and the analysis of various seascapes metrics at three scales: the patch, the type of patch (class) and the entire seascape. In the present study only the patch class and the entire seascape are investigated. No metric was calculated at the patch level. The analysis was performed using an eight cells neighborhood rule coupled with no specific sampling strategy to consider the whole part of meadow selected. Following the recommendations of Sleeman *et al.* (2005), seven metrics were chosen for the analysis of the seascapes patchiness: the mean patch area (AREA), the mean radius of gyration (GYRATE_MN), the area-weighted radius of gyration (GYRATE_AM), the coefficient of variation of the Euclidean nearest-neighbor distance (ENN_CV), the area-weighted perimeter-area ratio (PARA_AM), the landscape division index (DIVISION) and the number of patches (NP) (Tab. 10). The same metrics were chosen for the patch type (class). At the seascape level the patch density (PD) was also calculated.

2.4. REI calculation

In an effort to link the erosive structures observed and the landscape metrics measured with the local water movement, we investigated the exposure of the sites to different wind conditions by using the Relative wave Exposure Index (REI) developed by Keddy (1982) and modified by Murphey and Fonseca (1995):

$$\mathrm{REI} = \sum_{i=1}^{8} (V_i \times P_i \times F_i)$$

where i = 1 to 8 corresponding to cardinal points in 45° increments (N=1, NE = 2, etc.), V=mean monthly mean wind speed (ms-1), P= rate of wind direction occurrence and F= effective fetch (km) or the distance from the site to the land computed through the 8 compass headings. Daily wind direction and speed were obtained from forecast stations at a distance of 4, 3, 6, 35 and 12 km respectively for the sites of Calvi, Macinaggio, Biguglia, Urbinu, and Ajaccio. Due to the availability of meteorological data for all sites only for the year 2011, V and P were computed for this single year. Fetch was calculated using the method of Fonseca and Bell (1998) by using ArcGIS®.

Table 10: *The seven landscape metrics recommended by Sleeman et al. (2005) and their abbreviation in FRAGSTATS.*

Metric name	FRAGSTATS abbreviation	Equation	Unit
Number of patches	NP	-	None
Mean patch area	AREA_MN	-	m²
Mean radius of gyration	GYRATE_MN	$\frac{1}{n} * \sum_{i=1}^{n}\sqrt{\left(x_i - (x)\right)^2 + \left(yi - (y)\right)^2}$	m
Area-weighted radius of gyration	GYRATE_AM	$\frac{\sum_{s=1}^{m}(nsRs)}{\sum_{s=1}^{m} n_S}$	m
Coefficient of variation of the Euclidean nearest-neighbor distance	ENN_CV	$\frac{\sqrt{\frac{\sum_{i=1}^{i=NP} h_i - \left(\frac{\sum_{i=1}^{i=NP} h_i}{NP}\right)}{NP}}}{\frac{\sum_{i=1}^{i=NP} h_i}{NP}} * 100$	%
Area-weighted perimeter-area ratio	PARA_AM	$\frac{\sum_{i=1}^{i=NP} \frac{p_i}{a_i} a_i}{\sum_{i=1}^{i=NP} a_i}$	None
Landscape division Index	DIVISION	$\left[1 - \sum_{i=1}^{n}\left(\frac{a_i}{A}\right)^2\right]$	None
Patch density	PD	-	None

2.5. Statistical analysis

Two principal component analysis (PCA), one for each scale of study (class and seascape), were performed using R version 3 software. The landscapes indices and the REI values were computed to assess the difference of seascape characterization according to the spatial degree of consideration. The variable loadings were checked to make sure that the indices chosen were significantly informative about the *P. oceanica* seascape structure at both landscape and class level.

2.6. Patchiness Source Index (PaSI) calculation

In order to assess the main origin (natural or anthropogenic) of the patchiness observe in *P. oceanica* seascapes, we defined a Patchiness Source Index (PaSI) for a given area by computing surfaces of the different structures identified. The PaSI is based on the model of the Conservation Index (CI) developed by Moreno *et al.* (2001):

$$\mathrm{PaSI} = \frac{S_{NP}}{S_{NP}+S_{AP}}$$

where S_{NP} = percentage of the surface covered by the different types of natural patches (m^2) and S_{AP} = percentage of the surface covered by different types of anthropogenic patches (m^2). The PaSI ranges from 0 to 1 and has no unit. A value tending to 0 reflects a meadow patchiness mainly due to human activities. On the other hand, a value near 1 should reflect a natural patchiness. PaSI values are classified using five categories and a color code (Tab. 11).

Table 11: *Color code corresponding to the different values of the Patchiness Source Index (PaSI).*

PaSI Value	Description	Color
0.801 -1	High natural influence on the meadow patchiness	Blue
0.601 - 0.800	Major natural influence on the meadow patchiness	Green
0.401 - 0.600	Moderate anthropogenic influence on the meadow patchiness	Yellow
0.201 - 0.400	Major anthropogenic influence on the meadow patchiness	Orange
0 - 0.200	High anthropogenic influence on the meadow patchiness	Red

3. Results

3.1. Patch characteristics

The meadow of the South of Macinaggio shows bomb craters and natural sandy patches (Fig. 45a). In front of Biguglia lagoon the meadow is covered by trawling tracks, large marks made by tankers anchors and chains as well as several sandy natural patches (Fig. 45b). Many sandy corridors and ovoid patches of various sizes are observed in front of Urbinu lagoon (Fig. 45c). The meadow chosen in Calvi Bay shows various types of patches like anchoring tracks, fish farm impact, bare mat patches and other natural structures (Fig. 45d). Finally, a high patchiness near the fish farm is observed on the meadow selected in the Gulf of Ajaccio (Fig. 45e).

The analysis of the sonograms allowed the detection of 11 different types of patches in the meadows (Tab. 12). Five were likely to be of natural origins whereas five were induced by human activities. The origin of bare mat patches was hard or even impossible to be determined with the sonar images alone.

The shape of natural patches showed a bathymetric zonation. Thus, sand corridors (SC) were observed from 10 m to 20 m depth, small sand patches (SSP) at the same depth, large sand patches (LSP) and colonized patches (CP) from 15 to 25 m while ovoid patches (OP) were encountered between 15 m and the lower limit of the meadow (Table 4-10). This particular zonation was mainly observed on the sonograms of Biguglia, Urbinu and Calvi. All the natural patches presented various sizes, their surface ranging from 1 m^2 to 25 544 m^2 (Fig. 46).

The natural and anthropogenic bare mat patches presented various sizes and shapes so their sonar images can be very similar (Tab. 12). Due to their size and shape that greatly depended of the human activities involved in their creation, the anthropogenic patches were quiet easy to identify. The narrowest ones were the trawling tracks and the anchoring tracks (from 0.5 m to 4.0 m large) which were also the longest i.e. up to 1 800 m for the trawling tracks and 230 m long for the anchoring tracks (Tab. 12). Patches generated by the anchoring of cruise ships and/or tankers reached a surface of 1 254 m^2 with a characteristic "funnel" shape. The biggest surfaces were observed at the level of the bomb impacts (57 686 m^2) and of the patches generated by the fish farms (more than 100 000 m^2 for a single patch) (Fig. 46). Generally speaking, bare mats cover a small part of the *P. oceanica* seascapes studied, that is to say a mean coverage of 1.4% (SE ± 1.7%).

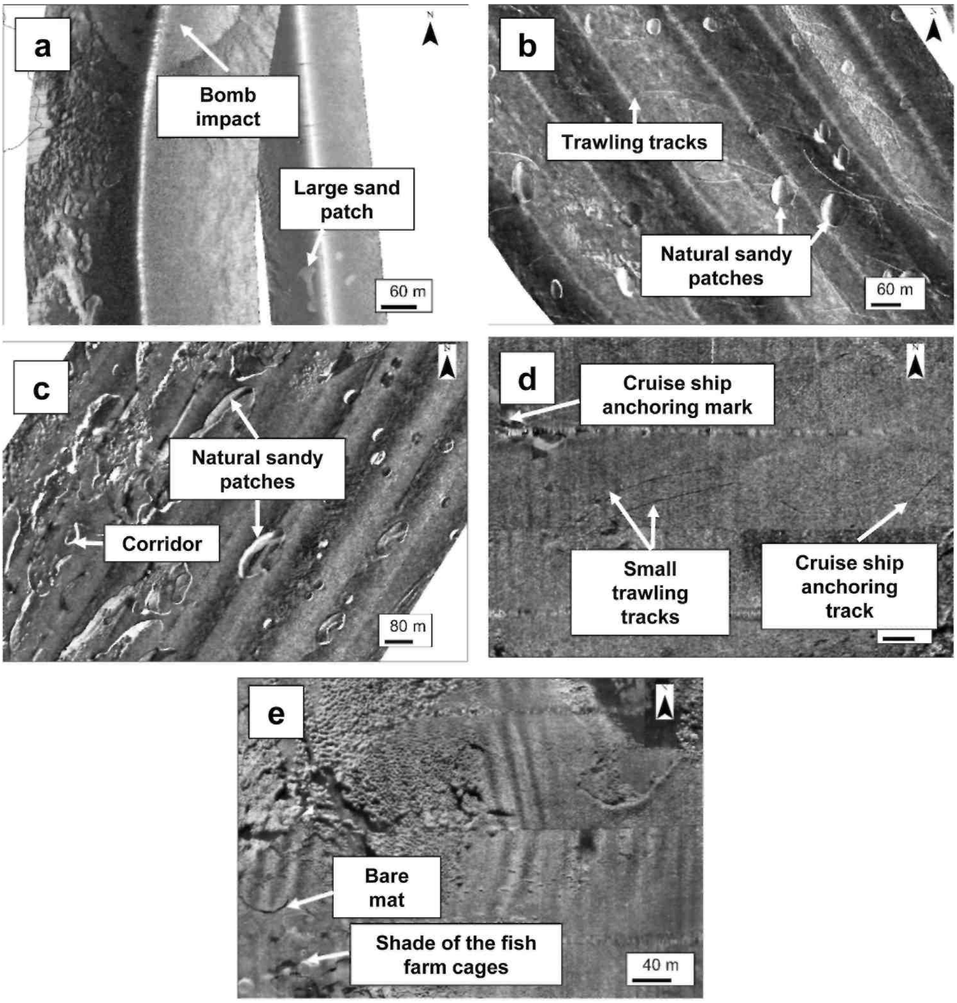
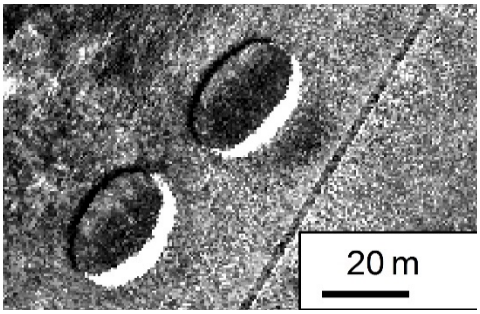
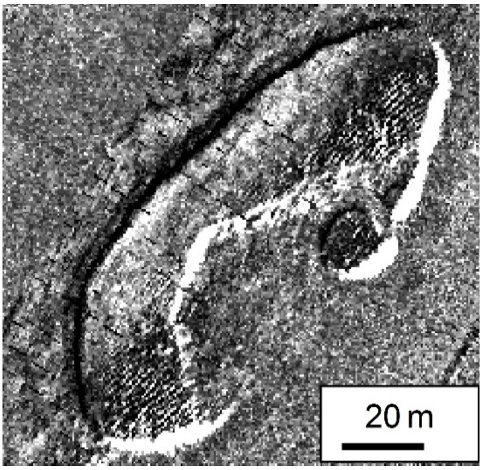
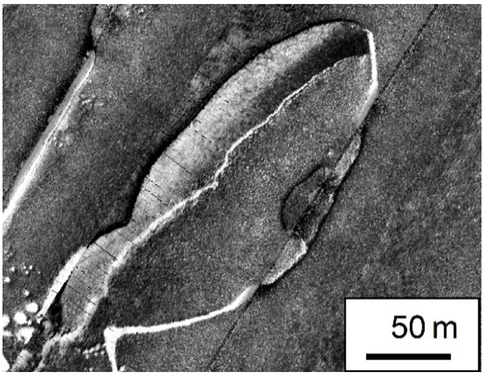
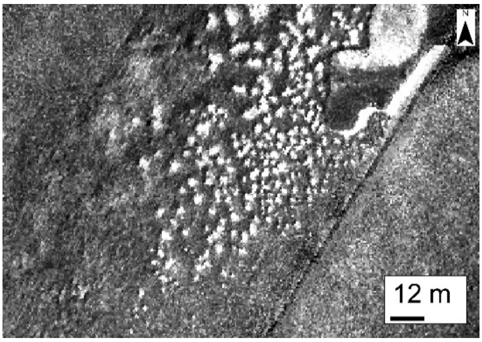
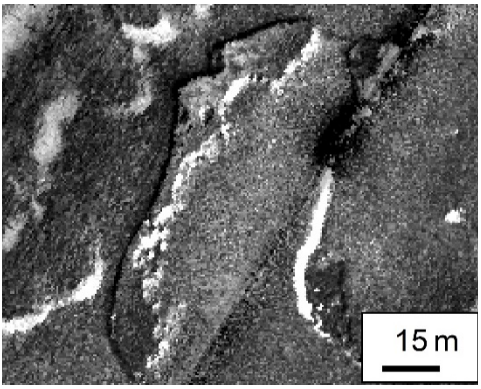
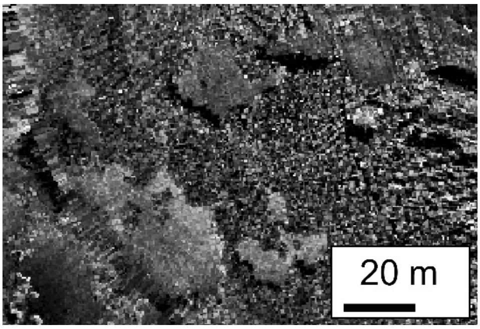
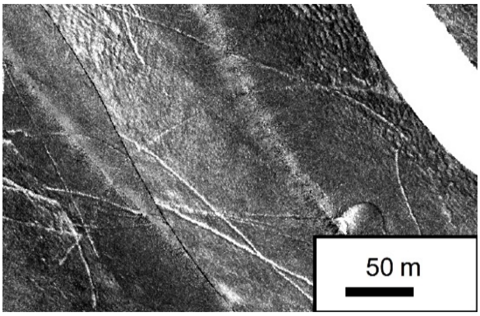
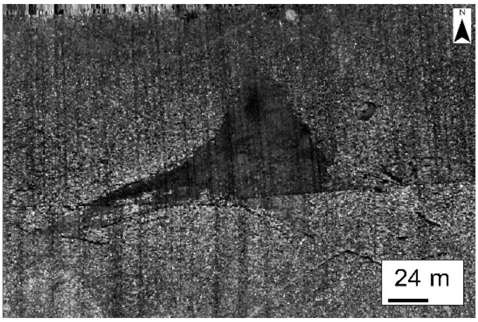
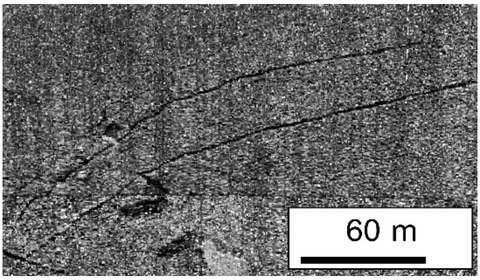
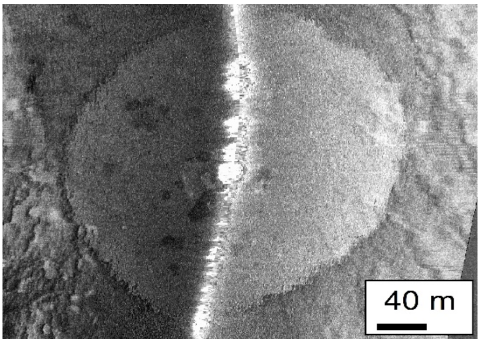
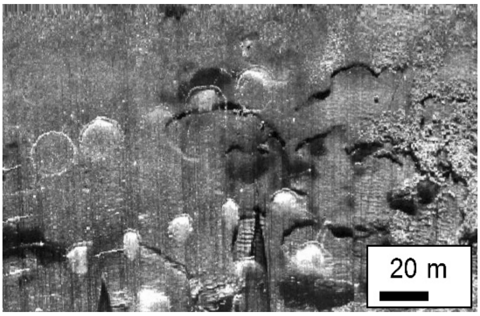


Figure 45: *Examples of sonar interpretation of patches inside* P. oceanica *meadows for each site considered (a) South Macinaggio, (b) Biguglia, (c) Urbinu, (d) Calvi and (e) Ajaccio.*

***Table 12**: Description of the different types of patches identified inside* P. oceanica *meadows during this study.*

Sonogram	Designation	Description
	Ovoid patch (OP)	Ovoid shape with a length ranging from 20 to 60 m and a width from 15 to 30 m. Parallel to the coast. Observed from the lower limit of the meadow to 20 m deep. Most probably generated by the water movement
	Colonized patch (CP)	Ovoid shape with a triangle-like part recolonized by the meadow with a length ranging from 20 to170 and a width from 15 to 65 m. Parallel to the coast. Observed from 15 to 25 m deep. Most probably generated by the water movement
	Large sand patch (LSP)	"Banana" shape with a length ranging from 70 to 500 m and a width from 30 to 50 m. Parallel to the coast. Observed from 20 to 15 m deep. Most probably generated by the water movement

	Small sand patch (SSP)	Small round craters with a width ranging from 1.5 to 6 m) that can link themselves and form narrow corridors. Mainly observed near larger patches like large sand patches or sand corridors from 20 to 10 m deep. Most probably generated by the water movement
	Sand corridor (SC)	Channel shape with a length ranging from 10 to 350 m and a width from 2 to 20 m. Parallel to the coast. Observed from 20 to 10 m deep. Most probably generated by the water movement
	Bare mat (BM)	Mainly observed nearby the lower limit of the meadow but also frequently observed at lower depths. Patches of bare mat have irregular shapes and sizes. Certainly generated by winter storms and also by human activities. Possible confusion between the natural and the anthropogenic origins
	Trawling tracks (TT)	Long (100 m - 1 km) and narrow (2-4 m) corridors generated by trawling in the meadow. Observed from 2 m to the lower limit of the meadows

	Anchoring patch (AP)	"Funnel" shape with a length ranging from 60 to 120 m. Parallel to the coast line certainly due to the main wind orientation. Observed from 20 to more than 30 m deep. Generated by the anchoring of cruise ships.
	Anchoring tracks (AT)	Corridors similar to trawling tracks but shorter (less than 250 m) and narrower (less than 2 m). Generated by both cruise ships and smaller leisure boats. Observed from 10 m to 35 m.
	Bomb impact (BI)	Circular patch generated by the impact of bombs mainly during the World War 2 or more recently by mines and explosive fishing. Their diameter ranges from several decameters to 250 m. Observed at all depths in the meadows
	Fish farm patch (FFP)	Bare mat patches nearby a fish farm generated by the shadow of the cages and the increase of the organic matter load. The acoustic image of the cages is visible. The extent of the patches varies according to the number of cages and their size. Generally, it occurs at a depth ranging from 15 to 25 m

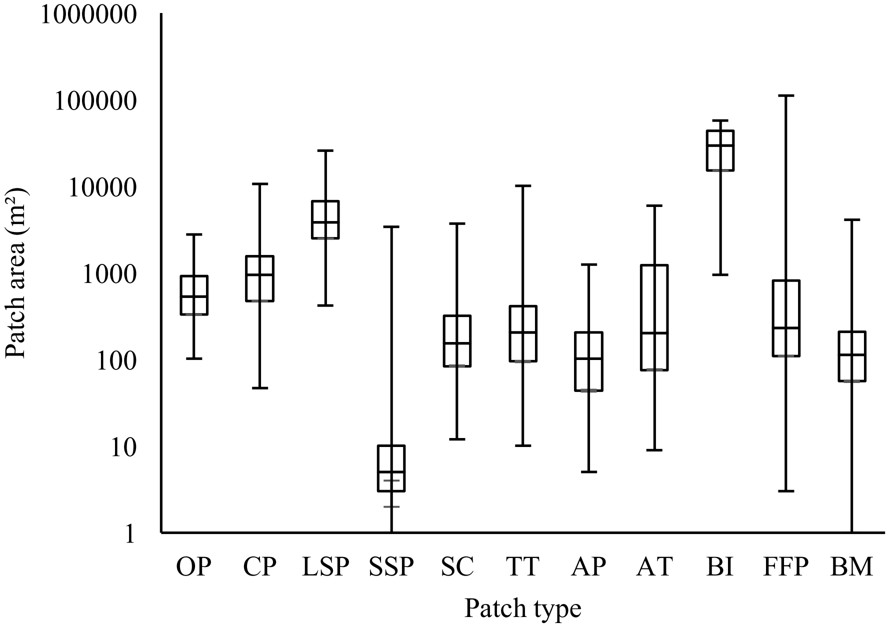


Figure 46: *Box plot representation of the surface areas of patches observed on all sites according to their type. The area is expressed through a logarithm scale. Black bars represent minimum and maximum patch areas. OP: ovoid patch; CP: colonized patch; LSP: large sand patch; SSP: small sand patch; SC: sand corridor; TT: trawling tracks; AP: anchoring patch; AT: anchoring tracks; BI: bomb impact; FFP: fish farm patch; BM: bare mat.*

3.2. Seascapes features

At a seascape level, the different sites showed great variations in their landscape indices and REI values leading to various *P. oceanica* seascapes (Tab. 13). The number of patches (NP), ranges from 66 in the South of Macinaggio to 1 473 in Urbinu. Concerning the patch density (PD) the site of Biguglia looked as the patchiest (291.5 patches.m^{-2}) whereas the South of Macinaggio was the lesser one (12.5 patches.m^{-2}) (Tab. 13). The mean size of patches (AREA_MN) reached its highest value in the South of Macinaggio (80 160 m^{2}) and its lowest in Calvi (4 186 m^{2}). The mean distance of patches gravity center from their border (GYRATE_MN) showed high variations too, from 33.34 m in the South of Macinaggio to 3.98 in Urbinu. By taking into account their area with the area-weighted radius of gyration (GYRATE_AM), its values greatly increased, from 1 056.50 m in the South of Macinaggio to 510 in Calvi. It means that in a landscape-centric perspective the necessary distance to reach the edge of a patch will grow longer respectively for Calvi, Urbinu, Ajaccio, Biguglia and the South of Macinaggio. A high coefficient of variation (ENN_CV) of the mean distance between each patch for each site was observed, describing a high spatial heterogeneity in patch arrangements for all sites (Tab. 13). The Landscape Division Index (DIVISION) values reflect low divided meadows for the sites of Calvi, the South of Macinaggio and Biguglia whereas the sites of Ajaccio and Urbinu are more fractionated. The exposition of the sites to wave action illustrated by the REI showed contrasted values that discriminate the sites in three groups. Ajaccio was relatively not exposed (253) whereas Calvi (1 855) and Urbinu (3 239) were well exposed to wave action, when Biguglia (11 038) and the South of Macinaggio (15 161) are very exposed (Tab. 13). Using the PaSI on the sites studied, it ranked 0.412 for Ajaccio, 0.350 for Calvi, 0.547 for the South of Macinaggio, 0.591 for Biguglia and 1 for Urbinu, revealing contrasted sources of patchiness (Tab. 13).

Table 13: *Surface of the area and the P. oceanica meadows, landscape indices, REI and PaSI values for the five sites studied. S: seascape: C: class.*

	Metric level	Ajaccio	Calvi	South Macinaggio	Biguglia	Urbinu
Surface of the area studied (km²)	S	2.451	1.858	3.583	4.423	2.129
Total meadow surface (km²)	S	2.201	1.765	3.394	4.167	1.849
Number of patches (NP)	C/S	98	444	66	1 290	1 473
Mean patch area (AREA_MN) (m²)	C/S	24 995	4 186	80 160	5 875	13 744
Patch density (PD) (patches.km^{-2})	S	40.0	238.9	12.5	291.5	72.8
Mean radius of gyration (GYRATE_MN) (m)	C/S	18.73	9.22	33.34	8.27	3.98
Area-weighted radius of gyration (GYRATE_AM) (m)	C/S	663.43	510.2	1 056.50	871.99	522.05
Coefficient of variation of the Euclidean nearest-neighbor distance (ENN_CV) (%)	C/S	203.35	213.4	253.24	383.51	291.19
Area-weighted perimeter-area ratio (PARA_AM)	C/S	180	578	108	809	470
Landscape Division Index (DIVISION)	C/S	0.185	0.098	0.1019	0.1222	0.2524
REI	C/S	253	1 855	15 161	11 038	3 239
PaSI	S	0.412	0.350	0.547	0.591	1.000

3.3. Seascape versus class scale

The analysis through PCA of the metrics at the scale of the landscape and the patch type presented contrasted results. The five sites appeared to be well discriminated (Fig. 47) but these differences are mainly due to the landscape characteristics of a small number of patch type (Fig. 47). Thus this phenomenon was partly driven by the small sand patches and the trawling tracks in Biguglia (SSP_BIG and TT_BIG), the anchoring patch in Calvi (AP_CAL), the fish farm patches and the anchoring tracks in Ajaccio (FFP_AJA and AT_AJA), the bomb impact in the South of Macinaggio (BLMAC) and the small sand patches in Urbinu (SSPJJRB) (Fig. 48). The large sand patches of Urbinu, South Macinaggio and Biguglia (respectively LSP_urb, LSP_MAC and LSP_BIG) form a group discriminated from the other patches because of their large surface (AREA_MN) and their elongated shape (GYRATE.MN) (Fig. 48).

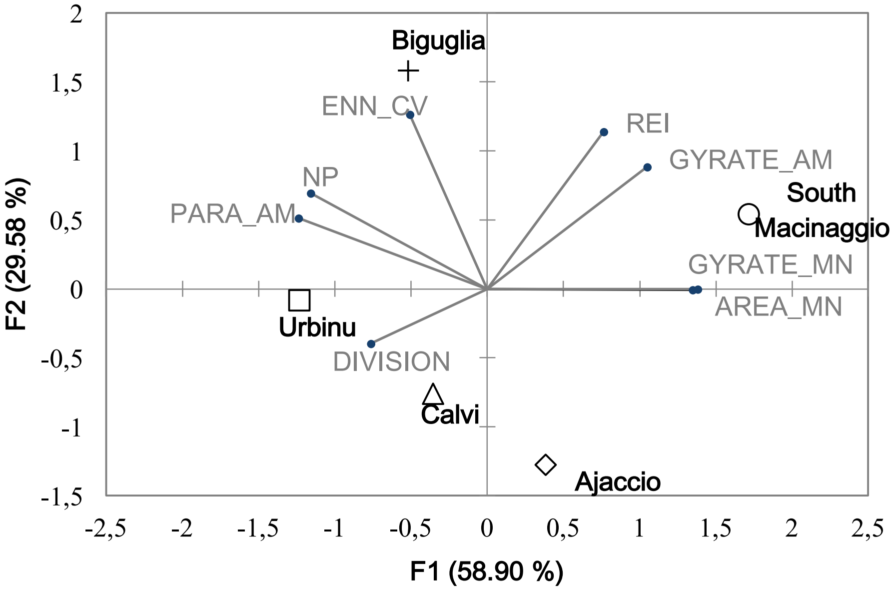


Figure 47: *Biplot of the principal components analysis (PCA) showing variations in landscape characteristics for the five sites studied according to the metrics selected (red lines). The percentage reflects the proportion of variance expressed by each axe. Ajaccio:◇; Calvi:△; South Macinaggio:○; Biguglia: +; Urbinu:□.*

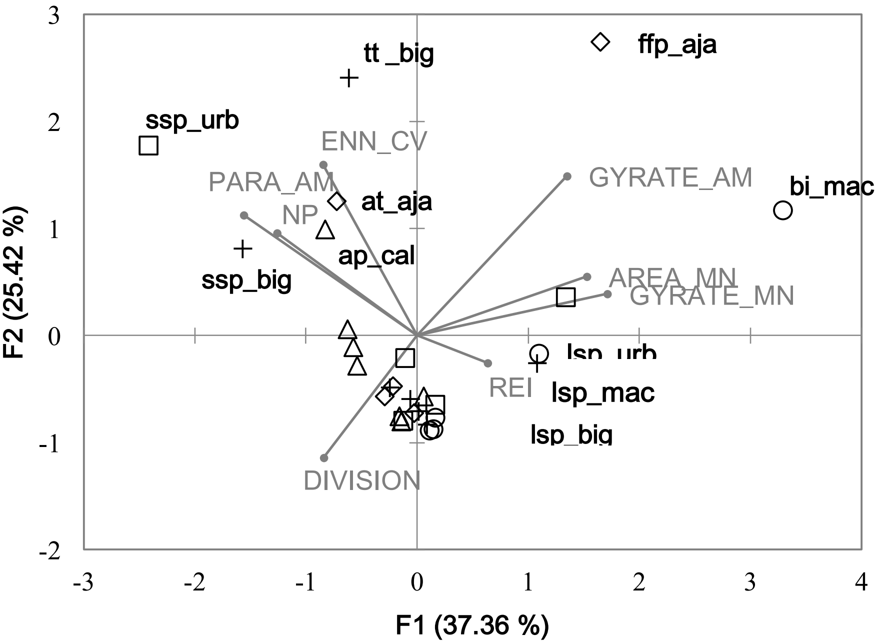


Figure 48: Biplot of the principal components analysis (PCA) of the metrics selected at the class level for the five sites studied. The percentage reflects the proportion of variance expressed by each axe. ap: anchoring patches: at: anchoring tracks: bi: bomb impact: ffp: fish farm patches: ssp: small sand patches: tt: trawling tracks: lsp: large sand patches: cal: Calvi (Δ): mac: South Macinaggio (○); big: Biguglia (+); aja: Ajaccio (◊); urb: Urbinu (□).

At the landscape scale the cumulative percentage of variance was almost 90% for the two axes. The variable loadings obtained from the PCA of the landscape metrics were high (>0.3 or < -0.3), except for the division index (DIVISION). This result indicates that the metrics selected were relevant to describe the patchiness of the landscape (Tab. 14). A different assessment was made concerning the variable loadings from the class level analysis. The two axes cumulated only 63% of the percentage of variance and the REI appears not to be relevant for a study at a patch type scale (Tab. 14).

Table 14*: Principal components analysis (PCA) eigenvalues and variable loadings for the selected indices at the landscape and the patch type scale. Variables in bold are considered strong (>0.3 or <-0.3).*

	Axis 1	**Axis 2**
Seascape level		
Eigenvalues	4.77	1.81
Percentage of variance	59.65	22.67
Cumulative percentage of variance	59.65	82.32
Variable loadings		
NP	**0.38**	**0.32**
AREA_MN	**-0.45**	0.00
GYRATE_MN	**-0.46**	0.00
GYRATE_AM	**-0.35**	**0.41**
PARA_AM	**0.41**	0.24
ENN_CV	0.17	**0.59**
DIVISION	0.25	-0.18
REI	-0.25	**0.53**
Class level		
Eigenvalues	8.50	6.32
Percentage of variance	35.65	25.93
Cumulative percentage of variance	35.65	61.58
Variable loadings		
NP	**-0.30**	**-0.36**
AREA_MN	**0.48**	-0.15
GYRATE_MN	**0.50**	-0.12
GYRATE_AM	**0.37**	**-0.49**
PARA_AM	**-0.40**	**-0.42**
ENN_CV	-0.20	**-0.56**
DIVISION	-0.25	**0.32**
REI	0.19	0.02

4. Discussion

4.1. From natural to anthropogenic *Posidonia oceanica* seascapes

This paper used side scan sonar images and cartographies of seagrass meadows in order to describe and establish a new nomenclature for *P. oceanica* patches and to perform an analysis of their characteristics at the large spatial scale of the seascape.

The first identifications and classifications of *P. oceanica* meadows were based on the observation of isolated patches at a small scale (Molinier & Picard 1952, Boudouresque & Meinesz 1982). This fact can be explained by the use of scuba diving prospections. Furthermore, anthropogenic patches were not considered as a component of the *P. oceanica* seascapes, only natural assemblages being described. Thus, the patches generated by human activities were studied independently. Our study demonstrated that nowadays certain *P. oceanica* seascapes are mainly characterized by some types of patches that can be of anthropogenic origin. That is why we advise to use a new nomenclature that define precisely each type of patch. The next step was the study of their relation to assess the *P. oceanica* seascapes structure. The patches attributes allow inferring on their possible origin.

Among the 11 types of patches, the five natural ones appear to be linked through their shape, size and bathymetric zonation (Fig. 49). The water movement should play an important role and this is true even at the level of the lower limit (Vacchi *et al.* 2012, Pergent *et al.* 2014). This hypothesis is supported by the fact that the majority of natural patches encompass a matt cliff facing the shore eroded by the water movement induced by wave action, and a part facing the lower limit recolonized by the surrounding meadow (Boudouresque *et al.* 1980b, Blanc & Jeudy De Grissac 1984, Boudouresque *et al.* 2012). Thus a scenario of the structures succession may be envisaged from the lower to the upper limit of the meadow and/or according to water movement intensity. Given the slow growth rate of *P. oceanica* rhizomes (Gobert *et al.* 2006a, Di Maida *et al.* 2013), these various types of patches would appear almost motionless at human time scale so the seascapes they form appear not to change. This pattern is in opposition with other seagrass meadows which show seasonal appearances and disappearances of gaps (Patriquin 1975, Bell *et al.* 1999).

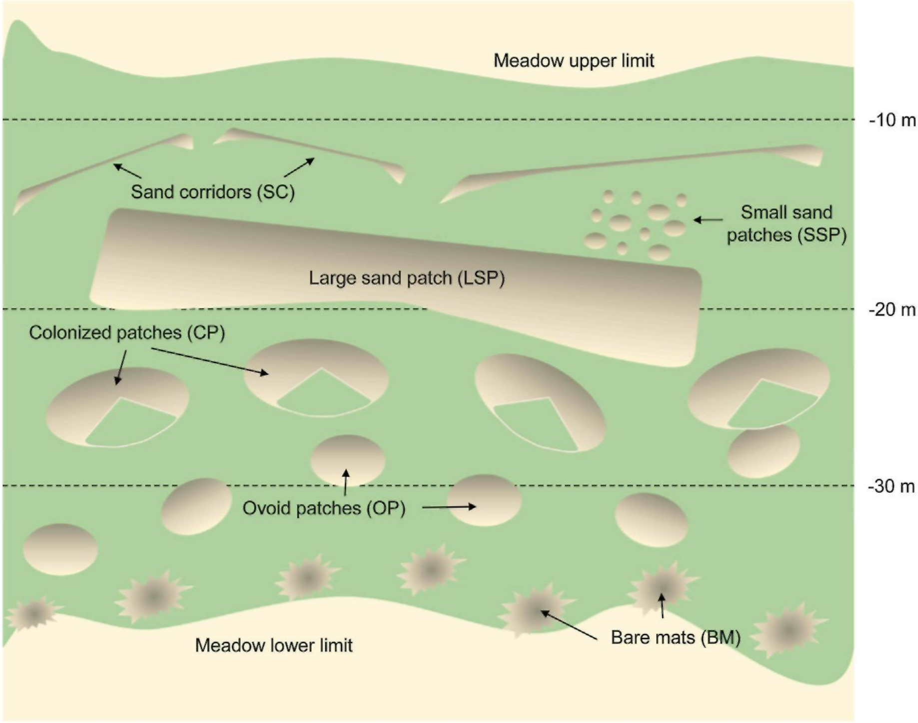


Figure 49*: Diagram of the bathymetric zonation of the different natural patches.*

Conversely, patches generated by anthropogenic activities (trawling, anchoring, bombs, fish farms) modify more rapidly their size and shape through the processes of recolonization or erosion (Meinesz & Lefèvre 1984, Francour *et al.* 1999, Pergent-Martini *et al.* 2006, Kiparissis *et al.* 2011). The natural and anthropogenic patches can be found at the same sites (Calvi, Biguglia) within a short range distance and often interact. For instance, the trawling tracks (TT) going through the matt cliff of ovoid (OP) and colonized patches (CP) at Biguglia should accelerate the erosion and create a corridor in the recolonized part, thus modifying the substrate nature and the faunal communities (Sánchez-Jerez & Ramos Esplá 1996).

Considering the bare mat (BM) areas it is hard to settle their origin (Moreno *et al.* 2001) using their shape and size only. However it is possible to determine it according to their location, like the anthropogenic ones near a sewage dredging (Pergent-Martini *et al.* 1995).

4.2. Metrics relevance

The landscapes indices advised by Sleeman *et al.* (2005) to investigate the patchiness of seagrass meadows look as being relevant in the study of the patches arrangement in *P. oceanica* meadows except for the division index (DIVISION). Thus, even if DIVISION loadings are strong (≥ 0.3 or ≤ -0.3) at the patch type level (Tab. 14), this metric does not vary enough in this study to describe patch class impact. This aspect is explained by its definition and the parameters this index encompasses (Tab. 10).

The Relative wave Exposure Index (REI) seems not informative enough at the scale of the type of patches. It does not encompass in its computation the depth (Infantes *et al.* 2009), a very important factor in the case of the seagrasses (van Katwijk & Hermus 2000, Sundblad *et al.* 2014). It is nevertheless interesting to notice that the bathymetric succession of natural structures was mainly observed in sites were the REI was high *i.e.* Biguglia, Urbinu and Calvi. Water movement being one of the main driver of fragmentation in seagrass meadows (Koch *et al.* 2006), more sensitive tools with the same easiness of use than the REI must be developed.

4.3. The Patchiness Source Index (PaSI)

The list of patches used to calculate the Patchiness Source Index (PaSI) is not exhaustive and can be modified according to the area studied. The bare mats ought to be associated with the natural or anthropogenic patches when their origin can be determined. In practical view, maps used for the calculation of the PaSI require more time of treatment because of the need of identifying at least the origin of each patch. This is why this index is more suitable for a use at a lesser or the same scale than in the present study *i.e.* on an area of several km². Although describing one aspect of the patchiness in *P. oceanica* meadows, this index doesn't make any assessment of its degree, other metrics being already available for this task (Moreno *et al.* 2001, Montefalcone *et al.* 2006a, Montefalcone *et al.* 2010b). It does not reflect the intensity of the human impact either. Finally, this index may also be applied on other seagrass meadows presenting both natural and anthropogenic patches.

Conclusion

The high resolution of side scan sonar images allows to study patches nature in *P. oceanica* meadows at a large scale and to investigate seascapes features. The different types of patches making up the meadows ought to lead to different *P. oceanica* seascapes according to their shape and their arrangement between one another. Their classification in accordance with landscape metrics leads to the assessment of the main origin (natural or anthropogenic) of the meadow patchiness for a given site. Patches should evolve at various speeds according to their origin, class and the impact of human activities. They are thus an important component in the functioning of the ecosystem based on *P. oceanica* meadows providing a wide variety of habitats. This approach, the examination of the seascapes structure, is only the first part of a study in the field of landscape ecology which also takes an interest in the function and the changes (Turner 1989, Sleeman *et al.* 2005).

The fragmentation (the evolution of patchiness) of the meadows leading to contrasted and complex *P. oceanica* seascapes takes place through several mechanisms and spatial scales. A natural long term process induced by water movement (Boudouresque *et al.* 2012, Vacchi *et al.* 2012) is thus opposed to an anthropogenic shorter one (Ardizzone *et al.* 2006). The anthropogenic processes show also different rates of fragmentation according to the type of impact, *e.g.* physical damages (anchoring, trawling) fragment the meadow more quickly than pollution. Nevertheless, this establishment should be modified in a near future. In the case of the natural patches, global climate changes and the increase of extreme events like storms could boost the erosion of the meadows

(Pergent *et al.* 2014). That is why a better understanding at a small scale of the natural patches dynamic (*e.g.* chemical processes in sediments, rate of erosion/recolonization) could bring a new light on the evolution of *P. oceanica* seascapes. Likewise, seascapes characteristics should be encompassed in indices that aim to assess the quality of the environment, these metrics being now interested in the whole functioning of the ecosystem based on *P. oceanica* meadows (Personnic *et al.* 2014).

Article 5: Seascape ecology, a gateway for the management of seagrass meadows

Abstract

Seagrass meadows are marine habitats found in shallow water temperate and tropical coastal areas worldwide that have a high ecological and economic importance. Amongst the 60 or so seagrass species, the endemic Mediterranean species *Posidonia oceanica* forms meadows that are arguably the most important shallow water coastal habitat in the region but which are subjected to high anthropogenic pressures. Because of the relatively large size of the plant, the meadows formed by this seagrass have high meadow architectural and morphological complexity, which results in different morphotypes or seascapes. While numerous studies of *P. oceanica* architectural characteristics for typical continuous meadows are available, few works have addressed seascape ecological features, and the influence of environmental factors (natural and anthropogenic) thereon. In the present review we give an overview of *P. oceanica* meadow architectural and morphological characteristics and how these contribute to Mediterranean landscapes and seascapes. Studies addressing the influence of natural and anthropogenic factors on morphometric features of different meadow types and landscape ecological characteristics of *P. oceanica* habitat are also reviewed, as well as their influence on the associated biota. Finally, by considering the available data and tools for seascape studies, we present a discussion on methods to assess seagrass seascapes within the framework of coastal management.

Keywords: seagrass; seascape; *Posidonia oceanica*; management; structure; function; review

1. Introduction

A landscape can be defined as a shifting arrangement of biotic structures and the resulting mosaic of patches (Fig. 1) (Robbins & Bell 1994). In turn, the patches are surrounded by a border called an 'edge' (Fig. 1), which delimits different adjacent habitats (Pickett & Cadenasso 1995). The whole structure is embedded within a matrix which plays a major role in connecting patches, thus ensuring landscape functioning (Fig. 50) (Forman & Godron 1986). Within this context, landscape (or 'seascape' when dealing with marine habitats) ecologists aim to study the structure (morphology and size), function (functional ecology) and changes (evolution) of these biotic systems (Turner 1989).

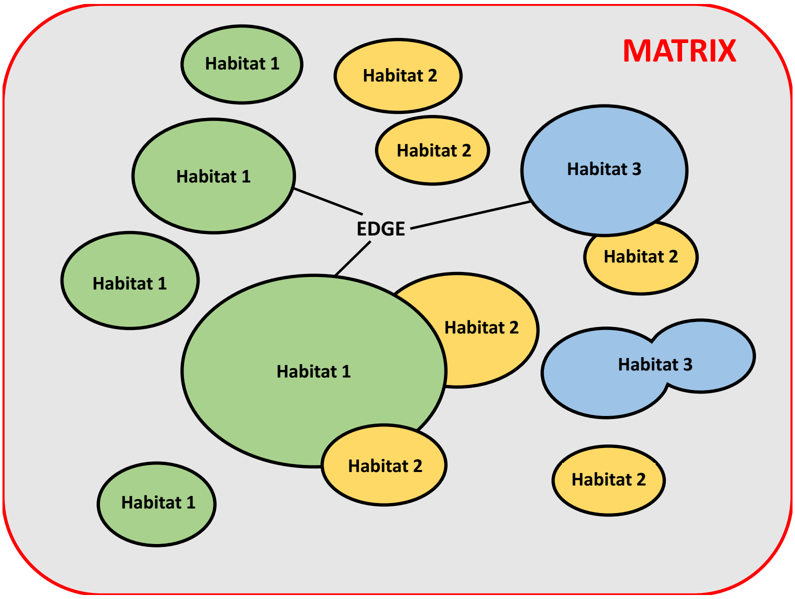


***Figure 50**: Conceptual representation of different habitat compartments forming a landscape (or seascape).*

Landscape ecology has been applied to terrestrial habitats in Europe since the beginning of the 1940s, mainly within the context of studies of small areas, which were partly based on classification systems and nomenclatural schemes originally developed by botanists focusing on terrestrial plant communities. In contrast to the 'European school', the 'American school', which has mainly featured since the early 1980s, has focused more on landscape modelling and studies carried out on a larger scale (McGarigal 2015).

In the mid- to late 1980s, one of the first seascapes to benefit from the attention of marine ecologists are those formed by seagrass meadows, with most studies focusing on the associated motile invertebrates and fishes (Bell & Westoby 1986, Bell & Hicks 1991). On the other hand, descriptions of different *Posidonia oceanica* meadow types and formations of the seagrass have been available since the early 1950s (Molinier & Picard 1952, 1954, Clairefond & Jeudy De Grissac 1979, Boudouresque *et al.* 1980b, Boudouresque & Meinesz 1982, Boudouresque *et al.* 1985a, Boudouresque *et al.* 1990c, Boudouresque *et al.* 2012). In the past 15 years or so, the number of seascape studies have increased sharply and numerous works have incorporated tools used in the study of seascape ecology to characterize meadows formed by marine magnoliophytes. This field of study has recently started to be referred to as ’marine space ecology’ (Li & Mander 2009, Boström *et al.* 2011).

The definition of a *P. oceanica* seascape (and more generally of any seagrass seascape) will vary according to substratum type *e.g.* sand, bare mat and rock (Pagès *et al.* 2014), while the meadows themselves also comprise a matrix (Abadie *et al.* 2015b). Seagrass habitat structure can be viewed at various levels - from within-meadow architectural features to gross meadow morphology; the latter ranging from continuous to patchy. The function of seagrass seascapes includes the influence of meadow structure on the associated biota. Lastly, change corresponds to the evolution over time of seagrass habitat structure and/or function. All these aspects can be studied at various spatial scales, from a few square centimeters to hundreds of kilometers. Hereafter, we use ‘small scale’ in the context of an area covering less than 1 km^2, and ‘large scale’ within the context of an area larger than 10 km^2.

The practical value of data from seascape studies is their use to manage marine habitats and to model their evolution taking into account the ecosystems’ key species (Boström *et al.* 2011). Although this approach is commonly used in terrestrial ecosystems management and conservation (Turner 1989, Zonneveld 1995), it is seldom applied to coastal seascapes (Li & Mander 2009), including seagrass meadows (Pittman *et* *al.* 2011). In part, this results from the lack of available data on the link between the occurrence and distribution of species associated and seagrass meadow structure (Boström *et al.* 2006a).

The present review aims to highlight the importance of the seascape approach in the management of seagrass meadows through use of a well-documented species - *P. oceanica* – as example. In the present work we assessed previous seagrass seascape studies in order to: (1) highlight the main architectural characteristics of different *P. oceanica* meadow types; (2) indicate the influence of main natural and anthropogenic factors on *P. oceanica* habitat; (3) describe the role played by *P. oceanica* seascapes on the associated biota; and (4) evaluate the contribution of *P. oceanica* meadows to the Mediterranean seascape. Finally, we identify gaps in knowledge to propose future work within the field of seascape ecology and management, as applied to *P. oceanica* and other seagrass habitats.

2. Bibliographical research

A bibliographical search of seagrass seascape studies was first undertaken without restricting to any one particular seagrass species. References to *in situ* studies were extracted from previous reviews concerning seagrass seascapes (Kendrick *et al.* 2005a, Boström *et al.* 2006a, Connolly & Hindell 2006, Horinouchi 2007, Heck *et al.* 2008, Grober-Dunsmore *et al.* 2009, Boström *et al.* 2011, Vacchi *et al.* 2016). In order to complete this first approach, a search was then performed using the Scopus and Google Scholar data bases, using the keywords ‘seagrass’, ‘landscape’, ‘seascape’, ‘patch’, ‘structure’ and ‘architecture’.

All references were then classified according to the field of study in seascape ecology, referring to the subjects of interest defined by Turner (1989), i.e. the structure (S), function (F) and changes (C). Furthermore, the method and spatial scale of each study was addressed by using a qualitative symbology scheme (Tab. 15).

Table 15*: symbology for sampling methods and spatial scales considered in seagrass meadow studies used in the present bibliographical search.*

	Area	Symbol
Method		
Quadrats and sampling spots	Tens of cm^2	Q
Transects (scuba diving, video, trawling)	Hundreds of m^2	T
Small patches	Less than 10 m^2	SP
Large patches	Tens of m^2	LP
Mapping (cartography, grid model)	Exhaustive	M
Area studied		
Small scale	<1 km^2	SSS
Medium scale	1-10 km^2	MSS
Large scale	>10 km^2	LSS

3. *Posidonia oceanica* seascape characteristics

3.1. Available literature on *Posidonia oceanica* seascape ecology

The first work that makes reference to *P. oceanica* seascape was undertaken by Molinier and Picard (1952) along the French Mediterranean Coast. This study described ‘intermatte’ features, *i.e.* sand patches or channels present amongst the *P. oceanica* meadows and presumably resulting from the effects of bottom currents that are a residual product of wave action. Following this relatively early study, it was not before 1998 that the number of seagrass seascape studies started to increase (Fig. 51), reaching a total of 157 scientific works to date. The main species studied are *Zostera marina* and *Posidonia oceanica*; 23 % and 34 % of all published works respectively. When considering the total number of works reviewed (Fig. 52), studies carried out at the small spatial scales (SSS) are more numerous and comprise 53 %. However, studies carried out at large spatial scales (LSS) increased in number since the mid-2000s, reaching 30 % of the total published works (Fig. 52). It is noteworthy that the first work undertaken at a large spatial scale was focused on *P. oceanica*. When considering study methods, mapping (M) at various spatial scales appears to be the most popular methodology to study seagrass seascapes (40 %), followed by quadrat sampling and discrete sampling (Q-DS) techniques, which represent 27 % of published works (Fig. 53). Details of the whole bibliographical search are available in Annex 10.

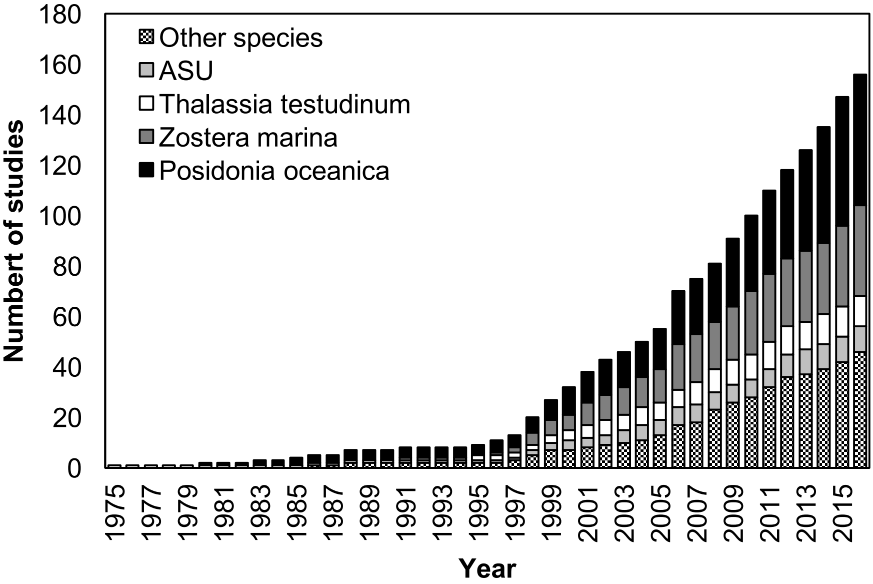


Figure 51*: Cumulative number of studies concerning seagrass seascape ecology published from 1975 to 2016. ASU: artificial seagrass unit.*

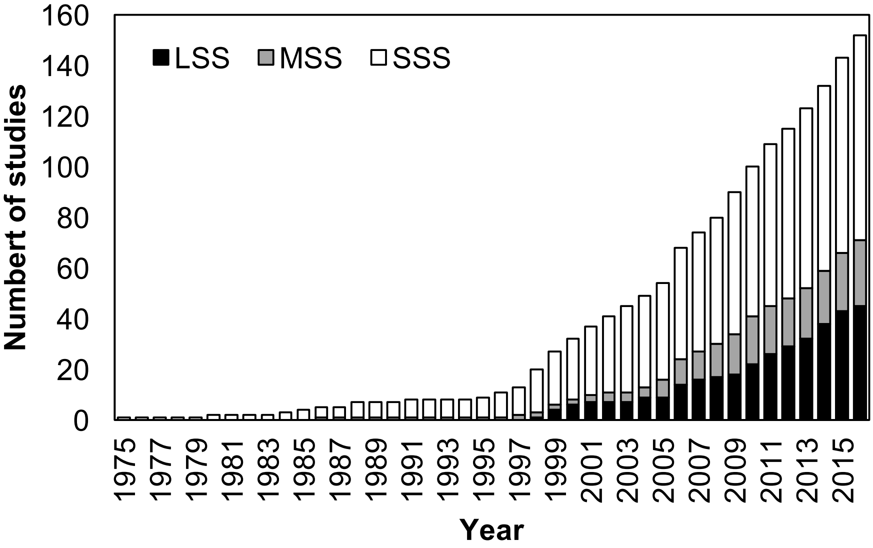


Figure 52: *Cumulative number of studies, categorized according to spatial scale addressed, published from 1975 to 2016. LSS: Large scale; MSS: medium scale; SSS: Small Scale.*

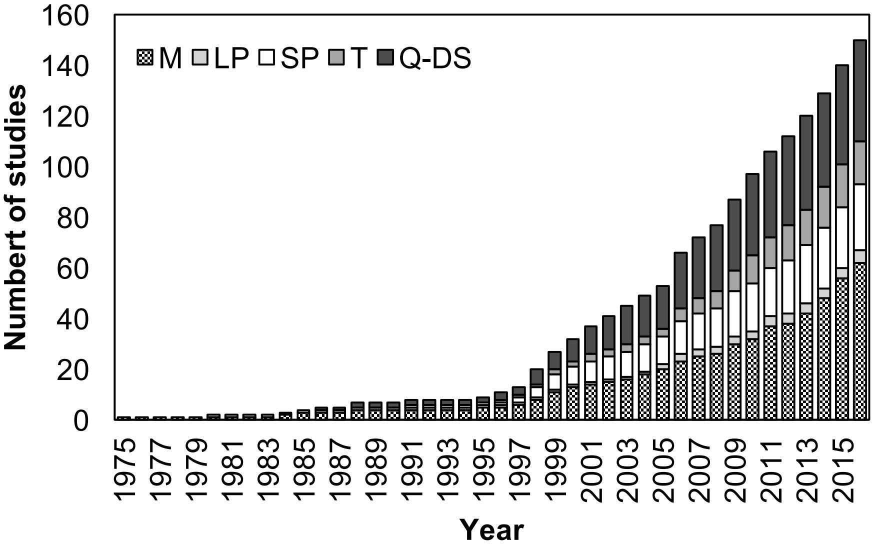


Figure 53: *Cumulative number of studies categorized according to study methodology, published from 1975 to 2016. SP: Small Patch; LP: Large Patch; M: Mapping; T: Transect; Q-DS: Quadrat-Discrete Sampling.*

3.2. *Posidonia oceanica* within-meadow architectural characteristics

3.2.1. Two-dimensional features

Development of heterogeneous *P. oceanica* seascapes at the large spatial scale starts at the genetic level. More specifically, genetic diversity is correlated with meadow shoot density; the slow stolonization rate (asexual reproductive process of a *P. oceanica* shoot) over a long temporal scale leading to an increase of shoot density at the center of isolated patches (Zupo *et al.* 2006a). The separation of two distinct branches on a single *P. oceanica* rhizome thus depends on an internal biological clock (Molenaar *et al.* 2000). After the development of new shoots, their orientation (orthotropic or plagiotropic) can be reversed (Molenaar *et al.* 2000) in order to adapt to a change in environmental factors, such as sedimentation or the availability of unvegetated substrata that can be colonized. No competition is observed between the new shoots and no increase in leaf size is observed when shoot density decreases (Panayotidis *et al.* 1981). However, an opposite phenomenon is observed when taking into account the sediments chemistry (*e.g.* pH, nutrients concentrations, redox potential) (Gobert 2002). Differences in morphology, growth rate, leaf length and density mainly occur at small spatial scales (Balestri *et al.* 2003, Borg *et al.* 2005, Zupo *et al.* 2006b). Under disturbances, Marbà *et al.* (1996) reported a shoot recruitment rate of *P. oceanica* that unbalanced the mortality rate, thus leading to a slowly decreasing shoot density.

Specific features of shoots making up *P. oceanica* seascapes that vary at a very small scale, *i.e.* < 1 m², lead to changes in shoot density at a larger spatial scale. This assertion has been verified at the spatial scale of hundreds of meters by Gobert *et al.* (2003) who noted the largest variation of meadow structure between 8 and 12 m depth, and which were attributed to some internal plant mechanism. Borg *et al.* (2005), who compared the within-meadow structure of reticulate and continuous meadows, observed no differences between the two meadow types over the different spatial scales. Differences in shoot density will lead to parts of a seagrass meadow that have less resistance against erosive forces (*e.g.* sea currents and physical damage from anthropogenic activities), leading to the generation of patches at the seascape scale (Panayotidis *et al.* 1981) and development of different meadow morphotypes.

3.2.2. Three-dimensional structure

Far from being a flat and homogenous structure, meadows of *P. oceanica* that contribute to a seascape are vertically structured as a result of their complex within-meadow architectural features. The leaf canopy acts as a trap of both organic and inorganic particles, with the leaves preventing their resuspension (Dauby *et al.* 1995). Gacia and Duarte (2001) assessed resuspension of particles within a *P. oceanica* meadow and noted that this was lower by a factor of 3 compared with a bare sediment bottom. The particle retention rate is increased by a factor of 5 during periods of exposure to erosion (*e.g.* during winter storms) (Gacia *et al.* 1999). Accumulation of the trapped sediment particle results in an elevation of the seabed, leading to corresponding vertical growth of *P. oceanica* rhizomes (Boudouresque & Meinesz 1982, Boudouresque *et al.* 1983). The complex formed by sediments, living/dead roots and rhizomes is called “matte” (Boudouresque & Jeudy De Grissac 1983, Gobert *et al.* 2006a). This structural component, which can be several meters thick (López-Sáez *et al.* 2009), serves as an important carbon store (Mateo *et al.* 1997, Pedersen *et al.* 2011) while its dynamics are strongly linked to the seascape structure of *P. oceanica* meadows.

3.3. Impacts of natural and anthropogenic factors on *Posidonia oceanica* seascapes and within bed architecture

Posidonia oceanica seascapes are strongly influenced by both natural and anthropogenic factors which define their shape, and thus their function, at various scales.

3.3.1. Natural factors

Among natural factors, water movement, such as that associated with waves and currents, appears to be a main factor influencing the *P. oceanica* meadow structure at both within-meadow and seascape scales.

However, this cannot always be verified as shown by Borg *et al.* (2009) who observed that high patchiness was not always linked with a high exposure (Tab. 16).

At shallow water depths, strong bottom currents and the mechanical action generated by wave breaking prevent establishment of *P. oceanica* meadows. This has been confirmed by Infantes *et al.* (2009) who report that a current velocity higher than 40 cm.s^{-1} compromises colonization by the plant (Tab. 16). Similarly, Pace *et al.* (in press) show that at shallow depth (6-11 m depth), high energy wave climate leads to an increase of meadow patchiness and a decrease in the architectural complexity. At greater water depths, even if negligible, currents derived from wave energy result in a decrease of meadow cover resulting in the generation of patches of different bottom type (bare matte or sandy bottom) (Vacchi *et al.* 2010, Gobert *et al.* accepted). Furthermore, *P. oceanica* meadows enhance sediment stabilization of sandy patches present in their vicinity (Vacchi *et al.* 2016). At the large spatial scale, sandy patches intermixed within a *P. oceanica* meadow are clearly recognizable thanks to side scan sonar images, and can occupy from 2 to 16 % of the total seagrass meadow area (Pasqualini *et al.* 1999, Pasqualini *et al.* 2000, Clabaut *et al.* 2014, Abadie *et al.* 2015b).

When considering smaller areas, *e.g.* a small bay (<1 km² in size), other causes of meadow fragmentation, such as those resulting from wave action generated by high winds, are noted. As a result, sandy patches called “return river” can be generated within a *P. oceanica* meadow (Tab. 16), the nature of which would depend on orientation of the coastal area concerned to the main winds influencing it (Boudouresque & Meinesz 1982). Furthermore, such a situation can lead to an increase in the number of sandy patches present within a meadow (Meinesz *et al.* 1988, Abadie *et al.* 2015b).

At the small spatial scale(*i.e.* several square meters) the architectural features of a *P. oceanica* meadows exhibit high heterogeneity as a result of several influencing local natural factors such as nutrient availability, granulometry and pH (Gobert *et al.* 2003, Borg *et al.* 2005). External abiotic factors are coupled with internal ones, as well as structural features to lead to development of a some particular *P. oceanica* seascape; one example is that described by Boudouresque *et al.* (1985b) concerning formation of a ‘barrier reef’ (Tab. 16), which results from long term sedimentation and the vertical growth rate of the plant (Fig. 54). In the same way, variation in horizontal growth of *P. oceanica* rhizomes leads to a heterogeneous seascape. This observation is based on a long term simulation which revealed colonization, over a period of 600 years, of an area measuring 0.3 ha, with the seascape being slowly modified throughout this period (Kendrick *et al.* 2005b). This process not be a linear dynamic one, with recruitment increasing with an increase in *P. oceanica* patch size (Almela *et al.* 2008). Seafloor morphology, as well as geology (*e.g.* sand, rock), also play an important role in the determination of seascape heterogeneity (Montefalcone *et al.* 2016). At the level of shoot density and plant growth dynamics, certain environmental factors lead to a high degree of patchiness which is manifested as nestlike patterns (Zupo *et al.* 2006b). Similarly, decreased light intensity may lead to alteration of seascape micro-structure (see Fig. 54), as for example demonstrated by Dalla Via *et al.* (1998) who recorded a decrease of 72 % in shoot density between a water depth of 3 m and 10 m (Tab. 16).

***Table 16**: Main outcomes from studies which refer to the influence of natural factors on* P. oceanica *meadows.*

Type of factor	Main seascape structural results	Study site	Reference
Multiple	Architectural characteristics of *P. oceanica* meadows are mainly influenced by local environmental factors	Ramla Bay, Mellieha Bay, White Rocks and St Thomas Bay (Malta)	Borg et al. (2005)
Water movement	Sand corridors (called “intermatte channels”) are assumed to be dynamic natural features aligned perpendicular to the shore	Calvi Bay, Corsica (France)	Boudouresque et al. (1980)
	Surface water pushed by main winds toward the shore could create unsuitable conditions for the meadow to grow and favor the formation of the sand corridors	Elbu, Corsica (France)	Meinesz et al. (1988)
	Meadow exposure to waves is not necessary linked to their patchiness	Ramla Bay, Mellieha Bay, White Rocks and St Thomas Bay (Malta)	Borg et al. (2009)
	Structure of the shallow portion of *P. oceanica* meadow is influenced by sea currents to different degrees depending on wave energy	Liguria (Italia)	Vacchi et al. (2010)
	Erosion and recolonization rate of natural sand patches are measured as well as their shifting speed within the seagrass meadow	Calvi Bay, Corsica (France)	Gobert et al. (accepted)
	High wave climate energy lead to meadows with higher a patchiness and a less complex architectural structure between 6 m and 11 m depth	Baħar ic-Cagħaq, Sel- mun Bay, Daħlet Qorrot, San Blas Bay and Ramla Bay (Malta)	Pace et al. (in press)
Light	Decreased light intensity leads to decreased shoot density of P. oceanica meadows	Calvi bay, Corsica (France)	Dalla Via et al. (1998)
Seafloor characteristics	Meadow structure is naturally heterogeneous even at a small scale as a result of the influences of various factors such as nutrients levels, sediment granulometric characteristics and variation of pH	Calvi Bay, Corsica (France)	Gobert et al. (2003)
	Seafloor morphology influences the architectural features of P. oceanica meadows, as well as their density and growth rate	Lacco Ameno, Island of Ischia (Italy)	Zupo et al. (2006b)
Plant physiology	*P. oceanica* seascapes are strongly influenced by the growth dynamics of the plant	Simulation	Kendrick et al. (2005b)
	Shoot recruitment of *P. oceanica* increases with patch size	Balearic Islands (Spain)	Almela et al. (2008)

3.3.2. Anthropogenic influence

Human activities, such as coastal development, trawling, anchoring, fish farms, are well known to directly modify *P. oceanica* meadow structure at all depths (Boudouresque *et al.* 2009, Giakoumi *et al.* 2015b), but such effects are less evident within the 35-43 m bathymetric range (Pasqualini *et al.* 1998). As in the case of naturally-occurring patches of the seagrass, patches resulting from anthropogenic activities can be clearly identified at large spatial scales according to their size and shape (Pasqualini *et al.* 1999, Clabaut *et al.* 2014, Abadie *et al.* 2015b).

In places characterized by intense human activities, anthropogenic impacts on *P. oceanica* habitat result in higher levels of fragmentation compared to natural processes (Leriche *et al.* 2006, Montefalcone *et al.* 2010b). However, in areas characterized by moderate anthropogenic pressures, *P. oceanica* seascapes are found to have a relatively low percentage of patches resulting from human impact. For example, in Corsica (France), patches resulting from anthropogenic impact comprise only a maximum of 6% the total seagrass area (Tab. 17) and no further significant regression has been recorded (Bonacorsi *et al.* 2013, Abadie *et al.* 2015b).

In general, increased levels of anthropogenic impact favors the development of bare matte areas (Tamburello *et al.* 2012), leading to decreased *P. oceanica* patch size and edge length (Nowell 2014). Anthropogenic impacts have different temporal scales of action, resulting in the creation of bare matte patches within the *P. oceanica* matrix. In the long term, if the adverse activities continue at the same intensity, a shift in the seagrass meadow matrix can occur, resulting in areas with bare sand or dead matte (Ardizzone *et al.* 2006). Among the human activities that operate over a long period to eventually lead to fragmentation of meadows, hence patch generation, are pressures linked with coastal development (pollution and high rates of sediment deposition, as well as urban expansion; see Fig. 54), will first lead to a decrease in shoot density (Tab. 17) and then to fragmentation of a *P. oceanica* meadow (Montefalcone *et al.* 2007, Montefalcone *et al.* 2010b, Rountos *et al.* 2012). On the other hand, anthropogenic activities causing direct physical damage (*e.g.* boat anchoring, trawling, explosives) immediately lead to seagrass meadow fragmentation and to formation of patches (Fig.

54), thus modifying the seascape configuration (Meinesz & Lefèvre 1984, Kiparissis *et al.* 2011, Okudan *et al.* 2011). Changes in the substratum's biogeochemistry as a result of mechanical damage can lead to intrusion of toxic compounds (*e.g.* hydrogen sulfide), which limit *P. oceanica* growth and meadow development (Abadie *et al.* 2016).

Table 17*: Outcomes from studies that include assessment of the influence of anthropogenic factors on* P. oceanica *meadows.*

Type of anthropogenic impact	Main observation concerning seascape	Study site	Reference
Multiple	The bathymetric range 35-43 m appears to be less affected by human activities compared to shallower water depths	Corsica (France)	Pasqualini et al. (1998)
	Natural and anthropogenic pressures can be identified and quantified using as the level of patchiness, using side scan sonar	Corsica (France)	Pasqualini et al. (1999, 2000)
	Human pressures cause regression of a *P. oceanica* meadows, leading to fragmentation and patch formation, hence decreasing the lower limit of a meadow	Cape Circeo and Sperlonga (Italy)	Ardizzone et al. (2006)
	Human activities lead to formation of 'intermatte' channels within *P. oceanica* meadows; such features may comprise up to 8% of the total seagrass area	Bay of Saint-Cyr (France)	Leriche et al. (2006)
	Urban activities cause a decline of the area covered by *P. oceanica* meadows	Genoa (Italia)	Montefalcone et al. (2007)
	Human activities have a higher impact, hence fragmentation, of *P. oceanica* meadows compared to natural impacts and seabed physical characteristics	Liguria (Italia)	Montefalcone et al. (2010b)
	Anthropogenic impacts lead to areas with dead *P. oceanica* matte	Tuscany (Italy)	Tamburello et al. (2012)
	Moderate human pressures cause no significant *P. oceanica* meadow regression	St. Florent, Corsica (France)	Bonacorsi et al. (2013)
	P. oceanica seascape is influenced by seabed type (sand, rock), by fresh water input, and by anthropogenic activities	Corsica (France)	Clabaut et al. (2014)
	P. oceanica patch and edge length decrease when human impacts increase	Balearic Islands (Spain)	Nowell (2014)
	P. oceanica patches generated by natural or anthropogenic factors can be used to assess seagrass habitat fragmentation	Corsica (France)	Abadie et al. (2015)
	A slow but clear fragmentation of seagrass meadows is observed over a long period, *e.g.* 85 years	South East coast of France	Holon et al. (2015a)
	Human activities are responsible for the destruction large areas with *P. oceanica* beds as indicated by the presence of mapped areas with dead matte	French Mediterranean Coast	Holon et al. (2015b)

Type of anthropogenic impact	Main observation concerning seascape	Study site	Reference
Anchoring	Formation of a P. oceanica barrier reef is driven by the sedimentation rate and the structure can be modified by anchoring activities	Elbu, Corsica (France)	Boudouresque et al. (1985b)
	Moderate anchoring activities are positively correlated with meadow fragmentation	Port-Cros (France)	Francour et al. (1999)
	Anchoring by cruise ships creates corridors with bare matte and patches within P. oceanica meadows	Port-Cros (France)	Ganteaume et al. (2005)
	Heterogeneity of meadow shoot density can be driven by pressure from anchoring activities	Lacco Ameno, Island of Ischia (Italy)	Zupo et al. (2006a)
	Anchoring activities reduce the number of leaves and meadow density at shallow water depths	Stagnone, Sicily (Italia)	Ceccherelli et al. (2007)
	Intensive anchoring on P. oceanica meadows creates large scars with bare matte	Fethiye Bay (Turkey)	Okudan et al. (2011)
	Mechanical damage by anchoring leads to physical disturbance of the substratum and intrusion of toxic compounds, leading to generation of patches with dead matte	Calvi Bay, Corsica (France)	Abadie et al. (2016)
Explosives	Explosions such as those resulting from detonated bombs during World War II create large circular patches that are hardly recolonized by P. oceanica	Villefranche (France)	Meinesz and Lefèvre (1984)
Trawling	Trawling activities lead to creation of large areas with bare matte that are suitable for settlement of invasive species such as Caulerpa cylindracea	Alykes Bay, Zakynthos Island (Greece)	Kiparissis et al. (2011)
Fish farm	Fish farms wastes can modify P. oceanica meadow structure within a distance of some 170 m	St. Paul's Bay (Malta)	Dimech et al. (2000, 2002)
	Fish farms activities, at low or high intensity, lead to a decrease in meadow shoot density, standing crop and leaf surface	Crete (Greece)	Rountos et al. (2012)

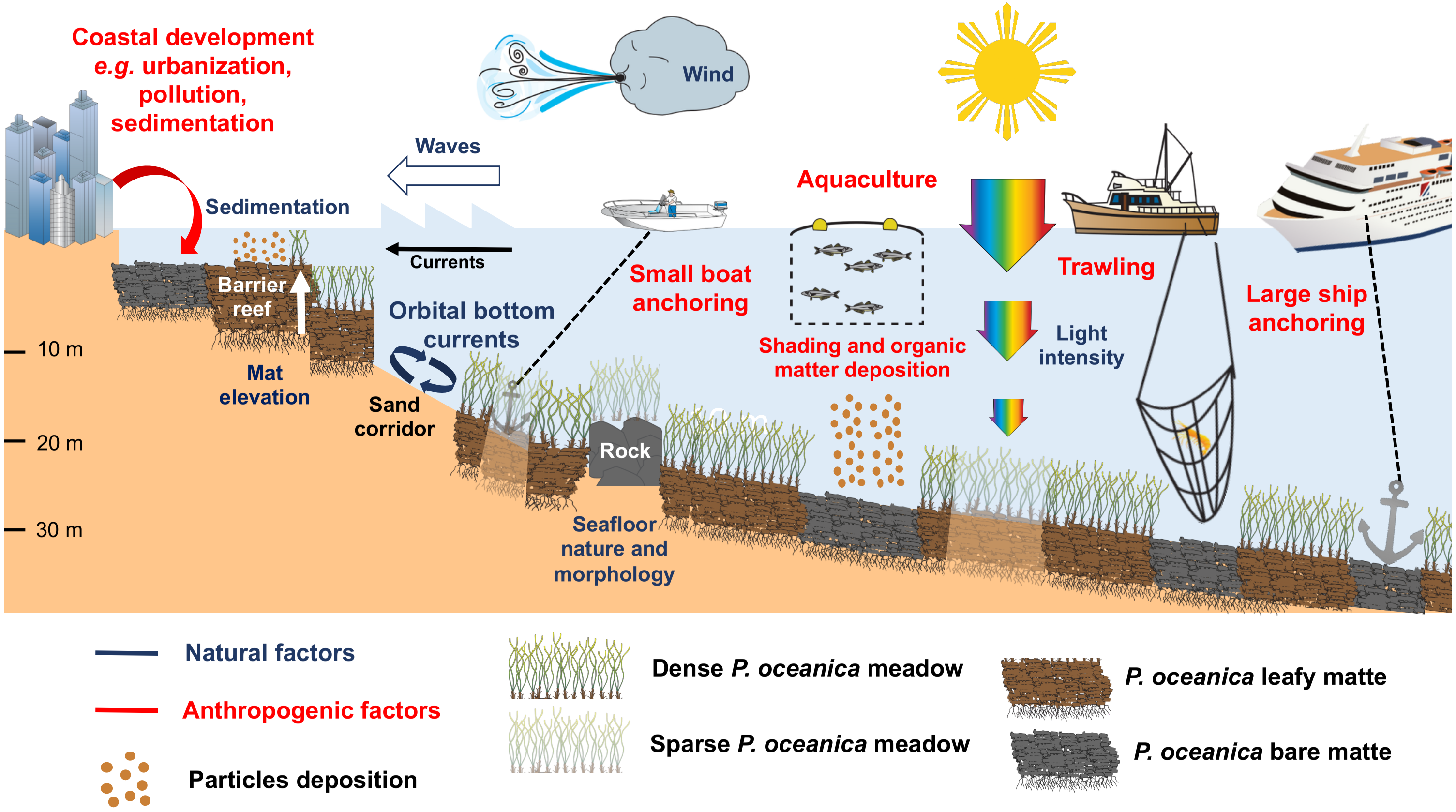


Figure 54: *Schematic diagram showing natural and anthropogenic factors that influence a* P. oceanica *seascape. The scale on the left indicates water depth.*

3.4. Influence of *P. oceanica* seascapes on the associated biota

The occurrence and distribution of species associated with a *P. oceanica* seascapes is mainly influenced by substratum type and meadow architecture (Boström *et al.* 2011). The transition between a surrounding different bottom type and a patch or that between two distinct patch types is called the ‘edge’ or ‘ecotone’ (Forman 1995). For several species, their abundance tends to be higher at the junction between two different substrates; this phenomenon being referred as the ‘edge effect’ (Odum & Barrett 1971). Recent studies in the field of seascape ecology have been aimed at linking meadow or patch structure to the species’ distribution, with emphasis being on a particular taxon, assemblage, or several functional species (Boström *et al.* 2006a).

3.4.1. Substratum type and benthic biotic characteristics

Benthic communities are known to change according to environmental characteristics, including substratum type, and anthropogenic influence (Eagle 1975, Borja *et al.* 2003). This has been confirmed in studies of interactions between *P. oceanica* meadows and bare sediment bottoms, the results of which have indicated a higher diversity and abundance of epifauna at the edge of a seagrass meadow (Fig. 55). For example, mysids are found to prefer the meadow edge (Tab. 18), while other taxa show no specific preference for substratum type, except at the level of the species (Sánchez-Jerez *et al.* 1999). Settlement of non-mobile benthic species like *Pinna nobilis* Linnaeus also shows a strong edge effect, with more than half of the bivalve population found at the border of a *P. oceanica* meadow (Coppa *et al.* 2010). Therefore, the occurrence and distribution of *P. nobilis* appears to be greatly influenced by structural features of the seascape (Tab. 18).

Amongst the substrata associated with *P. oceanica* meadows, dead matte areas (resulting from both natural or anthropogenic factors), although classically considered as an impoverished substratum in terms of colonizing biota, have been noted to support a similar species richness compared with living matte (Fig. 55). For example, Borg *et al.* (2006) highlighted a change in the community structure of macroinvertebrates associated with natural dead matte; a higher abundance of the amphipods *Leptocheirus guttatus* Grube and *Maera grossimana* Montagu, and the polychaeta *Nereis rava* Ehlers recorded from this substratum type compared to living matte (Tab. 18). Once again, when considering *P. nobilis*, populations of this bivalve have a higher density on bare matte (Fig. 55) compared to *P. oceanica* meadows and patches with bare sand (Coppa *et al.* 2010). In the case of dead matte resulting from anthropogenic activities such as illegal trawling, differences at microscale level (0.1 to 1 m) have been recorded for amphipods and isopods when compared to the same groups associated with living matte (Sánchez-Jerez & Ramos Esplá 1996).

In areas where the habitat is under the influence of nutrient enrichment, such as *P. oceanica* meadows located near fish farms, workers (*e.g.* Dimech *et al.* (2002) have observed a localized increase in species richness and abundance as a result of increased productivity (Fig. 55). This despite the change in meadow structure which was evident by the lower leaf length and shoot density of *P. oceanica* located near the fish farm (Tab. 18). Therefore, this study shows that meadow structure alone does not determine the occurrence and distribution of species associated with the seagrass, and other factors can modify the *P. oceanica* seascapes' function. Studies have also indicated that that small modifications of seagrass meadow structure may not have an appreciable influence on the associated macroinvertebrate assemblages (Tab. 18) but these are more influenced by other factors such as epiphyte biomass and sediment grain size (Borg *et al.* 2010).

***Table 18**: Outcomes from studies dealing with the influence of* P. oceanica *seascapes on associated benthic macroinvertebrates.*

Main seascape results	Study site	Reference
Trawling impacts lead to changes in fish and macroinvertebrates communities	El Campello, Alicante (Spain)	Sánchez-Jerez and Ramos Esplá (1996)
Difference between bare sediment and meadow edge are evident for the associated epifauna	El Campello, Alicante (Spain)	Sánchez-Jerez *et al.* (1999)
Localized higher species richness and abundance result from nutrient enrichment in the vicinity of a nearby fish farm	St. Paul's Bay (Malta)	Dimech *et al.* (2002)
Richness and abundance of motile macroinvertebrates is higher in dead matte habitat compared to living matte	Mellieha Bay (Malta)	Borg *et al.* (2006)
No differences in attributes of the macroinvertebrate community are noted observed between continuous and reticulate meadows	Ramla Bay, Mellieha Bay, White Rocks and St Thomas Bay (Malta)	Borg *et al.* (2010)
More than half of the individuals of a *P. nobilis* population are present close to the edge of a meadow. Their distribution is influenced by meadow structural characteristics	Gulf of Oristano, Sardinia (Italy)	Coppa *et al.* (2010)

3.4.2. Influence of seascape on the behavior of herbivores

The most studied functional aspect of *P. oceanica* seascapes is that concerning grazing of the canopy stratum by herbivores. Classically, the grazers are sea urchins *Paracentrotus lividus* Lamarck and the saupe *Sarpa salpa* Linnaeus, which attract intention as a result of their ability to consume and digest *P. oceanica* tissue (Peirano *et al.* 2001).

Study of the occurrence and distribution of benthic organisms often includes an assessment of their settlement preferences within the considered habitat. In *P. oceanica* seascapes, Prado *et al.* (2009)

observed that *P. lividus* (one-year cohort individuals) tends to prefer the matte as post-settlement habitat (Fig. 55), and absence of this substratum led to non-survival of 100% of the post-settled individuals (Tab. 19). Still, this process would depend on their proximity to *P. oceanica* habitat despite their ability to move toward a meadow (Fig. 55). Furthermore, the process does not depend on seagrass patch size (Ceccherelli *et al.* 2009), suggesting that even young individuals can reach the matte (Tab. 19). In this way, the abundance of *P. lividus* increases at the edge of the meadow on the seagrass matte (Pinna *et al.* 2013), where they are protected from fish predation by the longer leaves, as well as by the unburied roots and rhizomes (Farina *et al.* 2009).

When comparing the functional compartment of *P. oceanica* grazers, namely *S. salpa*, *P. lividus* and amphipods, all of which are motile consumers, it is not only the influence of meadow structure on their distribution which is useful for study but also their impact on seascape characteristics. For example, at the level of influence of seagrass meadow structure, the results of Pagès *et al.* (2014) show that *P. lividus* and *S. salpa* increase their grazing pressure at the center of *P. oceanica* patches rather that at the meadow edge (Fig. 55). This study also points out that *P. oceanica* patches established on a rocky bottom are more subject to grazing than those present on a sandy bottom (Tab. 19). The increase in grazing pressure, combined with natural fragmentation of the seagrass meadows, leads to loss of *P. oceanica* primary production (Gera *et al.* 2013).

Table 19*: Outcomes from studies on the influence of* P. oceanica *seascapes on herbivores*

Species concerned	Main seascape results	Study site	Reference
Paracentrotus lividus	The capacity of sea urchins to move toward a *P. oceanica* habitat does not depend on seagrass patch size. Those closest to the patches have more probability to reach them	Polt Agra Bay, Sardigna (Italy)	Ceccherelli *et al.* (2009)
	Unburied roots/rhizomes and longer leaves protect sea urchins from predation by fishes	Medes Islands (Spain)	Farina *et al.* (2009)
	Post-settlement processes are influenced by meadow structure, and are enhanced when a matte is present	Catalan Coast (Spain)	Prado *et al.* (2009)
	Abundance of *P. lividus* increases at the edge of the meadow and is influenced by shoot density and canopy height	Gulf of Alghero, Sardinia (Italy)	Pinna *et al.* (2013)
Paracentrotus lividus *Sarpa salpa*	Nutrient loading from a fish farm leads to an increase of epiphytes and higher herbivore abundance	Crete (Greece)	Rountos *et al.* (2012)
	Herbivore pressure combined with meadow fragmentation leads to a decrease in *P. oceanica* primary production	Fenals and Giverola (Spain)	Gera *et al.* (2013)
	Herbivory is higher at the center of *P. oceanica* patches and where patches of the seagrass are located on a rocky bottom compared to when present on a sandy bottom	Catalan Coast (Spain)	Pagès *et al.* (2014)

3.4.3. Settlement of alien Chlorobionta

The natural and human-induced heterogeneity of *P. oceanica* seascapes (*e.g.* sand and bare matte patches) provide substrata for colonization by non-indigenous species that have a fast growth rate. In the Mediterranean Sea this phenomenon has been especially studied for Chlorobionta of the genus *Caulerpa*. These organisms have the capacity to substitute *P. oceanica* faster than native species, increasing the rate of fragmentation of the meadows (Montefalcone *et al.* 2010a).

The first non-native species historically studied for its interaction with *P. oceanica* meadows is *Caulerpa taxifolia* (Vahl) C. Agardh; a circumtropical Chlorobionta member that was accidentally released in the NW Mediterranean Sea (Jaubert *et al.* 2003). De Villèle and Verlaque (1995) observed that when *C. taxifolia* When grows on *P. oceanica* meadows, it causes mortality of the seagrass, although the resistance of *P. oceanica* to this increases with an increase in shoot density (Tab. 20).A higher *P. oceanica* shoot density has a shading effect on *C. taxifolia* blades, thus reducing the size of the alga and, by extension, the colonization capacity of this species (Ceccherelli & Cinelli 1999). After several years of observation, Jaubert *et al.* (1999) reported no long-term impact of this alien species on adjacent *P. oceanica* meadows (Tab. 20). However, later it transpired that competitive processes between *P. oceanica* and *C. taxifolia* also occur through the release of chemical compounds into the substratum leading to changes in their growth pattern and structural development (Pergent *et al.* 2008). Currently, C. taxifolia has almost disappeared from the sites previously colonized, its regression being ascribed to a decrease of its dispersion capacity (Montefalcone *et al.* 2015).

Another non-indigenous Chlorobionta species, *Caulerpa cylindracea* Sonder, originates from south-western Australia and whose presence has been noted in the Mediterranean Sea since 1990 (Klein & Verlaque 2008). This species tends to prefer bare matte patches within *P. oceanica* seascape (Fig. 55) rather than bare sediment and rocky bottoms (Katsanevakis *et al.* 2010). *C. cylindracea* also colonizes impacted substrata, such as those exposed to trawling activities, including *P. oceanica* meadows affected by the activity (Kiparissis *et al.* 2011). *C. cylindracea* has been noted to be unable to penetrate dense *P. oceanica* meadows (Tab. 20) and only remains established along their edges (Ceccherelli *et al.* 2000).

***Table 20**: Outcomes from studies on the influence of alien Chlorobionta on* P. oceanica *seascapes.*

Species	Main seascape results	Study site	Reference
Caulerpa taxifolia	*P. oceanica* meadows invaded by *C. taxifolia* are subjected to higher shoot mortality during some seasons, but their resistance increases with an increase in shoot density	Menton (France)	De Villèle and Verlaque (1995)
	P. oceanica canopy causes a shading effect on *C. taxifolia* blades, such that the alga has a reduced size	Galenzana Bay, Elba Island (Italy)	Ceccherelli and Cinelli (1999)
	C. taxifolia does not have a long term impact on *P. oceanica* meadows	Menton (France)	Jaubert et al. (1999)
	Competition between *P. oceanica* and *C. taxifolia* induces changes in their growth and chemical characteristics	Cap Martin (France)	Pergent et al. (2008)
Caulerpa cylindracea	Higher shoot density at the edge of a *P. oceanica* meadow decreases the probability of invasion by *C. cylindracea* present in the vicinity of the seagrass	Antignano, Tuscan Coast (Italia)	Ceccherelli et al. (2000)
	C. cylindracea is more capable of settling on dead matte compared to rocky bottoms, bare sand and *P. oceanica* meadows	Zakynthos Island (Greece)	Katsanevakis et al. (2010)
	Trawling tracks (bare matte) within *P. oceanica* meadows are fully colonized by *C. cylindracea*	Alykes Bay, Zakynthos Island (Greece)	Kiparissis et al. (2011)
Caulerpa cylindracea *Caulerpa taxifolia*	At shallow depths, *P. oceanica* meadows can be impacted adversely as the plant is substituted by alien species. Non-indigenous species (*Cymodocea nodosa* and *Caulerpa prolifera*) are stronger invaders compared to native ones	Liguria (Italy)	Montefalcone et al. (2010a)

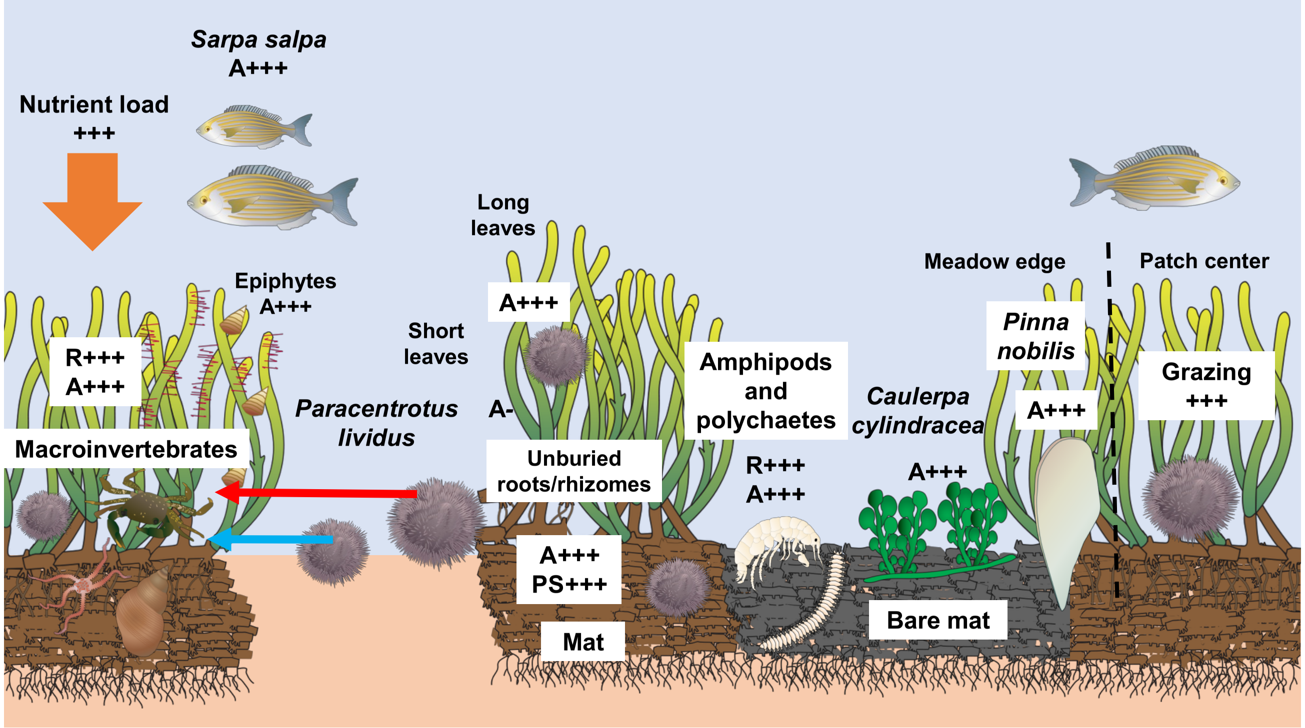


Figure 55: *Schematic diagram showing factors that influence the occurrence and distribution of species associated with a* P. oceanica *seascape, based on information from the published literature. R: specific richness; A: abundance; PS: post-settlement.*

3.5. Connectivity of *Posidonia oceanica* meadows with the Mediterranean seascape

Landscape/seascape connectivity is well studied in tropical areas which support a triangular network of mangroves, coral reefs and seagrass meadows (Grober-Dunsmore *et al.* 2009, Berkström *et al.* 2012). Although connectivity between marine and terrestrial Mediterranean habitats is not much studied at a large spatial scale, merging several isolated works provides an insight into the role played by *P. oceanica* meadows (Fig. 56). In this way, through exportation of primary production (Boudouresque *et al.* 2015a) and their influence on water movement (Vacchi *et al.* 2016), *P. oceanica* meadows interact with other habitats, both marine and terrestrial (Heck *et al.* 2008), thus connecting with the whole Mediterranean coastal landscape and seascape.

3.2.1. A link with terrestrial habitats

P. oceanica seascape is mainly linked with terrestrial habitats at the level of beaches. Through their structure, dense P. oceanica meadows attenuate wave energy in shallow depths (Manca *et al.* 2012). For example, Infantes *et al.* (2012) recorded a reduction of 50 % of wave height in places where *P. oceanica* meadows having a density around 600 shoots.m^{-2} were present. Moreover, by decreasing the wave energy reaching the shore, *P. oceanica* meadows also reduce the unvegetated landward slope, thus limiting the height of waves crashing on the beach (Manca *et al.* 2012). This phenomenon provides natural protection for beaches against coastal erosion in several ways (Gacia & Duarte 2001, Vacchi *et al.* 2016).

Through exposure to water movement and its seasonal physiological characteristics, *P. oceanica* meadows export part of its primary production to the shore (Boudouresque *et al.* 2006); this process occurring mainly during autumn and winter storms. The exported material comprises leaves, roots and rhizomes that accumulate on sandy beaches and forming ‘banquettes’ (Fig. 56); a pile of *P. oceanica* litter that can reach a height of several meters (Boudouresque *et al.* 2015a). Banquettes are eroded at their bases by waves, resulting in the formation of an arched overhang (Mateo *et al.* 2003), while the structure limits sediment losses from a beach, hence reducing coastal erosion (Chessa *et al.* 2000, De Falco *et al.* 2008). Banquettes act as a temporary sinks of biogenic elements, given that *P. oceanica* meadows are able to accumulate 50 % of their biomass, 71 % of their carbon, 27 % of their nitrogen and 9 % of their phosphorous (Mateo *et al.* 2003). Slow degradation of beach banquettes releases nutrients that are then available for terrestrial organisms (Guala *et al.* 2006). Such nutrient input has been assessed for the upper beach and fore dune vegetation (Fig. 56), and has been found to enrich terrestrial plant tissues by a factor of 1.5 fold for nitrogen and up to a factor of 2 for phosphorous (Cardona & García 2008, Del Vecchio *et al.* 2013). Such organic material is, however, of no benefit as food for beach macroinvertebrates (*e.g.* the sand hopper *Talitrus saltator* Montagu), as these do not feed on *P. oceanica* wrack. However, the physical structure of banquettes provides them with a shelter against environmental disturbances (Colombini *et al.* 2009).

3.2.2. Contribution to other marine seascapes

As already mentioned above, *P. oceanica* seascapes interact both with shallower and deeper marine ecosystems through export of detritus (Fig. 56). This output of *P. oceanica* ecosystems is called “necromass”, *i.e.* exported primary producers, leaves, broken rhizomes and roots as well as drift macrophytes (Boudouresque *et al.* 2015a). The amount of necromass exported ranges from 10 to 55 % (Boudouresque *et al.* 2015a), while this percentage varies strongly between one place and another; for instance 51-68% recorded from Marseille (France) and 37-49 % from Ischia (Italy) (Pergent *et al.* 1994, Pergent *et al.* 1997). Differences in the amount of exported necromass probably result from differences in water movement intensity during autumn and winter storms (Remy 2016), as well as from *P. oceanica* seascape structure, with patchy meadows accumulating less detritus than continuous ones (Ricart *et al.* 2015a).

Although the primary production exported from *P. oceanica* meadows is well studied, data on its destination and use in other marine seascapes are scarce. Presumably, the first marine habitats taking advantage of this input are those located adjacent the seagrass meadows, for example bare sediment habitat, algal forests and meadows formed by other seagrass meadows (Fig. 56). Thus, *P. oceanica* outputs are a carbon source for sand-dwelling species living close to the meadow, while this has not been established for more distant ecosystems (Cardona *et al.* 2007). More than a simple food source, *P. oceanica* necromass, in the form of 'litter', creates a temporary mobile habitat and also provides a structural shelter for a whole unique set of detritivore invertebrates (Dimech *et al.* 2006, Mascart *et al.* 2015, Remy 2016).

In the case of marine ecosystems located at a large distance from *P. oceanica* meadows, few studies have addressed the quantity and potential use of export of necromass from the seagrass ecosystem. It is assumed that most of this resource is consumed by the sea urchin *Paracentrotus lividus* present sublittoral rocky bottoms and reefs (Verlaque & Nedelec 1983) as well as serving as a source of organic matter for algal habitat on hard bottoms (Cardona *et al.* 2007) and marine caves (Picard 1965). However, such export is probably less than expected given the lower efficiency of *P. oceanica* energy transfer (2 to 10 times lower) toward higher trophic level when compared to other Mediterranean seagrasses, such as *Cymodocea nodosa* (Ucria) Ascherson and *Zostera noltii* Hornemann (Danovaro *et al.* 2002). Organic material exported by *P. oceanica* is also expected to reach deep water habitats to depths of around 600 m (Gobert, personal observation) (Fig. 56) (Wolff 1976).

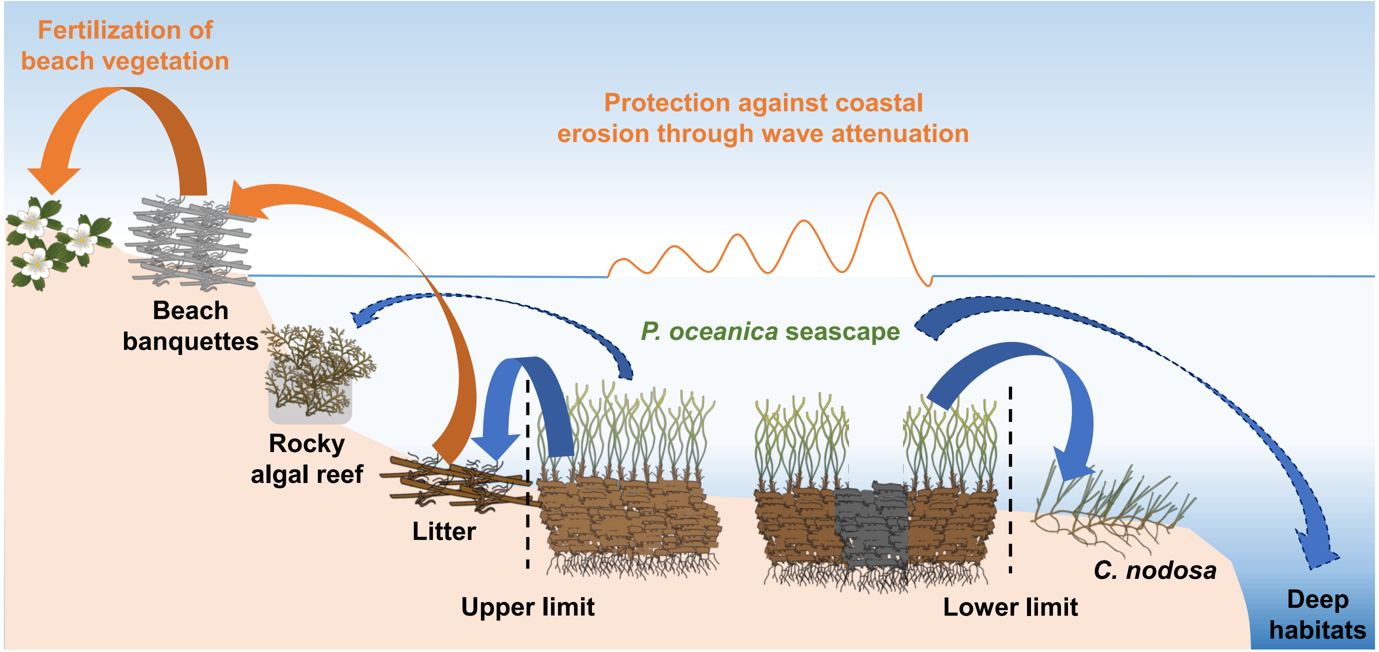


***Figure 56**: Schematic diagram showing connectivity of a* P. oceanica *seascape with terrestrial ecosystems and other marine habitats. Orange arrows: terrestrial connection; blue arrows: marine connection.*

4. Information on *P. oceanica* seascapes for management purposes

Although a large effort has been made on various aspects of seascape ecology over the last fifteen years, there are still limitations with regard to both data acquisition and mining and treatment when compared with terrestrial landscape studies. Moreover, there remain difficulties concerning the development of tools for managers and stakeholders who, after all, are the eventual users of information on this area of ecology. These assertions are particularly true for *Posidonia oceanica* seascapes and their management within the framework of European directives such as the Water Framework Directive (WFD) and the Marine Strategy Framework Directive (MSFD).

4.1. Data acquisition and treatment

4.1.1. Mapping *P. oceanica* seascapes

One of the most widespread tools used in landscape ecology to collect information on the largest spatial scales is habitat mapping. Currently, the most popular techniques associated with habitat mapping use Geographical Information Systems (GIS). Improvement of data acquisition techniques in recent years has enabled the production of extensive marine habitat maps (Leriche *et al.* 2004, Noël *et al.* 2012), which have become as important as the mapping techniques used in terrestrial ecological studies and the information generated thereof. Side scan sonar images (or sonograms), have a much higher resolution than other mapping techniques used in surveys of the marine environment, and can give a clear visual indication of seascapes formed by *P. oceanica* meadows*.* This information can highlight several impacts of human activities on seagrass beds (Pasqualini *et al.* 1999, Leriche *et al.* 2006, Abadie *et al.* 2015b). However, since side scan sonar requires use of a towed device, it cannot be maneuvered at depths shallower than 10 m (Augris & Clabaut 2001), thus limiting data acquisition on extensive shallow coastal areas that support seagrass meadows. To counteract this limitation, side scan sonar images are used in conjunction with aerial and satellite imagery techniques that allow delineation of the distribution of seagrass meadows and patches of the habitat.

4.1.2. The three-dimensional viewpoint

As already stated, *P. oceanica* seascapes present a heterogeneous vertical structure whose formation in influenced seafloor features and dynamics of the seagrass matte. A tri-dimensional approach is thus required to study the structural and functional features of the habitat. Mapping techniques currently used in landscape and seascape ecology utilize the two-dimensional (2D) aspect because this is simpler to generate and requires less data than ones having a three-dimensional (3D) aspect. The creation of 3D maps is, however, very widespread in terrestrial environmental studies, especially in programs that have an educational or informative aim (Schobesberger & Patterson 2008, Niedomysl *et al.* 2013). Besides the advantages and inconvenience of visual interpretations (Popelka & Brychtova 2013), 3D maps provide different results compared to the 2D ones according to the topography of the site studied. Moreover, some metrics traditionally used with 2D maps remain applicable to 3D analyses but, still, it is essential to create new ones (Parrott *et al.* 2008, Wu *et al.* 2012).

In the marine environment, particularly in the case of seagrass meadows, site topography has a strong influence on the species' spatial distribution in different habitats (Robinson *et al.* 2011). Within the context of gathering information for use in conservation measures, use of 3D mapping surveys could help managers understand the importance and functioning of marine habitats. In the case of *P. oceanica* meadows, it is clearly established that water depth (Elkalay *et al.* 2003) and seafloor features (Di Carlo *et al.* 2005) play an essential role in influencing seagrass meadow dynamics. Thus, beyond the purely visual aspect, use of 3D maps in a seascape study should provide a more realistic view of patch arrangement and function. For instance, it seems logical that a *P. oceanica* vertical edge having a height of 2 m which appears flat on classical maps (2D) would constitute a real obstacle for the movement of several benthic organisms. Moreover, this it is not only the aboveground structure that should be considered in a 3D analysis, but also the belowground properties (*e.g.* structure of the root-sediment matrix and chemical processes) that drive the shape of a *P. oceanica* seascape (Abadie *et al.* 2016).

4.1.3. Linking structure and function at the seascape level

P. oceanica habitat mapping studies as well as works assessing their functional role have increased over the last two decades (Boström *et al.* 2011, Telesca *et al.* 2015). It would thus be tempting to extrapolate functional features at a large spatial scale from the available maps in order to manage coastal habitats. However, several obstacles prevent such approach for marine habitats in general, including *P. oceanica* seascapes.

Although the number of available maps of *P. oceanica* habitat has increased, there are still problems concerning lack of data on their functioning, and on how to acquire the necessary information. While it would seem appropriate to study structural and functional processes at a small spatial scale (*i.e.* smaller than 1 km^2) using quadrats, discrete sampling techniques and transects (Pace *et al.* in press), such techniques are less adequate for studies at the medium (1 to 10 km^2) and large (> 10 km^2) spatial scales. A first obstacle thus lies in the methods used for large spatial scale studies. Even if 62 % of such studies have relied on mapping, 20 % of them have been made using quadrats and discrete sampling techniques (Table 21). Evidently, new field methods need to be developed in order to assess the functional aspect of seagrass seascapes at large spatial scales (*e.g.* automated fish and macroinvertebrate counting made using Remotely Operated Vehicles).

***Table 21**: Proportion (%) of sampling methods used in studies on* P. oceanica *that consider one or more spatial scales. SSS: Small Scale; MSS: medium scale; LSS: Large scale; Q-DS: Quadrat-Discrete Sampling; T: Transect; SP: Small Patch; LP: Large Patch; M: Mapping.*

	Q-DS	**T**	**SP**	**LP**	**M**
SSS	39	6	24	6	24
MSS	12	24	0	4	60
LSS	20	13	4	0	62

Furthermore, as described above, sampling effort has been focused on a small number of species that have contrasting mobility (Boström *et al.* 2006a, Connolly & Hindell 2006). Linking direct observations with maps requires an answer to aspects of interest described by a numerical data, such as width of the edge effect and maximal propagation/dispersal distance of species between one patch and another) (Boström *et al.* 2011). Unfortunately, even on obtaining such data, the results obtained using the available methods may not reflect the true situation due to the complexity of species-rich ecosystems such as *P. oceanica* seascapes (Green & Sadedin 2005, Duffy *et al.* 2007). Such an obstacle can be overcome by using new approaches to data management and treatment based on meta-analysis of available data, which help answer a specific question. However, such an approach first requires homogenization of databases as well as total and free access to data resources; this field being recently referred to as 'big science' (Hampton *et al.* 2013). When these conditions are met, it is possible to proceed with analysis of complex biological systems, such as *P. oceanica* seascapes, through data mining (Hochachka *et al.* 2007) and artificial intelligence (Rykiel 1989). From fundamental approaches, new simplified tools and land/seascape assessment procedures aimed for use by coastal managers have already emerged; these indicate the limitations of previous indicators.

4.2. New analysis tools for management purposes

4.2.1. Limitation of uses of landscape indices

Over the last few decades, several indices have been developed for use in landscape ecology to quantify the spatial features of terrestrial habitats (Schumaker 1996, McGarigal *et al.* 2014). These metrics have been transferred to marine studies and are currently widely used for management of seagrass seascapes, including ones formed by *P. oceanica* (Sleeman *et al.* 2005, Montefalcone *et al.* 2013b, Chefaoui 2014). However, recent studies concerning terrestrial ecosystem conservation have highlighted their limits (Kupfer 2012, Šímová & Gdulová 2012). Specifically, information on the relationship between some specific metrics and ecological processes (Fig. 57) are sometimes doubtful (Li & Wu 2004). Consequently, landscape indices should not be used alone when studying in *P. oceanica* seascapes, while and the outcomes should not be used as the ultimate tool for management decisions but rather coupled with other landscape procedures and interpreted using knowledge of ecological processes (Fig. 57). The limitations of landscape indices also highlight the need for new practical ways to provide information on seascapes to stakeholders.

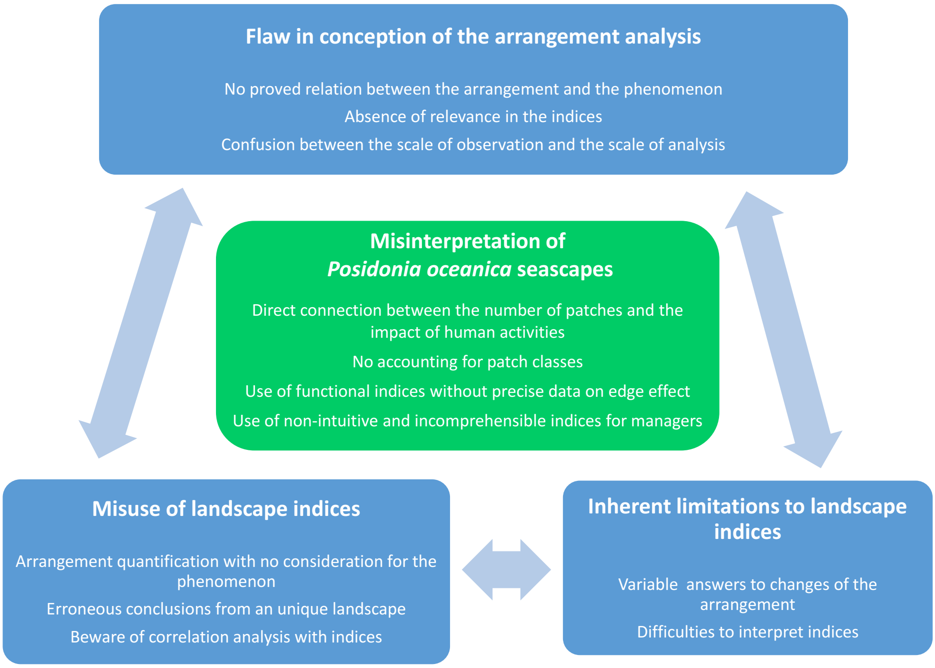


***Figure 57**: Issues encountered when using indices in landscape ecology (blue) and their impact on the study of* P. oceanica *seascapes (green) [modified from Li and Wu (2004)].*

4.2.2. Landscape graph

Traditionally studied as a patch mosaic, landscapes can also be described within the context of a more functional angle by using an approach called the 'landscape graph' (Fig. 58) (Kupfer 2012). Applying the mathematical theory underlying landscape graphs to landscape ecology results in nodes (2D patches) connected by links (from the perimeter or the center) inside a matrix (Fall *et al.* 2007). Links can be drawn as Euclidean distances (straight lines) as well as lowest cost (for instance according to relief or habitats) or else be weighted using ecological factors. Different types of graphs can be built and modeled, for example, making links between all nodes or only making nodes close to another (Galpern *et al.* 2011). The generation of landscape graphs requires the use of new metrics to study landscape characteristics. This type of model is, however, limited as it only takes into account the landscape connectivity characteristics but not habitat quality (Moilanen 2011).

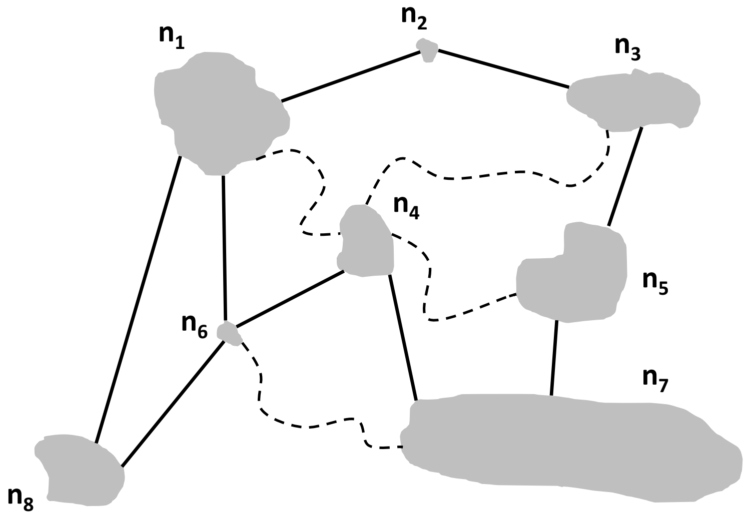


Figure 58*: Schematic diagram of the graph concept as applied to landscape ecology. Grey patches represent nodes (n), full black lines depict direct links (Euclidean distance) and dotted lines show links of lower cost.*

The use of landscape graphs for the study of *P. oceanica* seascapes will be an important breakthrough in understanding of the influence of meadow structure on the occurrence and distribution of associated biota. Within the context of conservation and management, graphs will help us gain insight of important aspects (Galpern *et al.* 2011) such as: (1) nodes are connected in a seascape; (2) which patch types are important for connectivity; (3) which patches are important for connectivity; (4) how connectivity differs between graphs; (5) the threshold of aggregation within a landscape. The knowledge gained will be very useful for managers involved in the conservation and management of seagrass habitat. The Landscape Graphs Model thus allows better communication of knowledge on important ecological aspects with decision-makers (Bergsten 2013).

Conclusion

Amongst the seascapes formed by different seagrasses, *P. oceanica* meadows are the most studied due to their peculiar and complex three dimensional structure and the large number of species they support. Over the last 15 years, there has been a large effort to study of their large-scale structural features and interactions with fauna and flora, which has resulted in important data being available for use in management of the habitat. However, much work still remains to be done at the level of data processing as well as to enhance transfer of information on seagrass seascape ecology to managers and stakeholders. New approaches and simplified procedures are currently available for landscape ecological studies but these cannot always be applied to seascape ecology due to lack of data. Hence, there is need for ecological studies aimed at gathering the necessary information as well as to develop new tools and procedures including ones aimed studying *P. oceanica* seascapes.

CHAPITRE 5

DISCUSSION, APPLICATIONS ET CONCLUSIONS : Utiliser les intermattes pour la conservation du paysage sous-marin

En partant de l'unité qui compose les paysages formés par *Posidonia oceanica*, *i.e.* 'l'intermatte', puis en s'intéressant à sa globalité, ces travaux de doctorat ont mis en lumière l'importance de telles structures dans la dynamique de cet habitat côtier primordial. Ainsi, l'influence de facteurs tant naturels qu'anthropiques change la morphologie des paysages à *P. oceanica*, modifiant les interactions avec la faune, la flore et d'autres systèmes marins. Ces influences se traduisent par des formes variées d'intermattes naturelles et artificielles.

Ainsi, les intermattes naturelles se révèlent être des sites particulièrement intéressants pour l'étude du processus de recolonisation du substrat nu par l'herbier. A l'opposé, les intermattes issues de l'impact des activités humaines montreront des faciès et des dynamiques plus variés, le phénomène prépondérant étant dans ce cas la fragmentation de l'herbier. Ceci est particulièrement étudié dans le cadre de l'ancrage de grosses unités avec un effet mécanique de destruction, débouchant sur l'intrusion de composés chimiques toxiques pour la plante limitant le processus de recolonisation.

Dans cette partie il est donc discuté du potentiel des intermattes en tant qu'indicateur de l'influence des facteurs naturels et anthropiques sur la dynamique des paysages sous-marins formés par *P. oceanica*. Ces réflexions s'appuient sur les résultats de travaux originaux réalisés dans le cadre du doctorat (dont l'encadrement de travaux de fin d'études), ainsi que sur des collaborations à d'autres programmes de recherches (GECOMED, gestion de la RNBB). Plusieurs outils et méthodes d'étude des herbiers sont ainsi passés en revu tout en discutant de leurs limites et de leur potentiel au travers d'applications concrètes. La réflexion sur l'utilité relative de tels outils est réalisée pour leur utilisation, dans le cadre d'études ponctuelles et de suivis réguliers, par des organisations d'étude du milieu marin généralistes (bureaux d'étude, aires marines protégées, collectivités locales, universités). Chaque application est illustrée par une représentation qualitative évaluant la pertinence du coût, du temps de terrain et de traitement des données, des connaissances requises et de la reproductivité de la méthode employée selon un code couleur familier des gestionnaires (bleu : très bon ; vert : bon ; jaune : moyen, orange : mauvais, rouge : très mauvais). Enfin, ces méthodes sont confrontées afin de proposer la base d'indice d'évaluation de l'impact de l'ancrage sur les herbiers à *P. oceanica*.

1. Les intermattes naturelles : Lieu d'étude du processus de recolonisation des herbiers

1.1. Etude spatiale de la dynamique des intermattes naturelles

Comme démontré dans le Chapitre 2, les intermattes naturelles sableuses sont des sites propices pour l'étude spatiale de la recolonisation de l'herbier. La méthode de balisage (Fig. 59) pour le suivi spatial des intermattes, mise au point au début des années 2000 et se poursuivant à ce jour, a ainsi prouvé son efficacité en permettant une mesure au centimètre près de l'évolution du processus de recolonisation et d'érosion (NOMATEC 2002, Gobert *et al.* accepted).

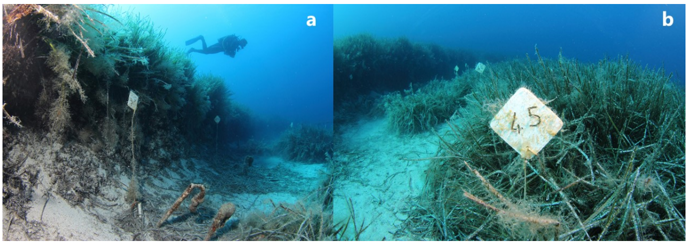


Figure 59 *: Balisage des intermattes en Baie de Calvi a) au niveau de l'érosion ; b) au niveau de la recolonisation.*

Cette méthode non-destructive permet donc un suivi à long terme des intermattes à moindre coût tout en requérant un faible temps de plongée sous-marine pour la mise en place, le suivi et/ou la récupération des balises. Le balisage est également utilisé pour l'étude de la limite inférieure des herbiers à *P. oceanica* depuis le des années 1990 dans le cadre du Réseau de Surveillance Posidonie (Boudouresque *et al.* 1990b) et du réseau mondial SeagrassNet (Pergent *et al.* 2015).

Par triangulation (mesure de la distance et de l'orientation entre les balises) il est ensuite possible de produire des micro-cartographies des intermattes et d'étudier leur évolution (Application n°1). Ce type d'évaluation se rapprochant alors de celles réalisées à l'aide d'un pointeur acoustique (Descamp *et al.* 2005, Descamp *et al.* 2011) cette dernière nécessitant cependant des moyens matériels, et humains plus conséquents ainsi que des compétences supplémentaires.

Application n°1 : Le cas de l'étude spatiale de la dynamique des intermattes naturelles

Site : STARESO, Baie de Calvi, Corse, France (42° 34.819'N 8° 43.522'E)

Méthode : Des balises sous la forme de piquets en PVC soutenus par des fers à béton délimitent les bords de l'intermatte sableuse à 15 m de profondeur. La distance entre les balises et leur orientation permet de réaliser une cartographie sous Système d'Information Géographique (SIG). Chaque année la distance de l'herbier par rapport au piquet est mesurée au centimètre près.

Résultats : La vitesse de colonisation moyenne est de 9 (± 5) $cm.a^{-1}$ entre 2014 et 2015 et de 10 (± 8) $cm.a^{-1}$ entre 2015 et 2016. Une vitesse d'érosion similaire est observée concernant l'érosion : 11 (± 9) $cm.a^{-1}$ entre 2014 et 2015 et 14 (± 12) $cm.a^{-1}$ entre 2015 et 2016. Comme mentionné dans le chapitre 2, ces vitesses de colonisation ne concernent pas seulement la seule croissance du rhizome mais l'avancée globale de l'herbier.

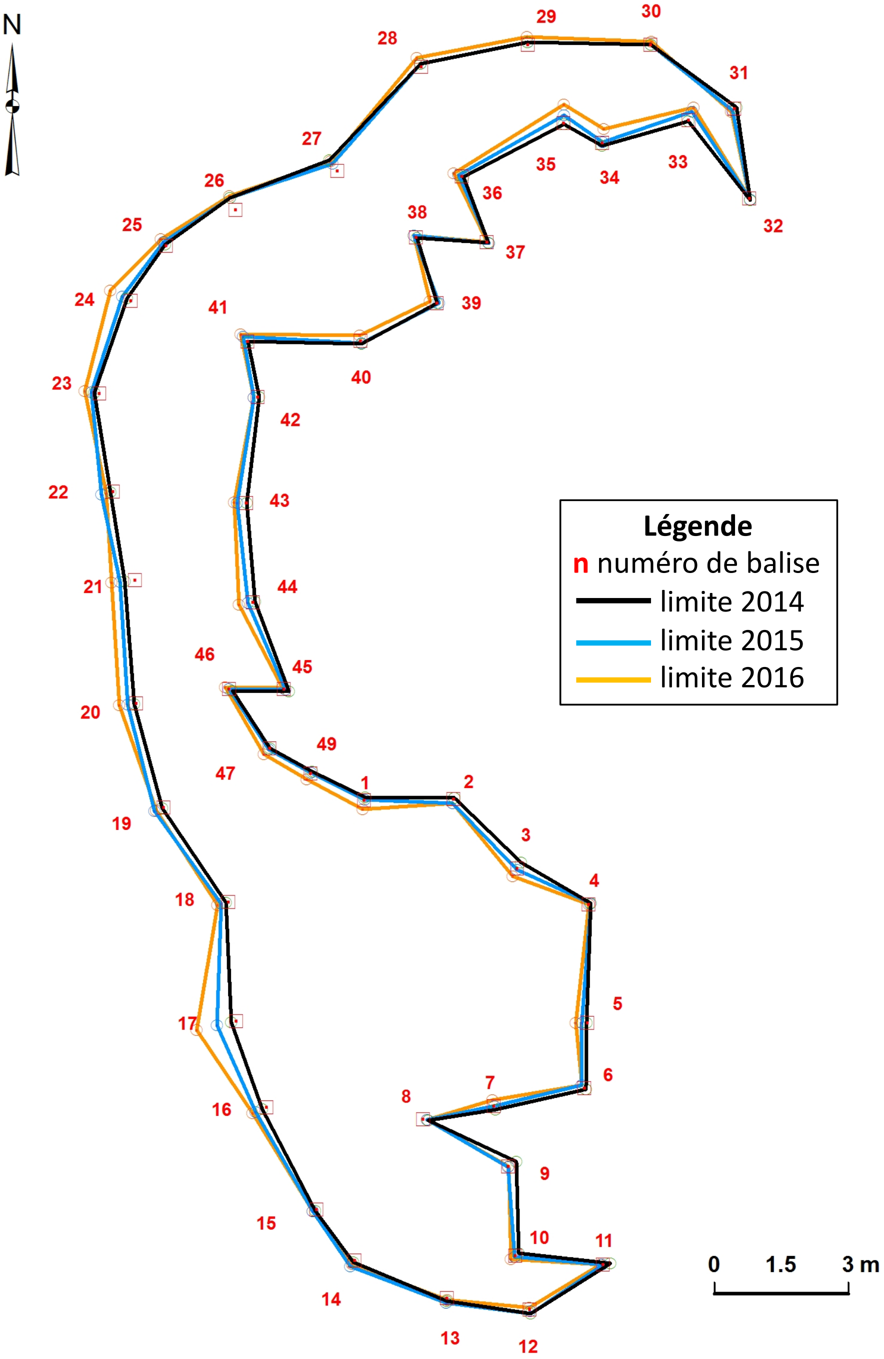


Figure 60 *: Evolution de la limite d'une intermatte naturelle sableuse à 15 m de profondeur au sein d'un herbier à* P. oceanica *de 2014 à 2016.*

Discussion : Ce système de représentation permet notamment d'identifier les lieux de plus forte érosion comme ici de la balise 16 à 18, ou de plus forte recolonisation comme de la balise 32 à 36 (Fig. 60). Le phénomène d'érosion et de colonisation n'apparaît donc pas comme homogène tant sur le plan spatial que temporel. Cette technique est peu onéreuse et nécessite peu de temps de terrain (Fig. 61), et peut également être utilisée pour le suivi de patchs de *P. oceanica*. Ces données sont similaires à celles observées depuis le début des années 2000 sur le même site (voir Chapitre 2 – Article 1). A ces mesures par balisage pourraient s'ajouter des photographies verticales pour une meilleure représentation de la limite.

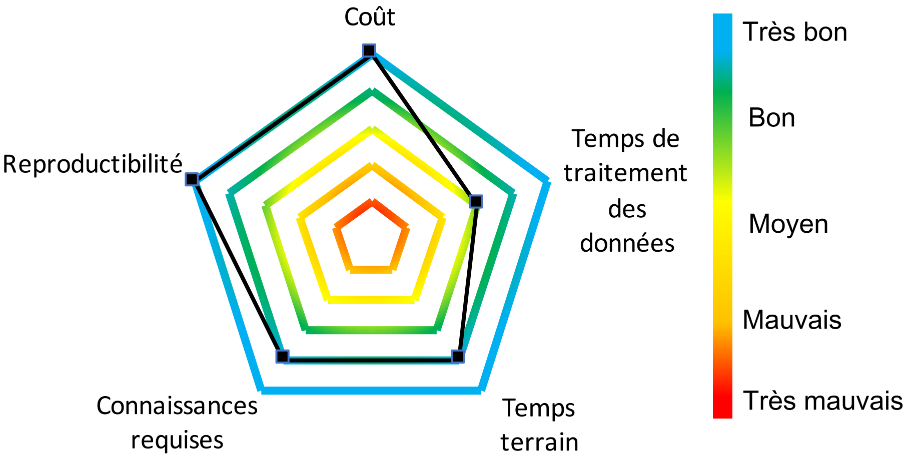


***Figure 61** : Représentation qualitative de l'utilisation du balisage pour la micro-cartographie des intermattes au sein des herbiers à* P. oceanica.

1.2. Efficacité photosynthétique en bordure d'herbier

La recolonisation de l'herbier peut donc être étudiée d'un point de vue spatial sur le long terme avec une bonne précision de mesure. L'étape suivante consiste logiquement à déterminer les facteurs intrinsèques et environnementaux influençant la dynamique de la bordure de l'herbier. Il est alors intéressant de faire appel à des notions d'écologie paysagère dont l'un des principaux buts est l'étude des phénomènes biotiques et structuraux dans les zones d'écotones, i.e. à la frontière entre deux habitats (Angelstam 1992, Forman 1995).

Dans le cas du processus de colonisation d'un substrat nu par les herbiers à *P. oceanica*, l'un des paramètres fondamentaux à prendre en compte est l'efficacité photosynthétique de la plante qui conditionne la dynamique de leur production primaire (Olesen *et al.* 2002, Zimmerman 2006). Au cours des vingt dernières années a été mise au point une technique de mesure *in situ* de l'efficacité photosynthétique de la végétation marine : la fluorimétrie à amplitude de pulsation modulée (pulse amplitude modulated – PAM – fluorometry en anglais). Le principe de fonctionnement de cet instrument de mesure repose sur l'émission de pulsations lumineuses sur les limbes et la détection de la réponse de la plante sous la forme d'une onde lumineuse (Fig. 62) (Lassauque 2009).

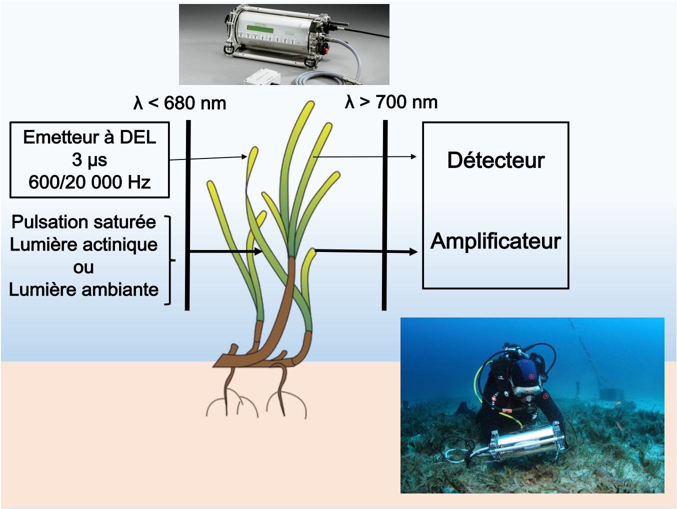


***Figure 62** : Principe de fonctionnement de la fluorimétrie à amplitude de pulsation modulée (PAM) sur les plantes sous-marines [traduit et redessiné d'après Lassauque (2009)].*

Le PAM est couramment utilisé depuis la fin des années 1990 pour l'étude de la photosynthèse chez les plantes sous-marines dont *P. oceanica* (Beer *et al.* 1998, Silva *et al.* 2009). Son utilisation pour mettre en évidence l'influence de facteurs naturels ou anthropiques sur l'activité photosynthétique des plantes sous-marines reste cependant limitée. Ceci est principalement due au manque de données sur les variations naturelles spatiales et temporelles mise en lumière par une telle technique (Gera *et al.* 2012).

En s'appuyant sur le protocole standardisé de Gobert *et al.* (2015) de mesure de l'activité photosynthétique dans les herbiers à *P. oceanica* grâce au PAM, une méthode d'étude de la photosynthèse en bordure d'herbier recolonisant les intermattes a été mise au point (Application n°2). Dans ce cas, l'adaptabilité du protocole de base a permis de mettre en évidence un lien entre la structure de la bordure de l'herbier et l'efficacité photosynthétique de *P. oceanica* en phase de recolonisation (Lapeyra 2016). L'utilisation de cette technique n'en est cependant qu'au stade de la recherche fondamentale, le protocole nécessitant des connaissances spécifiques et un certain temps d'apprentissage pour une calibration optimale et des mesures *in situ* exploitables (Fig. 65). Il n'apparaît donc pas encore envisageable d'utiliser le PAM en tant qu'outil de monitoring pour étudier l'impact des activités humaines sur les herbiers à *P. oceanica*. L'effort de recherche fourni actuellement présage cependant une utilisation future comme bioindicateur prometteuse à moyen terme.

Les seules mesures obtenues en utilisant le PAM ne semblent pas être capables de fournir une évaluation de l'état de conservation d'un herbier à *P. oceanica* et doivent être couplées à d'autres observations. Plus spécifiquement, l'étude des interactions chimiques entre la plante et le sédiment permet une compréhension plus complète des processus en jeu.

Application n°2 : Le cas de l'efficacité photosynthétique en bordure d'herbier

Site : STARESO, Baie de Calvi, Corse, France (42° 34.819'N 8° 43.522'E)

Méthode : Des mesures de réponse photosynthétique ont été réalisées avec un PAM en bordure d'intermatte et au sein d'herbiers continus à 15 m de profondeur sur des rhizomes orthotropes et plagiotropes en tenant compte de leur proportion. La réponse de la plante aux stimulations lumineuses croissante est exprimée en taux de transfert d'électrons maximum (ETR_{max}).

Résultats : Une structuration différente au niveau de la proportion des types de rhizomes est observée entre la bordure recolonisante de l'intermatte et l'herbier continu (Fig. 63).

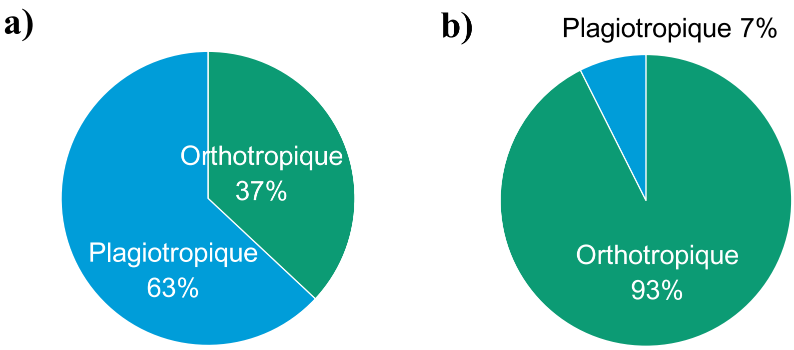


***Figure 63** : Proportion de rhizomes plagiotropes et orthotropes a) en bordure d'herbier ; b) dans un herbier continu (Lapeyra 2016).*

Les mesures d'ETR_{max} réalisées avec le PAM ne révèlent cependant aucune différence significative en comparant l'herbier continu et sa bordure (Fig. 5-7a ; t-test : p=0.0589, t=1.970, df=28). En revanche une différence significative est observée en comparant l'ETR_{max} des faisceaux plagiotropes et orthotropes (Fig. 64b ; Mann Whitney test : p=0.0224, U=292.5).

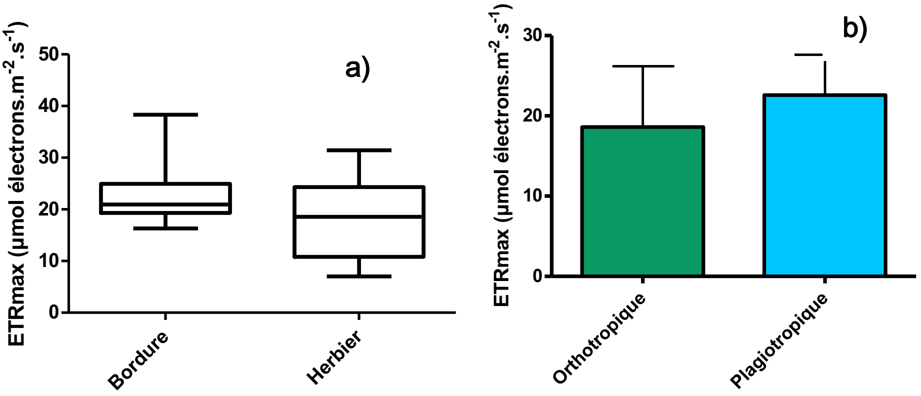


Figure 64 : Comparaison de l'ETRmax entre a) la bordure de l'intermatte et l'herbier continu ; b) les rhizomes plagiotropes et orthotropes (Lapeyra 2016).

Discussion : Ces résultats indiquent que le contraste physiologique induit par le type de rhizome n'entraîne pas de variation de l'efficacité photosynthétique en bordure de l'herbier malgré une quantité de lumière accrue. La capacité de l'herbier à coloniser un substrat nu ne dépendra donc pas seulement de la lumière mais également d'autres facteurs tels que la physico-chimie du sédiment.

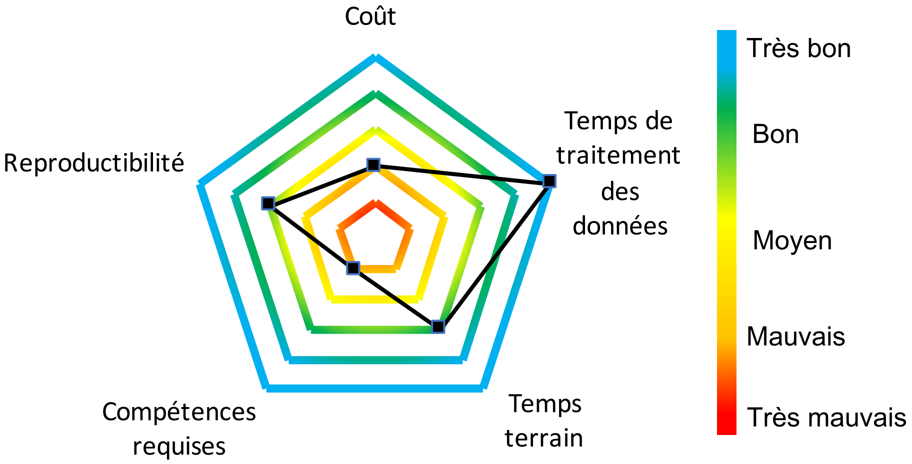


Figure 65 : Représentation qualitative de l'utilisation du PAM pour l'étude de la recolonisation des intermattes au sein des herbiers à P. oceanica*.*

1.3. Approche biogéochimique du sédiment

De par leur constante interaction avec le sédiment qu'elle colonise, *P. oceanica* modifie la biogéochimie de son substrat (Marbà *et al.* 2006). A l'inverse, les conditions physico-chimiques du sédiment influencent le développement de la plante, favorisant ou limitant ainsi sa croissance (Holmer *et al.* 2003, Pérez *et al.* 2007). L'étude des processus biogéochimiques se déroulant au sein du substrat colonisé par les herbiers à *P. oceanica* est ainsi un bon indicateur des facteurs naturels et anthropiques pouvant influencer leur dynamique physiologique et structurelle (Pergent-Martini *et al.* 2005).

Durant ces travaux de thèse plusieurs éléments chimiques de l'eau interstitielle du sédiment ont été mesurés au niveau des bordures des intermattes naturelles à différentes profondeurs et saisons, mettant en lumière une signature biogéochimique particulière au niveau de la recolonisation de l'intermatte par l'herbier (voir Chapitre 2 – Article 2). A partir de cette observation, il est alors nécessaire de déterminer quels éléments chimiques seront potentiellement les meilleurs indicateurs dans le cadre de travaux de suivi de la recolonisation de l'herbier nécessitant un coût et un temps d'acquisition de données optimisés.

Aux vues des études antérieures réalisées sur la biogéochimie du sédiment dans les herbiers à *P. oceanica* et des travaux réalisés durant ce doctorat, il est possible d'isoler un petit nombre de composés chimiques au fort potentiel d'indicateur mesurables dans l'eau interstitielle du sédiment :

- **pH** (potentiel hydrogène) : il peut notamment être relié de façon directe avec l'activité photosynthétique de *P. oceanica* et à divers autres phénomènes métaboliques (Invers *et al.* 1997, Marbà *et al.* 2006). Le pH est cependant plus utilisé comme un révélateur des processus se déroulant au sein du substrat, en particulier le cycle des carbonates (Invers *et al.* 2001, Pilson 2012).

- **Alcalinité totale** (TA = $[HCO_3^-] + 2[CO_3^{2-}] + [B(OH)_4^-]$ + [minor ions] + $[OH^-] - [H^+]$) : en complément du pH, l'alcalinité permet une meilleure appréciation du système des carbonates. En effet, les divers composant de ce système influençant la photosynthèse de *P. oceanica* au travers de la modification des concentrations en CO_2. A partir de cette mesure il est possible de calculer le carbone inorganique dissous (DIC = $[CO_2] + [HCO_3^-] + [CO_3^{2-}]$) qui est lié à la production primaire des herbiers à *P. oceanica*.
- **Sulfure d'hydrogène** (H_2S) : ce composé réduit du sulfate (SO_4^{2-}) est abondamment présent dans la couche anoxique du substrat sur lequel se développent les herbiers à *P. oceanica*. S'il a été rapporté qu'une exposition prolongée de la plante à des concentrations supérieures à 10 µM réduit son développement (Calleja *et al.* 2007), des concentrations supérieures son enregistrées durant les périodes chaudes (García *et al.* 2012). Le sulfure d'hydrogène est donc un indicateur ayant un fort potentiel pour les suivis saisonniers.
- **Nutriments** (ammonium, nitrate, nitrite, phosphate) : sous leur forme ionique ce sont des éléments limitants du développement des herbiers à *P. oceanica* (Romero *et al.* 2006). Bien que les quantités de nutriments mesurées dans les herbiers soient faibles (Gobert *et al.* 2002), les variations de leurs concentrations sont de bon indicateurs de développement de la plante.

Si l'identification de composés chimiques comme indicateurs est relativement aisée, il est très difficile de développer des outils et des méthodes de mesure simples et rapides pour un suivi régulier des éléments chimiques présents dans le sédiment marin. La première difficulté réside dans la l'importante variabilité temporelle (e.g. jour/nuit, saisons, météo) et spatiale (e.g. profondeur dans le sédiment, variations horizontales) de ces indicateurs, nécessitant le strict respect de protocoles définissant une heure solaire et un lieu de prélèvement. Le second obstacle à de telles analyses est le prélèvement de l'eau interstitielle du substrat. Bien que simplifié par Gobert *et al.* (2006b), une expérience importante du plongeur est requise pour ce type de prélèvement nécessitant une précision de manipulation maximum pour éviter toute contamination de l'échantillon. Enfin, il est nécessaire de procéder directement aux analyses en laboratoire, la stabilité des échantillons n’excédant pas quelques heures pour les composés les plus stables.

En laboratoire, bien que certaines mesures puissent être facilitées avec l’utilisation de sondes (Application n°3), le dosage des éléments chimiques requiert plusieurs heures de travail et des compétences techniques importantes (Fig. 67). La rigueur obligatoire à chaque étape du protocole découle de la précision de mesure nécessaire pour étudier des éléments souvent en faible concentration dans les herbiers à *P. oceanica.* Ainsi, l’utilisation de méthodes simplifiées pour la mesure d’éléments chimiques dans l’eau interstitielle du sédiment, comme par exemple les tests colorimétriques de qualité de l’eau, ne sont pas utilisables. En revanche, l’utilisation de méthodes de mesure indirectes, tel que le gradient de diffusion en couche mince (DGT) semble prometteuse. Ces petits dispositifs basés sur le principe de l’adsorption sur résine permettent ainsi une mesure différée de composés tels que le sulfure d’hydrogène et certains éléments traces(Naylor *et al.* 2004, Richir *et al.* 2011, Abadie *et al.* 2014). La simplification et l’automatisation des mesures d’éléments chimiques dans le sédiment marin sont donc une nécessité pour une étude complète et saisonnière de la dynamique de recolonisation des herbiers à *P. oceanica*.

Application n°3 : Mesure du sulfure d'hydrogène dans l'eau interstitielle du sédiment

Site : STARESO, Baie de Calvi, Corse, France (42° 34.819'N 8° 43.522'E)

Méthode : L'eau interstitielle du substrat à 10, 15 et 20 m de profondeur a été prélevée en bordure d'intermatte et dans un herbier continu en septembre 2014 à l'aide de seringues (fig. 66a) à 10 cm de profondeur dans le sédiment. Le sulfure d'hydrogène est immédiatement quantifié en laboratoire à l'aide d'une sonde équipée d'une électrode Ag/H_2S (à calibrer avant chaque jeu d'échantillons, Fig. 66b) mesurant directement le potentiel de l'échantillon. Les résultats sont ensuite interprétés à l'aide d'une droite d'étalonnage pour obtenir la concentration en H_2S de chaque échantillon (voir Annexe 6 pour le protocole détaillé).

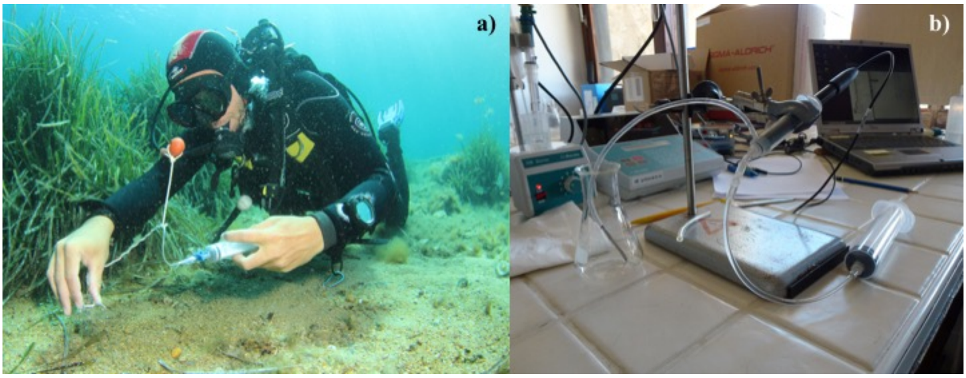


***Figure 66** : a) Echantillonnage de l'eau interstitielle à l'aide d'une seringue et d'une aiguille ; b) sonde de mesure du sulfure d'hydrogène.*

Résultats : Les concentrations en sulfure d'hydrogène sont plus grandes dans l'herbier qu'en bordure. Par exemple, à 10 m, 36.2 µM dans l'herbier continu contre 1.8 µM dans la bordure recolonisante et 0.5 µM en bordure dans le sédiment nu (Tab. 22).

***Tableau 22** : Concentration en sulfure d'hydrogène (µM) mesuré dans un herbier continu et en bordure d'herbier à 10, 15 et 20 m de profondeur en septembre 2014.*

Profondeur	Herbier continu	Bordure herbier	Bordure sédiment nu
10 m	36.2	1.8	0.5
15 m	35.5	0.2	0.0
20 m	41.8	11.0	1.7

Discussion : Ces résultats concordent avec ceux de précédents travaux où une concentration en sulfure d'hydrogène plus élevée est trouvée dans les herbiers à *P. oceanica* par rapport au sédiment nu (Barrón *et al.* 2006). On observe ici un gradient avec une décroissance de la concentration en H_2S de l'herbier continu jusqu'au sédiment nu en passant par l'herbier en état de recolonisation (Tab. 22). Ce phénomène s'explique par des conditions plus réductrices dans le sédiment colonisé de longue date, du fait de la décomposition de matière organique. Les faibles concentrations au niveau de la recolonisation sont reliées au manque de développement de la structure souterraine de la plante, diminuant ainsi la quantité de matière en décomposition.

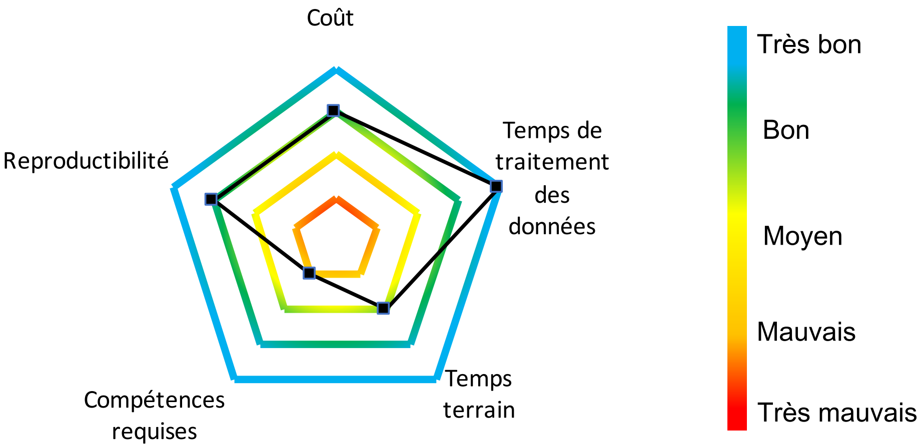


***Figure 67** : Représentation qualitative de la mesure du sulfure d'hydrogène avec une sonde pour l'étude de la recolonisation des intermattes au sein des herbiers à P. oceanica.*

2. Le paysage à *P. oceanica* influencé par les activités humaines : L'exemple de l'ancrage

A l'opposé des intermattes naturelles, structures propices pour l'étude du processus de recolonisation de l'herbier, les intermattes anthropiques permettent une meilleure compréhension des phénomènes limitant le développement de l'herbier. Dans ce but, les sites d'ancrage intensif de grosses embarcations fournissent de nombreuses intermattes dont l'origine est clairement identifiable. Plusieurs échelles d'approches sont possibles en utilisant les caractéristiques des intermattes comme indicateur de l'impact de l'ancrage à différentes échelles spatiales.

2.1. L'intermatte anthropique comme indicateur de l'impact de l'ancrage

La structure d'un herbier sous pression d'ancrage est généralement étudiée en utilisant des indicateurs classiques tels que la densité de l'herbier, son recouvrement et la compacité de la matte (Francour *et al.* 1999, Milazzo *et al.* 2004, Ceccherelli *et al.* 2007). Cependant, quelques études ont eu recours à une approche que l'on peut qualifier de paysagère en utilisant les intermattes (leur nombre et leur taille) pour qualifier l'état de conservation d'herbiers à *P. oceanica* soumis à la pression d'activités humaines diverses dont l'ancrage (Moreno *et al.* 2001, Ganteaume *et al.* 2005a, Ganteaume *et al.* 2005b). Dans la continuité de ce type d'approche, les travaux de recherches réalisés durant ce doctorat visent à étudier la dynamique des intermattes pour évaluer l'influence de l'ancrage sur les paysages à *P. oceanica*.

Dans un premier temps, c'est la dynamique spatiale des intermattes générée par l'ancrage qui doit être étudiée. La technique de balisage et de cartographie décrite dans la première étude de cas de ce chapitre est particulièrement efficace dans le cadre d'un suivi à long terme. Cette méthode, couplée à d'autres mesures *in situ*, a été notamment utilisée à partir de 2012 (Application n° 4) dans le parc marin international des bouches de Bonifacio (PMIBB) dans une zone d'ancrage intensif (Buron *et al.* 2012, Meziere 2016). Elle permet notamment d'évaluer si les mesures de gestions de l'ancrage (interdiction, mouillage écologique) permettent une recolonisation des intermattes par l'herbier.

Application n°4 : Recolonisation des intermattes d'ancrage après mesures de gestion

Site : Cala di u Grecu et Cala di u Ghiuncu, Lavezzu, Corse, France (41°20'27. N 9°15'33E)

Méthode : Cinq intermattes issues de la destruction mécanique par les ancres sont identifiées et leurs bordures balisées en 2012 à l'aide de piquets (voir Application n°1) dans une zone d'ancrage récemment interdite au mouillage. Une cartographie de chaque intermatte est réalisée pour suivre l'évolution de leur superficie. La quantité et la proportion de rhizomes plagiotropes/orthotropes à l'intérieur du périmètre balisé est également mesurée comme indicateur de la recolonisation de l'herbier. Ces mesures sont répétées en 2016 pour évaluer la dynamique de recolonisation des intermattes.

Résultats : Les photos des intermattes permettent de les cartographier précisément. Le nombre de rhizomes plagiotropes augmente ou reste stable augmente légèrement à toutes les stations tandis que le nombre de rhizomes orthotropes augmente nettement (Figure 69).

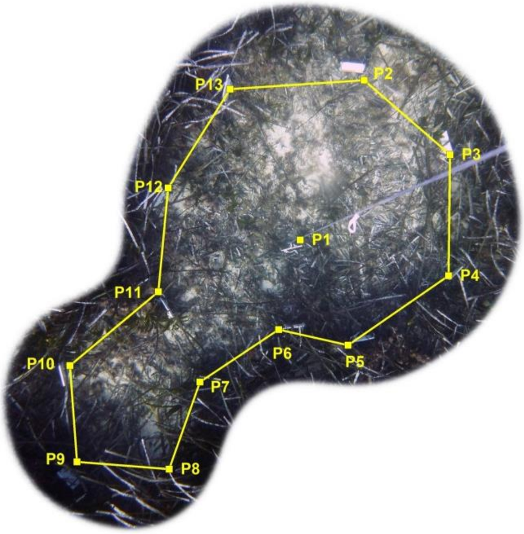


***Figure 68** : Photographies verticale d'une intermatte d'ancrage balisée (en jaune) en Décembre 2012 (Meziere 2016).*

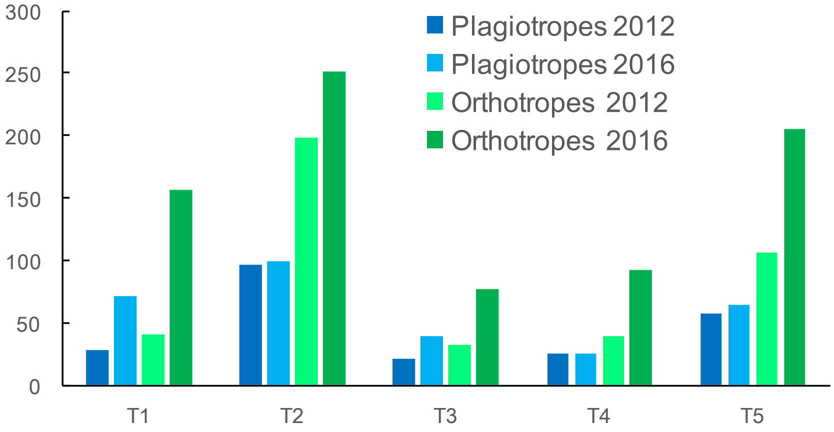


Figure 69 *: nombre de rhizomes plagiotropes et orthotropes observés dans chaque intermatte d'ancrage étudiées (T1 à T5) (Meziere 2016).*

Discussion : Les photographies verticales des intermattes d'ancrage permettent d'estimer la recolonisation par l'herbier. Le processus de recolonisation est principalement mis en évidence par le nombre de rhizomes plagiotropes et surtout par l'augmentation notable du nombre de rhizomes orthotropes. Ce dernier indique que l'herbier se 'stabilise' après une phase de recolonisation intensive et commence à se restructurer (i.e. édification de la matte). Le nombre constant de rhizomes plagiotropes révèle que le processus de recolonisation est toujours en cours.

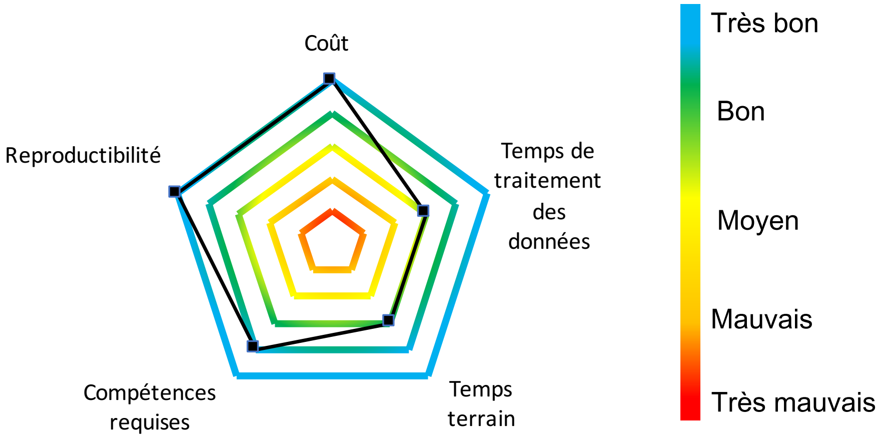


Figure 70 *: Représentation qualitative de l'étude de la recolonisation des intermattes d'ancrage au sein des herbiers à* P. oceanica*.*

Dans un deuxième temps, il est intéressant d'étudier la dynamique du flux de particules à l'intérieur des intermattes d'ancrage, un apport trop important de sédiments ne pouvant être compensé par la croissance verticale de *P. oceanica* (Boudouresque *et al.* 1983). Dans l'optique de mesurer *in situ* et modéliser le flux de particules au sein d'un herbier à *P. oceanica*, Gacia *et al.* (1999) ont mis au point une technique simple et peu coûteuse (Fig. 73) respectant les caractéristiques des pièges à sédiment classiquement utilisés en milieu côtier (Blomkvist & Kofoed 1981, Blomqvist & Hakanson 1981). Une resuspension plus importante des particules déposées sur le sédiment nu est observée par rapport à celle de la canopée des herbiers à *P. oceanica* (Gacia & Duarte 2001). Le même constat a été réalisé durant ces travaux de doctorat entre les intermattes naturelles et l'herbier continu adjacent (Abadie 2015). De plus, une resuspension encore plus importante a été observée au sein des intermattes d'ancrage (Application n°5), cette différence étant cependant vraisemblablement due à la différence d'exposition aux vents dominants des sites étudiés. Face à cette instabilité du sédiment au sein des intermattes d'ancrage, il est plus difficile pour *P. oceanica* de recoloniser le substrat.

Enfin, il est primordial d'étudier les processus chimiques se déroulant dans les intermattes anthropiques. Comme discuté dans le Chapitre 3, la destruction mécanique de l'ancrage mène à la génération de composés toxiques limitant le développement de *P. oceanica* (Calleja *et al.* 2007, Abadie *et al.* 2016).

Lors d'une investigation complète à long terme de la dynamique individuelle des intermattes générées par l'ancrage, et plus largement des intermattes issues d'activités anthropiques (e.g. ferme aquacole, explosifs, chalutage), il serait donc idéal d'étudier les trois aspects mentionnés dans cette partie, couplés à d'autres indicateurs classiques (e.g. densité de l'herbier, compacité, proportion de rhizomes plagiotropes/orthotropes). Cependant, aux vues des contraintes financières et pratiques d'une étude de phénomènes sous-marins, une étude spatiale de la dynamique spatiale des intermattes (Application n°4) semble suffisante pour estimer l'efficacité de mesures de gestions ou évaluer la vitesse d'érosion d'une zone soumise à l'ancrage. Ces observations devront être complétées par des données de fréquentation de la navigation de plaisance dans la zone d'étude (Abadie *et al.* 2016).

Application n°5 : Flux de particules dans une intermatte d'ancrage

Site : Baie de l'Alga, Corse, France (42°33'53.85"N 8°43'52.22"E)

Méthode : Des pièges à sédiments configurés pour mesurer la resuspension des particules dans les 80 premiers centimètres au-dessus du fond (Gacia *et al.* 1999) sont placés dans un herbier continu (Fig. 71a) et une intermatte d'ancrage (Fig. 71b) à 15 m de profondeur en juillet 2015 et en février 2016. Ils sont récupérés après huit jours complets de prélèvements et leur contenu est filtré en laboratoire en utilisant des filtres pré-pesés GF/F de 25 mm. Les filtres sont ensuite séchés en étuve pendant quatre jours à 60 °C puis pesés pour obtenir la quantité de matière sèche remise en suspension par mètre carré.

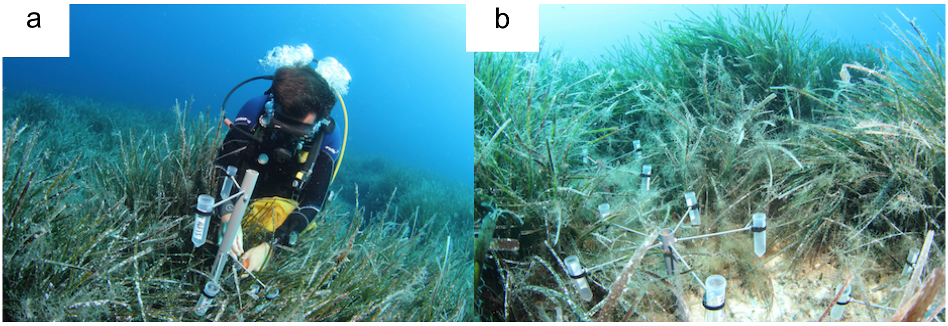
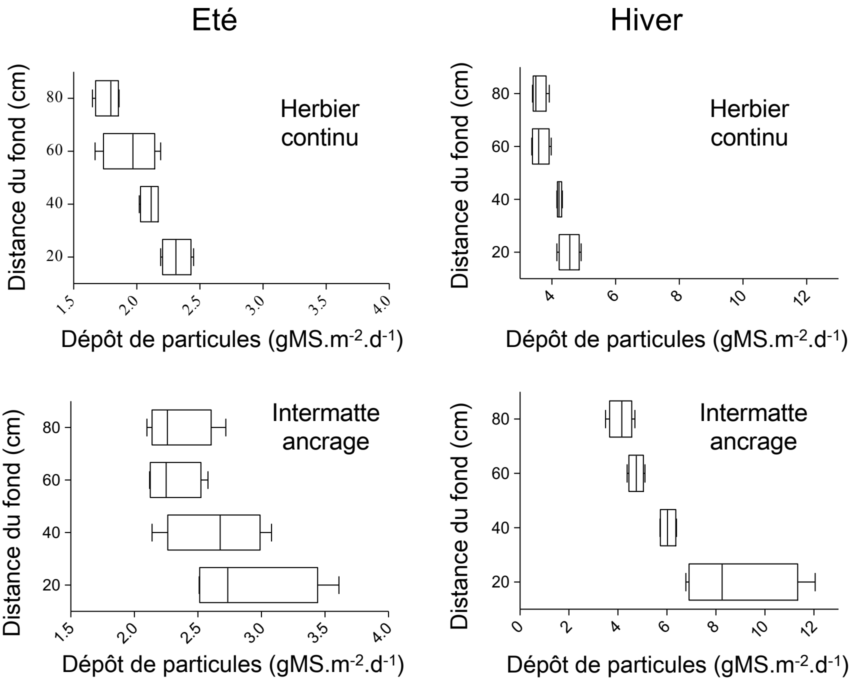


***Figure 71** : Pièges à sédiments à 15 m de profondeur en été dans a) un herbier continu ; b) une intermatte d'ancrage.*

Résultats : La resuspension est plus importante en hiver qu'en été (Fig. 72) ce phénomène étant principalement dû à l'hydrodynamisme plus turbulent durant la période hivernale avec des tempêtes beaucoup plus fréquentes. Une resuspension légèrement plus importante est observée dans l'intermatte d'ancrage aux deux saisons de l'année étudiées (Fig. 72), ce phénomène pouvant être accentué lors d'épisodes de tempête (Abadie, données non-publiées). Une déposition totale, i.e. 20 cm au-dessus du fond, significativement plus grande est observée dans l'intermatte d'ancrage (t-test : p=0.012 ; t=3.552 ; df=6), cette dernière agissant ainsi comme un piège à sédiment.


Eté

Hiver

Figure 72 : Resuspension des particules en été et en hiver dans un herbier continu et une intermatte d'ancrage.

Discussion : Dans le cas présent, le flux de particules n'est pas le seul fruit d'éléments intrinsèques au milieu marin. Des phénomènes naturelles (e.g. le ruissellement des eaux de pluie) et des activités anthropiques (e.g. les rejets des navires de plaisance) peuvent aussi influencer la dynamique sédimentaire et par extension, celle des intermattes d'ancrage.

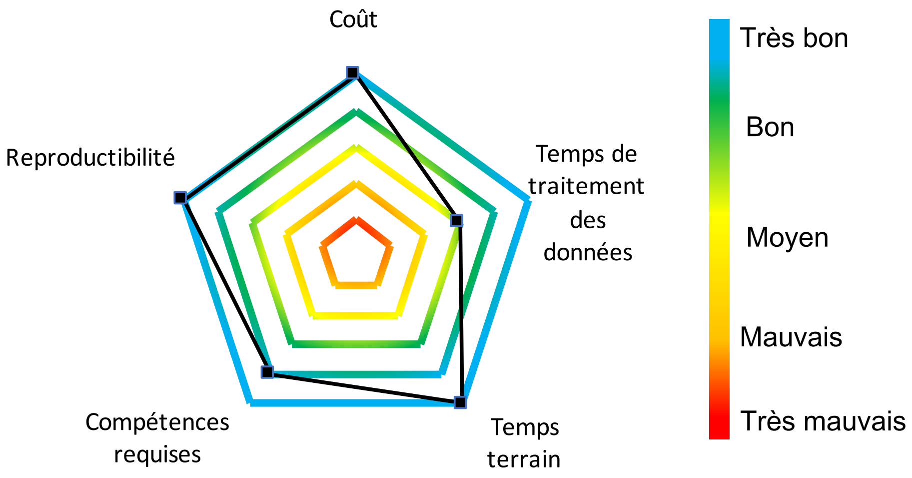


Figure 73 *: Représentation qualitative de l'utilisation de piège à sédiment pour l'étude du flux de particules dans les herbiers continus et les intermattes d'ancrage.*

2.2. Approche écosystémique et impact de l'ancrage

En complément, ou comme alternative à une étude individuelle des intermattes, il est possible d'envisager une approche dite 'écosystémique' (voir Chapitre 1). Ce ne sont ainsi plus les compartiments (intermattes) du paysage qui sont étudiés mais les compartiments fonctionnels de l'écosystème *P. oceanica* (Fig. 74). En faisant la synthèse des observations réalisées dans une partie des compartiments il est possible d'évaluer l'état écologique d'un herbier à l'aide de l'indice de qualité basé sur l'écosystème (EBQI).

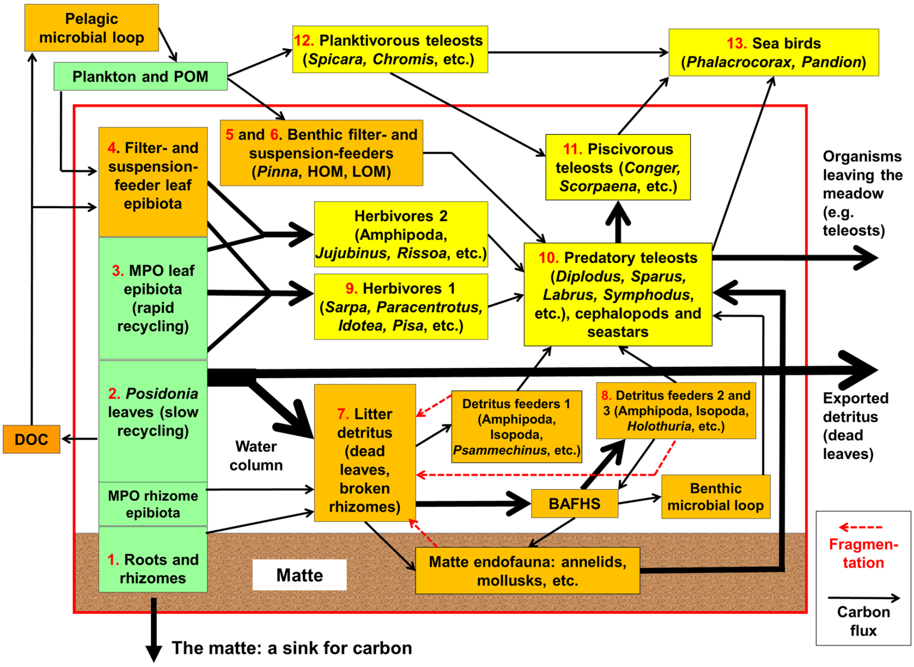


Figure 74 : Schéma conceptuel reliant les différents compartiments fonctionnels de l'écosystème à P. oceanica*. Les compartiments numérotés correspondent à ceux étudiés pour le calcul de l'indice d'état écologique (EBQI) (Personnic et al. 2014).*

Cette approche de conception récente semble prometteuse pour identifier les compartiments de l'écosystème nécessitant une attention particulière (e.g. manque de données, nécessité de mesures de gestion). L'étape suivante d'une telle approche est de définir l'impact des activités humaines sur chacun des compartiments de l'écosystème à *P. oceanica* afin de relier l'EBQI à des décisions de gestion ciblées. Une première réflexion a été réalisée dans cette optique par Giakoumi *et al.* (2015b) sur la base de la connaissance d'un groupement d'experts du fonctionnement de l'écosystème à *P. oceanica*. Cette approche a notamment permis de déterminer un facteur d'impact propre à chaque compartiment fonctionnel de l'écosystème pour un ensemble d'activités humaines en milieu côtier dont l'ancrage. L'ancrage est ainsi identifié comme une pression endommageant principalement la strate foliaire et souterraine des herbiers à *P. oceanica* ainsi que les épibiontes et les invertébrés filtreurs qui y vivent (Giakoumi *et al.* 2015b).

Lorsqu'une une zone d'ancrage intensif est étudiée via le calcul de l'EBQI, il apparaît que ces compartiments présentent un état de conservation moyen voir bon, alors que les compartiments comprenant des téléostéens présentent un mauvais état écologique (Fig. 75, Application n°6). Cette évaluation des compartiments des téléostéens ne reflète pas un impact direct de l'ancrage sur ce compartiment jugé peu ou pas impacté par ce type de pression (Giakoumi *et al.* 2015b).

L'impact mécanique des ancres sur le fond devrait cependant être visible sur la structure de l'herbier. Comme discuté dans le Chapitre 3, les indicateurs structuraux classiques se révèlent efficaces à une profondeur inférieure à 10 m pour des embarcations de petite taille (< 10 m de long). A plus grande profondeur (comme à 15 m pour l'échantillonnage de l'EBQI), l'impact des grandes unités se traduit par la création de larges intermattes de matte nue (voir Chapitres 3 et 4).

Dans le but de mettre en évidence via le calcul de l'EBQI les pressions anthropiques résultant en un impact mécanique sur les herbiers à *P. oceanica*, il semble donc nécessaire d'y ajouter des mesures paysagères simples telles que le Conservation Index (Moreno *et al.* 2001) ou à plus grande échelle le Patchiness Source Index (Abadie *et al.* 2015b). Cependant, l'ancrage peut avoir un effet indirect sur d'autres compartiments. Plus précisément, le bruit produit par les embarcations peu impacter la capacité de communication de certaines espèces comme *Chromis chromis* Linnaeus (Codarin *et al.* 2009). De même, la pêche récréative depuis les navires de plaisance, souvent sous-estimée, peut également mener à une diminution de la biomasse des téléostéens dans la zone (Lewin *et al.* 2006).

Il apparaît donc indispensable de créer de nouveaux outils faisant appel à des notions paysagères reliant directement la structure à la distribution des organismes vivants au sein des herbiers à *P. oceanica*. S'il est actuellement difficile de relier à grande échelle la structure à la distribution des organismes dans les paysages à *P. oceanica* (voir Chapitre 4 – Article 4), il est cependant possible de développer des outils d'analyse cartographique de la structure des paysages sous-marins sous pression d'ancrage.

Application n°6 : Utilisation de l'EBQI dans une zone d'ancrage intensif

Site : Baie de l'Alga, Corse, France (42°33'53.85"N 8°43'52.22"E)

Méthode : Les différents compartiments fonctionnels de l'écosystème à *P. oceanica* dans la baie de l'Alga sont évalués à 15 m de profondeur en juillet 2016 pour calculer l'état écologique du site selon la méthode de Personnic *et al.* (2014).

Résultats : L'EBQI dans la baie de l'Alga atteint 4/10 ce qui correspond à un état écologique 'médiocre'. Les compartiments fonctionnels de *P. oceanica* ont un état 'moyen' à 'bon' alors que ceux des téléostéens sont évalués en 'mauvais' état écologique (Fig. 5-18, détail des données en Annexe 10).

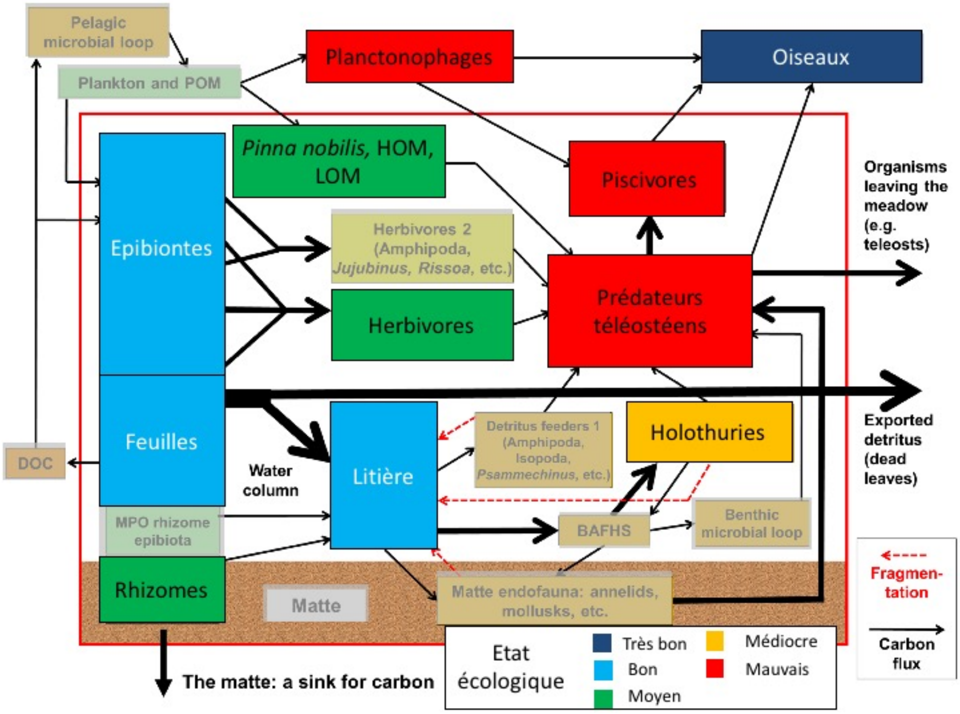


Figure 75 *: Modèle conceptuel de l'écosystème à* P. oceanica *dans la Baie de l'Alga après calcul de l'EBQI. Les compartiments grisés ne sont quantifiés.*

Discussion : Les compartiments structurels de la plante ne semblent pas impactés par l'ancrage ce qui correspond aux observations de Abadie *et al.* (2016) sur le même site à la même profondeur. En effet les dommages de l'ancrage se traduisent par de larges intermattes avec une chimie du sédiment modifiée, un phénomène non-détectable par les outils classique d'étude utilisés pour le calcul de l'EBQI. Le 'mauvais' état écologique des compartiments à téléostéens est plus surprenant. Il peut cependant s'expliquer naturellement par l'oligotrophie des eaux de la Baie de l'Alga (et plus largement de la Baie de Calvi) produisant un effet 'bottom up' à partir du plancton, réduisant ainsi la quantité de nourriture des planctonophages et par extension la quantité de proie des piscivores (Sommer *et al.* 2002, Hounboungo *et al.* 2016). Dans la baie de l'Alga, l'EBQI ne semble donc pas adapté à l'évaluation de l'impact de l'ancrage sur la structure du paysage. Il permet cependant une évaluation de plusieurs compartiments de l'écosystème avec un coût et un temps de terrain optimisé (Fig. 76).

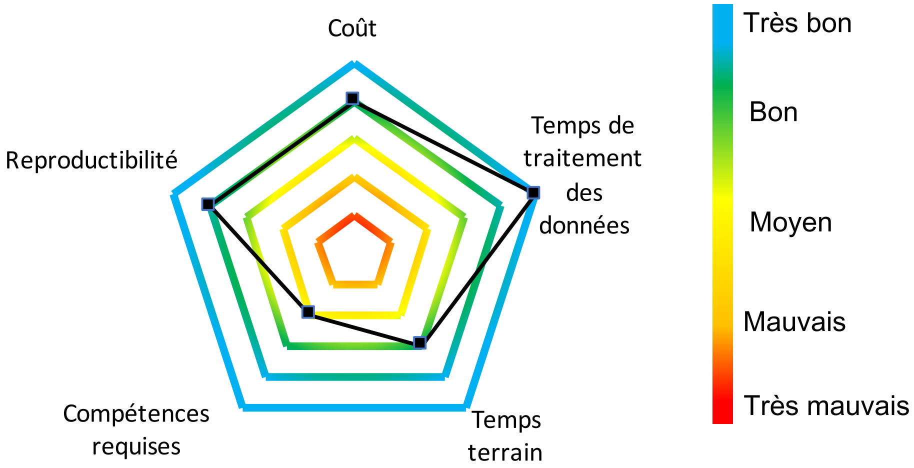


Figure 76 *: Représentation qualitative du calcul de l'EBQI dans une zone d'ancrage intensif.*

2.3. Vers de nouveaux outils d'analyse de la structure des paysages à *P. oceanica*

Les impacts mécaniques des activités humaines sont clairement identifiables au sein des herbiers à *P. oceanica* et peuvent être cartographiés et classifiés (voir Chapitre 4 – Article 5) à l'aide de données sonar. A partir de ce résultat cartographique, il est possible de réaliser des analyses paysagères des intermattes identifiées en fonction des propriétés de leur forme et de leur surface (Abadie *et al.* 2015b). Dans le cas de l'ancrage, il est possible de réaliser une étude des cartographies existantes en reclassant les intermattes en fonction de leur origine (naturelle ou anthropique) et du type d'impact dont elles sont issues (Application n°7). Il est alors possible d'obtenir très rapidement, via des logiciels d'analyse des paysages, certaines de leurs caractéristiques telles que leur nombre, leur surface, leur forme, la longueur de leur bordure ou la distance qui les séparent l'une de l'autre. Cette analyse paysagère permet non seulement d'avoir une information générale sur un site mais également d'étudier en détail chaque type d'impact anthropique recensé au travers des intermattes.

Application n°6 : Analyse paysagère de l'impact de l'ancrage

Site : Baie de l'Alga, Corse, France (42°33'53.85"N 8°43'52.22"E)

Méthode : Une carte précise de la baie est réalisée en utilisant des données sonar et bathymétriques ainsi que des orthophotographies (voir Chapitre 4 – Article 5). Les intermattes naturelles et anthropiques (ancrage) sont ensuite classées selon leur origine. Leurs caractéristiques paysagères (surface, longueur de la bordure, forme, distance de l'intermatte la plus proche) sont mesurées automatiquement en utilisant le logiciel d'analyse paysagère FRAGSTATS. Leurs caractéristiques sont enfin comparées à l'aide d'une analyse en composante principale suivie d'une classification hiérarchique.

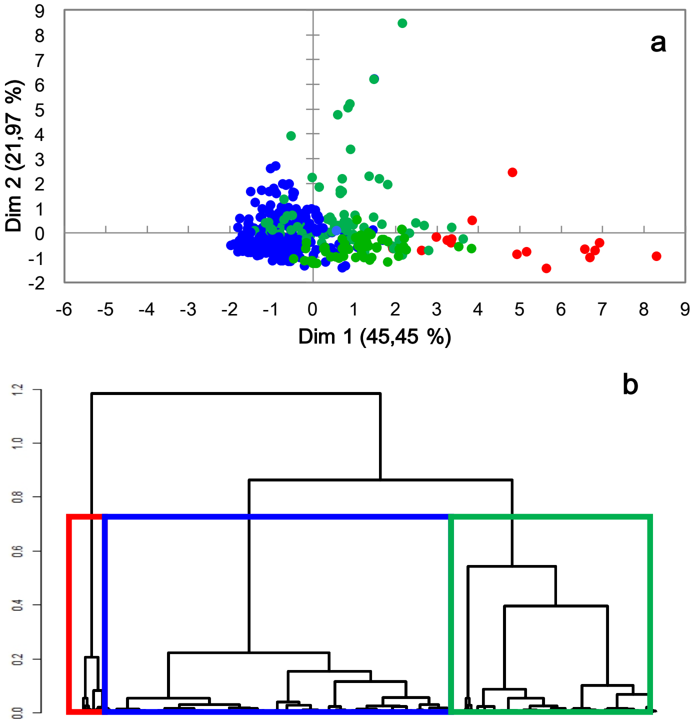


Figure 77 : a) analyse en composante principale des caractéristiques des intermattes naturelles (bleu) et d'ancrage (vert). Les points rouges représentent des intermattes naturelles et anthropiques ayant une taille et un périmètre extrême ; b) classification hiérarchisée des intermattes (Dussutour 2015).

Résultats : Les deux types d'intermatte de la baie de l'Alga sont dissociés par leurs caractéristiques paysagères (Fig. 77). Les intermattes d'ancrages ont ainsi une plus grande surface, ont une forme plus allongée et sont plus proches les unes des autres que les intermattes naturelles (Dussutour 2015).

Discussion : Du fait du plus grand nombre d'intermattes naturelles, le Patchiness Source Index (PaSI) atteint une valeur de 0.835 révélant un paysage sous-marin majoritairement d'origine naturelle (Abadie *et al.* 2015b). Les données sonar de cette cartographie ayant été obtenues en 2010, une nouvelle campagne de récolte de données cartographiques est à envisager pour évaluer l'évolution du paysage à *P. oceanica* de la Baie de l'Alga, dans laquelle la pression d'ancrage ne diminue pas au cours des années (Abadie, données non-publiées). La possibilité d'une telle comparaison est cependant subordonnée à la haute résolution de la cartographie du fait de la faible vitesse de croissance de la plante. Cette méthode qui permet de quantifier de façon exhaustive l'impact de l'ancrage à l'échelle d'une baie nécessite cependant un temps de traitement des données important ainsi que des connaissances poussées en cartographie (Fig. 78).

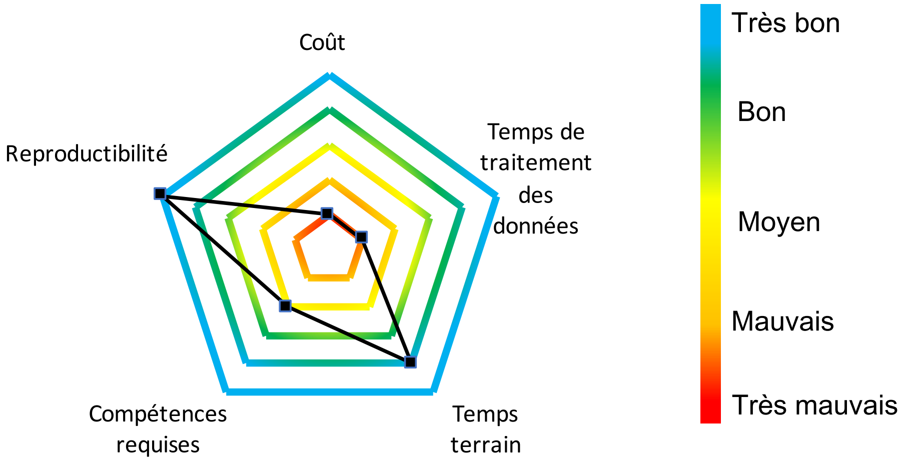


Figure 78 *: Analyse qualitative de l'analyse paysagère à partir de la cartographie d'une zone d'ancrage intensif.*

Si cette approche est très prometteuse pour la mise au point d'outils d'évaluation de l'état de conservation des paysages à *P. oceanica*, plusieurs obstacles pratiques restent à franchir pour réduire le coût et le temps de traitement des données acquises sur le terrain (Fig. 78).

Le premier obstacle est l'identification et la cartographie des intermattes. Elle est actuellement réalisée manuellement, requérant une connaissance et une expérience poussée de la structure de l'herbier puis un temps de dessin très important. Si cette technique requiert peu de temps pour une zone d'étude relativement réduite (< 1 km^2), elle devient fastidieuse à plus grande échelle. Afin de grandement améliorer le temps de traitement des données cartographiques, il est possible d'envisager une technique automatisée de cartographie moins classique : l'approche orientée objet (Saha *et al.* 2011). La classification orientée objet consiste à considérer la 'texture' et la forme des agrégations de pixels en plus de leur couleur classiquement analysée (Benz *et al.* 2004). Cette technique a déjà été testée avec succès en milieu marin (Lucieer 2008). Son utilisation pour cartographier les intermattes naturelles dans une matrice à *P. oceanica* semble très prometteuse, leur couleur et le texture étant très contrastés avec celles de l'herbier les entourant (Jousseaume, com. pers.).

Le second obstacle est la simplification d'analyse induite par la représentation en deux dimensions de paysages sous-marins ayant une structuration en trois dimensions complexe (Hoechstetter *et al.* 2008) (voir Chapitre 4 – Article 4). Depuis quelques années, de nouvelles techniques de cartographie fournissent une vision en 3D à haute résolution des fonds marins dont les herbiers à *P. oceanica* (Rende *et al.* 2015). Bien que cette technique en soit pour l'instant au stade expérimental et que seules de petites zones côtières soient cartographiées, les cartes géoréférencées obtenues semblent avoir un fort potentiel pour le développement d'outils de gestion paysagers (Fig. 79). L'effet de bordure prend alors une dimension verticale avec notamment l'écotone entre la canopée de l'herbier et la colonne d'eau. De même les tombants de matte ne sont plus un simple passage du substrat végétalisé au sédiment nu mais un véritable mur limitant le déplacement de certains organismes marins.

D’une façon concrète, quelles sont les métriques pertinentes lorsque l’on souhaite étudier une cartographie en trois dimensions d’un herbier à *P. oceanica* ? Dans un premier temps il est logique de transposer les indices paysagers classiques utilisés pour des cartographies en deux dimensions (Hoechstetter *et al.* 2008, Wu *et al.* 2012). Ainsi, le nombre d’intermattes, la longueur et leur distance l’une par rapport à l’autre de même que leur classification seront toujours des métriques pertinentes. Il est ensuite nécessaire d’identifier les paramètres ‘verticaux’ d’un herbier à *P. oceanica* fournissant une information utile à la gestion du paysage (Tab. 23). L’étape suivante nécessite d’automatiser le calcul de ces indices en développent des outils d’information géographique spécifiques. Il est ensuite primordial de tester la pertinence de ces métriques à grande échelle sur des sites géographiquement espacés le long des côtes de Méditerranée. Aux vues de la très faible disponibilité de cartographies 3D des herbiers à *P. oceanica*, la réalisation de cet objectif semble actuellement une perspective de développement plutôt qu’un but atteignable à court terme.

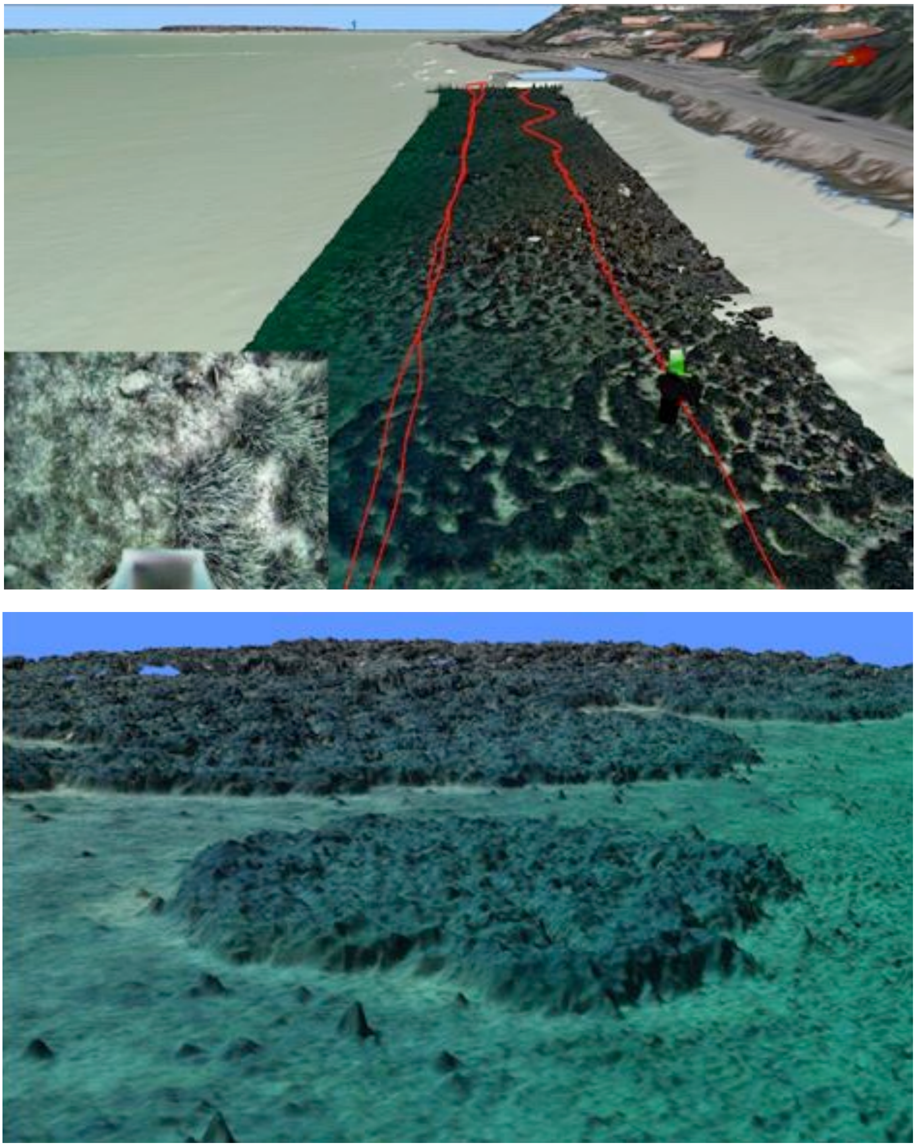


Figure 79 *: Visualisation en trois dimensions d’un herbier à* P. oceanica *dans le Golfe de Trieste (Slovénie). Cette représentation 3D a été créée à partir de photos aériennes, d’un modèle numérique de terrain et d’images sous-marines géoréférencées (Berden-Zrimec et al. 2015).*

Tableau 23 *: Proposition de métriques 3D descriptives des intermattes et de l'herbier à* P. oceanica.

Nom de la métrique	**Unité**	**Description**	**Intérêt pour la conservation**
Hauteur de la canopée	cm	Hauteur des patchs formés par la plante. Cette mesure ne correspond pas à la longueur réelle des feuilles du fait de leur courbure et de leur mouvement dû à l'hydrodynamisme. Elle varie significativement de façon saisonnière.	La hauteur de la canopée détermine la capacité d'un herbier à jouer son rôle de nurserie. Une faible valeur ou sa diminution peu indiquer l'influence d'un phénomène naturel ou anthropique sur la plante au niveau physiologique
Hauteur du tombant de matte	cm	Hauteur de la partie érodée des intermattes naturelles formant une bordure abrupte et verticale. La hauteur du tombant n'est pas homogène sur l'ensemble de la bordure.	Les tombants de matte sont des formations biologiques anciennes parfois âgées de plusieurs centaines d'années permettant d'étudier des couches de stockage de carbone autrement inaccessibles.
Hauteur totale de la bordure	cm	Hauteur de la canopée additionnée à la hauteur du tombant de matte.	Une bordure d'herbier est constituée de plusieurs compartiments de natures différentes abritant des communautés contrastées d'organismes.
Hauteur moyenne de la bordure	cm	La hauteur moyenne de la bordure comprend la hauteur de la canopée et la hauteur du tombant de matte. Une hauteur moyenne est calculée pour chaque patch ou type de patch.	La hauteur de la bordure influence le déplacement de nombreux organismes benthique. Elle peut représenter un obstacle ou un abris selon que ces derniers sont des proies ou des prédateurs.
Surface de la bordure	m^2	La surface de la bordure comprend sa hauteur et sa longueur totale. La longueur de la bordure au niveau du substrat et celle du sommet de la canopée sont considérées comme égales.	La bordure est le lieu de contact entre deux habitats distincts. Plus cette surface de contact est grande, plus le nombre d'interactions entre les organismes marins est important.
Volume de l'intermatte	m^3	Le volume de l'intermatte intègre la surface du substrat et la hauteur totale de la bordure.	Les phénomènes verticaux se déroulant au sein des intermattes (e.g. flux de particules) en font un espace particulier dons l'importance du volume détermine la distribution des espèces benthiques et pélagiques tels que les juvéniles de téléostéens.

3. Des nouveaux outils pour l'évaluation de l'impact de l'ancrage sur les herbiers à *P. oceanica*

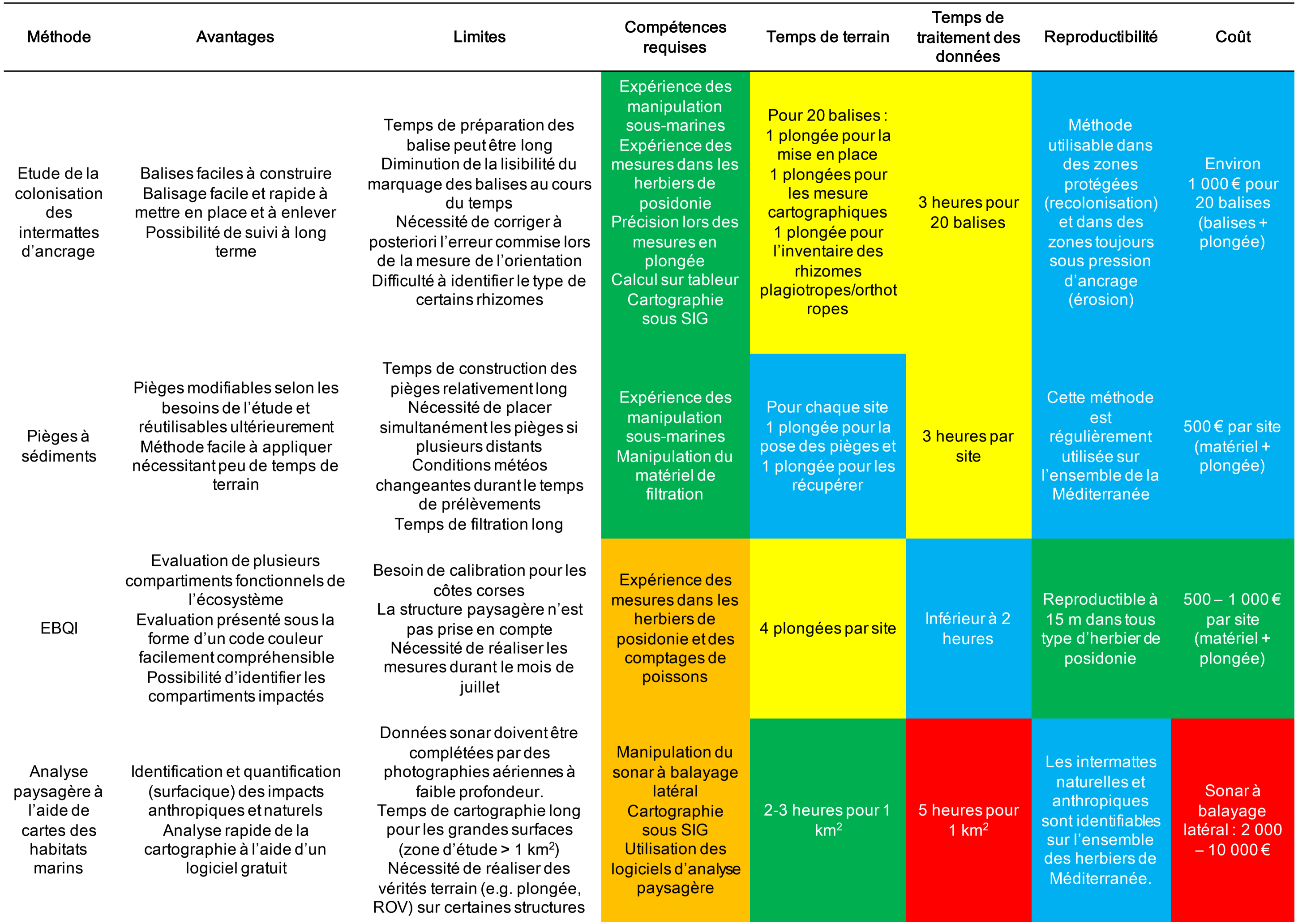
3.1. Comparaison des méthodes d'étude des intermattes

Chacune des méthodes décrites précédemment appliquées à des intermattes naturelles, peut être appliquée aux intermattes résultant d'un impact anthropique mécanique et donc l'ancrage. Afin d'évaluer l'impact des navires de plaisance dans une zone d'ancrage intensif (environ 1 km^2), il est nécessaire de coupler plusieurs de ces méthodes qui la plupart du temps sont complémentaires. Tous les protocoles nécessitent des observations et/ou des manipulations en plongée sous-marine (Tab. 23). Le temps nécessaire à l'obtention des résultats ne se limite cependant pas aux observations réalisées sur le terrain. Ainsi, les méthodes d'étude ayant recours à du matériel électronique de mesure, i.e. PAM, sonde de mesure du H_2S, nécessiteront peu de temps pour traiter et obtenir des résultats, alors que leur calibration sera relativement longue et les compétences requises importantes (Tab. 23). L'ensemble des techniques évaluées requièrent peu de temps de traitement des données, exceptée l'analyse paysagère de cartes des habitats marins qui demande également de l'expérience en cartographie (Tab. 23).

L'approche paysagère basée sur des cartes n'est pas un antagoniste de l'approche par observations en plongée sous-marine. Ces deux méthodes d'évaluation sont même complémentaires et nécessaires pour déterminer l'impact de l'ancrage. Pour un manager du milieu côtier, il est cependant rare d'avoir les ressources matérielles, humaines et budgétaires pour pouvoir utiliser les deux approches simultanément. A partir de ce constat, les bases de deux méthodes d'évaluation de l'impact de l'ancrage sur les herbiers à *P. oceanica* ont été élaborées dans le cadre de ces travaux de doctorat dans le but de répondre aux besoins des décisionnaires. Ces protocoles prennent la forme de deux indices d'évaluation, l'un sur base de cartographies et l'autre sur base de mesures en plongée sous-marine.

***Tableau 23** : Récapitulatif des caractéristiques des différentes méthodes d'étude des intermattes naturelles et anthropiques au sein des herbiers à* P. oceanica*.* Une plongée correspond à l'immersion de deux plongeurs durant environ une heure. La couleur indique l'évaluation qualitative de chaque caractéristique : bleu : très bon ; vert : bon ; jaune : moyen ; orange : mauvais ; rouge : très mauvais.

Méthode	Avantages	Limites	Compétences requises	Temps de terrain	Temps de traitement des données	Reproductibilité	Coût
Micro-cartographie par balisage	Balises faciles à construire (tige de métal + tuyau PVC) Balisage facile et rapide à mettre en place et à enlever Possibilité de suivi à long terme (plusieurs dizaines d'années) Transposable à des intermattes anthropiques	Temps de préparation des balise peut être long Diminution de la lisibilité du marquage des balises au cours du temps Nécessité de corriger à posteriori l'erreur commise lors de la mesure de l'orientation	🟩 Expérience des manipulation sous-marines Précision lors des mesures en plongée Calcul sur tableur Cartographie sous SIG	🟨 Pour 50 balises(soit une intermatte d'environ 100 m^2) 1 plongée pour la mise en place 2 plongées pour les mesure (distance et orientation) entre les balises	🟨 3-5 heures pour 50 balises	🟦 Méthode facilement transposable à d'autres intermattes naturelles quelle que soit sa localisation et sa profondeur	🟦 Environ 1 500 € pour 50 balises (balises + plongée)
Pulse Amplitude Modulated fluorometry (PAM) en bordure d'herbier	Mesure *in situ* instantanée de l'efficacité photosynthétique Grande quantité de mesures possibles à chaque plongée Obtention directe des résultats sous format exploitable	Coût du Diving-PAM Temps de calibration long Prélèvement à heure solaire fixe Requière une expérience et des connaissances poussées en matière de photosynthèse Nécessite des conditions de météo similaire entre chaque plongée (temps ensoleillé)	🟥 Expérience des manipulation sous-marines Utilisation du Diving-PAM	🟨 1 plongée par site 1-4 min par mesure (selon le type de mesure) Minimum 5 mesures par site	🟦 Inférieur à 1 heure après chaque plongée	🟨 Nécessite de respecter scrupuleusement le protocole pour comparer des sites	🟥 Diving-PAM : 20 000 €
Mesure du sulfure d'hydrogène dans l'eau interstitielle du sédiment à l'aide d'une sonde	Mesure non destructrice Faible volume d'eau interstitielle nécessaire Mesure rapide après calibration de la sonde	Contamination possible de l'échantillon Grandes variations spatiales des concentrations des éléments chimiques Prélèvement à heure solaire fixe Analyse des échantillons immédiatement après le prélèvement Longue calibration de la sonde	🟥 Expérience des prélèvement d'eau interstitielle à la seringue Mesures d'éléments chimiques dans des faibles volumes d'eau de mer	🟧 1 plongée par site 10 min par prélèvement Minimum 3 réplicas par site)	🟩 2 heures pour la calibration de la sonde (avant et après l'analyse des échantillons) 1 heure pour la mesure de 10 échantillons	🟩 Protocole utilisable dans tout type de sédiment sous réserve de pouvoir analyser les échantillons moins de deux heures après leur prélèvement	🟨 Sonde : 1 500 € Prélèvement et analyse de 10 échantillons (plongée, analyse, produits chimiques) : 500 €



Méthode	Avantages	Limites	Compétences requises	Temps de terrain	Temps de traitement des données	Reproductibilité	Coût
Etude de la colonisation des intermattes d'ancrage	Balises faciles à construire Balisage facile et rapide à mettre en place et à enlever Possibilité de suivi à long terme	Temps de préparation des balise peut être long Diminution de la lisibilité du marquage des balises au cours du temps Nécessité de corriger à posteriori l'erreur commise lors de la mesure de l'orientation Difficulté à identifier le type de certains rhizomes	Expérience des manipulation sous-marines Expérience des mesures dans les herbiers de posidonie Précision lors des mesures en plongée Calcul sur tableur Cartographie sous SIG	Pour 20 balises : 1 plongée pour la mise en place 1 plongées pour les mesure cartographiques 1 plongée pour l'inventaire des rhizomes plagiotropes/orthotropes	3 heures pour 20 balises	Méthode utilisable dans des zones protégées (recolonisation) et dans des zones toujours sous pression d'ancrage (érosion)	Environ 1 000 € pour 20 balises (balises + plongée)
Pièges à sédiments	Pièges modifiables selon les besoins de l'étude et réutilisables ultérieurement Méthode facile à appliquer nécessitant peu de temps de terrain	Temps de construction des pièges relativement long Nécessité de placer simultanément les pièges si plusieurs distants Conditions météos changeantes durant le temps de prélèvements Temps de filtration long	Expérience des manipulation sous-marines Manipulation du matériel de filtration	Pour chaque site 1 plongée pour la pose des pièges et 1 plongée pour les récupérer	3 heures par site	Cette méthode est régulièrement utilisée sur l'ensemble de la Méditerranée	500 € par site (matériel + plongée)
EBQI	Evaluation de plusieurs compartiments fonctionnels de l'écosystème Evaluation présenté sous la forme d'un code couleur facilement compréhensible Possibilité d'identifier les compartiments impactés	Besoin de calibration pour les côtes corses La structure paysagère n'est pas prise en compte Nécessité de réaliser les mesures durant le mois de juillet	Expérience des mesures dans les herbiers de posidonie et des comptages de poissons	4 plongées par site	Inférieur à 2 heures	Reproductible à 15 m dans tous type d'herbier de posidonie	500 – 1 000 € par site (matériel + plongée)
Analyse paysagère à l'aide de cartes des habitats marins	Identification et quantification (surfacique) des impacts anthropiques et naturels Analyse rapide de la cartographie à l'aide d'un logiciel gratuit	Données sonar doivent être complétées par des photographies aériennes à faible profondeur. Temps de cartographie long pour les grandes surfaces (zone d'étude > 1 km^2) Nécessité de réaliser des vérités terrain (e.g. plongée, ROV) sur certaines structures	Manipulation du sonar à balayage latéral Cartographie sous SIG Utilisation des logiciels d'analyse paysagère	2-3 heures pour 1 km^2	5 heures pour 1 km^2	Les intermattes naturelles et anthropiques sont identifiables sur l'ensemble des herbiers de Méditerranée.	Sonar à balayage latéral : 2 000 – 10 000 €

3.2. Le Map Anchoring Index (MAI) : Indice cartographique de l'impact de l'ancrage

Le MAI (Map Anchoring Index) est issu de l'analyse des paysages formés par les herbiers à *P. oceanica* (Dussutour 2015) et plus particulièrement des caractéristiques (taille et nombre) des intermattes résultant d'impacts anthropiques (voir Chapitre 4 – Article 4 et Chapitre 5 – partie 2.3.). Il intègre également la pression d'ancrage en tenant compte du nombre et de la taille (< 10 m ; 10–20 m ; 21–200 m ; > 200 m) des navires s'ancrant dans la zone d'étude, ainsi que leur impact potentiel dû à leur taille.

$$\mathrm{MAI} = (\mathrm{statut} \times \mathrm{poids}\ \mathrm{S_{IA}}/\mathrm{S_{totale}} + \mathrm{statut} \times \mathrm{poids}\ \mathrm{N_{IA}} + \sum \mathrm{statut} \times \mathrm{poids}\ \mathrm{N_{nav}})/45$$

Avec :

- S_{IA} la surface des intermattes anthropiques (m^2)
- S_{totale} la surface totale d'herbier à *P. oceanica* dans la zone d'étude (m^2)
- N_{IA} le nombre d'intermattes anthropiques
- N_{nav} le nombre moyen de navires par jour dans la zone d'étude durant la période estivale (juillet/août)

Chaque paramètre constituant l'indice est divisé en niveau de statut en fonction de ses valeurs théoriques (Tab. 24).

Tableau 24 *: Statut des paramètres constituant le MAI en fonction de leur valeur. La valeur entre parenthèses représente le poids attribué à chaque métrique.*

S_{IA}/S_{totale} (2)	N_{IA} (3)	Pression d'ancrage (N_{nav})				Statut
		< 10 m (1)	10-20 m (2)	21-200 m (3)	> 200 m (4)	
> 0.2	> 50	> 10	> 8	> 5	> 2	3
0.1-0.2	26-50	5-10	2-8	1-5	2	2
< 0.1	0-25	< 5	2	1	1	1
0	0	0	0	0	0	0

Enfin, la valeur du MAI est interprétée grâce à une classification par code couleur (Tab. 25) afin d'évaluer l'impact de l'ancrage sur la zone d'étude.

***Tableau 25** : Grille d'interprétation de la valeur du Map Anchoring Index (MAI) pour déterminer l'impact de l'ancrage.*

Description	**Valeur**	**Code couleur**
Impact de l'ancrage nul	0	Bleu
Faible impact de l'ancrage	0-0.250	Vert
Impact de l'ancrage modéré	0.251-0.500	Jaune
Fort impact de l'ancrage	0.501-0.750	Orange
Très fort impact de l'ancrage	0.751-1	Rouge

Le MAI a été développé à partir des données obtenues en Baie de l'Alga (Corse, France), une zone d'ancrage estival intensif d'environ 1 km^2 fréquentée par des navires de plaisances de tailles très contrastées (voir Chapitre 3). Dans la Baie de l'Alga, le MAI atteint une valeur de 0.578, indiquant ainsi un herbier à *P. oceanica* fortement impacté par l'ancrage. Il reste cependant à valider cet indice en calculant pour différentes zones de taille similaire sur l'ensemble des côtes méditerranéennes françaises.

Si le MAI semble capable de fournir une évaluation correcte des cartographies tout en prenant compte la pression d'ancrage dans une zone d'1 km^2, il est également nécessaire d'affiner sa calibration pour des zones plus vastes dans lesquelles des navires de croisière (> 200 m de long) pourront s'ancrer. De plus, l'impact de l'ancrage mis en évidence par cet indice correspond à un état de l'herbier à l'instant t de l'acquisition de données cartographiques (sonogrammes, photos aériennes).

Le MAI est donc un outil destiné à identifier les zones soumises à une forte pression d'ancrage dont l'impact se traduit par des intermattes détectables à l'aide de la télédétection. Il est également possible de calculer l'indice pour des cartographies anciennes sous réserve que des données sur la fréquentation de la zone soient disponibles. Pour réaliser un monitoring des zones ainsi identifiées à l'aide du MAI, il est nécessaire d'avoir recours à un autre protocole incluant des observations directes en plongée sous-marine.

3.3. Le Anchoring Index (AI) : la compilation d'observations *in situ*

Le Anchoring Index (AI) est un indice évaluant l'impact de l'ancrage s'appliquant à l'échelle d'une zone d'ancrage intensif (e.g. baie, plage, crique). Il regroupe sept paramètres mesurés à l'aide d'observations de terrain non-destructives dont la plupart sont réalisées en plongée sous-marine, i.e. la densité de l'herbier, la compacité de la matte, le déchaussement des rhizomes, le recouvrement de l'herbier, la proportion de matte morte, la concentration en sulfure d'hydrogène et la densité de navires (Tab. 26).

Tableau 26 *: Détail des paramètres constituant le Anchoring Index.*

Paramètre	Protocole	Unité
Densité de l'herbier	Mesure par quadrats de 40 cm x 40 cm répliquée dix fois. Les données sont interprétées à l'aide la grille de UNEP-MAP-RAC/SPA 2011	faisceaux.m^{-2}
Compacité de la matte	La distance de pénétration est mesurée dix fois avec une tige de 2 m de long est enfoncée perpendiculairement dans la matte à l'aide d'un poids de 5 kg	cm
Déchaussement des rhizomes	La distance entre le sommet des rhizomes et le substrat est mesuré 20 fois de façon aléatoire	cm
Recouvrement de l'herbier	20 quadrats de 40 cm x 40 cm sont photographiés et le recouvrement est estimé	%
Proportion de matte morte	Le substrat (herbier, sable, roche, matte morte) est observé tous les mètres sur cinq transects de 10 m de long	%
Concentration en sulfure d'hydrogène	L'eau interstitielle de la matte morte est prélevée (3 réplicas) à 10 cm de profondeur à l'aide d'une aiguille et d'une seringue. Les échantillons sont ensuite testé à l'aide de kits de mesure colorimétrique	µM
Densité de navires	Les navires ancrés sont comptés durant la période juillet - août et leur nombre est ramené à la surface de la zone d'étude	Navires.ha^{-1}

Les mesures sont réalisées durant la période estivale de plus grande affluence (juillet-août). Deux plongées en binôme sont nécessaires pour les observations sous-marines. Le AI peut être utilisé à toutes les profondeurs de développement de l'herbier.

En fonction de leur gamme de variation, une note de statut ainsi qu'un poids est attribué à chaque paramètre (Tab. 28). Enfin, le AI est calculé de la façon suivante :

$$AI = \sum_{i=1}^{7} P_i * S_i \Big/ 48$$

Avec :

- P_i le poids assigné au paramètre i
- Si le statut du paramètre i

Le Anchoring Index varie de 0 à 1 et sa valeur est interprété grâce à une classification par code couleur définissant l'impact de l'ancrage dans la zone d'étude (Tab. 27).

***Tableau 27** : Grille d'interprétation de la valeur du Anchoring Index (AI) pour déterminer l'impact de l'ancrage.*

Description	**Valeur**	**Code couleur**
Impact de l'ancrage nul	0	Bleu
Faible impact de l'ancrage	0-0.250	Vert
Impact de l'ancrage modéré	0.251-0.500	Jaune
Fort impact de l'ancrage	0.501-0.750	Orange
Très fort impact de l'ancrage	0.751-1	Rouge

Le calcul du AI dans la Baie de l'Alga à 10, 15 et 20 m de profondeur fait état d'un herbier impacté de façon modérée par l'ancrage à 10 m (AI = 0.396) et 15 m (AI = 0.500), et fortement impacté à 20 m (AI = 0.583).

***Tableau 28** : Statut de chaque paramètre en fonction de la valeur mesurée.*

Paramètre	Valeur	Statut	Poids	Statut max	Référence
Densité de l'herbier	Très basse	4	3	12	UNEP-MAP-RAC/SPA (2011)
	Basse	3			
	Moyenne	2			
	Haute	1			
	Très haute	0			
Compacité de la matte	> 100 cm	2	3	6	Francour *et al.* (1999)
	50-100 cm	1			
	< 50 cm	0			
Déchaussement des rhizomes	> 15 cm	2	1	2	Boudouresque *et al.* (1980a)
	5-15 cm	1			
	< 5 cm	0			
Recouvrement de l'herbier	< 20 %	4	1	4	Charbonnel *et al.* (2000)
	20-40 %	3			
	40-60 %	2			
	60-80 %	1			
	> 80 %	0			
Proportion de matte morte	> 50 %	4	3	12	Moreno *et al.* (2001)
	20-50 %	3			
	10-20 %	2			
	5-10 %	1			
	< 5 %	0			
Concentration en sulfure d'hydrogène	> 10 μM	3	2	6	Abadie *et al.* (2016)
	5-10 μM	2			
	1-5 μM	1			
	< 1 μM	0			
Densité de navires	> 10 navires.ha^{-1}	2	3	6	-
	5-10 navires.ha^{-1}	1			
	< 5 navires.ha^{-1}	0			

Lorsque différentes tranches bathymétriques sont concernées par un ancrage intensif, le AI permet ainsi de mettre en évidence un possible gradient de l'intensité de son impact. Le AI permet également un suivi régulier (par exemple trisannuel) d'une zone sous forte pression d'ancrage ou au contraire, d'une aire bénéficiant de mesures de gestion (interdiction d'ancrage, limitation de la taille des navires). Utilisé en réseau de monitoring, le AI permettrait un suivi à l'échelle de la Méditerranée. Tout comme le Map Anchoring Index, il reste à valider cet indice en le calculant pour différentes zones impactées.

Conclusions générales et perspectives

En étudiant les intermattes au sein des herbiers à *P. oceanica* à différentes échelles spatiales, ces travaux de doctorat ont mis en évidence l'importance de ces structures pour l'étude de processus naturels et anthropiques. Au travers des différentes méthodes utilisées, nous avons pu répondre aux trois interrogations formulées au début de ces travaux.

Les intermattes naturelles et anthropiques ainsi que l'herbier qui les entoure ont-ils des caractéristiques biologiques et physico-chimiques spécifiques ?

Nous avons observé que les intermattes naturelles et anthropiques sont caractérisées par des formes et des tailles différentes. Plus précisément, nous avons mis en évidence que ces particularités structurelles sont issues de processus biologiques et physico-chimiques particuliers se déroulant dans le substrat (sédiment nu, matte morte) et l'herbier qui les entoure. Ainsi, les intermattes naturelles présentent deux bordures structurellement distinctes avec un côté érodé formant un tombant de matte tandis que la bordure opposée est recolonisée. Chacune de ces bordures présente une chimie du sédiment (e.g. cycle du carbone, nutriments) et une morphologie (e.g. biomasse foliaire, densité) différente. Quant aux intermattes anthropiques et plus particulièrement celles issues de l'ancrage, nous avons constaté que les dommages mécaniques menant à la création d'un substrat de matte nue en décomposition créent des conditions chimiques défavorables à la recolonisation par l'herbier.

Comment ces structures si particulières s'insèrent-elles dans le paysage sous-marin ? Quelle est leur influence sur sa structure ?

Nous avons pu définir que la mosaïque formée par les intermattes structure le paysage à *P. oceanica*, leur nombre, leur forme, leur taille et la distance les séparant caractérisent ainsi le morcellement des herbiers. En utilisant des métriques issues de l'écologie paysagère terrestre, nous avons découvert que les caractéristiques propres à chaque type d'intermatte définiront la dynamique du paysage, i.e. sa fragmentation, à grande échelle spatiale. Nous avons notamment décrit la zonation bathymétrique des intermattes naturelles depuis la limite inférieure de l'herbier qui préfigure une évolution de leurs caractéristiques spatiales à long terme. En identifiant et classifiant chaque type d'intermatte observé sur les côtes corses, nous avons mis en évidence que l'impact des activités anthropiques modifie la structure des paysages sous-marins à *P. oceanica*, et par extension leur fonctionnement. Nous avons mis en avant ce principe en tentant de réaliser une synthèse des connaissances sur les paysages sous-marins à *P. oceanica*. Il apparaît ainsi au travers de cette étude que nos connaissances sur la répartition des organismes en fonction de la morphologie de l'herbier sont limitées, et qu'il semble donc impossible d'établir une telle relation à grande échelle spatiale dans un but de gestion.

Est-il possible d'utiliser les intermattes pour évaluer l'état de conservation des herbiers à *P. oceanica* ? Si oui, de quelle façon ?

Ces travaux de recherche montrent que les intermattes sont de bon indicateurs à plusieurs échelles spatiales. A l'échelle individuelle, elles permettent d'étudier les phénomènes de recolonisation et d'érosion dans des herbiers soumis ou non aux impacts anthropiques. Plus particulièrement, nous avons observé que la biogéochimie du sédiment conditionnera la colonisation des intermattes par l'herbier adjacent. Nous avons également mis en évidence une technique de mesure simple pour étudier leur dynamique spatiale. A l'échelle du paysage, il est possible de les utiliser comme indicateur de l'influence anthropique aux travers de métriques et d'indices paysagés couramment utilisés en milieu terrestre tout en développant de nouveaux spécifiques au milieu marin.

En étudiant les intermattes des herbiers à *P. oceanica*, ces travaux de doctorat en entreprise ont ainsi parcourus plusieurs méthodes d'analyses en allant de la plante au paysage entier en passant par une analyse écosystémique. Si ces techniques ont toutes un certain potentiel pour répondre à des problématiques de gestion et de conservation, elles se distinguent les unes des autres par leurs caractéristiques contrastées (coût, temps de terrain, temps de traitement des données, connaissances requises). Nous en concluons que deux échelles spatiales d'étude semblent nécessaires pour une évaluation complète de l'état de conservation des herbiers à *P. oceanica*.

La première échelle se situe au niveau d'une zone de taille restreinte (quelques dizaines de mètres carrés) avec des prélèvements en plongée sous-marine. Cette échelle d'étude requiert peu de moyen humains, matériels et financiers, et fourni des informations fonctionnelles sur l'herbier, mais ne permet cependant pas de gestion à grande échelle sans mise en place de réseaux de monitoring. La seconde échelle permet une évaluation sur de très grandes surfaces des paysages à *P. oceanica* mais nécessite un temps important d'acquisition et de traitement des données à un coût relativement élevé. Nous avons ainsi tenté de créer des outils à destination des gestionnaires en proposant la base pour deux indices évaluant l'impact de l'ancrage dans les herbiers à *P. oceanica*. Ces méthodes non-intrusives intègrent chacune des notions paysagères en tenant compte des changements de substrat (e.g. herbier, sable, matte morte) ou de la présence d'intermatte. Testés dans la baie de l'Alga (Corse, France), un site d'ancrage intensif des navires de plaisance, ces indices sont en cours de développement afin d'être plus largement utilisés pour la gestion du milieu côtier en Méditerranée.

Que ce soit d'un point de vu structurel ou fonctionnel et à toute échelle d'étude, les intermattes doivent donc être prises en compte lors de l'étude des herbiers à *P. oceanica*. Si leur structure est désormais mieux connue, les interactions des organismes marins avec la morphologie des paysages sous-marins (comme l'illustre la couverture de cette partie) restent à étudier en profondeur afin de développer d'autres outils indicateurs pour appuyer des mesures de gestion. Les herbiers à *P. oceanica* sont considérés comme un écosystème dont l'état de conservation doit être évalué dans le cadre de la directive européenne cadre stratégie pour le milieu marin (DCSMM), dans le but d'atteindre un bon état écologique d'ici 2020. Dans cette optique, inclure les caractéristiques des intermattes au sein des outils d'évaluation des herbiers fournirait une information sur la structure du paysage que les paramètres classiques (e.g. densité, recouvrement) ne renseignent pas.

L'étude des intermattes devrait nous amener à réviser le concept de morcellement des herbiers à *P. oceanica* à grande échelle spatiale. En effet, un herbier peut être naturellement morcelé avec un nombre important d'intermattes de grande taille. Il peut également être morcelé par les activités anthropiques qui entraîneront sa fragmentation à partir des intermattes artificiellement crées. Si ces points de départ de fragmentation artificiels sont multipliés, comme par exemple dans le cas de l'ancrage, le processus d'érosion sera alors accéléré. Les paysages à *P. oceanica* sont le résultat de ces deux phénomènes : un espaces complexe au sein duquel les intermattes naturelles et anthropiques interagissent et parfois même fusionnent. Une telle intrication entraîne très certainement des changements au niveau de la répartition des organismes inféodés à ces paysages. Afin de gérer et de conserver les paysages à *P. oceanica*, l'utilisation de l'écologie paysagère, appuyée par des outils pratiques d'évaluation, apparaît comme une approche prometteuse qui nécessite cependant une meilleure connaissance du fonctionnement des paysages sous-marins.

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Annexes

Annexe 1 : Justificatifs de publication, d’acceptation et de soumission des articles

Article 1
Objet: [MMS] Editor Decision
Date: 7 septembre 2016 07:39:04 UTC+2
À: "Arnaud Abadie" <arnaudabadie@aol.fr>
Cc: "Sylvie Gobert" <sylvie.gobert@ulg.ac.be>, "Gilles Lepoint" <g.lepoint@ulg.ac.be>, "Corinne Pelaprat" <corinne.pelaprat@stareso.com>, "François Remy" <francois.remy@ulg.ac.be>, "Pierre Lejeune" <pierre.lejeune@stareso.com>, "Jonathan Richir" <jonathan.richir@ulg.ac.be>

Arnaud Abadie:

We have reached a decision regarding your submission to Mediterranean Marine
Science, "Temporal evolution of sand corridors in a Posidonia oceanica seascape: a 15-years study".

Our decision is to: accept

CARLO NIKE BIANCHI
Università di Genova, Italy
nbianchi@dipteris.unige.it

Mediterranean Marine Science
http://www.medit-mar-sc.net

Article 2

De: "Estuaries and Coasts" <em@editorialmanager.com>
Objet: ESCO-D-16-00257 - Acknowledgement of Receipt
Date: 8 août 2016 14:46:41 UTC+2
À: "Arnaud Abadie" <arnaudabadie@aol.fr>
Répondre à: "Estuaries and Coasts" <estuariesandcoasts@erf.org>

Dear Mr Abadie:

Thank you for submitting your manuscript, "Sediment biogeochemistry in two edge types of Posidonia oceanica seagrass meadows and its influence on colonization processes", to Estuaries and Coasts.

The submission id is: ESCO-D-16-00257

Please refer to this number in any future correspondence.

During the review process you can keep track of the status of your manuscript by accessing the following web site:

http://esco.edmgr.com/

Your username is: Arnaud Abadie

Your password is: available at this link
http://esco.edmgr.com/Default.aspx?pg=accountFinder.aspx&firstname=Arnaud&lastname=Abadie&email_address=arnaudabadie@aol.fr

Alternatively, please call us at 001-630-468-7784 (outside the US)/(630)-468-7784 (within the US) anytime from Monday to Friday.

Sincerely,

Taylor Bowen, Editorial Coordinator
Abigail Cook Dommer, Editorial Assistant
Estuaries and Coasts
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Article 3

Marine Pollution Bulletin 109 (2016) 61–71

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From mechanical to chemical impact of anchoring in seagrasses: The premises of anthropogenic patch generation in *Posidonia oceanica* meadows

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ABSTRACT

Intensive anchoring of leisure boats in seagrass meadows leads to mechanical damages. This anthropogenic impact creates bare mat patches that are not easily recolonized by the plant. Several tools are used to study human impacts on the structure of seagrass meadows but they are not able to assess the indirect and long term implication of mechanical destruction. We chose to investigate the possible changes in the substrate chemistry given contrasted boat impacts. Our observations show that hydrogen sulfide concentrations remain high at 15 and 20 m depth (42.6 μM and 18.8 μM) several months after the highest period of anchoring during the summer. Moreover, our multidisciplinary study reveals that anchoring impacts of large boats at 15 and 20 m depth can potentially change the seascape structure. By taking into account both structural and chemical assessments, different managing strategies must be applied for coastal areas under anthropogenic pressures.

1. Introduction

Over the last decades, marine ecosystems all around the world have been facing impacts of human activities at various extents (Halpern et al. 2008; Jorda et al. 2012). This statement is particularly observed in the Mediterranean Sea at the level of the coastal habitat formed by seagrass meadows (Grech et al. 2012; Giakoumi et al. 2013). Seagrasses play a major ecological and economical role at the level of the global ocean, covering an area reaching up to 500,000 km^2 (Costanza et al. 1997; Short et al. 2007; Cullen-Unsworth and Unsworth 2013). Thus, they constitute a nursery (Beck et al. 2001), a large carbon sink (Fourqurean et al. 2012), as well as a protection against coastal erosion by attenuating waves and currents (Ondiviela et al. 2014). Among Mediterranean seagrasses, *Posidonia oceanica* (L.) Delile is the most studied due to its major ecological and economical role (Ruíz et al. 2009; Vassallo et al. 2013). The meadows it forms are observed from the surface to 40 m depth and are subject to the impact of human activities like coastal development, eutrophication, trawling, fish farms and anchoring (Boudouresque et al. 2009; Giakoumi et al. 2015b).

Along the French Mediterranean coasts, the main substrate affected by boat anchoring appear to be *Posidonia oceanica* (Holon et al. 2015). Anchoring inside *P. oceanica* meadows seems to have various degrees of impact according to its density, frequency, the type of anchor and the depth as well as the size of boats (Boudouresque et al. 2012). Thus, repeated anchoring of cruise ships, at depths greater than 15 m, causes large-scale degradations of the meadows (Ganteaume et al. 2005b; Abadie et al. 2015). In the same way small units, less than 10 m long, can have an important impact at a local scale (Francour et al. 1999; Milazzo et al. 2004; Ceccherelli et al. 2007).

At the present day, studies mainly targeted the degradation of small boats at shallow depths i.e. less than 10 m. Few works treat the effects of larger pleasure ships anchoring which can measure more than 80 m long and have an important impact in confined areas (Abadie 2012). In order to assess their impact, several parameters are classically measured: the meadow density, the mat structure and the bottom cover (Boudouresque et al. 1995; Francour et al. 1999; Pergent-Martini et al. 2005). However, some of these metrics seem not relevant enough to assess the damages observed on *P. oceanica* meadows. More specifically, classical indicators can indicate a good state of conservation of the meadow with no anthropogenic impact when tracks of bare mat (Fig. 1a) are clearly observed (Milazzo et al. 2004; Ganteaume et al. 2005a).

Intensive anchoring can lead to modifications of substrate qualities, passing from meadows to large bare mat areas in which anchoring tracks are visible (Fig. 1b). This phenomenon also induces a change in sediments nature going from carbonate sediments possibly oxygenized by the living plant to fine particles filling crevices inside decomposing

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Article 4

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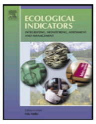

Marine space ecology and seagrasses. Does patch type matter in *Posidonia oceanica* seascapes?

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ABSTRACT

The use of landscape tools in the study of seagrass meadows (seascapes) begins to be widely spread but still require the establishment of several basis, i.e. a patch type classification based on numerical characteristics. Thanks to the complex seascapes created by the *Posidonia oceanica* meadows, they appear to be suitable for a study at a patch type level (class), which bring a new insight of their arrangement at the whole seascape scale. By interpreting side scan sonar images from the Corsican coast (France) through a GIS software, it was possible to describe 11 types of patches and to evaluate their natural or anthropogenic origin. Comparison of different landscape metrics and wave exposure (Relative wave Exposure Index, REI) at the seascape and the patch level showed that the particularity of *P. oceanica* seascapes are mainly characterized by certain types of patches often of anthropogenic origin. Furthermore the REI seems not to be a relevant index for a study at a class scale. A bathymetrical succession of natural patches was outlined from the lower to the upper limit of the meadow, with a long-term dynamic opposed to a shorter one concerning anthropogenic patches. In order to assess the origin (natural or induced by human activities) of the patches in *P. oceanica* meadows, as well as in any other seagrass, a Patchiness Source Index (PaSI), ranging from 0 to 1, was defined.

1. Introduction

Over the last three decades the interest in landscape ecology has grown and spread from land to marine ecosystems (Li and Mander, 2009; Sousa, 1984). A seascape can be defined as the varying arrangements of biotic structures with the resulting mosaic of marine habitat patches (Robbins and Bell, 1994). Thus, the study of their function and heterogeneity, including fragmentation and patchiness, should be called the Marine Space Ecology (Li and Mander, 2009). Fragmentation refers to a dynamic process which cannot be studied given a single temporal set of data (Boström et al., 2011). This term is often used in an erroneous way in place of patchiness which refers to a static state of a landscape.

The Mediterranean meadows of the seagrass *Posidonia oceanica* (Linnaeus) Delile play an important ecological and economic role e.g., fish nursery, carbon sink, protection from coastal erosion (Boudouresque et al., 2012; Costanza et al., 1997; Ruíz et al., 2009; Vassallo et al., 2013). Generally dense and continuous in the coastal zone from the surface to 45 m depth (Molinier and Picard, 1952), they are nevertheless subject to fragmentation due to natural phenomena and human activities (e.g. coastal development, pollution, anchoring) (Ardizzone et al., 2006; Boudouresque et al., 2009). In order to assess the role played by the heterogeneity of seagrass meadows, a landscape approach should be used (Bell and Hicks, 1991; Gobert et al., 2014; Robbins and Bell, 1994).

Heterogeneity in the physical structure of a seagrass meadow plays a major role in its functioning (e.g. juvenile survival, species-lined settlement, colonization, predator movements) thanks to the size and the shape of the patches (Bell et al., 2001; Borg et al., 2006; Boström et al., 2006; Connolly and Hindell, 2006; Micheli and Peterson, 1999). The habitats created by a natural fragmentation are essential for several key species (Prado et al., 2009).

Between 1950 and 1990 many types of *P. oceanica* seascapes have been described (Boudouresque et al., 2012, 1990, 1980a, 1985,

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Annexe 2 : Données de chimie du sédiment des intermattes naturelles (Article 2)

Station type	Depth	Month	H2S (µM)	pH	CH4 (nmol.l^{-1})	N2O (nmol.l^{-1})	pCO2 (ppm)	T in situ	Salinity	TA (µM)	DIC calc. (µM)
Meadow	10	February	0,27	7,60	41	4,3	1851	13,37	37,9	3416	3361
Meadow	10	February	0,14	7,56	52	3,1	1966	13,37	37,7	3342	3303
Meadow	15	February	0,65	7,50	69	4,4	2366	13,05	37,8	3497	3485
Meadow	15	February	0,59	7,60	80	2,9	1622	13,05	37,7	3033	2981
Meadow	20	February	1,05	7,60	66	4,0	1628	12,69	38,5	3032	2981
Meadow	20	February	0,58	7,48	144	3,0	2564	12,69	37,8	3608	3608
Natural patch colonization bare sand	10	February	0,05	7,84	21	8,5	759	13,37	38,5	2613	2465
Natural patch colonization bare sand	10	February	0,04	7,97	20	8,0	541	13,37	39,5	2601	2388
Natural patch colonization meadow	10	February	0,02	7,68	50	3,6	1272	13,37	37,8	2894	2809
Natural patch colonization meadow	10	February	0,02	7,62	26	4,3	1490	13,37	38,2	2943	2879
Natural patch erosion bare sand	10	February	0,01	7,77	30	9,3	898	13,37	38,1	2556	2442
Natural patch erosion bare sand	10	February	0,01	7,72	552	4,0	1142	13,37	38,3	2845	2745
Natural patch erosion meadow	10	February	0,01	7,73	63	5,1	1070	13,37	38,8	2799	2690
Natural patch erosion meadow	10	February	0,01	7,72	36	2,9	1080	13,37	38,9	2749	2645
Natural patch colonization bare sand	15	February	0,61	7,78	33	6,7	853	13,05	38,4	2510	2393
Natural patch colonization bare sand	15	February	0,67	7,73	40	4,5	927	13,05	37,9	2411	2317
Natural patch colonization meadow	15	February	0,66	7,41	50	4,0	2151	13,05	38,4	2559	2573
Natural patch colonization meadow	15	February	0,65	7,42	80	4,6	2357	13,05	37,9	2874	2890
Natural patch erosion bare sand	15	February	0,66	7,55	70	3,2	1575	13,05	37,8	2615	2583
Natural patch erosion bare sand	15	February	0,65	7,67	62	3,4	1225	13,05	38,8	2713	2634
Natural patch erosion meadow	15	February	0,65	7,68	30	7,1	1162	13,05	38,5	2632	2552
Natural patch erosion meadow	15	February	0,66	7,60	83	4,5	1496	13,05	37,9	2795	2744
Natural patch colonization bare sand	20	February	0,15	7,70	35	2,7	1071	13,4	37,9	2568	2480
Natural patch colonization bare sand	20	February	11,74	7,68	66	3,2	1171	13,4	37,8	2648	2568
Natural patch colonization meadow	20	February	0,32	7,47	70	4,2	2081	13,4	38,0	2826	2822
Natural patch colonization meadow	20	February	0,32	7,72	328	2,6	1097	13,4	37,9	2788	2687
Natural patch erosion bare sand	20	February	0,15	7,73	115	2,8	1027	13,4	38,0	2627	2528
Natural patch erosion bare sand	20	February	0,13	7,66	163	2,6	1184	13,4	38,0	2584	2510
Natural patch erosion meadow	20	February	0,00	7,57	194	3,5	1741	13,4	37,9	3001	2960
Natural patch erosion meadow	20	February	0,00	8,00	200	8,1	527	13,4	38,1	2703	2478

Station type	Depth	Month	H2S (µM)	pH	CH4 (nmol.l^{-1})	N2O (nmol.l^{-1})	pCO2 (ppm)	T in situ	Salinity	TA (µM)	DIC calc. (µM)
Meadow	10	June	0,01	7,45	58	3,5	2214	23,27	37,4	2757	2713
Meadow	10	June	20,59	7,49	79	4,8	2141	23,27	37,6	2949	2886
Meadow	15	June	1,12	7,53	73	2,9	1805	22,33	37,5	2757	2685
Meadow	15	June	3,07	7,48	84	2,9	2008	22,33	37,5	2706	2654
Meadow	20	June	0,92	7,69	35	6,4	1174	18,67	37,5	2692	2577
Meadow	20	June	18,21	7,51	41	3,7	1916	18,67	37,5	2803	2758
Natural patch colonization bare sand	10	June	0,13	7,54	31	2,5	1692	23,27	37,4	2635	2556
Natural patch colonization bare sand	10	June	0,08	7,50	34	24,7	1849	23,27	37,3	2589	2528
Natural patch colonization meadow	10	June	0,04	7,42	1278	2,8	3511	23,27	37,4	4024	3991
Natural patch colonization meadow	10	June	0,04	7,21	106	2,7	4676	23,27	37,4	3226	3291
Natural patch erosion bare sand	10	June	0,02	7,40	57	3,1	2455	23,27	37,4	2688	2664
Natural patch erosion bare sand	10	June	0,03	7,43	48	2,7	2176	23,27	37,4	2595	2558
Natural patch erosion meadow	10	June	0,02	7,36	59	3,7	3264	23,27	37,4	3215	3211
Natural patch erosion meadow	10	June	0,01	7,32	117	3,3	4441	23,27	37,5	4009	4029
Natural patch colonization bare sand	15	June	3,45	7,55	99	0,6	1702	22,33	37,6	2707	2629
Natural patch colonization bare sand	15	June	2,44	7,55	112	2,5	1816	22,33	37,6	2888	2807
Natural patch colonization meadow	15	June	1,65	7,26	66	2,6	5124	22,33	37,4	4052	4111
Natural patch colonization meadow	15	June	1,70	7,40	82	2,6	3800	22,33	37,5	4122	4108
Natural patch erosion bare sand	15	June	0,93	7,51	103	2,5	1925	22,33	37,5	2778	2715
Natural patch erosion bare sand	15	June	1,01	7,54	97	2,4	1734	22,33	37,5	2727	2651
Natural patch erosion meadow	15	June	5,90	7,49	144	3,0	2081	22,33	37,5	2880	2823
Natural patch erosion meadow	15	June	3,19	7,42	276	2,8	2671	22,33	37,5	3089	3061
Natural patch colonization bare sand	20	June	2,14	7,51	1622	2,5	2049	18,67	37,5	3018	2971
Natural patch colonization bare sand	20	June	55,43	7,57	1354	2,6	1742	18,67	37,5	2986	2914
Natural patch colonization meadow	20	June	69,25	7,48	193	1,8	2332	18,67	37,5	3183	3149
Natural patch colonization meadow	20	June	68,34	7,61	58	2,5	1420	18,67	37,5	2689	2605
Natural patch erosion bare sand	20	June	6,97	7,53	130	1,8	1807	18,67	37,6	2755	2704
Natural patch erosion bare sand	20	June	5,90	7,48	884	2,7	1943	18,67	37,6	2648	2615
Natural patch erosion meadow	20	June	1,97	7,40	71	6,5	2496	18,67	37,6	2769	2768
Natural patch erosion meadow	20	June	1,48	7,41	93	2,1	3230	18,67	37,6	3690	3690

Station type	Depth	Month	H2S (µM)	pH	CH4 (nmol.l^{-1})	N2O (nmol.l^{-1})	pCO2 (ppm)	T in situ	Salinity	TA (µM)	DIC calc. (µM)
Meadow	10	October	44,12	7,62	27	1,4	1389	23,09	38,2	2617	2507
Meadow	10	October	43,64	7,74	13	3,5	1007	23,09	38,2	2631	2464
Meadow	15	October	2,06	7,60	21	1,1	1484	22,78	38,1	2705	2600
Meadow	15	October	51,99	7,40	60	0,9	3458	22,78	38	3796	3774
Meadow	20	October	0,76	7,58	44	1,6	1587	22,87	38	2724	2629
Meadow	20	October	0,29	7,55	45	1,3	1733	22,87	38	2732	2650
Natural patch colonization bare sand	10	October	2,41	7,41	21	1,7	2933	23,09	38,1	3333	3302
Natural patch colonization bare sand	10	October	2,01	7,37	44	1,4	4293	23,09	38	4317	4314
Natural patch colonization meadow	10	October	0,23	7,81	6	5,0	794	23,09	38,2	2459	2269
Natural patch colonization meadow	10	October	0,26	7,88	6	4,5	659	23,09	38,1	2437	2215
Natural patch erosion bare sand	10	October	0,72	7,59	30	1,6	1580	23,09	38,1	2793	2689
Natural patch erosion bare sand	10	October	0,35	7,56	38	1,5	1750	23,09	38,1	2856	2765
Natural patch erosion meadow	10	October	0,26	7,51	28	1,4	2052	23,09	38,2	2935	2865
Natural patch erosion meadow	10	October	0,22	7,31	64	1,0	4687	23,09	38	4157	4183
Natural patch colonization bare sand	15	October	1,86	7,41	78	1,4	2867	22,78	38	3236	3208
Natural patch colonization bare sand	15	October	1,51	7,47	37	1,0	2263	22,78	38	2979	2925
Natural patch colonization meadow	15	October	1,36	7,65	69	1,6	1409	22,78	37,9	2873	2745
Natural patch colonization meadow	15	October	1,21	7,78	12	5,4	869	22,78	38,2	2510	2332
Natural patch erosion bare sand	15	October	0,73	7,52	72	1,1	1896	22,78	37,8	2782	2713
Natural patch erosion bare sand	15	October	0,66	7,52	73	1,3	1888	22,78	37,8	2763	2694
Natural patch erosion meadow	15	October	0,56	7,47	55	1,5	2078	22,78	38	2703	2653
Natural patch erosion meadow	15	October	0,59	7,51	62	1,2	1915	22,78	38,1	2756	2689
Natural patch colonization bare sand	20	October	0,18	7,55	53	1,2	1760	22,87	38,1	2814	2728
Natural patch colonization bare sand	20	October	0,95	7,82	12	4,0	824	22,87	38,1	2594	2396
Natural patch colonization meadow	20	October	0,15	7,31	542	1,2	4051	22,87	38	3600	3621
Natural patch colonization meadow	20	October	0,16	7,34	581	1,3	4011	22,87	37,9	3832	3840
Natural patch erosion bare sand	20	October	0,12	7,59	89	0,9	1466	22,87	38	2555	2461
Natural patch erosion bare sand	20	October	0,05	7,59	15	1,0	1290	22,87	38,2	2286	2195
Natural patch erosion meadow	20	October	12,34	7,54	58	1,3	1745	22,87	38,1	2700	2622
Natural patch erosion meadow	20	October	0,18	7,53	64	1,1	1945	22,87	38,1	2911	2835

Annexe 3 : Densité (en faisceaux.m^{-2}) des herbiers bordant les intermattes naturelles (Article 2)

10 m			15 m			20 m		
Continuous	Colonization	Erosion	Continuous	Colonization	Erosion	Continuous	Colonization	Erosion
550	760	340	250	240	530	290	90	30
410	370	530	450	220	510	240	120	200
230	480	400	290	250	610	420	170	240
420	500	790	570	440	320	250	180	120
430	490	600	400	290	560	480	190	70
510	700	970	530	360	530	300	100	120
590	770	570	570	350	550	20	200	250
630	510	650	500	310	340	150	240	120
430	810	310	450	310	630	120	130	50
460	910	490	360	450	330	200	210	160

Annexe 4 : Poids sec des feuilles (en grammes) des herbiers bordant les intermattes naturelles (Article 2)

10 m

February			June			October		
Continuous	Colonization	Erosion	Continuous	Colonization	Erosion	Continuous	Colonization	Erosion
0,5699	0,633	0,873	2,3695	2,2735	2,3149	0,4987	1,0893	0,8986
0,6852	0,7406	0,7646	2,1588	2,4841	2,7711	0,7859	0,9741	0,6417
0,6649	0,9014	0,7785	2,4414	1,006	2,2866	0,9157	0,3244	0,9607
0,7724	0,7996	0,8535	2,2316	2,3409	1,5591	1,6113	1,01	0,5851
0,8231	0,9338	0,7788	1,5124	1,323	2,3646	0,9783	1,3208	1,8917
0,9336	0,4306	0,678	2,5367	2,2035	1,6538	1,588	0,5533	0,5981
0,7637	0,4868	0,579	2,294	2,0876	2,3696	0,7907	1,0492	1,4994
0,6716	0,3195	0,5904	2,6481	2,6165	1,7191	1,0279	0,9483	0,6941
0,7449	0,4171	0,1732	2,2127	2,2073	3,1715	0,9234	1,237	0,5276
0,4416	0,2667	0,4425	2,8124	2,4391	2,3218	1,1874	2,4992	0,6619
0,5331	0,5489	0,4291	0,6734	2,12012	2,0914	0,9627	0,8494	1,0268
0,565	0,243	0,2137	2,2173	2,6206	1,1344	0,5551	1,3509	0,8712
0,5382	0,6736	0,2128	2,1876	2,6444	2,2258	0,2509	0,5185	0,6652
0,6006	0,1996	0,2876	2,1436	2,2387	2,2192	1,15	0,4631	0,1716
0,5839	0,3162	0,5725	2,14558	2,4875	2,6801	0,7934	0,6168	0,6898
1,1268	0,6803	0,4341	2,4409	1,6411	1,6037	1,7063	0,75058	0,7063
1,1704	1,0835	0,5354	1,9105	2,7957	2,284	0,568	0,7951	0,1441
0,5966	1,0623		2,9528	2,3775	0,6644	2,0801	0,9281	0,227
0,5285			0,8005	2,7755	1,3642	0,3863	0,9187	0,6942
			1,35824	2,0415	1,2912	0,9492	1,2915	0,5076

15 m

February			June			October		
Continuous	Colonization	Erosion	Continuous	Colonization	Erosion	Continuous	Colonization	Erosion
0,3007	0,7225	1,0153	3,4301	0,8748	2,3622	0,3626	1,2094	0,2841
0,5748	0,8642	0,5773	1,2609	2,7837	2,19008	0,4495	0,1861	0,2527
0,5758	0,7518	1,1717	2,3047	4,4344	0,9448	0,2388	1,4096	0,7668
0,8958	0,7511	0,7779	2,0776	2,8549	2,0962	0,5627	0,2113	0,2894
0,2397	0,4519	0,7519	2,1394	2,7639	2,1429	0,3736	1,5941	1,2127
0,4577	0,8605	0,5897	0,6885	3,501	1,0131	1,4851	1,2739	0,312
1,0307	0,5974	0,5251	2,6162	3,2697	1,3891	1,718	1,0716	1,5275
0,7804	0,5684	0,5532	3,3795	2,0561	1,8043	0,6527	1,2632	1,3998
1,0984	0,5798	0,2661	2,0603	2,7632	2,7763	0,3719	0,2771	0,5529
0,6294	0,9167	0,4692	1,4942	3,2757	1,5219	1,4973	0,6422	0,618
0,5485	0,3964	0,7795	1,4759	2,7834	2,6238	0,9464	1,1065	0,4726
0,5308	0,6352	1,1213	1,3205	4,1219	2,9747	0,8138	1,1843	0,2404
0,5167	0,6204	0,3878	2,1352	2,1979	1,0501	0,4094	0,4084	0,9022
0,7871	0,73	0,535	0,6972	1,3109	0,243	0,4914	0,4917	1,4278
0,4681	0,4304	0,5843	0,7091	2,1735	3,1591	0,3266	1,2391	0,13271
0,7643	0,7935	0,8208	0,9632	3,0219	0,9586	0,4955	0,8357	0,5726
0,6669	0,6486	1,0402	2,7898	2,0652	1,4979	0,6175	1,1345	0,8764
0,6522	0,5819	0,9453	2,6401	2,934	1,44092	1,686	2,1448	0,9862
	0,7286	0,2569	2,6879	3,4007	2,3536	1,8295	1,2424	0,1633

20 m

February			June			October		
Continuous	Colonization	Erosion	Continuous	Colonization	Erosion	Continuous	Colonization	Erosion
0,6029	0,3074	0,8503	2,3476	2,4321	0,3592	0,4317	0,4053	1,5067
0,4153	0,6785	0,2429	2,1218	2,1272	2,0939	1,0856	0,5307	1,0063
0,4728	1,0791	0,77	1,4035	2,3582	2,5208	0,8086	0,4776	0,6629
0,4992	0,5422	0,4153	2,2468	0,7844	1,5565	0,6128	0,3741	0,1802
0,2978	1,0713	0,551	1,9519	2,3765	1,4975	0,4028	1,2135	0,51241
0,3851	0,4092	0,3883	2,3123	2,4788	1,7957	0,1551	0,2351	1,202
0,57	0,9062	0,6286	1,4883	2,4748	1,259	0,4454	1,0243	0,5707
0,5057	0,4526	0,55101	2,5578	3,7084	1,3758	0,2455	2,1341	0,6842
0,5148	0,4669	0,46355	0,7953	2,7165	1,692	0,4824	1,5579	1,4553
0,5146	0,6392	0,4886	1,3105	2,1077	2,0687	0,7529	1,65371	1,0997
0,6665	0,2907	0,3193	1,1488	2,55904	2,5143	0,6067	0,2295	1,0928
0,4497	0,4549	0,934	2,0338	0,6612	1,435	0,2396	1,1747	0,5946
0,5392	0,9054	0,4905	1,8512	1,9624	3,1361	1,4742	2,2138	0,554
0,3816	0,6253	1,0444	0,6042	2,6488	1,8325	0,5314	1,2995	1,2094
0,3628	0,6352	0,4662	1,9284	2,0161	1,71664	0,7198	1,6714	1,4735
0,5226	0,752	0,6299	2,9478	2,5594	1,483	0,6346	1,3863	1,6726
0,5317	0,651	0,3893	2,5747	2,2608	1,6517	0,75004	0,5871	0,6343
0,7404	0,8016		2,2528	2,7475	1,5154	0,822	1,5682	0,3135
0,6232	0,4333		2,5661		1,6358	0,5554	0,22	0,1651

Annexe 5 : Protocole de dosage de l’oxygène dissout dans des micro-volumes

Principle: dissolved oxygen is titrated with a thiosulfate solution ($S_2O_3^{2-}$) using Winkler method titration of iodine adapted for microvolumes. The automatization of the procedure allows the treatment of a larger batch of samples.

Samples preparation: after collecting the pore water in syringes, samples are injected in small biological demand oxygen (BOD) bottles with a volume of 10 ml. Recipients are filled, with a special attention to not induced air bubbles, until the bottle volume flows out three times. 0.075 ml of each Winkler reagent (R1: $MnCl_2 + 4H_2O$ and R2: NaI + NaOH). At last, solutions are leaved in the shadow during at least three hours in order to allow the reagents to interact and the precipitate to form. After this period, the color of the precipitate indicates the presence (yellow) or absence (white) of dissolved oxygen in the solution.

Probe and software: the probe (a Metrohm 6.0451.100 for redox titrations) is linked to a multimeter Fluke®. Its signal is red through the O76 software developed by Renzo Biondo (Laboratory of Oceanology- University of Liege). The software allows the remote manipulation via a computer of the Metrohm 655 Dosimat device and the automatization of the oxygen concentration measurement. It integrates the precise volume of each BOD, the lab and in situ temperature as well as the sample salinity.

Standards titration: two solutions are titrated in order to calibrate the probe with microvolumes

A blank solution: 10 ml of filtrated sea water (SW) + 0.250 ml Winkler third reagent (R3: H_2SO_4) + agitation + 0.075 ml R2 + agitation + 0.075 ml R1

Standard solution: 10 ml of filtrated SW + 0.250 ml R3 + agitation + 0.075 ml R2 + agitation + 0.075 ml R1 + 0.2 ml standard (KIO_3)

The O76 software saves values obtained during these titrations and integrates them during the samples treatment.

Oxygen measurement: 0.250 ml of R3 is injected in each sample BOD when the precipitate is formed. 10 ml of the solution thus created is poured in a beaker with a pipette. Finally, the dissolved oxygen is measured via thiosulfate titration using the Metrohm 655 Dosimat.

Annexe 6 : Protocole de dosage du sulfure d'hydrogène

Probe: measures are realized using an ISM-146 FTH25-XS Micro hydrogen sulfide flow through measurement system. It measures the total free sulfide inside an aqueous solution. Measures are expressed in mV. The concentration is then determined thanks to a semi-logarithmic graph. The probe can measure concentrations of a range of 1.10-7 M to 1 M.

Software: the probe is linked to a multimeter Fluke®. Its signal is red through the ELM software developed by Renzo Biondo (Laboratory of Oceanology-University of Liege). This computer program displays the variations of signal (in mV) according to the time. The frequency of acquisition is 3 measures/sec, the mean of this three values being represented by a point. The time of measurement is customizable but should not be less than 120 sec according to Brooks (2001). Prior to each measure the graph must be rescaled to fit to the concentration of the new sample.

Calibration of the probe: a consequent amount (2 l) of sea water (SW) must be boiled in order to remove all the oxygen. Bottles of 70 ml are filled until the SW overflows and then are hermetically closed. They are used hereafter for the standards.

The calibration is done before each batch of samples (no more than 15 samples). The calibration requires at least five standards in order to obtain a linear line. The standards need a stock solution of Na2S (1.4 g Na2S.9H2O in 200 ml of distilled water) (Cline 1969). Due to its low concentration, another solution with a 100 x concentration was prepared. A working solution ($T Na2S) is finally prepared (3 ml Na2S stock solution + 37 ml distilled water). $T Na2S is titrated using the Winkler method before preparing the standards [Winkler standard solution (10 ml SW filtered + acid + reagent 2 + 0.2 ml Winkler standard) + 0.1 ml $T Na2S].

A basic sulfide antioxidant buffer solution (SAOB: 16 g NaOH, 14.4 g EDTA, 7 g ascorbic acid, 200 ml distilled water) is also necessary for the probe calibration.

The five standards are prepared as follows with their concentration calculated according to the dilution law C1V1=C2V2:

- Standard 1: 70 ml of boiled SW (blank)
- Standard 2: 70 ml of boiled SW + 0. 2 ml $TNa2S

- Standard 3: 70 ml of boiled SW + 0.4 ml $T Na2S
- Standard 4: 70 ml of boiled SW + 0.8 ml $T Na2S
- Standard 5: 70 ml of boiled SW + 1 ml $T Na2S

The five standards and the SAOB solution must be prepared prior to each batch of samples and are stable up to 3 hours. Each standard has to be titrated directly (without using a BOD) before the measure with the probe. Thus, at the same time as the probe measures the conductivity of a standard (10 ml SAOB + 10 ml of standard), standards are titrated (10 ml standard + acid + reagent 2 + 0.2 ml Winkler standard).

The mV values are recorded when the measure is stabilized and plotted on a semi-logarithmic graph. The standard concentrations are put on the logarithmic axe and the mV values on the linear axe.

Samples measurements: 10 ml from the sample are ejected in a 30 ml beaker containing 10 ml of SAOB. The beaker is then placed on a magnetic agitator and the probe is plunged into the solution. The electrode reading can take several minutes to stabilize. The electrode must be wiped after each measure but not rinsed. A new calibration must be performed at the end of each batch of samples in order to assess the possible deviation of the probe calibration during the measures.

References

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Annexe 7 : Densité de l’herbier, compacité de la matte, déchaussement des rhizomes et hauteur de la canopée dans un herbier de contrôle et un herbier sous pression d’ancrage (Article 3)

Control10	Anchoring10	Control15	Anchoring15	Control20	Anchoring20
Density (shoot.m-2)					
55	52	25	15	29	13
41	65	45	27	24	8
23	33	29	42	42	29
42	19	57	18	25	22
43	72	40	37	48	25
51	37	53	29	30	26
59	56	57	38	2	17
63	51	50	33	15	13
43	61	45	17	12	10
46	36	36	42	20	23
Compactness (cm)					
35	35	30	30	30	60
25	30	40	35	25	50
30	30	45	35	25	55
40	35	40	40	35	65
25	45	40	40	30	50
35	25	35	35	35	35
30	50	30	35	40	50
30	35	40	50	30	40
20	25	40	40	25	45
30	40	30	35	30	55
Rhzime baring (cm)					
5	9	4	9	9	1
2	21	3	3	4	1
4	20	7	14	0	2
6	12	2	12	5	3
6	5	14	5	7	1
1	0	14	12	5	2
5	19	6	21	4	4
1	14	4	6	12	1
3	14	5	8	3	1
2	15	3	9	10	3
3	13	12	4	9	4
2	6	5	0	13	1
7	5	5	6	3	3
4	19	4	8	13	2
3	3	7	3	15	1

Control10	Anchoring10	Control15	Anchoring15	Control20	Anchoring20
Canopy height in June (cm)					
125,6	121,8	109,3	102,3	108,1	47,3
121,3	121,2	103,4	102	105,6	50,6
119,5	120,9	101	98,1	105,5	65,3
119,3	116,2	98,5	97,3	104,6	66
119	113,3	98	93,5	97,3	68,9
116,6	106,4	97,1	92,8	96,7	70,1
115,5	102,3	95,2	86	95,1	70,3
106,5	97,4	93,6	77,8	90,6	70,7
106,2	95,6	92,4	69,4	90,3	72,1
105,6	93,5	88,5	64,7	86,2	72,2
105,5	91,7	87,4	64,4	84,6	73,6
102,7	90,8	86	64,1	82,3	75,2
99,8	89,8	85,2	62,7	82	78,3
89,1	87,7	61	61,4	79,5	78,8
87,1	82,9	60,5	55,8	78,2	83,5
87,1	82,1	59,9	54,5	76,6	85,6
85,8	81,1	54,8	50,6	75	87,2
73,8	75,3	50,1	45,6	68,7	93,1
70,6	67,3	47,4	42,4	63,2	96,2
65,5	66,1		32,5	56,3	99,6
Canopy height in September (cm)					
59	19,6	19,7	40	46,1	38,2
60,2	54,3	46,7	42	48,1	38,8
72,3	55,3	47,2	43,4	52	39,4
72,9	62	52	53,2	55,2	51
74	63,8	56,8	57,8	57,6	53
75,2	64	58,9	58,1	58,4	54,6
76,4	65,2	60	60,9	62	56
78,3	65,2	62,9	61,6	62,9	60
78,5	67,1	63,7	64,6	63,3	60,7
79,4	68	65	66,7	63,5	62,7
79,8	67,9	69	69	63,9	67,6
80	71	71,2	69,6	65,2	68,4
80,2	73,7	72,5	71,5	67	69,4
81,9	76,5	76,9	72,2	70,7	69,5
84,4	77	77	72,6	73,2	73,1
88,8	80,7	77,4	73,6	75,3	75,7
90,2	83,9	83,0	77	77,7	86
91	84,9	90	81,2	80	86
93,5	104,5	98,9	82,6	80	96,3
96	109,3	107,5	91,7	96	109

Annexe 8 : Concentrations en sulfure d'hydrogène et en nutriments dans un herbier de contrôle et un herbier sous pression d'ancrage (Article 3)

Station	H2S (µM)		NO2 (µM)		NO3 (µM)		NO4 (µM)	
	September	November	September	November	September	November	September	November
C10	2,9	0,2	0,06	0,06	0,24	0,3	2,52	2,7
	78,2	0,1	0,06	0,24	0,3	3,36	4,2	4,74
	36,2	0,1	0,06	0,3	0,12	2,1	7,32	5,76
Am10	6,2	2,0	0,06	0,06	0,3	0,18	2,7	4,38
	3,6	1,6	0,12	0,06	0,24	0,18	5,58	3,6
	26,2	1,4	0,06	0,06	0,12	0,54	5,94	5,34
Ap10	3,9	2,2	0,06	0,06	0,12	0,24	7,2	2,58
	2,1	3,2	0,06	0,06	0,18	0,24	3,96	2,7
	55,3	6,1	0,06	0,06	0,12	0,24	19,38	3
C15	0,0	0,2	0,06	0,06	0,78	0,42	3,78	3,18
	1,0	0,1	0,06	0,06	0,24	0,18	11,1	10,56
	0,2	1,1	0,06	0,12	0,24	0,54	16,14	5,22
Am15	3,6	3,4	0,12	0,06	1,56	0,36	4,56	4,02
	2,8	2,7	0,12	0,12	0,3	0,78	13,56	21,3
	17,8	40,2	0,12	0,06	0,42	0,12	14,16	11,82
Ap15	17,7	1,4	0,12	0,06	0,18	0,36	4,02	11,88
	3,5	7,3	0,06	0,06	0,18	0,12	5,46	25,68
	8,6	51,3	0,06	0,06	0,12	0,18	10,62	12,9
C20	5,0	1,2	0,12	0,06	0,48	0,48	5,16	3,72
	2,6	0,6	0,06	0,12	0,18	0,42	18,78	10,08
	41,8	0,5	0,06	0,06	0,24	0,12	19,2	8,52
Am20	0,5	1,6	0,12	0,06	0,78	0,24	3,24	2,64
	0,4	1,4	0,06	0,12	0,3	0,36	16,56	13,98
	1,8	14,1	0,06	0,06	0,12	0,18	21,66	6,48
Ap20	0,8	8,8	0,06	0,06	0,24	0,3	2,82	4,68
	0,6	2,5	0,06	0,18	0,12	1,02	8,34	4,26
	37,0	2,2	0,06	0,06	0,12	0,18	51,06	30,48

Annexe 9 : Synthèse de la recherche bibliographique sur les paysages formés par les plantes sous-marines

Summary of the bibliographical researches on seascapes formed by seagrass meadows. S=structure; F=function; C=changes; LSS: Large scale; MSS: medium scale; SSS: Small Scale; SP: Small Patch; LP: Large Patch; M: Mapping; T: Transect; Q-DS: Quadrat-Discrete Sampling

Study site	Seagrass species	Landscape aspect	Area studied	Method	Reference
French Mediterranean Coast (France)	*Posidonia oceanica* *Cymodocea nodosa*	S	SSS	T	Molinier and Picard (1952)
Barbados and Carriacou, West Indies (Barbados)	*Thalassia testudinum* *Syringodium filiforme*	S/C	SSS	M	Patriquin (1975)
Calvi Bay, Corsica (France)	*Posidonia oceanica*	S	SSS	LP	Boudouresque *et al.* (1980b)
Villefranche (France)	*Posidonia oceanica*	S	SSS	M	Meinesz and Lefèvre (1984)
Elbu, Corsica (France)	*Posidonia oceanica*	S	SSS	M	Boudouresque *et al.* (1985b)
Botany Bay, New South Whale (Australia)	*Zostera capricorni* *Posidonia australis*	S/F	MSS	Q-DS	Bell and Westoby (1986)
Elbu, Corsica (France)	*Posidonia oceanica*	S	SSS	M	Meinesz *et al.* (1988)
Tampa Bay, Florida (USA)	*Halodule wrighrii*	S/C	SSS	Q-DS	Pangallo and Bell (1988)
Pauatahanui Inlet (New Zealand)	ASU	S/F	SSS	SP	Bell and Hicks (1991)
Indian River Lagoon, Florida (USA)	*Halodule wrighrii* *Syringodium filifonne* *Halophila englemannii* *Halophila decipiens* *Halophila johnsonii* *Thalassia testudinum* *Ruppia maritima*	S	SSS	M	Virnstein (1995)
Back Sounds, North Carolina (USA)	*Zostera marina* *Halodule wrightii*	S/F	SSS	Q-DS	Irlandi (1996)

El Campello, Alicante (Spain)	*Posidonia oceanica*	S/F	SSS	T	Sánchez-Jerez and Ramos Esplá (1996)
Back Sounds, North Carolina (USA)	*Zostera marina* *Halodule wrightii* *Ruppia maritima*	S/F	SSS	SP	Irlandi (1997)
Alfacs Bay (Spain)	*Cymodocea nodosa*	S/C	MSS	M	Vidondo *et al.* (1997)
Back Sounds, North Carolina (USA)	ASU	S/F	SSS	SP	Eggleston *et al.* (1998)
Core et Back Sounds, North Carolina (USA)	*Zostera marina* *Halodule wrightii*	S	SSS	M	Fonseca and Bell (1998)
Tampa Bay, Florida (USA)	*Ruppia maritima* *Syringodium filifonne*	S/F	SSS	Q-DS	Knowles and Bell (1998)
Corsica (France)	*Posidonia oceanica*	S	LSS	M	Pasqualini *et al.* (1998)
Maasholm, Kiel Bight, Baltic Sea (Germany)	*Zostera marina*	S/F	SSS	Q-DS	Reusch (1998)
Phuket and Ko Talibong (Thailand) Balinao, Pto. Galera and El Nido (The Philippines)	*Thalassia hemprichii* *Cymodocea rotundata* *Cymodocea serrulata* *Syringodium isoetifolium* *Halodule uninervis* *Halophila ovalis*	S	SSS	Q-DS	Terrados *et al.* (1998)
Beaufort, North Carolina (USA)	*Zostera marina* *Halodule wrightii*	S/C	SSS	SP	(Townsend & Fonseca 1998)
Tampa Bay, Florida (USA)	*Halodule wrightii* *Thalassia testudinum* *Syringodium isoetifolium*	S/C	SSS	M	Bell *et al.* (1999)
Back Sounds, North Carolina (USA)	ASU	S/F	SSS	SP	Eggleston *et al.* (1999)
Success Bank (Australia)	*Amphibolis griffithii* *Posidonia coriacea*	S/C	LSS	M	Kendrick *et al.* (1999)
Bay of Sant'Amanza and Macinaggio, Corsica (France)	*Posidonia oceanica*	S	LSS	M	Pasqualini *et al.* (1999)
San Diego, California (USA)	*Zostera marina*	S/F	SSS	Q-DS	Reusch and Williams (1999)
El Campello, Alicante (Spain)	*Posidonia oceanica* *Cymodocea nodosa*	S/F/C	SSS	T	Sánchez-Jerez *et al.* (1999)

Manukau Harbor and Whangapoua Harbor (New Zealand)	*Zostera novazelandica*	S/F/C	LSS	SP	Turner *et al.* (1999)
St; Joseph Bay, Florida (USA)	ASU	S/F	LSS	SP	Bologna and Heck (2000)
Antignano, Tuscan Coast (Italia)	*Posidonia oceanica* *Cymodocea nodosa*	S/F	SSS	Q-DS	Ceccherelli *et al.* (2000)
St. Paul's Bay (Malta)	*Posidonia oceanica*	S	SSS	Q-DS	Dimech *et al.* (2000)
Corsica (France)	*Posidonia oceanica*	S	LSS	M	Pasqualini *et al.* (2000)
Tampa Bay, Florida (USA)	*Halodule wrightii* *Thalassia testudinum*	S/C	SSS	M	Robbins and Bell (2000)
Tampa Bay, Florida (USA)	*Halodule wrightii*	S/F	SSS	Q-DS	Bell *et al.* (2001)
Isles of Scilly (England)	*Zostera marina*	S/F	SSS	SP	Bowden *et al.* (2001)
Chesapeake Bay (USA)	*Zostera marina*	S/F/C	LSS	M	Hovel and Lipcius (2001)
Tampa Bay, Florida (USA)	*Halodule wrightii* *Thalassia testudinum*	S/C	SSS	Q-DS	Jensen and Bell (2001)
Core Sound, North Carolina (USA)	*Zostera marina* *Halodule wrightii*	S/C	LSS	M	Kelly *et al.* (2001)
Coast of Almeria (Spain)	*Posidonia oceanica*	S	MSS	T	Moreno *et al.* (2001)
Mombasa Lagoon (Kenya)	*Thalassodendron ciliatum*	S/F	SSS	SP	Alcoverro and Mariani (2002)
Tampa Bay, Florida (USA)	*Thalassia testudinum*	S/F	SSS	Q-DS	Bell *et al.* (2002)
St. Paul's Bay (Malta)	*Posidonia oceanica*	S/F	SSS	Q-DS	Dimech *et al.* (2002)
Goodwin Islands, Virginia (USA)	*Zostera marina* *Ruppia maritima*	S/F	MSS	M	Hovel and Lipcius (2002)
Calvi Bay, Corsica (France)	*Posidonia oceanica*	S/C	SSS	Q-DS	Gobert *et al.* (2003)
Bodega Harbor, California and Back Sounds, North Carolina (USA)	*Zostera marina* *Halodule wrightii*	S/F	SSS	Q-DS	Hovel (2003)

Bonavista Bay, Newfoundland (Canada)	ASU	S/F	SSS	SP	Laurel *et al.* (2003)
Bolinao, Pangasinan (Philippines)	*Enhalus acoroides* *Thalassia hemprichii* *Cymodocea rotundata* *Cymodocea serrulata* *Syringodium isoetifolium* *Halodule uninervis* *Halophila ovalis* *Halophila minor*	S/F/C	SSS	M	Salita *et al.* (2003)
Velje, Amager and Samsø (Danemark)	*Zostera marina*	S/C	LSS	M	Frederiksen *et al.* (2004)
San Diego Bay, California (USA)	ASU	S/F	SSS	SP	Healey and Hovel (2004)
Moreton Bay, Queensland (Australia)	*Zostera capricorni*	S/F	LSS	Q-DS	Pittman *et al.* (2004)
Tampa Bay, Florida (USA)	*Halodule wrightii* *Thalassia testudinum* *Syringodium isoetifolium*	S/C	SSS	M	Robbins and Bell (2004)
Ramla Bay, Mellieha Bay, White Rocks and St Thomas Bay (Malta)	*Posidonia oceanica*	S	MSS	Q-DS	Borg *et al.* (2005)
Ria Formosa (Portugal)	*Zostera noltii*	S/C	MSS	M	Cunha *et al.* (2005)
Back Sounds, North Carolina (USA)	*Zostera marina* *Halodule wrightii* *Ruppia maritima*	S/F	SSS	LP	Hovel and Fonseca (2005)
Simulation	*Posidonia oceanica*	S/C	SSS	-	Kendrick *et al.* (2005b)
Fremantle (Australia)	Not specified	S	MSS	M	Sleeman *et al.* (2005)
Cape Circeo and Sperlonga (Italy)	*Posidonia oceanica*	S/C	LSS	M	Ardizzone *et al.* (2006)
Tampa Bay, Florida (USA)	-	S/F/C	SSS	-	Bell *et al.* (2006)
Mellieha Bay (Malta)	*Posidonia oceanica*	S/F	SSS	Q-DS	Borg *et al.* (2006)
Archipelago Sea (Finland)	*Zostera marina*	S/F	LSS	Q-DS	Boström *et al.* (2006b)
Ninigret Pond, Rhode Island (USA)	*Zostera marina*	S	MSS	M	Bradley and Stolt (2006)

Island of Zanzibar (Tanzania)	*Thalassodendron ciliatum* *Enhalus acoroides* *Thalassia hemprichii* *Cymodocea rotundata*	S/F	LSS	Q-DS	Dorenbosch *et al.* (2006)
Jersey (England)	*Zostera marina*	S/F	LSS	T	Jackson *et al.* (2006b)
Jersey (England)	*Zostera marina*	S/F	LSS	T	Jackson *et al.* (2006a)
Pittwater estuary (Australia)	*Zostera capricorni*	S/F	MSS	LP	Jelbart *et al.* (2006)
Bay of Saint-Cyr (France)	*Posidonia oceanica*	S/C	MSS	M	Leriche *et al.* (2006)
San Diego Bay, California (USA)	*Zostera marina*	S/F/C	SSS	SP	Reed and Hovel (2006)
St Kilda (Australia)	*Heterozostera tasmanica* *Posidonia australis* ASU	S/F	SSS	SP	Tanner (2006)
Lacco Ameno, Island of Ischia (Italy)	*Posidonia oceanica*	S	SSS	Q-DS	Zupo *et al.* (2006b)
Lacco Ameno, Island of Ischia (Italy)	*Posidonia oceanica*	S	SSS	Q-DS	Zupo *et al.* (2006a)
Chesapeake Bay (USA)	*Zostera marina*	S	SSS	SP	Harwell and Rhode (2007)
Genoa (Italia)	*Posidonia oceanica* *Cymodocea nodosa*	S	MSS	T	Montefalcone *et al.* (2007)
Hervey Bay, Queensland (Australia)	*Halodule uninervis* *Halophila ovalis* *Zostera capricorni* *Halophila spinulosa*	S/F	LSS	Q-DS	Sheppard *et al.* (2007)
Bath (Barbados)	*Thalassia testudinum* *Syringodium filiforme*	S	SSS	Q-DS	Tewfik *et al.* (2007)
Charlotte Harbor, Florida (USA)	*Halodule wrightii* *Thalassia testudinum* *Syringodium ifiliforme*	S/F	LSS	M	Whaley *et al.* (2007)

Okinawa Island (Japan)	*Cymodocea rotundata* *Cymodocea serrulata* *Thalassia hemprichii* *Halodule uninervis* *Halodule pinifolia* *Syringodium isoetifolium* *Halophila ovalis*	S/C	SSS	M	Yoshida *et al.* (2007)
Balearic Islands (Spain)	*Posidonia oceanica*	S/C	SSS	SP	Almela *et al.* (2008)
West Florida Shelf (USA)	*Halophila decipiens*	S/C	MSS	M	Bell *et al.* (2008)
West Florida Shelf (USA)	*Halophila decipiens*	S	MSS	T	Fonseca *et al.* (2008)
Chwaka Bay (Tanzania)	*Cymodocea rotundata* *Cymodocea serrulata* *Enhalus acoroides* *Thalassia hemprichii* *Thalassodendron ciliatum*	S/F	LSS	Q-DS	Gullström *et al.* (2008)
Simulation based on Chesapeake Bay (USA)	Not specified	S/F	SSS	-	Hovel and Regan (2008)
Port Phillip Bay (Australia)	*Heterozostera nigricaulis*	S/F	SSS	Q-DS	Smith *et al.* (2008)
Ramla Bay, Mellieha Bay, White Rocks and St Thomas Bay (Malta)	*Posidonia oceanica*	S	MSS	M	Borg *et al.* (2009)
Polt Agra Bay, Sardigna (Italy)	*Posidonia oceanica*	S/F/C	SSS	SP	Ceccherelli *et al.* (2009)
Ria Formosa (Portugal)	*Zostera noltii* *Zostera marina* *Cymodocea nodosa*	S/C	MSS	M	Cunha and Santos (2009)
Medes Islands (Spain)	*Posidonia oceanica*	S/F	SSS	Q-DS	Farina *et al.* (2009)
Red Fish Bay, Texas (USA)	*Halodule wrightii* *Thalassia testudinum* *Syringodium ifiliforme* *Halophila engelmannii* *Ruppia maritima*	S/C	MSS	M	Fletcher *et al.* (2009)

Bonavista Bay, Newfoundland (Canada)	*Zostera marina*	S/F/C	SSS	SP	Gorman *et al.* (2009)
Papanui Inlet and Harwood (New Zealand)	*Zostera muelleri*	S/F	SSS	SP	Mills and Berkenbusch (2009)
Catalan Coast (Spain)	*Posidonia oceanica*	S/F/C	SSS	Q-DS	Prado *et al.* (2009)
Outer Puck Bay, Baltic Sea (Poland)	*Zostera marina* *Potamogeton sp.* *Zanichellia palustris Ruppia maritima*	S	SSS	M	**Erreur ! La référence de lien hypertexte est incorrecte.**
Indian River Lagoon, Florida (USA)	*Halophila johnsonii*	S/C	LSS	T	Virnstein *et al.* (2009)
Brittany (France)	*Zostera marina*	S/F	LSS	Q-DS	Becheler *et al.* (2010)
Ramla Bay, Mellieha Bay, White Rocks and St Thomas Bay (Malta)	*Posidonia oceanica*	S/F	MSS	Q-DS	Borg *et al.* (2010)
Hanko Peninsula (Finland)	*Zostera marina* *Potamogeton pectinatus*	S/F	SSS	Q-DS	Boström *et al.* (2010)
Gulf of Oristano, Sardinia (Italy)	*Posidonia oceanica*	S/F	MSS	T	Coppa *et al.* (2010)
Brisbane Water, Lake Macquarie, Wallis Lake and Smiths Lake (Australia)	*Zostera capricorni*	S/F/C	LSS	M	Ford *et al.* (2010)
Zakynthos Island (Greece)	*Posidonia oceanica*	S/F/C	MSS	T	Katsanevakis *et al.* (2010)
Liguria (Italia)	*Posidonia oceanica*	S/C	LSS	T	Montefalcone *et al.* (2010b)
Gullmarsfjord (Sweden)	*Zostera marina*	S/F	SSS	SP	Nohrén and Odelgård (2010)
Port Phillip Bay, Victoria (Australia)	*Heterozostera nigricaulis*	S/F	SSS	Q-DS	Smith *et al.* (2010)
Newfoundland (Canada)	*Zostera marina*	S/F	LSS	M	Thistle *et al.* (2010)
French Mediterranean Coast (France)	*Posidonia oceanica*	S	SSS	M	Descamp *et al.* (2011)

Chwaka Bay (Tanzania)	*Cymodocea rotundata* *Cymodocea serrulata* *Enhalus acoroides* *Thalassia hemprichii* *Thalassodendron ciliatum*	S/F	LSS	Q-DS	Gullström *et al.* (2011)
Alykes Bay, Zakynthos Island (Greece)	*Posidonia oceanica*	S/F	LSS	M	Kiparissis *et al.* (2011)
Model based on Chesapeake Bay (USA)	*Zostera marina*	S/F/C	SSS	M	Mizerek *et al.* (2011)
Fethiye Bay (Turkey)	*Posidonia oceanica*	S	LSS	Q-DS	Okudan *et al.* (2011)
Biscayne Bay, Florida (USA)	Not specified	S	LSS	M	Santos *et al.* (2011)
Port Phillip Bay, Victoria (Australia)	*Heterozostera nigricaulis*	S/F	SSS	LP	Smith *et al.* (2011)
Gulf of Veracruz (Mexico)	*Thalassia testudinum*	S	SSS	T	Terrados and Ramírez-García (2011)
Tokyo Bay (Japan)	*Zostera marina*	S/C	SSS	M	Yamakita and Nakaoka (2011)
Fårö, Baltic Sea (Finland)	ASU	S/F	SSS	SP	Arponen and Boström (2012)
Heuningnes Estuary (South Africa)	*Zostera capensis*	S/F	SSS	Q-DS	Källén *et al.* (2012)
Lakshadweep Islands (India)	Not specified	S	LSS	M	Nobi *et al.* (2012)
Crete (Greece)	*Posidonia oceanica*	S/F	LSS	Q-DS	Rountos *et al.* (2012)
Trinity Bay, Newfoundland (Canada)	ASU	S/F	SSS	SP	Ryan *et al.* (2012)
Port Phillip Bay (Australia)	*Zostera nigricaulis*	S/F	SSS	SP	Smith *et al.* (2012)
Tuscany (Italy)	All marine habitats of which *Posidonia oceanica*	S	LSS	T	Tamburello *et al.* (2012)
Emmapolder (Netherlands)	*Zostera noltii*	S/F/C	SSS	T	van der Heide *et al.* (2012)
New Brunswick (Canada)	*Zostera marina*	S	MSS	M	Barrell and Grant (2013)

St. Florent, Corsica (France)	*Posidonia oceanica*	S/C	SSS	M	Bonacorsi *et al.* (2013)
Hallock Bay, Long Island (USA)	ASU	S/F	SSS	SP	Carroll and Peterson (2013)
Fenals and Giverola (Spain)	*Posidonia oceanica*	S/F/C	SSS	SP	Gera *et al.* (2013)
Moreton Bay (Australia)	Not specified	S/C	LSS	M	Lyons *et al.* (2013)
Palma Bay, Balearic Islands (Spain)	*Posidonia oceanica*	S	LSS	Q-DS	Massot-Campos and Codina (2013)
Liguria (Italia)	*Posidonia oceanica*	S/C	LSS	M	Montefalcone *et al.* (2013b)
Gulf of Alghero, Sardinia (Italy)	*Posidonia oceanica* ASU	S/F	SSS	Q-DS	Pinna *et al.* (2013)
Provence (France)	*Posidonia oceanica*	S	LSS	M	Andromede Oceanologie (2014)
Spanish Coast	All marine habitats of which *Posidonia oceanica*	S	LSS	M	Chefaoui (2014)
Corsica (France)	*Posidonia oceanica*	S	LSS	M	Clabaut *et al.* (2014)
Calvi Bay, Corsica (France)	Several Mediterranean species of flora and fauna of which *Posidonia oceanica* and *Cymodocea nodosa*	S/F	LSS	T	Gobert *et al.* (2014)
Aransas Bay and Corpus Christi Bay, Texas (USA)	*Halodule wrightii*	S/F	MSS	M	Hensgen *et al.* (2014)
Yucatan Peninsula (Mexico)	*Thalassia testudinum* *Syringodium filiforme,* *Halodule wrightii*	S/F	SSS	T	Molina Hernàndez and van Tussenbroek (2014)
Balearic Islands (Spain)	All marine habitats of which *Posidonia oceanica* and *Cymodocea nodosa*	S	LSS	M	Nowell (2014)
Catalan Coast (Spain)	*Posidonia oceanica*	S/F	SSS	SP	Pagès *et al.* (2014)

Moreton Bay (Australia)	*Halophila spinulosa* *Halophila ovalis* *Halodule uninervi* *Zostera muelleri* *Cymodocea serrulata* *Syringodium isoetifolium*	S/C	LSS	M	Roelfsema *et al.* (2014)
Corsica (France)	*Posidonia oceanica*	S	LSS	M	Abadie *et al.* (2015b)
Core et Back Sounds, North Carolina (USA)	*Zostera marina* *Halodule wrightii*	S/F/C	MSS	T	Baillie *et al.* (2015)
Halifax Harbour, Nova Scotia (Canada)	*Zostera marina*	S/F/C	SSS	M	Barrell and Grant (2015)
Willapa Bay, Washington (USA)	*Zostera marina* *Zostera japonica*	S	LSS	M	Dumbauld and McCoy (2015)
South East coast of France	*Posidonia oceanica*	S/C	LSS	M	Holon *et al.* (2015a)
French Mediterranean coast including Corsica	*Posidonia oceanica* *Zostera marina* *Zostera noltii* *Cymodocea nodosa*	S	LSS	M	Holon *et al.* (2015b)
Capo Rizzuto, Calabria (Italy)	*Posidonia oceanica*	S	SSS	M	Rende *et al.* (2015)
Aiguablava, Giverola and Rustella (Spain)	*Posidonia oceanica*	S/F	SSS	Q-DS	Ricart *et al.* (2015a)
Port Curtis Harbour, Queensland (Australia)	*Zostera muelleri*	S/F	SSS	Q-DS	Ricart *et al.* (2015b)
Biscayne Bay, Florida (USA)	Not specified	S/C	MSS	M	Santos *et al.* (2015)
Schleswig-Holstein (Denmark and Germany)	*Zostera marina*	S	LSS	M	Schubert *et al.* (2015)
Calvi Bay, Corsica (France)	*Posidonia oceanica*	S	SSS	Q-DS	Abadie *et al.* (2016)
The entire species' geographic range	*Cymodocea nodosa*	S	LSS	M	Chefaoui *et al.* (2016)
Parc National du Banc d'Arguin (Mauritania)	*Zostera noltii* *Halodule wrightii* *Cymodocea nodosa*	S/C	MSS	M	de Fouw *et al.* (2016)

Several sites along the coast of Black Sea (Bulgaria, Romania, Turkey, Crimea)	*Zostera noltii*	S/F	LSS	M	Jahnke *et al.* (2016)
Chesapeake Bay (USA)	*Zostera marina*	S/F/C	SSS	SP	Lefcheck *et al.* (2016)
Thomson Bay and Stark Bay, Rottnest Island (Australia)	*Posidonia sinuosa* *Amphibolis griffithii*	S	MSS	M	Serrano *et al.* (2016)
West coast of Sweden	*Zostera marina*	S/F			Staveley *et al.* (2016)
Albemarle-Pamlico Sound Estuary System, North Carolina (USA)	*Zostera marina* *Halodule wrightii* *Ruppia maritima*	S	MSS	M	Uhrin and Townsend (2016)
Calvi Bay, Corsica (France)	*Posidonia oceanica*	S/C	SSS	LP	Gobert *et al.* (accepted)
Baħar ic-Cagħaq, Selmun Bay, Daħlet Qorrot, San Blas Bay and Ramla Bay (Malta)	*Posidonia oceanica*	S	SSS	M	Pace *et al.* (in press)

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Annexe 10 : Détail des données utilisées pour le calcul de l’EBQI dans l’herbier de la Baie de l’Alga

Boites	Poids	Paramètres	Statut					IDC	Protocoles	Matériel (taille en cm)
			4	3	2	1	0			
1 – *P. oceanica* racines et rhizomes	3	Croissance des rhizomes orthotropes (mm a^{-1})	9 to 19	20 to 40	3 to 8	> 40	< 3	3	30 mesures au hasard et in situ (croissance des rhizomes correspondant à la base des 8 dernières feuilles)	Regle Inox metal / Plaquette
2 - *P. oceanica* feuilles	5	Densité (nombre de feuilles m^{-2})	≥ 490	489 to 370	369 to 250	249 to 130	< 130	3	20 mesures au hasard et in situ de la densités des "shoot" dans un quadrat de 0,16 m^2	Quadrat 40*40 / Plaquette
		Recouvrement (%)	> 80	80 to 61	60 to 41	40 to 20	< 20	3	30 mesures au hasard du recouvrement	Appareil photo
3 - Epibiontes MOP des feuilles	4	Biomasse (g MS $feuilles^{-1}$)	0.3 to 0.7	0.1 to 0.3	0.8 to 1.5	< 0.1	> 1.5	3	Prélévement des 2 plus vielles feuilles externes sur 30 "shoot" prélevéss au hasard pour estimer la biomasse d'épibiontes	Sac / Plaquette
4 - Epibiontes filtreurs et suspensivores des feuilles									Prélévement des 2 plus vielles feuilles externes sur 30 "shoot" prélevéss au hasard pour estimer la biomasse d'épibiontes	Sac / Plaquette
5 – Filtreurs benthiques (*Pinna nobilis*)	2	Densité (nombre d'individus $100m^{-2}$)	> 3.0	3.0 to 1.1	1.0 to 0.6	0.5 to 0.1	< 0.1	4	Densité de *Pinna nobilis* le long de 20 transects de 10 mètres et 1 mètre de large	Decamétre / Plaquette / barre de 1 metre
6 – Autres filtreurs et suspensivores benthiques	2							4	Abondance des filtreurs et suspensivores (autres que *Pinna nobilis*) dans un quadrat de 1 m^2, en réalisant 30 réplicats au hasard	Quadrat 100*100 / Plaquette
-HOM		Densité (nombre m^{-2})	< 0.1	0.1 to 0.9	1.0 to 1.9	2.0 to 5.0	> 5.0			
-LOM		Densité (nombre m^{-2})	> 10.0	10.0 to 5.1	5.0 to 1.1	1.0 to 0.1	< 0.1			
7 - Litière détritique	2	g MS m^{-2}	> 350	350-251	250-151	150-51	≤ 50	3	Collecte de la litière détritique dans 5 quadrat aléatoire de 0,1 m2	5 Sacs / Plaquette / Quadrat 10*10
8 - Détritivores	2	Individus 10 m^{-2}	1.0 to 4.9	0.2 to 0.9	5.0 to 24.9	< 0.2	≥ 25.0	4	Abondance des Holothuria spp.dans un quadrat de 1 m2, en réalisant 30 réplicats au hasard	Quadrat 100*100 / Plaquette

Boites	Poids	Paramètres	Statut 4	3	2	1	0	IDC	Protocoles	Matériel (taille en cm)
9 - Herbivores 1	5	Densité de Paracentrotus lividus (nombre d'individus m^{-2})	1.0 to 4.9	0.1 to 0.9	5.0 to 9.9	< 0.1	≥ 10	4	Abondance *de Paracentrotus lividus* dans un quadrat de 1 m2, en réalisant 30 réplicats au hasard a 5 mètres	Quadrat 100*100 / Plaquette
		Indice de broutage (% feuilles)	30 to 59%	5 to 29%	60 to 95%	< 5%	> 95%	4	Sur 30 faisceaux échantillonnés de manière aléatoire % des feuilles (adultes et intermédiaires) montrant des traces de scarifications engendrés par *S. Salpa*	Plaquette
10 - Predateurs teleosteens (cephalopodes et etoiles de mer)	5	poids frais de teleosteens (kg 100 m^{-2})	> 1.5	1.5 to 1.1	1.0 to 0.6	0.5 to 0.3	< 0.3	4	Comptage de l'ensemble des téléostéens sur 10 transects de 50 mètres de long et 5 mètres de large pour une durée de 5 minutes	Plaquette / decametre
11 - Piscivores teleoststeens	5	poids frais de teleosteens (kg 100 m^{-2})	> 1.0	1.0 to 0.6	0.5 to 0.3	0.2 to 0.1	< 0.1	4	Comptage de l'ensemble des téléostéens sur 10 transects de 50 mètres de long et 5 mètres de large pour une durée de 5 minutes	
12 - Planktivores teleosteens	3									
-Zooplankton feeders		poids frais (kg 100 m^{-2})	> 3.0	3.0 to 1.6	1.5 to 0.8	0.7 to 0.3	< 0.3	4	Comptage de l'ensemble des téléostéens sur 10 transects de 50 mètres de long et 5 mètres de large pour une durée de 5 minutes	
-Omnivores		poids frais (kg 100 m^{-2})	> 3.0	3.0 to 1.6	1.5 to 0.8	0.7 to 0.3	< 0.3	4		
9-12 - SRDI	3	Indice specifique de diversité relative (SRDI)	> 10	10 to 8	7 to 5	4 to 3	< 3	4	Comptage de l'ensemble des téléostéens sur 10 transects de 50 mètres de long et 5 mètres de large pour une durée de 5 minutes	
13- Oiseaux	1							2		
-*Phalacrocorax spp.*		Distance par rapport au site de nidification (km)	< 4	4 to 7	8 to 12	13 to 17	> 17			
-*Pandion haliaetus*		Distance par rapport au site de nidification (km)	< 4	4 to 7	8 to 12	13 to 17	> 17			