UNIVERSITÉ DU QUÉBEC À MONTRÉAL

EFFETS SIMPLES ET CUMULÉS DES PERTURBATIONS ET DES STRESS MULTIPLES SUR LES COMMUNAUTÉS BENTHIQUES INTERTIDALES : RÔLE DES MACROPHYTES

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RÉSUMÉ

Les écosystèmes côtiers sont sujets à de nombreux stress et perturbations (stress ci-après) naturels et anthropiques. Ceux-ci agissent sur la stabilité et le fonctionnement des écosystèmes qui peuvent aller jusqu'à une disparition d'habitats et une perte de biodiversité. Bien que ces milieux soient généralement soumis à plusieurs stress à la fois, peu d'études se sont intéressées à la nature et aux conséquences potentielles des effets cumulatifs. Les études mettant l'accent sur de multiples stress sont importantes pour aider à la compréhension des mécanismes qui façonnent les communautés dans un environnement complexe et changeant.

L'objectif principal de cette thèse est d'évaluer les effets des stress et leurs interactions sur les communautés macrobenthiques littorales. Pour répondre à cet objectif, mon projet cible le rôle des macrophytes structurants sur leurs communautés associées lorsque des stress affectant les contrôles descendant et/ou ascendant (« *top-down* » et « *bottom-up* ») sont présents. Des expériences *in situ* ont été mises en place dans deux habitats du littoral de l'estuaire maritime du Saint-Laurent : herbiers de zostères et les macroalgues. Le premier chapitre évalue le rôle des macroalgues en milieu médiolittoral rocheux en combinaison avec un enrichissement de la colonne d'eau et une réduction des gastéropodes brouteurs sur la résilience des communautés macrobenthiques associées. Le second chapitre évalue le rôle de la densité des zostères marines en combinaison avec un enrichissement des sédiments et une réduction de la lumière sur l'épifaune associée et les zostères en soi. Le dernier chapitre porte sur les effets de bordure et la densité de zostères marines sur leur épifaune associée sur cinq sites de l'hémisphère Nord (côte ouest de l'Atlantique, côte est du Pacifique, Québec et France) afin de vérifier si les effets de la complexité de l'habitat et du paysage à petite échelle est le même dans des herbiers de zostères pouvant avoir des caractéristiques différentes. Dans chacun des chapitres, des mesures de diversité univariées (richesse, diversité, équitabilité, abondances) et multivariées (structure et composition) au niveau des invertébrés et des algues ont été évaluées. Les types d'interactions entre stresseurs ont aussi été déterminé dans les chapitres 1 et 2 (addition, dominance, synergisme, antagonisme). Des mesures sur la zostère marine ont été ajoutées pour les chapitres 2 et 3 (densité des plants et masse des épibiontes ; chapitre 2 seulement : élongation relative des plants et glucides non-structuraux). Le dernier chapitre utilise une approche par traits biologiques pour comparer des sites qui ont très peu d'espèces communes. Les effets de l'habitat sont ainsi mesurés sur des traits

communs à tous les sites. Cette approche permet de faire des rapprochements entre les communautés et leurs fonctions.

Les résultats de ma thèse montrent que les espèces structurantes en présence de stress multiples jouent un rôle primordial pour les communautés des habitats côtiers et confirment leurs rôles structurant et protecteur sur les différentes composantes de la biodiversité. Également, les milieux rocheux dominés par les macroalgues et les herbiers de zostères peuvent présenter de la résistance (chapitre II) et sont résilients (chapitres I et II) selon le type de stress temporairement appliqués. Contrairement aux attentes, les parcelles ayant subi les traitements triples n'ont pas été plus affectées que les traitements simples ou doubles à l'exception du traitement triple dans les macroalgues de milieux rocheux (chapitre I) qui a démontré un taux de récupération plus lent que les autres traitements. Ma thèse démontre que lorsque les stress interagissent, les effets ne sont pas systématiquement *additifs* ou *synergiques* tels que fréquemment sous-entendus dans la littérature. Plusieurs des interactions mesurées étaient de type *dominant*, c'est-à-dire que l'effet d'un stress vient éclipser celui d'un second alors qu'en majorité du temps, il n'y a pas eu d'interaction entre stress. Des interactions *synergiques négatives*, *additive*s et *antagonistes* ont aussi été observées. Le dernier chapitre montre que l'effet de la complexité des espèces structurantes et l'effet de bordure peuvent être importants ou pas, ainsi ils ne se généralisent pas entre des sites distants, et ce, même en utilisant des traits biologiques. Les résultats suggèrent que la répartition des espèces et les traits biologiques sont influencés par d'autres aspects que seulement l'effet de bordure ou la complexité des zostères, et qu'aucun de ces deux effets ne domine les effets observés sur les assemblages.

Ma thèse met en valeur l'importance des expériences *in situ* qui utilisent des perturbations et des stress multiples pour déterminer leurs effets cumulatifs. Entre autres, la détermination des types d'interaction entre stress est importante au niveau de la gestion des écosystèmes et qu'une simple additivité des stress ne devrait pas être supposée sans tests *in situ*. Il est primordial que les gestionnaires reconnaissent que les stress pourront avoir des effets locaux spécifiques et que les interactions entre les stress présents sont imprévisibles. Effectivement, les résultats de cette thèse suggèrent que les stress multiples peuvent interagir différemment sur les indices liés à la biodiversité des communautés, leurs structures et leurs fonctions et que leurs interactions ne peuvent pas être prédites en utilisant des mesures sur des stress simples seulement. Effectivement, il sera important pour les gestionnaires d'inclure plusieurs mesures de la diversité, particulièrement des mesures multivariées et des mesures de fonctionnement, dans le but d'évaluer la santé des écosystèmes. Il devient donc prioritaire de maintenir la présence de macrophytes structurants qui soutiennent directement les capacités de résilience et de résistance des communautés face aux

stress. Ma thèse permettra une meilleure gestion des écosystèmes en invitant les différents acteurs à porter une attention particulière aux différents indices de biodiversité, aux interactions imprévisibles des stress présents ou prédits, tout en tenant compte de l'unicité dans les caractéristiques et réponses de certains habitats.

Mots clés : diversité, effets cumulatifs, espèces structurantes, résistance et résilience, perturbations et stress multiples

ABSTRACT

Coastal ecosystems are exposed to many natural and anthropogenic stress and disturbances (stress afterwards). These stresses affect the stability and functioning of ecosystems and their effect may lead to a loss in biodiversity and habitat. Although coastal systems are exposed to multiple simultaneous stresses, few studies investigated the interaction type and the cumulative effect of stress. Such studies are important for the understanding of how communities are shaped in a complex and changing environment.

The main objective of this thesis is to measure the effects of stresses and their interactions on intertidal macrobenthic communities. To reach this goal, this thesis is centered on the role of habitat-forming macrophytes over their associated communities when they are facing stress affecting top-down and bottom-up controls. In situ experiments were performed in two different habitats: eelgrass meadows and rocky intertidal dominated by fucoids. The first chapter evaluates the role of macroalgae in a rocky intertidal system combined to water column enrichment and a reduction of grazing gastropod on the associated macrobenthic community resilience. The second chapter estimates the role of eelgrass shoot density combined to sediment nutrient enrichment and light reduction on associated epifaunal assemblages and eelgrass itself. The last chapter assesses the effect of edge and eelgrass shoot density on associated epifaunal assemblages on five different sites from the northern hemisphere (West Atlantic Coast, East Pacific Coast, Québec and France) to verify if the effects of habitat complexity and small-scale seascape are the same in different eelgrass meadows. In each chapter, diversity univariate and multivariate invertebrates and algae diversity measures were analyzed: abundance, richness, diversity, evenness, structure, composition. The type of interaction among stressors were determined in chapters 1 and 2 (addition, dominance, synergism, antagonism). Some eelgrass measures were added in chapters 2 (shoot density, shoot relative elongation, non-structural carbohydrates, epibionts biomass) and 3 (shoot density, epibionts biomass). The last chapter uses a biological traits approach in combination to the species approach. The biological trait approach allows to compare the effect of habitat on species among sites that have almost no species in common.

My results indicate that habitat-forming species play an important role when communities are facing multiple stresses which confirms their structuring and

protecting roles over different biodiversity components. Moreover, rocky systems dominated by macroalgae and eelgrass meadows may present resistance (chapter II) and are resilient (chapters I and II) depending on the temporary stress they are facing. Contrary to expectations, plots that were facing three stresses were not more affected than were single or double stressed plots except for the triple stress in chapter I that had the slowest recovery. My thesis shows that interacting stresses are not systematically *additive* or *synergistic* as is regularly assumed in the literature. Indeed, many of the interactions were of the type *dominant*, that is, the effect of one stressor overshadows the effect of the other stressor, while we mainly measured no interactions. Some *negative synergistic*, *additive* and *antagonistic* interactions were also observed. The last chapter shows that the effect of the complexity of habitat-forming species and edge effect may be or may not be important. Indeed, no common general results were observed on five distant sites even when using biological traits.

My thesis highlights the importance of in situ experiments using multiple disturbances and stresses in order to determine the cumulative effects. Determining the interaction type between stresses is essential for system management since additivity of stresses should not be assumed without proper testing. It is important that managers know that stresses can have local and specific effects, and that the interactions among stresses can not easily be predicted. Indeed, the results of this thesis indicate that multiple stresses will not have the same impact depending on the identity of the investigated variables. Moreover, it is impossible to predict the interaction of stresses based only on their single effect. Managers should include complementary diversity measures as well as functioning measures to insure the health of ecosystems. Notably, it is of a great importance to maintain the presence of habitat-forming macrophytes since they promote the resistance and resilience of communities facing stress. My thesis will allow a better management of ecosystems by inviting decision makers to look at various biodiversity indices, to take into account that the interaction of stresses are unpredictable, and that every habitat or system may show unique characteristics that will affect their responses to stressors.

Key words: cumulative effect, diversity, habitat-forming species, multiple disturbances and stresses, resistance and resilience

INTRODUCTION GÉNÉRALE

0.1 Mise en contexte

Au cours des deux derniers siècles, les activités humaines ont causé beaucoup de changements dans la nature, notamment dans le paysage terrestre ou dans les océans (p. ex. : destruction d'habitat, surexploitation des ressources naturelles), les cycles biogéochimiques, le climat et la biodiversité (IPCC, 2014; Vitousek *et al.*, 1997b). Il n'existerait aucun écosystème marin non affecté par les activités humaines et une grande partie de ces derniers seraient influencés par des stress et des perturbations d'origines multiples (Halpern *et al.*, 2008).

Les facteurs externes affectant les communautés sont généralement subdivisés en deux catégories : les stress et les perturbations. Les stress se caractérisent par des conditions pouvant changer la production de biomasse (p. ex. réduction en luminosité et enrichissement en nutriments). Les perturbations occasionnent une perte totale ou partielle de biomasse et peuvent être issues de phénomènes biotiques (p. ex. consommation par niveau trophique supérieur, enlèvement par l'homme) ou abiotiques (p. ex. dommage par les vagues, le froid et la dessiccation) (Grime, 1977). Dans le but d'alléger le texte, le terme stress sera utilisé pour les généralités autant à titre de stress que de perturbation et les termes précis seront utilisés pour les cas spécifiques. Cependant, veuillez noter que les changements induits sur les communautés dans cette thèse sont des stress dans les cas d'enrichissement en nutriment et de réduction de luminosité, et sont des perturbations dans le cas de roche mise à nue, d'enlèvement

manuel d'algues et de brouteurs, et de réduction de densité de zostères (voir dans les différents chapitres correspondants).

Près de 40 % de la population humaine habite à moins de 100 km des côtes (Agardy *et al.*, 2005). Les écosystèmes côtiers sont sujets à de nombreux stress induits par les activités humaines p. ex. : destruction d'habitat, eutrophisation, augmentation de sédimentation, perte de biodiversité et espèces envahissantes (Airoldi et Beck, 2007; Halpern *et al.*, 2008; IPCC, 2014; Short et Wyllie-Echeverria, 1996; Vitousek *et al.*, 1997b). Ces stress altèrent la structure et le fonctionnement des écosystèmes (Cardinale *et al.*, 2012; Hawkins *et al.*, 2009; Hooper *et al.*, 2012).

En général, les producteurs primaires des estuaires et des zones côtières sont limités par l'azote (Howarth, 1988). La fixation artificielle de l'azote par l'homme a doublé la quantité d'azote disponible pour les organismes vivants (Vitousek *et al.*, 1997a; Vitousek *et al.*, 1997b). L'eutrophisation des milieux côtiers peut mener à des changements dans la structure des communautés benthiques (Kraufvelin, 2007; Worm et Lotze, 2006) allant jusqu'à la disparition de macrophytes structurants (Duarte, 2002; Short et Wyllie-Echeverria, 1996).

Les écosystèmes côtiers peuvent également être touchés par les changements globaux tels que l'augmentation de la température, l'augmentation du niveau de la mer, les changements au niveau de la salinité, l'augmentation de la concentration en dioxyde de carbone et des rayonnements ultraviolets (Harley *et al.*, 2012; Short et Neckles, 1999). Il est primordial de développer des connaissances dans le but de restreindre les effets nocifs des activités humaines sur les écosystèmes puisqu'une récupération est possible là où des efforts de conservation sont mis en place (Lotze *et al.*, 2006).

L'augmentation des stress sur les côtes pourrait affecter les assemblages benthiques, d'abord au niveau de leur structure d'abondance et ensuite sur leur composition en espèces allant jusqu'à une perte en biodiversité locale (Arevalo *et al.*, 2007; Hillebrand *et al.*, 2008; Kraufvelin, 2007). Un changement au niveau de la structure de dominance, même seul, est suffisant pour avoir un impact sur les communautés (Doak *et al.*, 1998; Hillebrand *et al.*, 2008). Ces changements au niveau des assemblages provoqueraient des modifications dans le fonctionnement des communautés (p. ex. : respiration, productivité) et dans la stabilité temporelle de leurs propriétés (Bokn *et al.*, 2003; Lotze *et al.*, 2006; Stachowicz *et al.*, 2002).

On sait qu'une perte en biodiversité et des changements dans la composition des assemblages peuvent altérer les biens et services rendus par les écosystèmes (Chapin *et al.*, 2000; Hooper *et al.*, 2005; Worm *et al.*, 2006). Les écosystèmes offrent notamment des fonctions écosystémiques (p. ex. : production algale, production de poissons, purification, recyclage, détoxification) (Daily, 1997) et ont une très grande valeur tant pour l'homme que pour la planète (Barbier *et al.*, 2011; Costanza *et al.*, 1997). Ces biens et services étant nécessaires, il devient capital de comprendre les conséquences écologiques que les altérations anthropiques ont sur les écosystèmes (Barbier *et al.*, 2011; Hooper *et al.*, 2005).

Dans la nature, des stress peuvent se produire en simultané et les effets cumulatifs sont difficilement prédictibles à partir d'études simples qui mesurent les effets d'un stress arrivant seul. Effectivement, les effets cumulatifs des stress peuvent être additifs (sans interaction) ou non-additifs (c.-à-d., synergiques ou antagonistes; Fig. 0.1) (Côté *et al.*, 2016 pour différentes interactions possibles; Galic *et al.*, 2018; voir Piggott *et al.*, 2015). Une synergie sera présente lorsque l'effet combiné des stress sera plus grand que l'effet additif anticipé à partir des effets simples, tandis qu'il s'agira d'un antagonisme si cet effet cumulatif est plus petit que la prédiction (Fig. 0.1). Il est aussi

possible que les effets d'un stress soient masqués ou annulés par les effets d'un stress dominant (réaction antagoniste de type dominance; Fig. 0.1). Cependant, il est généralement sous-entendu dans la littérature que les effets sont additifs étant donné un manque de connaissances sur les possibles effets interactifs (Halpern *et al.*, 2007). De plus en plus, les interactions entre stress sont souvent considérées comme étant synergiques sans effectuer de tests (Côté *et al.*, 2016). Il n'existe pas de consensus sur l'incidence relative des différents effets. Par exemple, Strain *et al.* (2014) rapportent que la majorité des effets sont additifs, tandis que Darling et Côté (2008) rapportent que la majorité sont non-additifs et impossibles à prédire, car menant à ce qu'on appelle des « surprises écologiques » non anticipées. Crain *et al.* (2008) estiment que le pourcentage d'interactions synergiques en milieux marin et côtier change de 33 à 66 % lorsqu'on passe de deux à trois stress. Il existe peu d'études *in situ* sur les effets de la multiplication des stress sur les communautés marines (Crain *et al.*, 2008), néanmoins plusieurs études ont documenté des interactions entre des stress (p. ex. : Atalah et Crowe, 2010; Eklof *et al.*, 2009; Guerry, 2008; Lange *et al.*, 2011; Strain *et al.*, 2014).

Il est donc nécessaire d'effectuer des études incluant trois stress ou plus; de telles études sont rares en milieux rocheux marins côtiers dominés par les macroalgues (voir Strain *et al.*, 2014) et presque inexistantes dans les herbiers marins (Blake et Duffy, 2010 en mésocosme; Eklof *et al.*, 2009 en milieu naturel).

Au Canada, même si l'on y a recensé des réductions importantes dans l'abondance de certains groupes taxonomiques, le golfe du Saint-Laurent reste un système relativement peu dégradé par rapport à d'autres systèmes similaires (Lotze *et al.*, 2006). Au Québec, une eutrophisation (Gilbert *et al.*, 2007; Thibodeau *et al.*, 2006), de même qu'une augmentation de la température, des précipitations et de l'érosion côtière sont prévues sur les régions bordant l'estuaire Saint-Laurent (DesJarlais *et al.*, 2010). Les zones côtières peuvent facilement s'éroder sous l'influence des précipitations, du gel-dégel,

du vent et des vagues (DesJarlais *et al.*, 2010). L'augmentation de l'érosion côtière est liée à la hausse de la température de la mer, donc du niveau moyen des mers et aux redoux hivernaux (cycle gel-dégel), à la diminution de la durée de la période d'inhibition des vagues par les glaces, et aux changements du régime des tempêtes (Savard *et al.*, 2008). Les communautés côtières seront donc davantage touchées par ces stress au cours des décennies à venir. Plus particulièrement, les communautés de l'étage médiolittoral seront affectées par les changements du régime de couvert de glace par une augmentation des glaces mobiles pouvant racler les substrats, et par une diminution de la protection par les glaces contre les vagues et les températures froides en hiver. On peut s'attendre à ce que les espèces structurantes de ces milieux soient affectées par ces stress soit par plus de perte de biomasse par les glaces et les gelées.

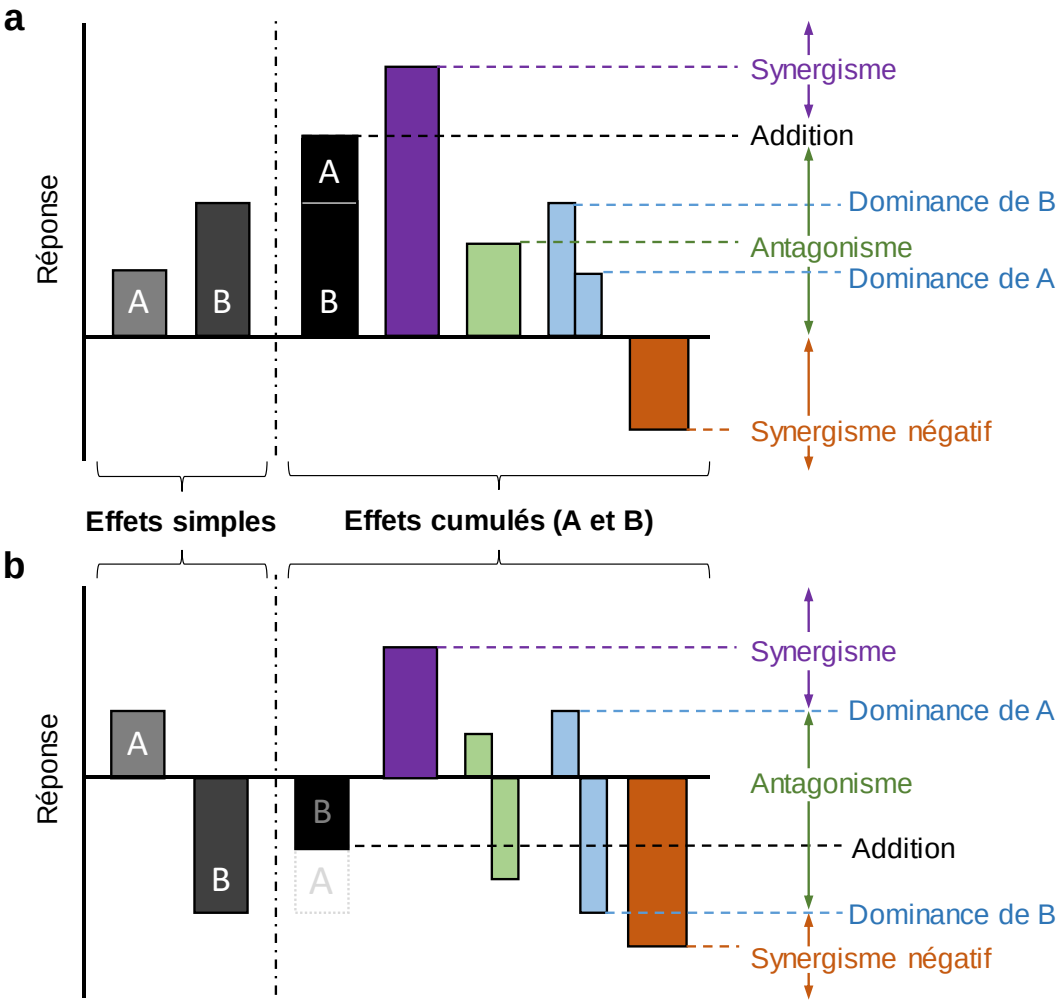

Figure 0.1. Représentations graphiques montrant les types d'effets cumulatifs possibles entre deux stress (A et B) : addition (noir), synergisme (violet), antagonisme (vert), dominance (bleu) et synergisme négatif (orange). (a) et (b) sont deux scénarios possibles utilisés à titre d'exemple. De façon générale, une interaction synergique aura lieu lorsque l'effet cumulé sera plus grand que l'effet anticipé de l'addition des réponses (a); un synergisme négatif, lorsque l'effet cumulé est de signe opposé à la réponse des stress (a); un antagonisme positif, lorsque l'effet cumulé est plus petit que l'effet anticipé additif (a,b); et dominant, lorsque l'effet n'est pas différent de l'un des deux stress (a,b). Les interactions sont un peu différentes lorsque les effets sont de sens opposé tel qu'en (b) : synergisme si la réponse est plus élevée que le stress A, relation antagoniste négative si la réponse cumulée est moins négative que l'addition des deux stresseurs, et synergisme négatif si la réponse est plus négative que celle du stress B. Figure modifiée de Côté *et al.* (2016). Consulter Galic *et al.* (2018) pour d'autres représentations graphiques semblables.

0.2 État des connaissances

0.2.1 La biodiversité

Les changements climatiques anticipés et l'éventuelle perte en espèce ont poussé les écologistes à se pencher sur la relation entre la biodiversité et le fonctionnement des écosystèmes (Hooper *et al.*, 2005; Loreau, 2000; Stachowicz *et al.*, 2007). Généralement, les études sur la biodiversité montrent qu'un nombre d'espèces élevé affecte positivement le fonctionnement des écosystèmes (Gustafsson et Bostrom, 2011; Hooper *et al.*, 2005; Worm *et al.*, 2006). Cependant, la diversité ne se limite pas au nombre d'espèces (ou richesse spécifique); d'autres indicateurs peuvent être utilisés. Ainsi, l'équitabilité ou la dominance (abondances relatives), la composition (identité des espèces) et la structure des abondances sont des variables à prendre en compte (Chapin *et al.*, 2000; Clarke *et al.*, 2014). Ces différents indicateurs liés à la diversité sont donc à considérer pour expliquer et comprendre la stabilité des écosystèmes. De plus, chaque espèce doit être jugée importante puisque même les interactions les plus faibles peuvent perturber la composition et la structure d'une communauté entière (McCann, 2000).

Les diverses composantes de la biodiversité telles que la composition en espèces, l'équitabilité et la richesse sont importantes dans le maintien de la stabilité structurelle et fonctionnelle. Dans un contexte d'augmentation des stress sur les communautés, il devient primordial d'évaluer l'influence de la biodiversité sur les fonctions des écosystèmes telle que la stabilité des communautés lorsqu'elles font face à des stress.

0.2.2 Stabilité des communautés

La stabilité est un concept d'écologie vaste et complexe. Il est accepté que la stabilité se décompose en plusieurs composantes qui ne font toutefois pas l'unanimité quant aux

termes à utiliser. Déjà, le terme stabilité ainsi que ses composantes ont été utilisés par différents auteurs pour décrire plusieurs composantes distinctes de la stabilité, parfois les mêmes avec différents mots (Donohue *et al.*, 2016; Grimm et Wissel, 1997; Lehman et Tilman, 2000). Il devient donc important de bien cibler la définition de la stabilité utilisée dans chaque article de la présente thèse.

0.2.2.1 Composantes de la stabilité

La définition de la stabilité par Grimm et Wissel (1997) se divise en trois propriétés : constance, résilience et persistance. La constance se définit comme un état essentiellement inchangé par rapport à un état de référence et est nommée résistance lorsqu'un système fait face à des stress tout en restant inchangé. La résilience se caractérise par un retour à un état de référence après un stress temporaire ; il sera question d'élasticité si on parle de la vitesse à laquelle la résilience a lieu. La persistance est la pérennité/conservation d'un système écologique dans le temps qui est à l'opposé du renouvellement d'espèces. Les divisions des composantes de la stabilité sont légèrement différentes pour Pimm (1984) qui compte cinq composantes avec les équivalents de Grimm et Wissel (1997) (entre parenthèses) : la stabilité (résilience), la résilience (élasticité), la persistance, la résistance et la variabilité (constance). À ces composantes sont parfois ajoutés le nombre d'extinctions (robustesse) et le nombre d'invasions qui sont des propriétés de la persistance (Donohue *et al.*, 2013).

0.2.2.2 Stabilité des communautés

Une communauté stable/constante, présentant naturellement une variabilité temporelle et spatiale, conservera ses diverses fonctions et son abondance totale dans le temps par divers mécanismes impliquant la complémentarité : asynchronie, diminution de la stochasticité démographique, diversité de réponses aux stress et réduction des forces de compétition (de Mazancourt *et al.*, 2013; Loreau et de Mazancourt, 2013). La stabilité peut être influencée par plusieurs facteurs, dont la richesse (Tilman, 1996),

l'équitabilité (dominance) (Hillebrand *et al.*, 2008), les liens interspécifiques (Rooney et McCann, 2012), les espèces structurantes (Paine, 1969) et les perturbations (Donohue *et al.*, 2013). La stabilité peut être évaluée par plusieurs variables d'intérêt : abondances ou biomasse et composition des espèces, et les abondances par niveau trophique (Pimm, 1984).

0.2.2.3 Relation entre diversité et stabilité

De manière générale, plus la diversité en espèces est grande, plus les chances sont élevées qu'il y ait présence de complémentarité entre deux ou plusieurs espèces, d'inclure des espèces résistantes à certains stress, ou encore d'inclure une espèce ayant la capacité de dominer la communauté par ses traits spécifiques (Loreau *et al.*, 2001; Yachi et Loreau, 1999).

Plusieurs études rapportent des effets positifs de la richesse sur la stabilité des systèmes (p. ex. Gustafsson et Bostrom, 2011; Macarthur, 1955), d'autres rapportent qu'elle peut avoir des effets négatifs (p. ex. Cusson *et al.*, 2015; May, 1973; Valdivia et Molis, 2009), ou encore aucun effet (Goodman, 1975). Toutefois, l'effet de la diversité sur la stabilité peut dépendre du niveau trophique étudié (Jiang et Pu, 2009), des échelles auxquelles elle est mesurée ainsi que de sa nature (richesse ou équitabilité; Cusson *et al.*, 2015). Par exemple, la richesse peut stabiliser au niveau de l'écosystème, mais déstabiliser au niveau des populations (effet portfolio ou effet de l'assurance) (Lehman et Tilman, 2000; Tilman, 1996; Tilman *et al.*, 2006). C'est-à-dire qu'à grande échelle, il y aura un effet stabilisant de la moyenne de la biomasse totale des diverses espèces dans le temps, tandis qu'à l'échelle d'une population, l'effet sur la biomasse peut être non négligeable (Schindler *et al.*, 2015). En d'autres mots, même si une espèce échoue, l'effet portfolio assure que la biomasse totale restera stable peu importe l'identité et l'abondance respective des espèces présentes. Aussi, un assemblage riche en espèces a plus de chance de posséder des espèces ayant la capacité de se remettre qu'un

assemblage pauvre lorsqu'il fait face à un stress (Hillebrand *et al.*, 2008; Yachi et Loreau, 1999).

La complémentarité entre espèces correspond à une meilleure utilisation des ressources par des espèces semblables mais qui occupent des niches différentes ou par facilitation entre espèces ; la productivité de l'assemblage sera ainsi plus élevée que la productivité de chaque espèce seule (Loreau, 2000; Loreau et Hector, 2001). Aussi, la complémentarité entre les espèces permet une meilleure résistance des communautés contre les espèces envahissantes et facilite le rétablissement de la richesse spécifique à la suite d'un stress (Aquilino et Stachowicz, 2012; Stachowicz *et al.*, 2002). Il existe aussi l'effet d'échantillonnage (« sampling effect ») qui peut annuler l'effet de complémentarité et qui est décrit comme une sélection d'une catégorie extrême d'un trait qui mène à une dominance de la communauté et de sa productivité par une seule espèce (Loreau, 2000; Loreau et Hector, 2001). D'ailleurs, il est anticipé que les stress, qu'ils soient d'origine naturelle ou anthropique, entraineront une modification dans la structure de dominance avant d'entrainer une perte en richesse (Hillebrand *et al.*, 2008). Une modification dans la structure de dominance peut engendrer des changements dans les processus écosystémiques, la dynamique des communautés et la stabilité (Doak *et al.*, 1998; Hillebrand *et al.*, 2008).

Finalement, les effets des stress sur les populations vont varier en fonction des propriétés des espèces et donc il ne devrait pas y avoir d'effet constant et cohérent entre les différentes espèces d'une communauté (Elmqvist *et al.*, 2003; Yachi et Loreau, 1999).

0.2.2.4 Mesure de la stabilité des assemblages

L'évaluation de la stabilité d'un assemblage devrait prendre en compte la richesse et l'équitabilité (Cusson *et al.*, 2015; Hillebrand *et al.*, 2008; Hooper *et al.*, 2005), les liens trophiques (Rooney et McCann, 2012), le renouvellement d'espèce, les variabilités temporelle et spatiale, la résistance et la résilience (Donohue *et al.*, 2013; Grimm et Wissel, 1997; Pimm, 1984). Toutefois, la plupart du temps, les études se concentrent sur un seul de ces aspects qui peuvent cependant être corrélés entre eux de façon positive ou négative (Donohue *et al.*, 2013). De plus, ces relations sont appelées à être modifiées de façon imprévisible en présence de stress. Les études devraient donc évaluer davantage ces diverses mesures dans le but d'évaluer la stabilité générale des assemblages (p. ex. : Cusson *et al.*, 2015).

Une autre approche dans l'évaluation de la diversité d'un système passe par l'utilisation de traits biologiques qui peut, par exemple, être utilisée pour déterminer pourquoi certaines espèces sont présentes à certains endroits, informer sur la répartition des ressources ou encore pour déterminer comment elles participent au fonctionnement des écosystèmes. L'analyse des traits biologiques (« *Biological Trait Analysis* » ou BTA) utilise une combinaison de traits tels que les cycles biologiques, des attributs morphologiques et des caractéristiques comportementales qui sont utilisés pour relier les espèces et leurs fonctions écologiques et déterminer la niche occupée (Bremner *et al.*, 2006b). Par leur définition générale, les traits biologiques seront retrouvés chez une multitude d'espèces même si elles sont géographiquement ou taxonomiquement éloignées (Statzner *et al.*, 2001; Usseglio-Polatera *et al.*, 2000). Chaque espèce présente sera ainsi caractérisée par une multitude de traits qui sont une base commune entre les espèces. Aussi, les traits biologiques ne sont pas influencés par les variations biogéographiques à grandes échelles et devraient permettre de meilleures prédictions de changements au niveau du fonctionnement des écosystèmes (Bremner *et al.*, 2003; Wong et Dowd, 2015). Finalement, il est possible de faire des analyses de diversité

fonctionnelle en utilisant des traits biologiques ainsi que d'analyser les proportions des traits à l'intérieur d'une communauté, un peu de la même manière que la diversité en espèces serait analysée. On mesurera souvent la dispersion des traits dans l'espace pour déterminer la répartition des ressources et le rôle de la compétition dans la structure des communautés.

0.2.2.5 Résistance, résilience et rétablissement

La résistance et la résilience sont deux aspects de la stabilité qui sont reliés à l'exposition aux stress. Comme pour la stabilité ci-haut, ces aspects ont souvent eu des appellations différentes dans la littérature (voir Grimm et Wissel, 1997). Par exemple, parmi les premiers auteurs décrivant ces aspects, Holling (1973) décrit la résistance (résilience dans son vocabulaire) et la résilience (stabilité dans son vocabulaire).

Malgré une variabilité temporelle et spatiale stable, il est possible qu'une communauté ne puisse pas résister face à certains stress que ce soit dû à l'identité, à l'intensité, à la durée ou à la fréquence du stress. La résistance d'une communauté se définit comme étant la capacité d'un système à demeurer inchangé lorsqu'il fait face à un ou des stress (Grimm et Wissel, 1997). Une perte en résistance sera d'abord identifiée par une augmentation de la variabilité au sein d'une communauté (Warwick et Clarke, 1993). La disparition d'une espèce structurante (voir ci-dessous) peut par exemple diminuer la résistance des communautés et ce manque de résistance peut être amplifié par l'addition de stress (Joseph et Cusson, 2015).

Une autre composante de la stabilité est la résilience (ou rétablissement, *sensu* Ingrisch et Bahn, 2018) qui se définit comme étant le retour à un état de référence, ou état alternatif, d'un système écologique à la suite d'une perturbation temporaire (Grimm et Wissel, 1997). Selon Ingrisch et Bahn (2018), la résilience est en fait une fonction d'un

écosystème qui maintient sa biodiversité et son fonctionnement et qui est définie comme une habileté d'un système à mitiger les effets d'un stress et à le rétablir. La résilience d'un système est possible tant que les limites du domaine d'attraction de l'état de stabilité n'ont pas été dépassées (voir Holling, 1973). La résilience est un facteur important dans la conservation des assemblages pour le maintien de la biodiversité et des services rendus par les écosystèmes (Elmqvist *et al.*, 2003). Le potentiel de résilience d'un écosystème serait dépendant de la richesse régionale, de la diversité et de l'identité des espèces présentes initialement (Allison, 2004; Hillebrand *et al.*, 2008; Lotze *et al.*, 2006). Donc, l'assortiment de réponses en réaction aux changements environnementaux parmi les espèces remplissant la même fonction écosystémique est crucial à la résilience (Elmqvist *et al.*, 2003). Le rétablissement des communautés peut être influencé par l'intensité et le moment (« *timing* ») des stress, la présence d'espèces structurantes et la disponibilité des propagules (O'Leary *et al.*, 2017; Oliveira *et al.*, 2011; Oliveira *et al.*, 2014). Les études sur la résilience sont importantes dans la détermination de ce qui pourrait à la fois empêcher ou favoriser le retour à l'état de référence d'un écosystème. Étant donné la variabilité naturelle des écosystèmes, il devient nécessaire d'utiliser des références non stressées en comparaison pour bien définir l'impact des stress sur les écosystèmes (Ingrisch et Bahn, 2018; Underwood, 1989).

0.2.3 Les espèces structurantes

La composition en espèces peut avoir d'énormes impacts sur un écosystème : par exemple la présence de certaines espèces peut changer la disponibilité en ressources, créer un habitat ou encore contrôler la productivité (Chapin *et al.*, 2000; Jones *et al.*, 1994). De telles espèces sont dites structurantes ou ingénieures (sensu Jones *et al.*, 1994) et augmentent la stabilité des communautés (Bulleri *et al.*, 2012a; Maggi *et al.*, 2009). La perte d'espèces structurantes affecte négativement les communautés en causant une perte en richesse et en abondances, ainsi que par des changements dans la

structure et composition des communautés (Herkul et Kotta, 2009; Rueda *et al.*, 2009; Watt et Scrosati, 2013).

En milieu médiolittoral, les macrophytes telles que les macroalgues et les herbes marines sont souvent considérés des espèces structurantes. Aussi, des groupes fonctionnels tels que les brouteurs peuvent jouer un rôle capital (espèce clé) dans la composition en espèces et l'apparence physique d'une communauté tel que mentionné dans la section suivante (Duffy *et al.*, 2003).

0.2.3.1 Les macroalgues structurantes

Les macroalgues en milieux rocheux et les herbiers marins en milieux meubles subissent des déclins prononcés depuis une centaine d'années (Airoldi et Beck, 2007; Burkholder *et al.*, 2007; Waycott *et al.*, 2009). Les macroalgues capables de former une canopée protectrice remplissent plusieurs rôles : elles diminuent le stress dû aux variations de la température et de la dessiccation (en milieu médiolittoral), elles offrent un habitat complexe, elles jouent un rôle de pouponnière pour les poissons, elles jouent un rôle important dans la structure de diversité des communautés qu'elles abritent, et enfin, elles contrôlent la production nette de biomasse (Benedetti-Cecchi *et al.*, 2001; Bertness *et al.*, 1999; Eriksson *et al.*, 2006; Heck *et al.*, 2003; Jenkins *et al.*, 1999; Lemieux et Cusson, 2014). Les macroalgues sont d'autant plus importantes dans les milieux intertidaux situés plus haut dans l'estran à cause de l'importance qu'y jouent les facteurs physiques (Bertness *et al.*, 1999; Watt et Scrosati, 2013); par exemple, la dessiccation et les fortes températures y sont plus prononcées et les macroalgues contribuent à la conservation de l'humidité et à tamponner les extrêmes de température (Bertness *et al.*, 1999). Leur disparition peut, entre autres, augmenter le recrutement d'algues éphémères qui sont des algues moins complexes (Joseph et Cusson, 2015; Schiel et Lilley, 2007). La disparition ou des modifications dans la composition d'espèces macroalgales ont des effets négatifs directs sur les communautés :

changement en composition, réduction d'abondances et de richesse et altération de la structure (Benedetti-Cecchi *et al.*, 2001; Lemieux et Cusson, 2014; Watt et Scrosati, 2013).

0.2.3.2 Les herbiers marins

Les herbiers marins sont écologiquement importants notamment puisqu'ils offrent un habitat complexe qui peut protéger certaines espèces de la prédation (Orth *et al.*, 1984), jouer un rôle de pouponnière à poisson (Heck *et al.*, 2003) et jouer un rôle important dans la structure des communautés (Connolly, 1995; Herkul et Kotta, 2009; Reed et Hovel, 2006). Ils stabilisent les sédiments (Bostrom et Bonsdorff, 2000; Gustafsson et Bostrom, 2011) et affectent la sédimentation (Herkul et Kotta, 2009; van Katwijk *et al.*, 2010), affectent la dynamique des nutriments et du carbone, modifient les courants et les vagues, et sont d'importants producteurs primaires (Hemminga et Duarte, 2000).

Le déclin des herbiers de zostères peut être dû à plusieurs causes p. ex. : le développement côtier, l'eutrophisation, les espèces invasives, la croissance de macroalgues éphémères, et l'augmentation de la turbidité et du niveau de l'eau (Airoldi et Beck, 2007; Duarte, 2002; Orth *et al.*, 2006). Les herbiers sont particulièrement touchés par les stress reliés à la qualité de l'eau et des sédiments (Duarte, 2002). Ces stress peuvent provoquer une diminution de la densité des plants, une fragmentation ou la disparition d'un herbier, et peuvent causer des modifications au niveau de la structure et de la productivité des communautés (Connolly, 1995; Duarte, 2002; Herkul et Kotta, 2009; Reed et Hovel, 2006).

La perte et la fragmentation des habitats causent un déclin de la complexité d'habitat, une diminution de la grandeur des parcelles et une augmentation de la proportion des bordures (Fahrig, 2003) ce qui influencera la richesse spécifique et les autres

composantes de la diversité (Airoldi *et al.*, 2008; Fahrig, 2003). Typiquement, la disparition d'herbes marines, ou une diminution en densité d'herbes marines, diminuera la stabilité de la communauté, la richesse spécifique et les abondances totales, influencera la composition et la structure des communautés, et diminuera la capacité de soutien de l'habitat (Calizza *et al.*, 2017; Edgar et Robertson, 1992; Herkul et Kotta, 2009; Lundquist *et al.*, 2018; Reed et Hovel, 2006). Les effets négatifs drastiques d'une perte d'habitat pourraient cependant être observés seulement à partir d'un seuil particulier de perte en complexité (Pittman *et al.*, 2004; Reed et Hovel, 2006).

Généralement on associe la perte des herbiers comme étant négative. Toutefois, la réduction en densité d'herbes marines peut avoir l'effet inverse. En effet, une diminution de la densité peut diminuer l'auto-ombrage, ce qui augmente la surface des feuilles, la biomasse des plants, la croissance des plants et le nombre de feuilles (Rattanachot *et al.*, 2016). De tels changements sur les plants pourraient avoir un effet positif sur les communautés associées. Effectivement, l'aire de surface des feuilles semble plus importante que la densité des plants pour expliquer la biomasse de l'épifaune (Sirota et Hovel, 2006). Finalement, la disparition complète d'herbes marines peut aussi favoriser les organismes habitant les sédiments puisque les rhizomes des plants sont parfois limitants pour ces derniers (Rueda *et al.*, 2009).

Contrairement à la perte d'habitat, la fragmentation d'habitat peut avoir des effets autant positifs que négatifs sur la biodiversité (Bell *et al.*, 2001; Fahrig, 2003). Des études mesurant les effets de la fragmentation sur la faune associée rapportent des effets positifs, neutres ou négatifs sur les densités fauniques, la diversité spécifique, la diversité fonctionnelle et la composition (p. ex. Arponen et Bostrom, 2012; Healey et Hovel, 2004; Lefcheck *et al.*, 2016). De plus, les réponses semblent être dépendantes de la composition en espèces, du paysage environnant et à la qualité des habitats

adjacents (Ries *et al.*, 2004; Tanner, 2005, 2006). Un effet accompagnant la fragmentation d'habitat est l'augmentation du ratio périmètre : aire. L'effet de bordure peut affecter les herbiers marins de multiples façons; la bordure peut par exemple diminuer la richesse spécifique parce que souvent les habitats de bordure sont moins complexes (Christie *et al.*, 2009; Moore et Hovel, 2010), mais souvent, les bordures auront une plus grande richesse taxonomique et de plus grandes abondances fauniques (Bologna, 2006; Bologna et Heck, 2002; Pierri-Daunt et Tanaka, 2014; Warry *et al.*, 2009). La densité faunique, la composition en espèces, la distribution des tailles et la production secondaire peuvent être différentes à la bordure ou à l'intérieur d'un herbier (Bologna, 2006), mais le sens de la relation dépend de plusieurs processus (Bell *et al.*, 2001). Effectivement, la densité épifaunique et sa biomasse peuvent augmenter ou diminuer de la bordure jusqu'à l'intérieur (Bologna, 2006; Moore et Hovel, 2010), tandis que certains groupes peuvent ne pas être affectés du tout par l'effet de bordure (Bologna, 2006; Tanner, 2005). Enfin, l'établissement des larves est généralement plus élevé aux bordures, mais les bordures sont souvent plus hostiles à la survie de ces dernières étant donné une plus forte exposition, p. ex. vitesse du courant et resuspension des sédiments plus élevés, et une stabilité des sédiments réduite (Bostrom *et al.*, 2010).

0.2.4 Contrôles descendant et ascendant

Le contrôle descendant (« *top-down* ») de la structure des communautés se fait par les niveaux trophiques plus élevés, soit des prédateurs et des consommateurs primaires vers les producteurs primaires. Des changements au niveau des contrôles descendants peuvent être perçus comme des perturbations puisqu'ils vont venir influencer les biomasses. Les études effectuées jusqu'à maintenant suggèrent que la complexité d'habitat peut avoir un fort impact sur le contrôle *top-down* des communautés (p. ex. Hovel et Fonseca, 2005; Moore et Hovel, 2010). Aussi, les consommateurs (espèces clés) peuvent avoir un effet important sur la structure et la composition des communautés (Anderson et Underwood, 1997; Atalah et Crowe, 2010; Blake et Duffy,

2012; Navarrete, 1996). L'intensité (densité des consommateurs), la fréquence ainsi que la variabilité temporelle et spatiale de consommation peuvent être importantes au niveau de la composition des communautés et des abondances de certaines espèces (Atalah *et al.*, 2007a; Butler, 1989; Navarrete, 1996). Par exemple, une densité de prédateurs variable peut changer la composition d'une communauté d'invertébrés (Butler, 1989; Navarrete, 1996); elle peut aussi aider certains individus à trouver refuge lorsque la densité de prédateurs est faible, permettant ainsi de diversifier les tailles de proies (Butler, 1989) ou encore de devenir assez gros pour échapper à la prédation (Navarrete, 1996). Finalement, il est possible d'avoir des effets interactifs entre l'intensité et la variabilité temporelle de consommation. Par exemple, Navarrete (1996) a remarqué que la variabilité temporelle de prédation par *Nucella* sp. (fréquences faible et modérée) modulait la composition en espèces en comparaison avec un régime de prédation constant ou l'absence de prédateurs.

Les effets du broutage sur les assemblages sont particulièrement importants lors des premiers stades de la colonisation d'un milieu par les algues (Guerry, 2008; Korpinen *et al.*, 2007) et sont variables en fonction du milieu (Burkepile et Hay, 2006; Freidenburg *et al.*, 2007), du niveau des nutriments et de la saison (Lotze *et al.*, 2001). La succession des algues sur un substrat rocheux mis à nu peut être accélérée par le broutage via une consommation préférentielle de certaines espèces (facilitation par les brouteurs) (Lubchenco, 1983). Le broutage a un effet considérable sur la densité et la diversité des macroalgues (Aquilino et Stachowicz, 2012; Bertness *et al.*, 1999; Jenkins *et al.*, 1999; Korpinen *et al.*, 2007). Par exemple, la présence de brouteurs peut prévenir l'établissement d'une espèce d'algue susceptible au broutage (algues éphémères) et favoriser des espèces plus résistantes (algues pérennes) (Boaventura *et al.*, 2002; Jenkins *et al.*, 1999; Lotze *et al.*, 2000, 2001). La présence de prédateurs peut aussi influencer l'abondance et la diversité des algues via une cascade trophique en

changeant la structure de tailles des brouteurs (Eriksson *et al.*, 2009; Jochum *et al.*, 2012).

Les brouteurs peuvent également jouer un rôle crucial dans les herbiers marins notamment en contrôlant l'abondance des algues épiphytes sur les feuilles des herbes marines (Hughes *et al.*, 2004; Valentine et Duffy, 2006). La quantité d'algues épiphytes sur les feuilles des herbes marines est corrélée avec la diminution du pourcentage de PAR (rayonnement photosynthétique actif) reçu au niveau des herbes et est inversement corrélé à leur activité photosynthétique (Drake *et al.*, 2003). Ainsi, les brouteurs d'algues épiphytes contribuent au maintien des populations d'herbes marines.

Le contrôle ascendant (« *bottom-up* ») de la structure des communautés se fait par les ressources p. ex. les nutriments et la lumière (végétaux), et la nourriture (animaux). Les effets de l'enrichissement sur la diversité dépendraient du contexte; par exemple, en milieu limité par les nutriments, un enrichissement peut augmenter la diversité des macroalgues en permettant l'établissement d'espèces limitées par le taux d'azote (Bracken et Nielsen, 2004), tandis qu'un fort taux de nutriments changerait la dominance algale (p. ex. *Cystoseira mediterranea* à taux modérés vers *Ulva rigida* à taux très élevés) et diminuerait la diversité des macroalgues (Arevalo *et al.*, 2007). Les macrophytes structurants jouent un rôle protecteur en augmentant la résistance de la communauté à l'eutrophisation (Eriksson *et al.*, 2006) possiblement via une absorption des nutriments en excès. L'eutrophisation pourrait permettre le recrutement d'algues éphémères ou améliorer la qualité nutritionnelle des algues attirant ainsi plus de brouteurs (p. ex. Korpinen et Jormalainen, 2008; Kraufvelin, 2007). La recolonisation des milieux enrichis exempts d'algues peut se faire par des espèces d'algues opportunistes (Kraufvelin, 2007) et l'identité des espèces peut varier selon le niveau d'enrichissement (Korpinen *et al.*, 2007).

Dans les herbiers marins, l'enrichissement en nutriments peut augmenter la quantité d'algues épiphytes (Jaschinski et Sommer, 2008) et la quantité de macroalgues (Hauxwell *et al.*, 2003). L'enrichissement en nutriments peut augmenter la quantité d'algues épiphytes (p. ex. Sand-Jensen, 1977) ou celle des macroalgues (p. ex. Hauxwell *et al.*, 2003) et ainsi avoir des effets négatifs sur les herbiers marins en diminuant la biomasse des plants par une diminution de l'accès à la lumière (Hughes *et al.*, 2004). L'enrichissement peut aussi avoir des effets positifs p. ex. l'addition de nutriments au niveau des sédiments peut augmenter la biomasse des herbes marines lorsque les nutriments sont limités (Hughes *et al.*, 2004).

La diminution de la lumière par l'augmentation de la turbidité de l'eau, l'augmentation des apports en sédiments et de leur suspension dans l'eau ou l'augmentation des algues (phytoplancton, macrophytes et épiphytes) peut avoir des impacts négatifs sur les herbes marines notamment par une diminution de la biomasse, du taux croissance, du taux de sucres solubles dans les tissus, de la densité des plants et du taux de reproduction (p. ex. Burke *et al.*, 1996; Collier *et al.*, 2009; Gustafsson et Bostrom, 2013; Leoni *et al.*, 2008; Ralph *et al.*, 2007; Salo *et al.*, 2015; Short *et al.*, 1995; Silva *et al.*, 2013; van Lent *et al.*, 1995). Parfois, les effets peuvent entrainer la mort des plants dans le cas d'un sévère manque de lumière (Lee et Dunton, 1997; Ruiz et Romero, 2001). En revanche, la diminution de lumière peut aussi réduire la biomasse des algues épiphytes (Collier *et al.*, 2009; Ruiz et Romero, 2001) et augmenter la concentration de chlorophylle dans les herbes ainsi que leur longueur (Fokeera-Wahedally et Bhikajee, 2005).

Les contrôles « *bottom-up* » et « *top-down* » ne sont pas exclusivement indépendants; ils peuvent interagir et jouer un rôle plus ou moins important sur la diversité à différents stades d'une colonisation (Lotze *et al.*, 2000; Vaz-Pinto *et al.*, 2013) et ce rôle peut varier en fonction de la productivité (Worm *et al.*, 2002), des régions, des habitats

(Bulleri *et al.*, 2012b) et des saisons (Jaschinski et Sommer, 2008). Par exemple, la présence de brouteurs pourrait pallier jusqu'à un certain point un enrichissement en nutriments en milieu rocheux par une consommation préférentielle de certaines algues (Bulleri *et al.*, 2012b); les algues épiphytes poussant sur les herbes marines sont avantagées en situation d'enrichissement, mais leur développement est contrôlé par les brouteurs (Jaschinski et Sommer, 2008). Il est donc nécessaire d'étudier ces phénomènes conjointement (Worm *et al.*, 2002).

0.3 Importance de mon doctorat

Les effets simples des stress tels que la perte de biomasse en espèces structurantes ou l'enrichissement en nutriments ont largement été étudiés. Cependant, les stress multiples et leurs interactions à la fois sur les macrophytes et la structure des macroinvertébrés y étant associés n'ont pas encore été bien explorés, et ce particulièrement dans le milieu subarctique de l'estuaire marin du Saint-Laurent. De plus, les études portant sur la biodiversité et le fonctionnement des écosystèmes en milieu marin manquent de réalisme puisque la majorité des études sont réalisées en mésocosmes, à petite échelle et sur de courtes durées (Crowe *et al.*, 2012; Stachowicz *et al.*, 2007). Par exemple, les études réalisées en mésocosmes comportent un nombre d'espèces restreint avec des échanges à moyenne et grande échelles inexistants. Puisque les stress peuvent se produire en simultané, que leurs interactions sont souvent impossibles à prédire et que les études sur les stress multiples sont rares, il devient primordial d'effectuer des expériences factorielles *in situ* étudiant la multiplicité des stress en milieu marin. Les expériences *in situ* réalisées dans le cadre de mon doctorat étudient à la fois les macrophytes et leurs communautés associées faisant face à un, deux ou trois stress pour les deux premiers chapitres. Le troisième chapitre vérifie quant à lui si les effets structurants de la zostère marine montrent des tendances générales en

utilisant plusieurs sites distants sur trois côtes océaniques. Un diagramme conceptuel illustre comment les trois chapitres se complètent à la figure 0.2.

Étant donné que mon doctorat porte sur la multiplicité des stress en lien avec les espèces structurantes, nos résultats apporteront des informations précieuses sur les éventuels effets des changements anticipés dans la structure et dans le fonctionnement des écosystèmes littoraux. Les résultats permettront de discerner le rôle des espèces structurantes sur les différentes composantes de la biodiversité dans les habitats côtiers marins, et ce particulièrement dans les situations où les stress sont individuels et multiples. Des traitements (p. ex. : présence des producteurs primaires, brouteurs et nutriments) seront en mesure de vérifier les effets *top-down* et *bottom-up* dans ces systèmes. Aussi, nous utilisons nos résultats dans le but de montrer que les effets des stress ne sont pas toujours additifs, que des études comprenant des interactions sont nécessaires pour bien comprendre le fonctionnement des écosystèmes dans un environnement changeant, que les effets de la complexité d'habitat varient en fonction du site/région étudié et qu'il est donc probable qu'il en soit de même pour les effets des stress sur les macrophytes et leurs espèces associées. Nous souhaitons également utiliser nos résultats pour confirmer que l'utilisation seule de la richesse comme indicateur de résilience ou de dynamique face à des stresseurs multiples est insuffisante et incomplète.

Les résultats de cette thèse encourageront les décideurs à se baser soit sur des études à très grande échelle soit sur des études ciblées et reproduites localement dans la région gérée pour la préservation des ressources et des services rendus par les écosystèmes. Bien entendu, les décideurs devront aussi prendre en compte l'identité des stress pertinents au milieu géré et les effets cumulatifs de ces stress testés ensemble et non pas séparément. Finalement, en identifiant les stress ayant des effets sur les macrophytes structurants les habitats ainsi que les ressources trophiques, une meilleure

gestion des écosystèmes est assurée en prévenant des changements dans les assemblages d'invertébrés et donc dans la cascade trophique qui s'ensuivrait.

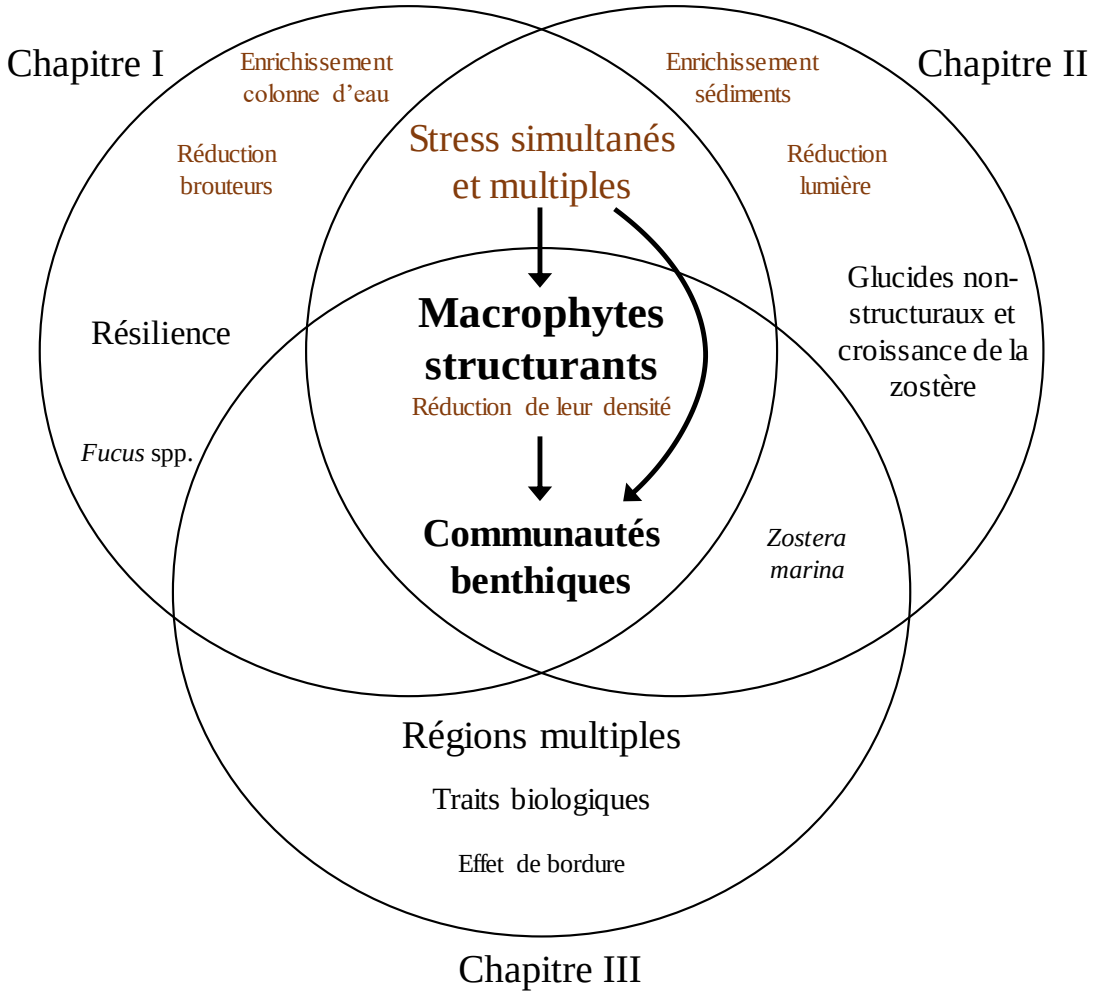

Figure 0.2. Diagramme conceptuel des trois chapitres de la thèse doctorale. L'élément central de la thèse est le rôle des macrophytes structurants (*Fucus* spp. ou *Zostera marina*) sur les différentes mesures de biodiversité relatives aux communautés benthiques des habitats côtiers marins. À cela s'ajoute les effets des stress multiples sur les macrophytes structurants et leurs communautés associées aux chapitres I et II. De plus, la résilience des communautés est évaluée au chapitre I et des mesures sur les macrophytes structurants sont ajoutées au chapitre II. Quant au chapitre III, il évalue si les effets des macrophytes structurants sur les communautés associées varient en fonction des régions en utilisant une approche par traits biologiques.

0.4 Objectifs et hypothèses

Cette thèse vise à évaluer les effets multiplicateurs des stress et leurs interactions sur les communautés dans deux habitats benthiques du littoral marin, présents dans l'estuaire maritime du Saint-Laurent. Cette thèse évalue également les généralités des effets des macrophytes structurants sur les communautés qui y sont associées. Chaque chapitre présentera soit une expérience à stress multiples et leurs effets sur les communautés, soit une expérience reproduite sur plusieurs sites en contrôlant la complexité d'habitat. Étant donné que nous sommes limités dans les manipulations réalisables *in situ*, donc enchâssés dans des échelles spatiale et temporelle réduites, les stress appliqués ne sont pas forcément toujours réalistes. Ces stress permettront tout de même une meilleure compréhension des mécanismes qui régissent la dynamique des communautés pouvant être en situation de stress. Avec les éléments mentionnés dans la section précédente, nous sommes en mesure d'émettre les hypothèses générales suivantes qui seront explorées dans chacun des chapitres de ma thèse :

1) les espèces clés (brouteurs et macrophytes) joueront un rôle important dans la structure des communautés associées et réduiront les effets de l'eutrophisation;
2) la multiplication des stress aura un plus grand impact sur les communautés que les stress uniques ou doubles; l'impact mesuré sur les communautés (ou au niveau physiologique) sera fonction du nombre de stress appliqués;
3) les macrophytes structurants joueront un rôle similaire prépondérant pour les communautés qui y sont associées.

0.4.1 Chapitre I

L'objectif principal du premier chapitre est d'évaluer la résilience des assemblages macrobenthiques intertidaux en milieu rocheux faisant face à des stress uniques ou multiples. Dans cette expérience *in situ*, nous avons manipulé les macroalgues de la

canopée (*Fucus* spp.), les consommateurs primaires (majoritairement les Gastéropodes du genre *Littorina* spp.) et les nutriments dissouts dans la colonne d'eau sur 14 mois en 2012-2013. Le retrait de la canopée macroalgale est réaliste seulement dans la mesure où elle est enlevée par un évènement ponctuel tel que le raclage par les glaces, une tempête ou encore la récolte par l'homme. Toutefois, ici les algues et les gastéropodes brouteurs sont retirés de façon chronique, donc ces stresseurs sont de type « *press* » (*sensu* Underwood, 1989). Nous avons choisi cette méthode pour cibler le rôle que les algues et les brouteurs ont sur les communautés. L'enrichissement en nutriments fait référence à l'eutrophisation anticipée dans l'estuaire du Saint-Laurent tel que mentionné plus tôt.

Les hypothèses testées étaient : 1) la présence des macroalgues de la canopée facilitera le rétablissement des communautés en situation d'eutrophisation et sera nécessaire à la résilience plus rapide et complète des communautés; 2) les divers stress influenceront les indices de diversité des algues et des invertébrés, notamment l'enlèvement de la canopée augmentera la richesse et l'abondance des algues de sous-canopée et diminuera la richesse et l'abondance des invertébrés, et la présence des brouteurs compensera les effets d'un enrichissement par consommation préférentielle des algues éphémères laissant l'espace aux fucales structurantes; 3) l'addition des stress devrait ralentir la résilience notamment au niveau de la structure des communautés.

0.4.2 Chapitre II

Le second chapitre a pour principal objectif d'évaluer le rôle de la densité des zostères (*Zostera marina* L.) en combinaison avec un changement dans les ressources sur les communautés associées et la zostère elle-même. Dans cette expérience *in situ*, nous avons manipulé la densité des plants de zostères marines, la lumière incidente et les nutriments dissouts dans les sédiments à l'été 2015. La réduction en densité et en aire de répartition de la zostère marine est une réalité mondiale des dernières décennies.

Une diminution de la densité des zostères pourra être occasionnée par des conditions non favorables telles qu'une augmentation de la turbidité de l'eau ou une augmentation des algues épiphytes. Une réduction de la luminosité peut être attendue au niveau de ces communautés par exemple par l'augmentation du niveau de la mer, des pluies diluviennes ou une gestion des eaux de rétention de barrages sur les tributaires à proximité, ou par des évènements favorisant les algues épiphytes sur les feuilles de zostères. Puisqu'un enrichissement en nutriments est anticipé au niveau de l'estuaire du Saint-Laurent, on peut en déduire qu'il s'ensuivra un enrichissement au niveau des sédiments également. Nous avons choisi d'appliquer le stress au niveau des sédiments puisque nous avons déjà effectué une expérience d'enrichissement au niveau de la colonne d'eau dans un herbier en 2011 sans voir d'effet sur les zostères, les épiphytes et les communautés épifauniques. Nous avons donc préféré une réduction temporaire de la luminosité.

Les hypothèses testées étaient : 1) la densité des herbes marines augmente l'abondance, la diversité et la richesse des assemblages d'invertébrés et modifie leur structure; 2) l'enrichissement en nutriments des sédiments et la réduction de densité (« *self shading* ») devraient augmenter le taux de croissance de l'herbe et la réduction de lumière la diminuer; il y a de fortes chances pour que la réduction de lumière ait un effet additif avec la réduction de densité ou l'enrichissement annulant ainsi les impacts sur la croissance; 3) la réduction de lumière devrait occasionner des effets physiologiques (p. ex. : diminution des réserves en sucres solubles) au niveau des zostères et diminuera la quantité d'algues épiphytes; ces changements engendrés par la diminution de lumière pourraient être atténués en présence de la diminution de densité de zostère; 4) l'addition des stress (réduction de densité de zostère de 80 %, réduction de la lumière de 70 % et enrichissement des sédiments en nutriments) devrait causer une plus grande dissimilarité dans les communautés. Nous attendons possiblement des effets non additifs et non prévisibles pour les stress triples des deux premiers chapitres.

0.4.3 Chapitre III

Le troisième chapitre a pour objectif d'évaluer le rôle de la proximité avec les bordures de l'herbier en combinaison avec une réduction de la densité de zostère marine sur les assemblages épifauniques associés et leurs traits biologiques. Une expérience manipulant la distance avec la bordure et la densité de zostères sur les communautés associées a été réalisée à l'été 2015 dans cinq herbiers de zostères variés issus de régions différentes et ayant un groupe d'espèces différentes (Californie, France, Mexique, Québec, Virginie). Nous avons privilégié l'analyse des résultats avec une approche par trait biologiques pour tenter de mieux généraliser et expliquer les effets de bordure et de complexité étant donné que nos sites avaient très peu d'espèces en commun. Cette expérience s'est déroulée dans le cadre d'une collaboration internationale avec le regroupement ZEN (*Zostera Experimental Network*).

Les hypothèses testées étaient : 1) la proximité avec la bordure de l'herbier et la densité des zostères sont importantes pour la structure des assemblages d'invertébrés ainsi que leurs traits biologiques. C'est-à-dire que nous nous attendons à ce que la structure des assemblages soit différente entre l'intérieur et la bordure des herbiers, et entre les parcelles à densités ambiantes et réduites. Nous pensons aussi que la richesse et la diversité seront plus faibles à la bordure ainsi que dans les parcelles réduites en densité; 2) une densité minimale de zostère est nécessaire à la stabilité des assemblages (p. ex. 50 % *versus* 80 % de réduction); 3) l'accumulation de ces stress montrera des effets non additifs sur les indices de diversité et devrait causer une plus grande dissimilarité dans les communautés.

0.5 Structure de la thèse

Cette thèse est basée sur trois articles de recherche originaux qui sont appelés chapitres I à III. Le chapitre I est publié dans la revue Ecosphere ; le chapitre II en révision dans *Marine Ecology Progress Series* ; le chapitre III est un manuscrit en préparation pour lequel nous n'avons pas encore ciblé la revue et qui sera envoyé à nos coauteurs après le dépôt initial de cette thèse. Toutes les références de l'introduction à la conclusion, en passant par les chapitres et les annexes, se trouvent combinées à la fin de la présente thèse et sont basées sur un style francophone.

0.5.1 Chapitre I : Impact of multiple disturbances and stress on the temporal trajectories and resilience of benthic intertidal communities.

Dans ce chapitre, nous avons mesuré l'effet de stress seuls et cumulés sur des communautés macrobenthiques et leur résilience en milieu rocheux sur un seul site. Dans le but de mesurer la résilience des communautés, une mise à nue accompagnée d'un brûlage de la roche a d'abord été fait avant d'induire les stress qui ont été maintenus sur 14 mois. Les stress incluaient un enlèvement de la canopée macroalgale, un enlèvement des brouteurs rampants et un enrichissement en nutriments. Le plus gros effet observé venait de l'enlèvement de la canopée et cela traduit son importance d'espèce structurante. Nous avons observé quelques effets non additifs et que la résilience était moins rapide en présence des trois stresseurs.

0.5.2 Chapitre II : Multiple stressors and disturbance effects on eelgrass and epifaunal macroinvertebrate assemblage structure.

Comme dans le premier chapitre, nous avons mesuré l'effet des stress seuls et cumulés sur des assemblages macrobenthiques sur un seul site, mais cette fois, dans un herbier de zostères marines sur une période de 10 semaines. Nous avons également mesuré

quelques paramètres autres que les assemblages dans le but de mesurer des effets sur l'habitat. Effectivement, nous avons regardé l'élongation, la densité et la concentration en glucides non structuraux des zostères, ainsi qu'évalué la quantité d'algues à la surface des feuilles de zostères. Les stress incluaient une réduction de la densité des herbes marines, une réduction d'accès à la lumière et un enrichissement en nutriments au niveau des sédiments. Nous avons observé que l'accès à la lumière était le plus influant sur les aspects reliés à la zostère marine. Nous avons aussi observé quelques effets non-additifs ainsi qu'un effet additif. Nous suggérons qu'une grande partie des effets observés sur nos assemblages d'invertébrés sont reliés à la disponibilité de l'habitat et aux ressources trophiques disponibles.

0.5.3 Chapitre III : Site dependent effects of proximity to patch edge and eelgrass complexity on epifaunal communities within Zostera marina L. meadows

Le dernier chapitre évalue la généralité des effets de l'habitat sur les assemblages d'invertébrés en répétant la même expérience sur plusieurs sites plutôt que les effets cumulatifs des stress sur un seul site. Effectivement, nous avons mesuré les effets de la complexité d'habitat et de la bordure d'habitat sur des assemblages macrobenthiques sur 5 sites ayant des environnements très différents en combinant une approche par espèce et une approche par trait biologique (taille, habitudes de vie et de déplacements, habitudes alimentaires, mode de dispersion de la reproduction, mode de nutrition des larves). Dans ce chapitre, nous voulions vérifier si la structure de l'habitat influence l'épifaune de la même manière partout. Nous avons observé quelques points communs, mais surtout des effets dépendants des sites étudiés. Cette expérience met en évidence qu'en utilisant la même méthode sur différents sites, il est possible d'obtenir des résultats tout à fait différents, voire des effets opposés. Par exemple, la plupart des sites étudiés avaient une plus grande richesse spécifique à la bordure de l'herbier, tandis qu'un site n'a pas montré de différence entre la position dans l'herbier et un autre site avait plutôt une plus grande richesse à l'intérieur de l'herbier.

CHAPITRE I
IMPACT OF MULTIPLE DISTURBANCES AND STRESS ON THE TEMPORAL TRAJECTORIES AND RESILIENCE OF BENTHIC INTERTIDAL COMMUNITIES

PUBLISHED ARTICLE

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Keywords: assemblage structure; cumulative impact; epifauna; field experimentation; foundation species; grazers, macroalgae; manipulative study; non-additive interaction; nutrient addition; recovery; rocky shores.

Supplementary material
Supplements link to main article: ecs22467-sup-0001-AppendixS1.pdf
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1.1 Abstract

Coastal ecosystems face severe environmental change and anthropogenic pressures that affect both the structure and functioning of communities. Understanding the response and resilience of communities that face multiple simultaneous disturbances and stresses becomes essential. We observed the recovery of a rocky intertidal subarctic macrobenthic community dominated by a macroalgal canopy (*Fucus* spp.), a habitat-forming species, over a period of 14 months. Using 0.25 m^2 plots, we ran an in-situ one-pulse experiment (removal of all material to bare rock and then burning of the surface) followed by a full orthogonal factorial design of three press-type disturbances or stresses: grazer reduction, canopy removal, and nutrient enrichment. We evaluated the single and interactive effects of the three disturbances and stresses on species diversity and abundance structure. Of all the main effects, canopy removal has the most severe impact, resulting in decreased biomass, richness, and diversity, as well as an altered community structure. Canopy-removed plots had fewer invertebrates and more ephemeral algae; beyond this, however, there was minimal effect from grazer reduction and nutrient enrichment acting individually. We categorized the interaction types of all significant interaction effects: canopy removal had a dominant effect over grazer reduction on richness, and it also dominated over nutrient enrichment on diversity and evenness. Nutrient enrichment and canopy removal had a negative synergistic interaction effect on richness at the end of the experiment. Without stressors, 11 months were required to achieve full recovery. The three stressors affected recovery time differently, depending on the identity and the number of stressors. Three stressors generally increased the time of recovery or even prevented recovery from being fully attained. Moreover, community structure and composition of plots subjected to the triple-stressor treatment had not fully recovered by the end of the study. Our results suggest that multiple stressors may interact on community indices and structure and that their interaction cannot be predicted from the outcome of single stressor studies.

The inclusion of multiple disturbances and stresses in field experiments provides a better understanding of the mechanisms that shape community structure and their functioning following various forms of disturbance.

1.2 Introduction

Coastal ecosystems are subjected to both natural and anthropogenic disturbances and stresses, e.g., eutrophication, sedimentation, and habitat loss (Airoldi et Beck, 2007; Halpern *et al.*, 2007). These various changes can have drastic negative effects on ecosystems, such as biodiversity loss, that impact community functioning and stability (Hooper *et al.*, 2012; Lotze *et al.*, 2006; Stachowicz *et al.*, 2002). Climate change and biodiversity loss are driving ecologists to study the relationship between biodiversity and ecosystem functioning (Gamfeldt *et al.*, 2015; Worm *et al.*, 2006).

Biodiversity plays an important role in ecosystem stability (Hillebrand *et al.*, 2008; Loreau *et al.*, 2001), ecosystem functioning (Hooper *et al.*, 2005; Yachi et Loreau, 1999), as well as offering resistance and resilience to disturbance and stress (Allison, 2004; Aquilino et Stachowicz, 2012). Resilience (or engineering resilience) is an essential ecosystem function that helps maintain biodiversity and functioning. It is defined as the ability of a system to mitigate an impact and recover following a disturbance. Recovery is the ability of a system to return to a reference state following a disturbance (Ingrisch et Bahn, 2018). Recovery can be measured in various ways. This includes temporal trajectories of different community characteristics, such as its abundance structure and recovery rate (Duarte *et al.*, 2015; Lotze *et al.*, 2001). All measured variables should be compared to an undisturbed reference (Ingrisch et Bahn, 2018; Underwood, 1989) to account for spatial and temporal variation. Recovery can be influenced by the intensity and timing of a disturbance, the presence of intact stands

of habitat-forming species, and the availability of propagules (O'Leary *et al.*, 2017; Oliveira *et al.*, 2011; Oliveira *et al.*, 2014). On rocky shores, the rapid recovery of communities (within 1 to 5 years) following a disturbance may be due to the open nature of this system that provides high numbers of propagules and larvae from unaffected shores (Crowe *et al.*, 2000; Hawkins *et al.*, 1999).

The presence of habitat-forming species can increase community stability (Bulleri *et al.*, 2012a; Maggi *et al.*, 2009). Habitat-forming species (or foundation species; ecosystem engineers sensu Jones *et al.*, 1994) play an essential role in ecosystem functioning by sheltering and protecting numerous organisms (Bertness *et al.*, 1999). The loss of habitat-forming species negatively affects the surrounding community by reducing species richness and abundance as well as through changes in community structure and composition (Herkul et Kotta, 2009; Rueda *et al.*, 2009; Watt et Scrosati, 2013).

Intertidal zones of rocky shore habitats are often dominated by habitat-forming macroalgae that are considered as key species in these systems (Hawkins et Hartnoll, 1983). These macroalgae provide complex habitats, dampen stresses—such as desiccation and extreme temperatures—limit water movement, provide shelter, and control biomass production and species diversity (Benedetti-Cecchi *et al.*, 2001; Bertness *et al.*, 1999; Eriksson *et al.*, 2006; Heck *et al.*, 2003; Jenkins *et al.*, 1999). Presently, habitat-forming macroalgae are declining worldwide as a consequence of climate change and more regional and local-scale human impacts (Airoldi et Beck, 2007; Hawkins *et al.*, 2009). Their loss can increase the recruitment of ephemeral algae (Schiel et Lilley, 2007). Consequently, the disappearance of habitat-forming macroalgae has a deleterious impact on the associated assemblages through a reduction in community richness and abundance (Watt et Scrosati, 2013) and an altering of composition structures (Lemieux et Cusson, 2014).

Similarly, grazers play an important role in structuring communities within rocky intertidal shore habitats (Anderson et Underwood, 1997; Atalah et Crowe, 2010). The influence of grazers is particularly important during the first stages of algal colonization (Guerry, 2008; Korpinen *et al.*, 2007), and this influence varies depending on the environment, nutrient levels, and season (Freidenburg *et al.*, 2007; Lotze *et al.*, 2001). Grazer presence may accelerate the succession of macroalgae through the preferential consumption of ephemeral algae, and thus affect algal density and diversity (Alestra et Schiel, 2014; Aquilino et Stachowicz, 2012; Lubchenco, 1983).

Coastal ecosystems experience constant stress due to human impacts (Cloern *et al.*, 2016; Halpern *et al.*, 2015). Among the many forms of stress, eutrophication exerts a marked pressure on coastal communities. Nitrogen fixation by humans has increased the usable forms of nitrogen for organisms by almost two-fold over the last century (Fowler *et al.*, 2013; Vitousek *et al.*, 1997a). Eutrophication caused by an excess of nitrogen impacts the benthic community structure by changing species composition and reducing macroalgal diversity (Arevalo *et al.*, 2007; Worm et Lotze, 2006). Depending on the nutrient limitations at a site, higher nutrient loading may promote ephemeral algae settlement and growth (Bertocci *et al.*, 2017; Bracken et Nielsen, 2004; Kraufvelin, 2007). Community resistance to eutrophication may be enhanced by habitat-forming macroalgae (Eriksson *et al.*, 2006). Grazers may reduce the effects of nutrient enrichment by preferential consumption of ephemeral algae (Atalah et Crowe, 2010).

Multiple interacting anthropogenic and natural disturbances and stresses often co-occur in ecological communities. Their cumulative effects are often considered as being additive, although they may accumulate in a multiplicative manner, or they may not even accumulate, or they may show dominance from one stressor (Côté *et al.*, 2016; Halpern *et al.*, 2007). Interactions may be synergistic or antagonistic, and they are

unpredictable (Côté *et al.*, 2016; Darling et Côté, 2008; Lyons *et al.*, 2015). Moreover, the frequency of synergistic interactions in the marine environment may be higher when communities are exposed to three stressors instead of two (Crain *et al.*, 2008). However, the mention of synergistic interactions in the literature is growing much faster than mention of antagonistic or additive effects, and these claims are often being made without proper testing (Côté *et al.*, 2016). It is rare to find studies that include three or more disturbances or stresses in intertidal rocky habitats dominated by macroalgae (Strain *et al.*, 2014); therefore, more of such studies are necessary. Single effects of canopy or grazer removal and enrichment are well known, yet few studies have looked at the interaction of biodiversity loss and stressors. Multiple interactive effects on both macroalgal and macroinvertebrate assemblage structures remain poorly studied, especially when following a major destructive event.

Here, based on measurements of diversity, structure, and resilience, we evaluate the response of subarctic rocky intertidal benthic communities subjected to single and interactive effects of canopy removal, grazer reduction, and nutrient enrichment. This study will improve our understanding of the role of top-down controls, habitat-forming species, and bottom-up forcing in the shaping of community structure. These roles and their interactions are not yet understood for the subarctic ecosystem of the St. Lawrence Estuary. This area was selected as it is exposed to both natural and anthropogenic stressors, including ice-scouring (Archambault et Bourget, 1983; Bergeron et Bourget, 1984), expected increases in water movement (Savard *et al.*, 2008), and eutrophication (Gilbert *et al.*, 2007; Thibodeau *et al.*, 2006). These stressors may affect the abundance and make-up of macroalgae and grazers in benthic intertidal communities. We hypothesize that in addition to a significant individual impact from canopy removal and grazer reduction, univariate and multivariate community characteristics and resilience will be even more affected by synergistic effects when coupled with the stress of nutrient enrichment. Although canopy removal and grazer reduction

treatments are disturbances (see Grime (1977) and Sousa (1984) where disturbance is related to biomass removal), only the terms stress and stressors will be used hereafter to simplify the reading.

1.3 Methods

1.3.1 Study site

We conducted the experiment from June 2012 to August 2013 on the south shore of the St. Lawrence Estuary near the municipality of Sainte-Flavie, Quebec, Canada (48°37′42.5″ N, 68°11′55.7″ W). The site is a flat, mid-intertidal rocky shore having a flora and fauna characteristic of a moderately wave-disturbed environment (Archambault et Bourget, 1983; Bergeron et Bourget, 1984). This subarctic location has a temperature and salinity range from 4–16 °C and 24–29 PSU, respectively (Archambault et Bourget, 1983; Fradette et Bourget, 1980). The tidal regime is mixed, dominated by semi-diurnal tides having a 3.5-m tidal range on average (see www.tides.gc.ca). *Fucus* spp. (*F. distichus edentatus* and *F. vesiculosus*) structures the natural communities of this mid-intertidal zone, and gastropod grazers (*Littorina obtusata* and *L. saxatilis*) and filter feeders (composed of *Mytilus edulis*, *M. trossolus* and hybrids, hereafter referred to as *Mytilus* spp., see Moreau *et al.* (2005)) are the dominant invertebrates. Ice often covers the shores of the estuary during winter (from mid-December until the end of March); this ice cover provides protection for the underlying biological assemblages against strong variations in water levels, storm waves, and extreme temperatures. However, the ice may also act as an indiscriminate disturbance factor on the flat rock surfaces and exposed crevices through heavy ice-scouring (Bergeron et Bourget, 1984; McKindsey et Bourget, 2001).

1.3.2 Experimental design

We used an orthogonal factorial experimental design to evaluate the loss of key species (macroalgal canopy [Ca], 2 levels; grazer [Gr], 2 levels; press-type disturbances) and nutrient enrichment ([Nu], 2 levels; press-type stressor) on the resilience of intertidal benthic communities in terms of their diversity and structure following a complete biomass removal (pulse disturbance) as a pretreatment: in June 2012, all organisms, algae and sediments were scraped off the plots, and the remaining rock was burned once with a bitumen torch (Figure 1.1). We added natural reference plots having no pretreatment to our design as a ninth treatment to evaluate community resilience (Fig. 1.1). All treatments were replicated four times ($n = 4$) and assigned randomly to 36 experimental plots (50 × 50 cm) on emergent rocky substrates. We positioned these plots within mature macroalgal bed zones respecting the following criteria: minimum of 80% cover of *Fucus* spp., homogeneous flat substrate, lack of pools or crevices, similar mid-intertidal height (1.33 ± 0.21 m; no differences of height among treatments, $F_{8,35} = 0.4878$, $p = 0.8540$), and a minimum of 3 m between plots. We applied the treatments within 50 × 50 cm plots and only sampled the center, a 30 × 30 cm area, so as to avoid edge effects.

The canopy factor had two levels: natural recruits of fucoids were either left intact (canopy untouched, C+) or completely handpicked (canopy removed, C-). We applied such maintenance twice a month from June to early September 2012, once in October 2012, and twice a month from May to the end of August 2013.

The grazer reduction factor had two levels: natural density (G+) or reduced density (G-). In the latter, we manually removed invertebrate grazers (periwinkles: *Littorina obtusata*, *L. saxatilis*, *L. littorea*, *Margarites* sp., *Lacuna vincta*; limpets: *Testudinalia testudinalis*, and isopods: *Jaera albifrons*) every 9–11 days in 2012 and every 4–8 days in 2013 (the reasons for this change in frequency are presented below). We maintained

a reduced abundance of grazers with two physical barriers: a small twisted wire brush (2-cm diameter) screwed on the rock along the plot contour and a thin layer of a natural sticky barrier (5-cm-wide; Tree Tanglefoot Insect Barrier, The Tanglefoot Company, Grand Rapids, USA) that was renewed twice a month at the outer limit of the brush. Before installing the barriers, we cleared the surfaces, added a small quantity of concrete (when required) on rough surfaces (Poly-Plug Bomix, Daubois Inc., Saint-Leonard, Canada), and covered the bare rock or the concrete with epoxy (West Systems Inc, Bay City, USA) to ensure the adhesion of the Tree Tanglefoot. We preferred this cageless system to avoid any cage effects on the community, especially as the mesh size would be small (1–2 mm). We tested the method in 2012 with incomplete exclusion procedural controls (n = 4), and we observed no difference with the reference plots for all response variables, with the sole exception in September 2012 for richness, obtained by destructive sampling (cf. Joseph et Cusson, 2015). We reduced *Littorina* spp. abundance in the G- treatment for up to four consecutive days using this method; we therefore maintained the plots more frequently in 2013 (i.e., about 40% of the time in 2012 and 66% of the time in 2013 with significantly less individuals in G- than in G+) (Cimon, Joseph, and Cusson, unpublished data). Moreover, the G- treatment significantly reduced the abundance of *Testudinalia testudinalis* and small individuals of *Littorina* sp. throughout the entire experiment (RM ANOVA with the same design as below (see Table 1 for example) with abundance transformed by square root, between subjects (all periods pooled together) and Gr contrast, respectively $F_{1,27}$ = 33.37, p = 0.0001 and $F_{1,27}$ = 122.58, p = 0.0001).

Two levels of enrichment were used: ambient (N-) and enriched (N+) conditions. Plots were enriched with 200 g of slow-release fertilizer pellets (N-P-K = 14-14-14, Smartcote® Plant Prod, Canada) split equally into two screen-mesh bags installed in opposite corners inside the plots but outside the sampling area. Enrichment using slow-release fertilizer pellets has been used in many habitats (e.g., Worm *et al.*, 2000). We

replaced fertilizer pellets with washed pebbles in ambient nutrient treatments to consider any effects from the bags (i.e., additional substrate). We changed all bags each month during the sampling periods; we washed the pebbles and replaced the pellets with new ones. We collected, dried, and weighed the pellets at each replacement to estimate the amount of nutrient diffused. We observed an average of 32.5 ± 0.4% weight loss, with a total estimated diffusion of 8.66 ± 0.13 g of total nitrogen per month into each plot. This level of enrichment is similar to a moderate eutrophication in the St. Lawrence Estuary (Gilbert *et al.*, 2007). Pilot tests in the field showed a 3- to 6-fold increase in total nitrogen concentrations in water samples from an enriched quadrat compared to the natural concentration of the St. Lawrence Estuary. The tissues of *F. distichus edentatus* were analyzed for total nitrogen in a concomitant study, and they confirmed that the additional nutrients were assimilated by the algae (see Joseph et Cusson, 2015).

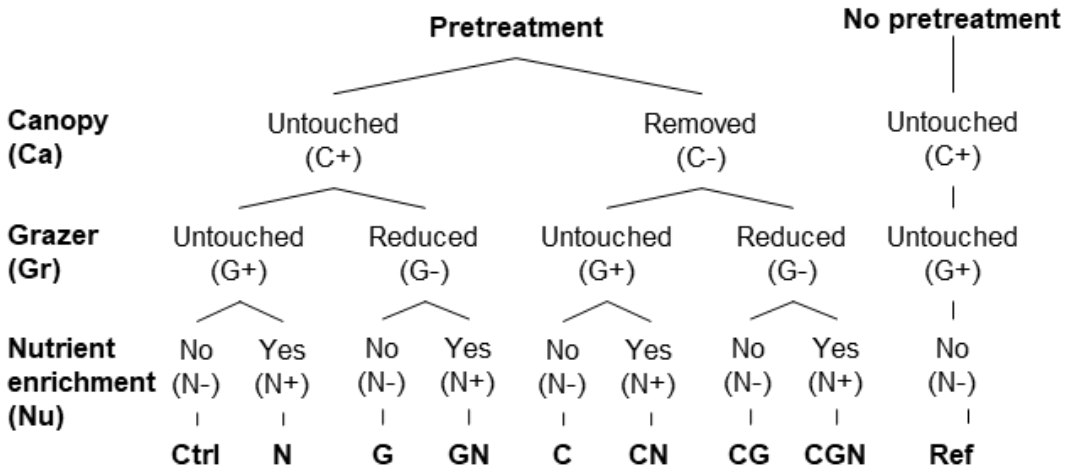

Figure 1.1. Schematic of the experimental design showing the three stress treatments (canopy, grazer, nutrient enrichment; two levels each) following pretreatment (plots scraped to bare rock and then burned), and reference plots left untouched (see the Methods section for details). Bottom row shows letter codes for treatments with one, two, or three letters representing the quantity of stress applied. Ctrl and Ref represent Control and Reference, respectively.

We took out the brushes and bags on October 20, 2012, and we reinstalled them between May 8 and 11, 2013 (a 29-week gap), to prevent the potential loss of material during winter due to ice-scour. There was at least one ice-scouring event during that winter. Reference plots were not the same in 2013 as those in 2012, as the latter were collected in September 2012 and were used as controls in another study (cf. Joseph et Cusson, 2015). We selected new reference plots (n = 4) that encompassed our abovementioned criteria, except for canopy percent cover that averaged lower (72%) than our criteria of 80%. In addition, the references did not show any significant differences in community abundance structure between corresponding months from the two growing seasons.

1.3.3 Sampling

We sampled the plots using non-destructive techniques by visually estimating the percentage cover for algae and mussels and by counts for other invertebrates within a 30 × 30 cm quadrat separated into 25 units each representing 4%of the surface area. Each individual (having a size >1 mm) was identified to the lowest taxonomic level possible, usually species, using local guides and taxonomic keys. These monthly inventories took place from June to October 2012, and from May to August 2013: Period 1 (June 2–9; pretreatment), Period 2 (July 1–8), Period 3 (July 31–August 6), Period 4 (August 28–September 4), Period 5 (October 17–20), Period 6 (May 23–24), Period 7 (June 21–23), Period 8 (July 20–23), and Period 9 (August 18–21). We counted invertebrates, other than *Mytilus* spp., then transformed the counts into percentage cover (e.g., regression to convert density into % cover with $n = 129$, $R^2 = 0.66$ for *Littorina saxatilis* and *L. obtusata*; arbitrary value of 0.25% for each individual of *L. littorea*, *T. testudinalis*, and *Nereis* sp.; 0.1% for each individual of *Lacuna vincta* and *Margarites* sp.; 0.01% for each *J. albifrons*) to have the same abundance unit for all taxa and permit the calculation of diversity estimates. Total percentage cover can exceed 100% as we estimated the cover by taxa. We maintained

(e.g., *Fucus* spp. removal and grazer reduction) the plots after performing the inventories. After the last sampling date (Period 9) and after the usual inventories, we destructively collected all biomass (except crustose species) within the 30 × 30 cm plot. In the laboratory, we filtered the samples through a 1-mm sieve, then counted and weighed all remaining organisms by taxon to the nearest 0.01 g (0.00001 g for tiny organisms). Biomass was converted into energy (kJ) by applying conversion factors from Brey *et al.* (2010).

1.3.4 Data analysis

We performed all analyses on non-manipulated associated species (unless mentioned), i.e., we excluded *Fucus* spp. and removed grazers, such as *Littorina* spp., prior to any analyses (see the list above and *Annexe A*: *Tableau 5.1* for further details). We excluded Period 1 from the analyses as it was the application of the pretreatment (June 2012).

To test for simple or interactive effects of the treatments on total abundance (N), species richness (S), Simpson's index of diversity ($1\text{-}\lambda$) and Pielou's evenness (J'), we used mixed models of repeated measures analysis of variance (RM ANOVA) with one fixed factor (Treatment; nine levels including the reference treatment) and eight repetitions over time (Period, fixed) using the identity of the plots as a random factor. To test our three factors of interest (Ca, Gr, Nu; two levels each), we ran orthogonal contrasts (a total of seven contrasts). If the main factor 'Treatment' or 'Period' was significant, we ran Tukey's HSD test to assess the differences between treatment levels or periods. Where the factor 'Period' had a significant interaction with a contrast of interest (e.g., Period × Ca × Nu), we used comparisons of means (*t*-test, one test for each period) to determine at which period the difference occurred, and we then ran multiple comparisons of means (*t*-test, only required for interactions, e.g., Ca × Nu) with Bonferroni sequential corrections on the contrast for that specific period. We performed a 1-way ANOVA with the same design (Treatment and seven contrasts) for

total biomass, as this variable was only available for the last period. We also used the same RM ANOVA as above to assess recovery time in terms of *N*, *S*, 1-λ, and *J'*, and we used comparisons of means (*t*-test) for each treatment *versus* references (eight contrasts, e.g., CG vs. Ref) at each period. We considered that each treatment was recovered for a given variable when no significant difference between that treatment and reference plots was observed until the end of the experiment. We then compared the recovery time of each treatment to the controls to assess if stressors had any impact on recovery time. Finally, we evaluated the resilience time at our site by comparing controls to references, using all species present, by applying the same method as above (RM ANOVA; with Treatment having only two levels). Normality and homogeneity assumptions were checked by graphical examination of the residuals (Montgomery, 2012; Quinn et Keough, 2002); only total abundance in percentage cover was transformed by square root prior to analyses. We characterized the interaction type of each significant double or triple interaction effect as either antagonistic, synergistic, additive, or dominant (sensu Côté *et al.*, 2016) using a calculated 95% confidence limit of the expected additive effect (Darling et Côté, 2008).

To examine the effects on community structure (for both % cover and biomass, based on Bray–Curtis similarities), we used repeated measures of permutational multivariate analysis of variance (RM PERMANOVA; Anderson *et al.*, 2008) run with 9999 permutations based on the same design as described above (Treatment + seven contrasts, eight repetitions over time). We tested the dispersion of data around a centroid using PERMDISP for each stress at each period. We evaluated recovery as presented above (1-way PERMANOVA; Treatment; eight contrasts of interest). For the latter, only 35 permutations per contrast were possible; as such, we used a Monte-Carlo procedure to obtain *p* values. Abundance data as percent cover and biomass were pretreated using dispersion weighting by Treatment × Period (Treatment only for biomass) (Clarke *et al.*, 2006) and transformed by square root according to shade plot

method (Clarke *et al.*, 2013), while data were transformed into presence-absence for the effects on compositional community structure. Dummy variables were used to deal with small species numbers (zero-adjusted Bray–Curtis; value of 0.1 for % cover and 0.02 for biomass) (Clarke *et al.*, 2014). We visualized the effects of the treatments using non-metric multidimensional scaling (nMDS) ordinations. We evaluated the contribution of each taxon to the observed similarities/dissimilarities between treatments using a similarity percentage analysis (SIMPER).

At the end of the experiment, we characterized the stress level among treatments using combined *k*-dominance curves of species biomass and % cover data (abundance/biomass comparison or ABC curves). Stable (i.e., undisturbed) communities are usually dominated by the biomass of a few individuals (*K*-selected), while disturbed communities are dominated by many small individuals (*r*-selected, opportunistic) (Warwick, 1986). We used the W statistic, which is a summary statistic of ABC curves ranging from -1 to +1, where +1 represents undisturbed communities, and -1 represents disturbed ones (Clarke, 1990). To test the effect on W values, we performed a 1-way ANOVA with the fixed factor 'Treatment' and our contrasts of interest.

Univariate analyses were run using SAS university edition v3.5 (PROC MIXED), while multivariate analyses and ordinations were run using PRIMER+PERMANOVA v.7 (Anderson *et al.*, 2008; Clarke et Gorley, 2015). We used a significance level of $\alpha = 0.05$ for all statistical analyses. We applied no corrections to *p* values to our planned contrasts.

1.4 Results

We identified a total of 39 different taxa (see the list in *Annexe A*: *Tableau 5.1*) for all inventories with averages (± SE) of 6.8 ± 0.2 species in 2012 and 8.6 ± 0.2 species in 2013 within the 30 × 30 cm plots. We observed 14 algal taxa, the most abundant being *Fucus distichus edentatus*, *Stragularia clavata*, and *Porphyra* sp., along with 25 invertebrate taxa with the grazers *Littorina saxatilis*, *L. obtusata*, *Testudinalia testudinalis*, and the filter feeder *Mytilus* spp. being the most common. For both % cover and biomass data, invertebrates were generally more abundant when the macroalgal canopy was untouched, and ephemeral algae were more abundant when the canopy was removed.

1.4.1 Effects of single and multiple stresses

Abundance and diversity indices. — Our experimental treatments (canopy removal, grazer reduction, and nutrient enrichment) affected the associated community (i.e., non-manipulated species only) abundance and diversity profile, and some of their effects varied in time. As expected, abundance in % cover, species richness, and Simpson's diversity values were all higher at the end of the experiment (e.g., from periods 2 to 9 with respective averages of 7 ± 3 to 25 ± 3 in % cover, from 1.4 ± 0.2 to 3.4 ± 0.2 in richness, and from 0.14 ± 0.04 to 0.38 ± 0.03 for Simpson's diversity). We observed the highest values of richness (3.6 ± 0.3) and diversity (0.5 ± 0.03) in periods 8 and 6, respectively. Evenness values, on the contrary, remained rather stable with a maximum and only significant difference between periods 3 and 6 (respectively 0.48 ± 0.09 and 0.70 ± 0.04; $F_{1, 148} = 9.54$, $p = 0.0024$).

Canopy removal affected abundance in % cover differently over time (see Period × Ca, in Table 1.1a); its effect was only significant in Period 8 with % cover values of the

associated community more than doubled in the canopy-removed plots (C-, Fig. 1.2a). Canopy removal enhanced species richness values (all periods pooled together; 3.1 ± 0.2 compared to 2.4 ± 0.1 when the canopy was untouched; Table 1.1b). However, the effect of the interaction between canopy removal and grazer reduction varied over time (see Period × Ca × Gr; Table 1.1b). In Period 8, richness values were higher in the canopy-removed and grazer-reduced plots (C- G-) than with all other combinations of these two stressors, while grazer-reduced plots (C+ G-) were lower than with all other combinations of these two stressors (Fig. 1.2b). The resulting interaction (C- G-) is a dominance-type interaction as the effect of canopy removal overshadows the effect of grazer reduction (Fig. 1.2b). Canopy removal significantly increased diversity values (all periods pooled together; Simpson diversity: 0.38 ± 0.02 compared to 0.29 ± 0.02 when the canopy was untouched; Table 1.1c). The interaction effect between canopy removal and nutrient enrichment varied over time (see Period × Ca × Nu; Table 1.1c). In Period 5, diversity values were lower in the presence of both the canopy and nutrient enrichment treatments (C+ N+) than with all other combinations of these two stressors (see Fig. 1.2c). This result may be due to a significant low evenness observed at the same period in the same plots (cf. Fig. 1.2c,d). As with grazer reduction, canopy removal dominates the effect of nutrient enrichment for the cumulative impact (C- N+) for both diversity and evenness.

At the end of the study (Period 9), we observed different effects when using biomass data compared to percent cover. Canopy removal reduced biomass (Table 1.2a; Fig. 1.2e), but it did not affect the abundance in % cover in this final period. Furthermore, treatment, canopy removal (Ca), and the triple interaction (Ca × Gr × Nu) all affected richness; a pattern that we did not observe when using % cover data. The addition of cryptic taxa—mainly amphipods due to sampling methods—can partly explain these differences (see *Annexe A: Table 5.1* for further details). Canopy removal reduced the total biomass of associated taxa by more than 50% (Table 1.2a; Fig. 1.2e). Richness

values were affected by the triple interaction (Ca × Gr × Nu in Table 1.2b) showing a negative synergism interaction type as we measured lower values in canopy-removed nutrient-enriched (CN) plots than in single treatments of enrichment (N) or grazer reduction (G) (Fig. 1.2f). Canopy removal reduced diversity (Table 1.2c; Fig 1.2g) and induced lower W statistic values (Fig. 1.2h; $F_{1, 27} = 4.94$, $p = 0.0349$).

1.4.1.1 Community structure

Canopy removal significantly affected the associated community structure (Table 1.3a), beginning at Period 5 (about 135 days; see *Annexe A: Table 5.2*) with differences remaining significant (or close to with a $p = 0.052$ at Period 6) until the end of the experiment (see *Annexe A*: *Table 5.2*, Fig. 1.3a showing the canopy effect over time and Fig. 1.3b showing Period 9). Differences were mainly due to more ephemeral algae (e.g., *Stragularia clavata* and *Petalonia fascia*) as well as fewer filter feeders (*Mytilus* spp.) and carnivorous anthozoans (*Aulactinia stella*) in the C- treatment. Grazer reduction or nutrient enrichment did not affect the associated community abundance structure. Canopy removal significantly increased the dispersion of the associated community structure in both periods 6 and 7 (see *Annexe A: Table 5.3*) where average distance among plots was higher in canopy-removed plots (distance from the centroid for canopy-untouched and canopy-removed plots, respectively: Period 6: 31 ± 3 and 43 ± 3; Period 7: 32 ± 3 and 44 ± 2). Grazer reduction significantly increased the dispersion of the associated community structure in Period 8 (see *Annexe A*: *Table 5.3*; Fig. 1.3c). We observed the highest abundance and richness of ephemeral algae in Period 8. Canopy removal significantly affected the associated community in biomass structure and increased dispersion among plots (Table 1.2e and see *Annexe A: Tableau 5.3*; Fig. 1.3d). We did not observe any significant effect of grazer reduction or enrichment on the associated community biomass structure (Period 9). We observed comparable results with both % cover and biomass data in compositional structure (all abundances being transformed into presence-absence data; Tables 1.3b and 1.2f).

Canopy removal altered the species composition within the community throughout the experiment (Table 1.3b).

Table 1.1. Summary of RM ANOVAs showing the effects of treatment, full factorial contrasts of canopy (Ca), grazer (Gr), and nutrient enrichment (Nu) factors on abundance in % cover, richness, Simpson's index of diversity, and Pielou's evenness of non-manipulated species of the community for all periods. Significant values are shown in **bold**.

	df	*F* ratio	*p*
a) % Cover			
Between subjects			
Treatment	8	1.12	0.3808
Ca	1	0.42	0.5223
Gr	1	0.16	0.6899
Nu	1	0.42	0.5208
Ca × Gr	1	0.05	0.8264
Ca × Nu	1	0.88	0.3576
Gr × Nu	1	0.68	0.4158
Ca × Gr × Nu	1	0.16	0.6884
Residual	27		
Within subjects			
Period	7	23.93	**<0.0001**
Period x Treatment	56	1.86	**0.0011**
Period × Ca	7	3.45	**0.0017**
Period × Gr	7	0.16	0.9929
Period × Nu	7	1.05	0.4006
Period × Ca × Gr	7	1.33	0.2387
Period × Ca × Nu	7	0.70	0.6740
Period × Gr × Nu	7	0.53	0.8090
Period × Ca × Gr × Nu	7	1.14	0.3401
Residual	189		

	df	*F* ratio	*p*
b) Richness			
Between subjects			
Treatment	8	1.43	0.2304
Ca	1	5.20	**0.0308**
Gr	1	0.83	0.3699
Nu	1	0.94	0.3413
Ca × Gr	1	1.87	0.1827
Ca × Nu	1	0.00	0.9550
Gr × Nu	1	0.03	0.8655
Ca × Gr × Nu	1	0.00	0.9550
Residual	27		
Within subjects			
Period	7	24.10	**<0.0001**
Period × Treatment	56	2.27	**<0.0001**
Period × Ca	7	5.03	**<0.0001**
Period × Gr	7	0.81	0.5797
Period × Nu	7	0.14	0.9945
Period × Ca × Gr	7	2.43	**0.0209**
Period × Ca × Nu	7	0.52	0.8226
Period × Gr × Nu	7	1.32	0.2449
Period × Ca × Gr × Nu	7	1.04	0.4031
Residual	189		

	df	*F* ratio	*p*
c) Diversity			
Between subjects			
Treatment	8	1.39	0.2465
Ca	1	6.70	**0.0152**
Gr	1	0.61	0.4412
Nu	1	0.23	0.6337
Ca × Gr	1	0.02	0.8883
Ca × Nu	1	0.10	0.7497
Gr × Nu	1	0.06	0.8016
Ca × Gr × Nu	1	0.01	0.9160
Residual	27.2		
Within subjects			
Period	7	13.99	**<0.0001**
Period × Treatment	56	1.29	0.1068
Period × Ca	7	1.56	0.1489
Period × Gr	7	0.82	0.5744
Period × Nu	7	1.86	0.0786
Period × Ca × Gr	7	0.48	0.8472
Period × Ca × Nu	7	2.75	**0.0097**
Period × Gr × Nu	7	1.04	0.4047
Period × Ca × Gr × Nu	7	0.39	0.9071
Residual	178		

	df	*F* ratio	*p*
d) Evenness			
Between subjects			
Treatment	8	2.85	**0.0187**
Ca	1	1.41	0.2447
Gr	1	2.98	0.0944
Nu	1	2.30	0.1398
Ca × Gr	1	0.54	0.4676
Ca × Nu	1	0.75	0.3945
Gr × Nu	1	0.06	0.8133
Ca × Gr × Nu	1	0.88	0.8133
Residual	28.5		
Within subjects			
Period	7	2.38	**0.0249**
Period × Treatment	56	1.82	**0.0024**
Period × Ca	7	1.04	0.4045
Period × Gr	7	0.81	0.5777
Period × Nu	7	2.36	**0.0258**
Period × Ca × Gr	7	0.54	0.8068
Period × Ca × Nu	7	3.33	**0.0026**
Period × Gr × Nu	7	0.82	0.5727
Period × Ca × Gr × Nu	7	1.84	0.0835
Residual	146		

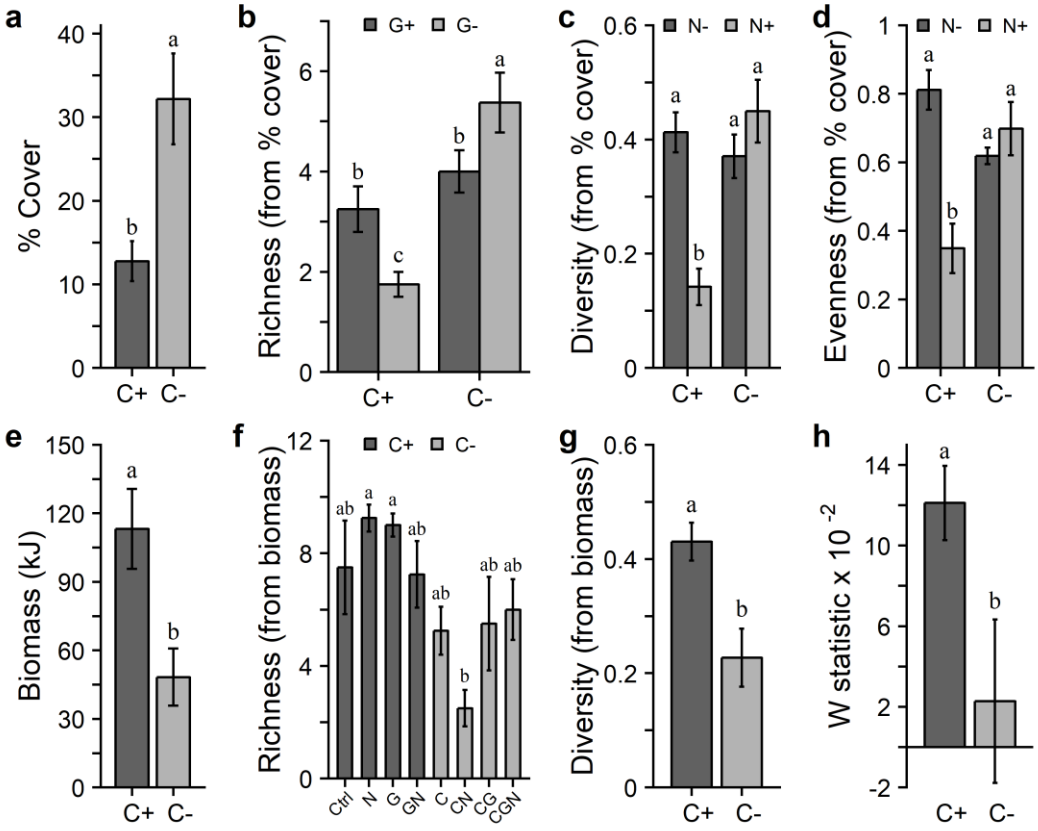

Figure 1.2. Mean (±SE) values of (a) abundance in % cover, (b, f) species richness, (c, g) Simpson's diversity index (1-λ), (d) Pielou's evenness, (e) biomass (kJ), and (h) the W statistic among various treatments for non-manipulated species. Values are from data in percent cover from Period 8 (a–b), percent cover from Period 5 (c–d), biomass from Period 9 (e–g), and counts and biomass from Period 9 (h). Dark and light gray bars are the respective treatments with C+: canopy untouched; C-: canopy removed; G+: grazers untouched; G-: grazers reduced; N+: nutrients added; N- no nutrients added. See Fig. 1.1 for details of the different treatments in (f). The number of replicates used to obtain the averages were n = 16 in (a), (e), (g), and (h); n = 8 in (b), (c), and (d); n = 4 in (f). Different letters above the bars indicate significant differences ($p < 0.05$).

1.4.2 Community trajectory over time and community resilience

The total abundance, in % cover, increased in all treatments over the first summer, yet understandably being at much lower levels in plots where species were removed (i.e., C- and G- treatments) (Fig. 1.4a). After the winter (Period 6), we observed lower values

and a higher variability due to moderate ice-scouring followed by a rapid recovery (Fig. 1.4a).

Table 1.2. Summary of (a–d) ANOVAs and (e–f) PERMANOVAs from biomass data obtained by destructive sampling (Period 9 only) showing the effects of treatment, full factorial contrasts of canopy (Ca), grazer (Gr), and nutrient enrichment (Nu) factors on biomass, richness, Simpson's index of diversity, Pielou's evenness, structure, and composition of the non-manipulated species of the community. Significant values are shown in **bold**.

	df	*F* ratio	*p*
a) Biomass			
Treatment	8	1.71	0.1408
Ca	1	9.81	**0.0041**
Gr	1	0.11	0.7459
Nu	1	1.09	0.3065
Ca × Gr	1	0.36	0.5550
Ca × Nu	1	0.01	0.9408
Gr × Nu	1	0.04	0.8441
Ca × Gr × Nu	1	0.19	0.6642
Residual	27		

	df	*F* ratio	*p*
b) Richness			
Treatment	8	3.99	**0.0031**
Ca	1	21.27	**<0.0001**
Gr	1	1.19	0.2853
Nu	1	0.57	0.4570
Ca × Gr	1	2.03	0.1655
Ca × Nu	1	0.57	0.4570
Gr × Nu	1	0.01	0.9338
Ca × Gr × Nu	1	5.13	**0.0318**
Residual	27		

	df	F ratio	*p*
c) Diversity			
Treatment	8	2.25	0.0555
Ca	1	11.49	**0.0022**
Gr	1	2.97	0.0963
Nu	1	0.08	0.7858
Ca × Gr	1	0.53	0.4718
Ca × Nu	1	0.08	0.7782
Gr × Nu	1	0.35	0.5606
Ca × Gr × Nu	1	0.70	0.4115
Residual	27		

	df	F ratio	*p*
d) Evenness			
Treatment	8	0.92	0.5187
Ca	1	2.36	0.1367
Gr	1	1.32	0.2617
Nu	1	0.62	0.4374
Ca × Gr	1	0.25	0.6215
Ca × Nu	1	0.58	0.4525
Gr × Nu	1	0.18	0.6749
Ca × Gr × Nu	1	0.05	0.8267
Residual	26		

	df	*Pseudo-F*	*p* (perm)
e) Structure (biomass)			
Treatment	8	2.7609	**0.0001**
Ca	1	11.786	**0.0001**
Gr	1	1.0841	0.3304
Nu	1	0.6080	0.7590
Ca × Gr	1	0.9499	0.4821
Ca × Nu	1	0.4381	0.9059
Gr × Nu	1	0.6079	0.7570
Ca × Gr × Nu	1	1.0415	0.3522
Residual	27		

	df	*Pseudo-F*	*p* (perm)
f) Composition (biomass)			
Treatment	8	3.5971	**0.0001**
Ca	1	12.632	**0.0001**
Gr	1	1.2561	0.2833
Nu	1	0.8395	0.4987
Ca × Gr	1	1.0910	0.3526
Ca × Nu	1	0.7464	0.5553
Gr × Nu	1	0.8879	0.4673
Ca × Gr × Nu	1	1.6744	0.1576
Residual	27		

Of all treatments, those that included canopy removal (C-) had greater average dissimilarities over time when compared to the reference plots (Fig. 1.4b). Only the canopy-removed treatment, combined with another stress (i.e., CG, CN and CGN), maintained a significant difference with the references throughout the entire

experiment (Fig. 1.4b). These differences were mainly due to ephemeral algae (e.g., *Ectocarpus* sp., Ulvaceae, *Porphyra* sp.) being more abundant in the canopy-removed treatments, and invertebrates (e.g., *Mytilus* spp., *Aulactinia stella*, *Pectinaria gouldii*) being more abundant in the references.

Table 1.3. Summary of RM PERMANOVAs showing the effects of treatment and full factorial contrasts of canopy (Ca), grazer (Gr), and nutrient enrichment (Nu) factors on abundance structure and species composition for non-manipulated species of the community for all periods. Significant values are shown in **bold**.

	df	***F* ratio**	***p***		**df**	***F* ratio**	***p***
a) Structure (% cover)				**b) Composition (% cover)**			
Between subjects				**Between subjects**			
Treatment	8	2.1286	**0.0028**	Treatment	8	2.8774	**0.0004**
Ca	1	1.7071	0.1283	Ca	1	7.0348	**0.0001**
Gr	1	1.0230	0.3752	Gr	1	1.9330	0.1183
Nu	1	1.3764	0.2140	Nu	1	0.8872	0.4610
Ca × Gr	1	1.2557	0.2676	Ca × Gr	1	1.1170	0.3385
Ca × Nu	1	1.5609	0.1568	Ca × Nu	1	0.9441	0.4370
Gr × Nu	1	0.2645	0.9671	Gr × Nu	1	0.1817	0.9268
Ca × Gr × Nu	1	1.0792	0.3404	Ca × Gr × Nu	1	0.4168	0.7922
Residual	27			Residual	27		
Within subjects				**Within subjects**			
Period	7	13.617	**0.0001**	Period	7	17.528	**0.0001**
Period x Treatment	56	1.4096	**0.0001**	Period × Treatment	56	1.5230	**0.0003**
Period × Ca	7	2.7227	**0.0001**	Period × Ca	7	3.4849	**0.0001**
Period × Gr	7	0.6753	0.9520	Period × Gr	7	0.8017	0.7161
Period × Nu	7	0.7989	0.8253	Period × Nu	7	0.8360	0.6748
Period × Ca × Gr	7	0.9316	0.6069	Period × Ca × Gr	7	1.0079	0.4597
Period × Ca × Nu	7	0.8706	0.7122	Period × Ca × Nu	7	0.7169	0.7965
Period × Gr × Nu	7	0.8190	0.7958	Period × Gr × Nu	7	0.6855	0.8274
Period × Ca × Gr × Nu	7	0.9956	0.4819	Period × Ca × Gr × Nu	7	1.1928	0.2660
Residual	189			Residual	189		

Throughout the consecutive periods of the experiment, the trajectories of the average community structure within each treatment were all positively correlated with the trajectories of the controls (see correlations and *p* values in *Annexe A*: *Figure 5.1*). Thus, the period-to-period recovery process was similar to that observed in the controls. We summarized these trajectories using a second-stage nMDS; The nMDS illustrates that treatments having two stressors had more different period-to-period trajectories for community structure (relative to the controls) than single stressor treatments, as

expected. Surprisingly, these differences were even greater than for the triple-stressor treatment (CGN) (Fig. 1.5).

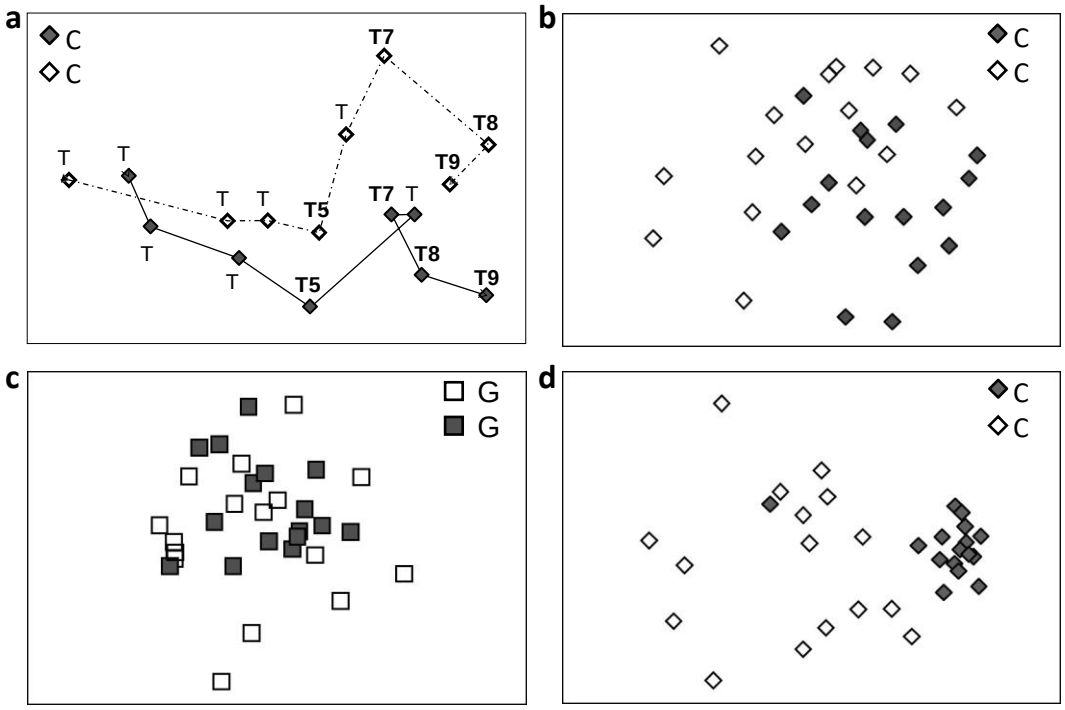

Figure 1.3. Non-metric multidimensional scaling (nMDS) plots illustrating the effect on community structure of (a) the canopy treatment across all periods (showing centroids), (b, d) the canopy treatment at Period 9, and (c) the grazer treatment at Period 8. Values were calculated based on Bray–Curtis similarities of the non-manipulated species based on percent cover data (a), (b), and (c) or biomass (d). C+: canopy untouched; C-: canopy removed; G-: grazers untouched; G+: grazers reduced. In (a), an asterisk (*) indicates a significant difference ($p < 0.05$) in community structure between C+ and C- at the given period. Stress from a to d: 0.07, 0.17, 0.19, and 0.12, respectively.

When all species are considered, controls showed complete recovery after 11 months for all measured variables, although richness recovered after two months, while requiring four months for diversity. At the end of the experiment, after 14 months, controls also recovered in terms of biomass and cryptic species. When using only non-manipulated species, all measured variables in the controls were similar to the reference

plots after 11 months (cf. Table 1.4). Prior to that, controls had lower richness and higher evenness values compared to the reference plots. In general, richness and species composition required the most time to recover. The treatments of N and GN recovered faster than the controls for total % cover, richness (N only), evenness, and diversity (see Table 1.4). All other treatments (C, CG, CN, and CGN) had longer or similar recovery times to the controls.

Table 1.4. Recovery time (in months) of the non-manipulated species community in terms of diversity profile characteristics (total % cover; species richness *S*; evenness *J'*; Simpson diversity 1-λ) and the structure (square root abundance) or composition (presence/absence) for each treatment. Recovery was achieved when no significant differences ($p > 0.05$) were observed between a given treatment and the reference plots before the end of the experiment. If not reached by the end of the study, then the recovery time is deemed to be >14 months. Grayscale is based on controls (Ctrl) where no shading (white) represents cases where recovery happened faster than in the controls (light gray), and dark gray signifies where recovery was slower than observed in the control plots. Note the sampling gap between months 4 and 11 due to winter (i.e., it was not possible to determine recovery time values from months 5 to 10). See Fig. 1.1 for details regarding the treatment codes.

	Effect of univariate factors on community characteristics				Effect of multivariate factors on community structure	
	Tot % cover	*S*	1-λ	*J'*	Structure	Composition
Ctrl	11	11	11	11	11	11
C	11	13	11	>14	11	14
G	11	14	14	11	14	14
N	4	2	1	4	11	11
CG	14	14	11	11	11	13
CN	11	13	11	>14	11	14
GN	1	11	1	4	11	13
CGN	11	14	14	13	>14	>14

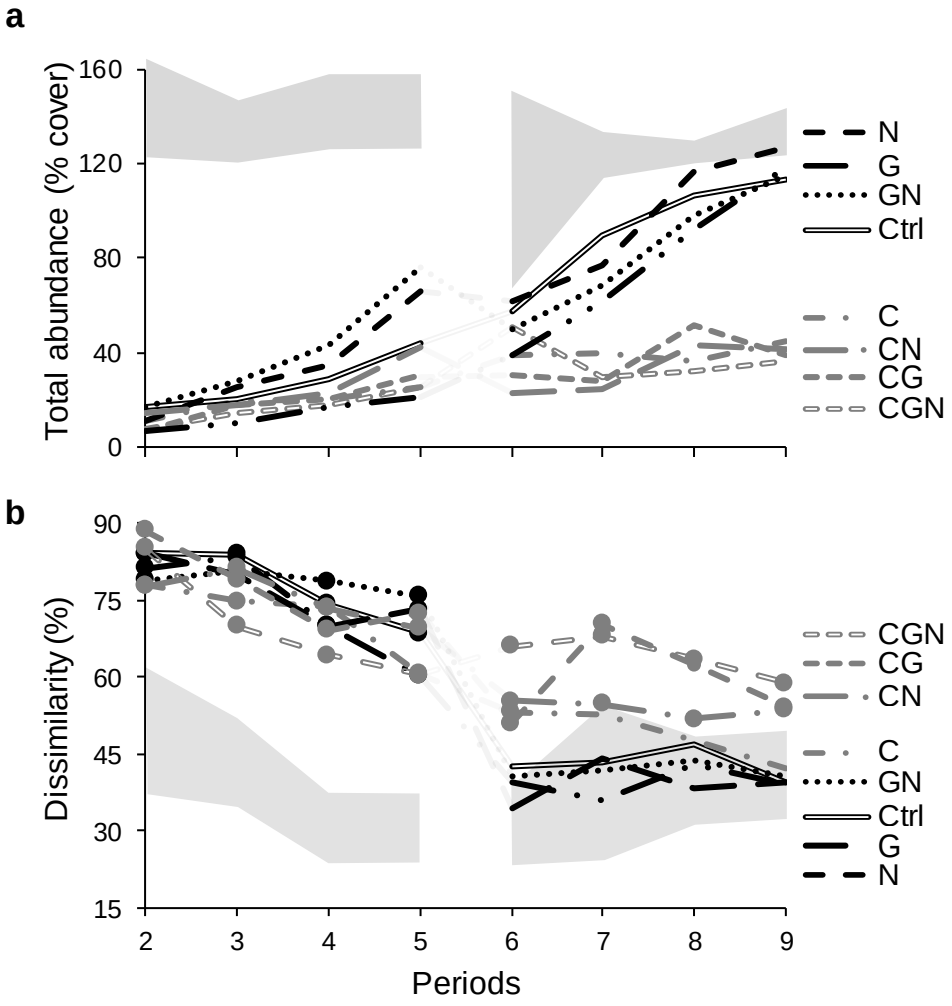

Figure 1.4. Community evolution over time. (a) Mean total abundance in percent cover of all species from visual observations in the field by treatment (n = 4). (b) Average dissimilarities between pairs of reference and treatment plots (n = 16) of each period for abundance in % cover structure of non-manipulated species. Light gray areas are 95% confidence intervals of the mean of reference plots (n = 4 in (a); within dissimilarities n = 6 in (b)). (b) Significant values between references and treatments are shown by filled circles (t-tests, $p < 0.05$). See Fig. 1.1 for treatments and definitions of C, G, N; number of letters in the treatment labels represents the amount of stress applied.

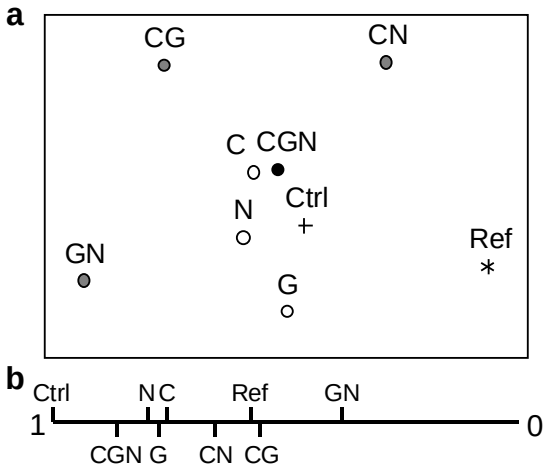

Figure 1.5. Second-stage nMDS ordination illustrating the change in average community structure patterns over time for each treatment (a) and Spearman correlations with controls (b) using non-manipulated species. (a) Second-stage nMDS is calculated from Spearman correlations of Bray–Curtis similarity coefficient matrices of average community structure pattern over time. Open circles represent single stressor treatments, gray circles represent two-stressor treatments, and black circles represent triple-stressor treatments. Stress = 0.08. (a,b) Ctrl and Ref refer to Control and Reference, respectively. See Fig. 1.1 for treatments and definitions of C, G, N; the number of these letters in the treatment labels represents the quantity of stress applied.

1.5 Discussion

Macrobenthic community resilience depends of the nature and the number of stressors to which the community is subjected. Macroalgal canopy removal, i.e., removal of habitat-forming species, had the greatest single effect by modifying in several ways diversity indices, community structure, as well as delaying or even preventing resilience. In general, we saw no significant individual impact of grazer reduction or nutrient enrichment. Some non-additive interactions occurred between canopy removal and grazer reduction as well as canopy removal and nutrient enrichment. The community structure of the triple stress treatment (CGN) differed from that of the

reference plots throughout the entire experiment suggesting a slower or even non-occurring resilience when faced with multiple stresses. Canopy removal alone (C) or combined with another stress (CG, CN, CGN) increased the resilience time, as did grazer reduction (G) on its own. Therefore, we partly confirmed our initial hypothesis that canopy removal and grazer reduction would have an individual impact on diversity indices, community structure, and resilience, and that communities would be affected to a greater extent via synergistic effects when coupled with nutrient enrichment stress.

1.5.1 Structure, abundance, and diversity of communities

Of all the main effects, canopy removal most affected the community diversity, abundance, and structure. Canopy-removed plots had a higher abundance (% cover), richness, and diversity, as well as a different structure in terms of abundance of associated communities at specific times. The differences were mainly due to ephemeral algae being more abundant in the canopy-removed plots, and invertebrates being more abundant in untouched-canopy plots, as expected (see Schiel et Lilley, 2011 for similar results). Indeed, *Scytosiphon* sp., *Ectocarpus* sp., *Petalonia* sp., *Chordaria* sp., and Ulvaceae were absent where the macroalgal canopy was untouched (C+). Although our pretreatment allowed space and light for ephemeral algae to establish, we did not see any delay in fucoid development in C+ plots due to potential competition with ephemeral algae; this observation contrasts with a number of other studies (e.g., Korpinen et Jormalainen, 2008; Sousa, 1979). Therefore, the presence of ephemeral algae is not essential for fucoids to establish and for succession to occur on these sites. Indeed, the recruitment of ephemeral algae occurred mainly during the second summer (2013); this period of the year was too late to result in any competition in the C+ plots. The late recruitment of ephemeral algae could be due to the timing of the experiment. Archambault et Bourget (1983) followed experimentally denuded and reference communities in the St. Lawrence Estuary, and they observed that ephemeral algae were more abundant in experimentally denuded plots only the year after the denuding of the

rock and after suffering an ice-scouring event. The reduced presence of invertebrates, when the canopy was removed, can be explained by the reduced habitat availability and increased stress level (e.g., higher temperatures, desiccation, and exposition to ultraviolet radiation) (Bertness *et al.*, 1999). Differences in average surface temperature between the reference plots and the canopy-removed plots ranged from 5–16 °C, temperatures measured using an infrared camera.

When using biomass (Period 9), we saw the opposite trend than with % cover data: lower biomass, richness, and diversity in the canopy-removed plots. The same data transformed into percentage cover no longer showed significant differences in abundance and diversity. This indicates a smaller individual mass of species in canopy-removed plots as suggested by the lower W statistic values that are characteristic of a more affected community (Clarke, 1990). The sampling method explains the opposite effect of canopy removal on richness between biomass and % cover data as cryptic species were added and were generally more present in untouched-canopy plots (see *Annexe A*: *Table 5.1* for the list of species). Indeed, when we removed those taxa from the analyses, differences in richness were eliminated, and diversity values increased where the canopy was removed (results not shown). Canopy removal strongly affected the structure in terms of biomass for both location and dispersion (a higher deviation from the centroid when the canopy is absent) indicating a sign of non-resistance to a stress (Warwick et Clarke, 1993).

We expected to observe a positive effect of the grazer reduction treatment on ephemeral algae recruitment and growth, as reported by many studies (e.g., Aquilino et Stachowicz, 2012). The grazer reduction treatment had no single effect on community diversity indices except for a higher community dispersal at Period 8 (based on % cover). The late recruitment of ephemeral algae could explain the lack of a single effect by grazer reduction in the first year. Small grazers, which dominated the plots but have

a limited grazing capacity, could also explain this lack of effect as also seen by Archambault et Bourget (1983). Yet, there was an interaction effect on richness with canopy removal in Period 8 where two ephemeral species (*Ectocarpus* sp. and Ulvaceae) were only present in the canopy-removed grazer-reduced plots (C- G-), and anemones (*Aulactinia stella*) were significantly more abundant in canopy-untouched grazer-untouched plots (C+ G+). Low richness values in reduced-grazer plots having an untouched canopy (C+ G-) are not easily explained. The latter generally had fewer encrusting algae, anemones, and barnacles than where grazers were not removed (C+ G+). The canopy removal effect overshadows the effect of grazer reduction when they are combined. This highlights the importance of the macroalgal canopy. On the other hand, the reduced presence of grazers significantly increased the abundance of ephemeral algae over the course of the entire experiment (results not shown). These results indicate that crawling grazers have no or little implication on community succession and structure in this rocky coastal system.

Primary producers of coastal zones are primarily nitrogen limited (Howarth, 1988). Many studies have shown an increase of ephemeral algae—which are fast-growing species—with high nutrient loading, especially when coupled to low grazing or space availability (e.g., Korpinen *et al.*, 2007). Surprisingly, the single effect of the nutrient-enrichment treatment decreased community evenness only in periods 3 and 5; it had, however, an interactive effect with canopy removal that decreased diversity and evenness only when the canopy was present in Period 5 (C+ N+). Those interactions had a combined impact that was strongly dominated by canopy removal, indicating a low importance of nutrient enrichment when facing such high stress. Low evenness in Period 5 for the enriched canopy-present plots (C+ N+) induced a lower diversity as the encrusting algae *Stragularia clavata* dominated the enriched plots. Nutrient enrichment did not affect total *Fucus* spp. abundance even though we measured higher nitrogen content in the macroalgae of the enriched treatments (results not shown). Once

again, the late recruitment of ephemeral algae in the first year could be responsible for a lack of response to nutrient enrichment, or that the enrichment level was lower than a specific threshold to have a significant effect on our assemblages, or that opportunistic algae were more limited by other abiotic factors on our site. Bertocci *et al.* (2015) have shown that nutrient enrichment combined with high disturbance intensity may enhance susceptibility to species invasion in rock pools. Our results indicate that our nutrient enrichment level may not have been sufficient to influence succession or community structure (see Bokn *et al.*, 2003 for similar results).

1.5.2 Community resilience

The studied macrobenthic community showed a high capacity of resilience following a pulse-type disturbance. Richness in control plots recovered after only two months, even though the complete recovery of all tested variables required 11 months. Such recovery is relatively fast after the pretreatment removal of all biomass. In contrast, Schiel et Lilley (2011) detected community effects (lower fucoid abundance, lower richness, more ephemeral algae, and different community structure) eight years after a similar disturbance, while Aquilino et Stachowicz (2012) measured a recovery of 18 months for perennial algae % cover. Subarctic communities recover quickly after ice-scouring events, especially when crevices can be used as refuges (Bergeron et Bourget, 1986). Within all our plots, there were no large crevices, although there was some limited relief that increased substrate heterogeneity and promoted recruitment (personal observations). According to O'Leary *et al.* (2017), community resilience is promoted by the presence of habitat-forming species, the supply of new recruits, and favorable physical settings. In our study, the recovery of the habitat-forming species *Fucus* sp. occurred 11 months after the pretreatment; this coincided with the full recovery of the controls. Finally, gross primary production (see Joseph et Cusson, 2015 for methods) did not differ between the controls and the reference plots at the end of the experiment, confirming a recovery in function (results not shown).

The addition of stressors generally slowed down resilience, in agreement with other studies (reviewed in O'Leary *et al.*, 2017). Nutrient enrichment alone (N) or combined with grazer reduction (GN) sped up the recovery of abundance, richness, diversity, and evenness; however, these plots had a different composition and abundance structure than the references, indicating that recovery was incomplete. Indeed, the encrusting algae *S. clavata* dominated in nutrient-enriched plots, while *Mytilus* spp. dominated the reference plots. Moreover, nutrient-enriched plots had little cover of habitat-forming macroalgae compared to the reference plots. This likely results in the lack of recovery in total biomass and in function (primary production). In contrast, removal of macroalgal canopy (C), grazer reduction (G), and all other combinations reduced resilience capacity. This indicates that even though some stressors did not affect the main tested general community metrics, they can affect stability in terms of recovery time. For this reason, studies need to address as many aspects as possible when examining communities, including stability (recovery and resistance) and function, to reveal a more complete set of responses of the assemblages to multiple stressors.

1.6 Concluding remarks

Further manipulative studies, such as our study, are required to have a better understanding of the effects of multiple stressors on assemblages. Indeed, the lack of resilience of the triple-stressor treatment demonstrates the necessity for studies including more than two stressors and, inevitably perhaps, longer-term studies that last until the combined treatments reach a complete recovery. Stressors affected species differently indicating that the nature of the stress has an influence on community characteristics and their functions. For instance, macroalgal canopy facilitates the recovery of the community. Single or multiple stressors differently affected richness, diversity, evenness, structure, and recovery. This confirms that complementary metrics

are needed to document these effects on community stability and persistence. As such, we do not recommend using single diversity measures, such as species richness, especially when habitat-forming species are absent or cannot be included in the analyses, as those measures provide an incomplete picture and can be misleading in terms of the actual state of a community. Rather, we recommend prioritizing the addition of multivariate measures, such as community structure and composition, to include subtle changes in dominance and identity. As our study suggests, multiple stressors may interact differently (dominant, additive, synergistic) on community characteristics and resilience, and the effects cannot be predicted from studies on a single stressor or that assume an additive cumulated impact of multiple stressors.

1.7 Acknowledgments

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CHAPITRE II
MULTIPLE STRESSORS AND DISTURBANCE EFFECTS ON EELGRASS AND EPIFAUNAL MACROINVERTEBRATE ASSEMBLAGE STRUCTURE

SUBMITTED to Marine Ecology Progress Series (in revion at the time of final thesis submission)

Title: Multiple stressors and disturbance effects on eelgrass and epifaunal macroinvertebrate assemblage structure

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Keywords: habitat complexity, cumulative effect, non-additive interaction, foundation species, field experimentation, manipulative study, shading, nutrient addition

2.1 Abstract

Multiple forms of environmental change and anthropogenic pressure co-occur in coastal marine ecosystems. These external forces affect ecosystem structure, functioning, and eventually, services to humans. Studies that include more than two simultaneous stressors are necessary to understand potential interactions among multiple stressors. We evaluated single and interactive effects of density reduction of *Zostera marina* L., a habitat-forming species, shading, and sediment nutrient enrichment on the response of *Z. marina* and its associated epifauna over 10 weeks. Shading had the greatest effect on reducing the eelgrass relative leaf elongation rate (RLE), non-structural carbohydrate reserves, and eelgrass shoot density. A reduced eelgrass shoot density sustained higher epifaunal densities and increased the eelgrass RLE. Sediment nutrient enrichment increased eelgrass shoot density but decreased epifaunal richness, diversity, and total abundance. Our three disturbance and stressors influenced diversity measures differently, but all affected assemblage structure. Most of the changes to the epifaunal assemblage and diversity likely occurred due to altered habitat availability and epiphytic algae load. We observed additive, antagonistic, and negatively synergistic interactions among our treatments, while most of the cumulative effects showed dominance by one stressor over another. Our results highlight the importance of field experiments that are based on multiple disturbances and stressors to determine the type of their interaction on communities.

2.2 Introduction

Seagrasses, which are habitat-forming species (or foundation species sensu Dayton 1972; ecosystem engineers sensu Jones et al. 1994), provide a complex habitat offering

several roles for many coastal species, such as reducing water movement, providing shelter from predation, stabilizing sediments. Their presence provides not only habitat, but also protection and food for fauna and plays an important role in structuring communities (Christie *et al.*, 2009; Duffy, 2006; Herkul et Kotta, 2009). At a global scale, eelgrass beds are declining due to multiple causes that may be interdependent, e.g., coastal development, eutrophication, sea-level rise, increased water temperature, and increased water turbidity (Airoldi et Beck, 2007; Duarte, 2002; Lefcheck *et al.*, 2017b; Orth *et al.*, 2006; Waycott *et al.*, 2009). These various stressors decrease shoot density, increase habitat fragmentation, and can result in the complete disappearance of the eelgrass bed, thereby changing the community structure and function of associated organisms (Connolly, 1995; Duarte, 2002; Herkul et Kotta, 2009; Reed et Hovel, 2006).

Habitat loss and fragmentation diminish habitat complexity and patch size and increase the edge effect at both the landscape and local scales; these modifications alter species richness and other components of diversity (Airoldi *et al.*, 2008; Fahrig, 2003). Eelgrass complexity influences the associated communities. Typically, the presence of seagrass—at low or high densities—will increase the associated community stability, species richness and abundance, influence assemblage composition, and increase the habitat carrying capacity (Calizza *et al.*, 2017; Edgar et Robertson, 1992; Lundquist *et al.*, 2018). On the other hand, a reduction in seagrass density decreases seagrass self-shading; therefore, leaf surface area, shoot biomass, growth, and number of leaves all increase (Rattanachot *et al.*, 2016). This could, in turn, support a greater epifaunal density as seagrass surface area could be more important than shoot density or length in explaining epifaunal biomass (Sirota et Hovel, 2006). Epiphytic algae can also play a trophic role in concert with this habitat complexity for increasing epifaunal density (Gartner *et al.*, 2013). Finally, a threshold of habitat loss may exist that, once crossed, leads to a negative effect on epifaunal communities (Reed et Hovel, 2006); this would

suggest that a decrease in shoot density may represent one of the foremost signs that the structure and, eventually, the functioning of the entire seagrass bed will be affected.

Coastal eutrophication is a major cause of seagrass bed decline. Nutrient enrichment of the water column increases the abundance of epiphytic algae and increases competition from macroalgae; therefore, seagrass biomass decreases due to a reduced access to light (Hauxwell *et al.*, 2003; Hughes *et al.*, 2004; Jaschinski et Sommer, 2008; Sand-Jensen, 1977). Nutrient enrichment in the water column can also alter overall richness, increase epifaunal density and biomass, cause a shift in species composition, and increase macrophyte and epiphyte abundance, particularly in nutrient-limited environments (Gil *et al.*, 2006; Schmidt *et al.*, 2017; Tuya *et al.*, 2013). Epifaunal grazers can control epiphyte biomass and even benefit from epiphyte presence (Baggett *et al.*, 2010; Reynolds *et al.*, 2014). Nutrient enrichment of underlying sediment may have a positive effect on eelgrass biomass (Hughes *et al.*, 2004), unless the nutrient supply is too great and the sediments become toxic (e.g., vanKatwijk *et al.*, 1997).

The light accessibility, which can be reduced by turbidity related to eutrophication, suspended sediments, sea-level rise, and macroalgae and epiphytes on leaves, is important to seagrass health and the maintaining of habitats and food for the numerous epibenthic communities. Depending on its duration and severity, a reduction in accessible light can negatively affect seagrasses by decreasing seagrass biomass, growth, shoot density, carbohydrate reserves, and overall survival (e.g., Ralph *et al.*, 2007; Ruiz et Romero, 2001; Silva *et al.*, 2013). Reduced water clarity, combined with warming temperatures, has had a negative effect on seagrasses in Chesapeake Bay, USA (Lefcheck *et al.*, 2017b). The effects of light reduction might be influenced by the season (Wong *et al.*, 2019). Light reduction can also decrease epiphytic algae and increase seagrass chlorophyll concentrations and plant length (Collier *et al.*, 2009; Fokeera-Wahedally et Bhikajee, 2005). Studies examining the effects of light reduction

on epifauna within seagrasses remain rare. Experimental shading has shown that a decrease in associated species abundance was related to a reduced abundance of epiphytic algae or habitat complexity (Edgar et Robertson, 1992; Gartner *et al.*, 2010).

Multiple anthropogenic and natural disturbances and stressors co-occur in coastal habitats (see Grime, 1977; Sousa, 1984, for disturbance and stress definitions). Nonetheless, their cumulative effects are often considered as additive or synergistic without proper testing; these effects may accumulate in a multiplicative manner or may not even accumulate and rather show the dominance of one stressor (Halpern et al. 2007, Côté et al. 2016). The cumulative effects may interact in a synergistic or antagonistic manner, and, depending on the system under consideration, the resulting effects may be unpredictable (Darling and Côté 2008, Lyons et al. 2015, Côté et al. 2016). The occurrence of synergistic interactions in the marine system may be greater when communities are exposed to three stressors rather than to a pair of stressors (Crain et al. 2008). Multiple interactive effects on both seagrass and macroinvertebrate epifaunal assemblage structures remain poorly understood and in situ studies that include three or more disturbances or stressors in seagrass beds are rare (e.g., Moreno-Marín *et al.*, 2018; Ruesink *et al.*, 2012; York *et al.*, 2013). Furthermore, such studies rarely measure the in situ effect of disturbance and stressor on invertebrate assemblages (e.g., Cardoso *et al.*, 2008; Stoner *et al.*, 2014).

Here, we aim to evaluate the structural and physiological responses of a *Zostera marina* L. bed and its associated epifaunal communities to single and interactive effects of a reduced shoot density of *Z. marina*, sediment nutrient enrichment, and shading. Although the effects of seagrass density/complexity have been studied (see above), few studies have explored the two other stressors, and none have studied their potential interactions. We measured the structural and physiological responses of *Z. marina* using shoot density counts, the relative leaf elongation rate, and the concentrations of

non-structural carbohydrates (shoot and rhizome). We assessed the response of the associated epifaunal communities through diversity indices, abundance structure, and the epiphytic algae load. We hypothesize that in addition to the significant individual influence of reduced eelgrass shoot density, univariate and multivariate assemblage characteristics will be affected by non-additive interactions. We hypothesize that both a reduction in eelgrass shoot density and shading will negatively affect eelgrass functioning and diversity, while nutrient enrichment will have a positive effect. We also hypothesize that shading will have the greatest effect on *Z. marina*. This study will improve our understanding of bottom-up controls and the complexity of habitat-forming species in shaping the associated diversity and functioning of eelgrass bed habitats. It will also provide useful insight into how eelgrass, and its associated communities, react in the presence of multiple stressors. Note that even though eelgrass shoot density reduction is considered a disturbance (see Grime, 1977; Sousa, 1984), we will use only the word 'stressor' to simplify the reading.

2.3 Methods

2.3.1 Study site

The experiment was conducted from July to September 2015 on the north shore of the St. Lawrence Estuary near the municipality of Baie-Comeau, Quebec, Canada (49°05'11″N, 68°19'09″W). The site is dominated by the habitat-forming seagrass *Zostera marina* L. that forms a quasi-continuous monospecific meadow, with some fragmented zones, having an approximate size of 15 km² around the Manicouagan Peninsula (Grant et Provencher, 2007). The year-round average water temperature is ca. 6 °C (12 °C, summer; up to 18 °C at low tide in July), and salinity ranges between 20–30 PSU. The site lies at ca. 0.16 m under the zero datum of sea level. The tidal regime is mixed, dominated by semidiurnal tides having a mean tidal range of ca. 2.6 m

(www.tides.gc.ca). Our experiment took place within a non-fragmented flat zone of the meadow having an average eelgrass shoot density of 690 shoots·m^{-2} at the beginning of the experiment.

2.3.2 Experimental design

We used a complete factorial experimental design (see Fig. 2.1) to evaluate the reduction in density of a habitat-forming species (eelgrass shoot density reduction [De], 2 levels: 0% [D-] or 80% reduction [D+]; pulse-type disturbance), nutrient enrichment of the sediments (enrichment [Nu], 2 levels: no addition [N-] or 75 g N m^{-2} [N+]; pulse-type stress), and reduction of light (shading [Sh], 2 levels: natural light [S-] or 68% reduction [S+]; pulse-type stress) on the diversity and structure of epifaunal eelgrass–associated assemblages and some of the physiological aspects of eelgrass. All eight treatments were replicated five times (n = 5) and randomly assigned to 40 experimental plots (1 × 1 m) that were dispatched haphazardly within the bed. A minimum distance of three meters was maintained between plots. We sampled only the center of the plots, a region of ca. 50 x 50 cm.

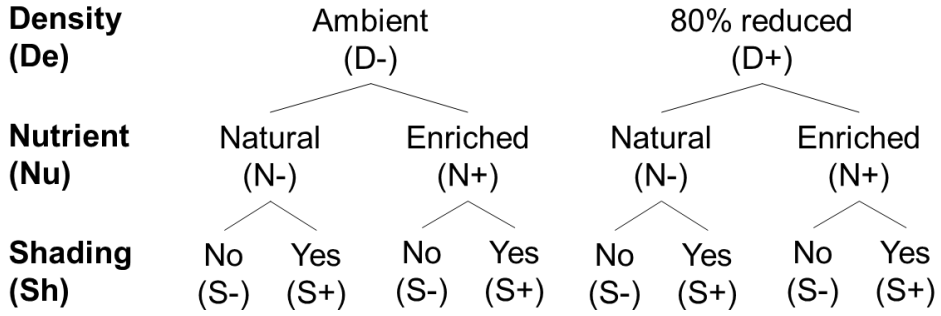

Figure 2.1. Schematic of the experimental design displaying the three stressor treatments (eelgrass shoot density reduction, sediment nutrient enrichment, shading, each with two levels; – stressor absent, + stressor present).

Density reduction was applied using 1 m^2 quadrats quadrilled with 100 cells (each 10 × 10 cm), where the cells occupied with shoots were counted. We then manually cleared 0% or 80% of the occupied cells at random; clearing included all eelgrass shoots, including rhizomes and roots. We recorded the biomass of 10 collected cells to evaluate aboveground biomass. Plots of natural eelgrass densities (D-) were gently hand-disturbed to avoid manipulation effects.

Plots were enriched with four sticks of synthetic nutrients added to the sediments (N:P:K = 15:3:3, 75 $g \cdot N \cdot m^{-2}$; Jobe's Fertilizer Spikes Trees and Shrubs, Easy Gardener Products Inc.) at each corner of a 50 × 50 cm quadrat in the middle of the plot. Plots without enrichment (N-) were similarly disturbed with inert sticks. We decided to test sediment nutrient enrichment rather than column nutrient enrichment because we had tested the latter in the context of a previous study, and we did not find any effect on epiphyte load or the associated epifauna at our site (see Duffy *et al.*, 2015).

Light was reduced using fiberglass screens of 1.25 × 1.25 m, suspended at ±30 cm above the sediments. Photosynthetically active radiation (PAR) was measured underwater within the first few centimeters at low tide with an LI-192 sensor (LI-COR). We measured PAR under six screens at their center (5 to 9 stable measures averaged), and since we only had one sensor, we immediately measured PAR without screen as a control for each of those six screens (5 to 9 stable measures averaged). PAR reduction was then calculated using the mean PAR attenuation between each of those six screens and their respective control. Mean PAR reduction was 68 ± 4%. Screens were kept in place for 19 days and were cleaned once a week to prevent any fouling.

Eelgrass shoot density reduction was applied in the first week of July (Period 0, see below). Two weeks later, we applied the sediment nutrient enrichment and shading (Period 1).

2.4 Sampling and sorting

Sampling occurred in four different periods from July to September 2015: Period 0 (July 1–4, eelgrass shoot density reduction), Period 1 (July 16–20, nutrients and shading added two weeks after the start of the experiment), Period 2 (August 5–7, shading removed five weeks after the start of the experiment), and Period 3 (September 10–12, 10 weeks after the start of the experiment). Data were collected by direct measures in the field and by sample collections followed by lab analysis.

2.4.1 Eelgrass measurements

Initial eelgrass shoot density was measured using 20-cm diameter rings (3 estimates/plot; Period 0). Eelgrass shoot density was thereafter evaluated only in eelgrass ambient plots (D-) (Periods 2 and 3).

We estimated the relative leaf elongation rate (RLE) of eelgrass once as a proxy for growth (in Periods 1 to 2) using five shoots per plot that were each marked with a reference hole at the top of the sheath using a pushpin. After 19 days, we collected the shoots and brought them back to the lab where leaf elongation was measured as the displacement of the mark relative to the reference mark on the oldest nongrowing leaf (Olesen et Sand-Jensen, 1994). Total leaf elongation was then divided by sheath length and number of days of elongation.

Analyses of non-structural carbohydrates were performed on four vegetative shoots pooled together, including their roots and rhizomes, that had been randomly collected from each plot, vacuum-sealed in plastic bags, and stored at -20 °C. Shoots were quickly washed under running water, stored at -80 °C for a week to stop all enzymatic activity, and then freeze-dried for five days. All samples (above- and belowground separately) were then ground into a fine powder (1 μm) by using a ball mill (Retsch MM200 Vibrant) for 5 min and stored at -20 °C until analysis. As root material was insufficient (<5 mg), the root material was pooled with rhizomes for analysis [Root-rhizome]. Soluble sugar extraction was performed on 40 mg of dried powder (dried at 50 °C overnight) of shoots [Shoots] and root-rhizome (Chow et Landhäusser, 2004; Deslauriers *et al.*, 2018). Soluble sugars were extracted three times with 80% ethanol at room temperature (4 mL) and centrifuged after each extraction (2000 g, 6 minutes). The supernatant was collected and treated with phenol (2%) and sulfuric acid (96%). The absorbance of the sample was measured at 490 nm with a UV-VIS spectrophotometer, and the concentration of soluble sugars was converted to mg per g of dry weight ($mg \cdot g^{-1}_{dw}$) using glucose standard curves. Enzymatic digestion of the remaining pellet was used to determine starch concentrations (Bellasio et al. 2014). We added α-amylase (3000 U/L, Megazyme) and amyloglucosydase (3260 U/L, Megazyme) to split the glucose chains and then chemically treated the pellet with a reagent and sulfuric acid (75%). The absorbance was read at 530 nm with a UV-VIS spectrophotometer. Starch concentrations were then converted to mg per g dry weight ($mg \cdot g^{-1}_{dw}$).

2.4.2 Epibenthic community measurements

We estimated the epiphyte load on eelgrass using eelgrass leaves scraped with a microscope slide under filtered seawater. During Period 1, we selected and scraped the leaves of three randomly selected shoots. We then filtered the water containing the scraped epiphytes through preweighed GF/F filters, and we assessed the epiphyte load

as the dry weight of epiphytes divided by the dry weight of the collected scraped shoots; $mg \cdot g^{-1}_{dw}$). For Period 2, our main sampling period, we used chlorophyll extraction, as this method is more precise. We scraped the leaves of one randomly selected shoot; we then filtered the water containing the epiphytes on GF/F filters that were then kept wrapped in aluminum foil at -80 °C until analysis. Epiphyte load was assessed using chlorophyll extraction with 90% acetone, following Parsons *et al.* (1984). For logistical reasons, we did not determine epiphyte load for Period 3.

We collected epifaunal macroinvertebrate communities of the eelgrass meadow using mesh bags (~500 µm, diameter ~18 cm); samples were collected during ebb tide (Period 1, 2, and 3). The opened mesh bag was pushed on eelgrass canopy towards the sediments, then closed right above the sediment surface. Once closed, eelgrass shoots sticking out were cut with scissors and the mesh bag placed in an identified plastic bag. This method excludes organisms that are in direct contact with the sediment interface. We separated fauna from eelgrass shoots in the laboratory by shaking the shoots under freshwater. We then collected the epifauna with a 500-µm sieve and preserved the epifauna in 70% ethanol for further sorting. Individuals were identified to the smallest taxon possible, usually species, and were then passed through a nested series of sieves (8.0, 5.6, 4.0, 2.8, 2.0, 1.4, 1.0, 0.71, 0.5 mm) to estimate the ash-free dry weight (AFDW) biomass using corrected empirical equations from Edgar (1990). Shoots were dried and weighed to standardize organism abundances by eelgrass biomass (individuals by grams of dry weight of *Zostera marina*; $N \cdot g^{-1}_{dw}$) as total abundance is correlated with *Z. marina* biomass (see Orth *et al.*, 1984).

2.5 Data analysis

We used an orthogonal three-way analysis of variance (ANOVA) for each relevant period to test for simple and interactive effects of our three fixed factors (density reduction, nutrient enrichment, shading) and their interaction on eelgrass shoot density (2-way analysis only), RLE, soluble sugars and starch, epiphyte load, epifaunal standardized abundance ($N \cdot g^{-1}_{dw}$, see above), species richness (S), Simpson's diversity index ($1-\lambda$), Pielou's evenness (J'), and assemblage structure and composition. We preferred not to first perform a repeated measures analysis as sampling was destructive and experimental conditions varied between the periods. We ran a Tukey's HSD multiple comparison test on the significant interactions of factors. We verified assumptions of normality and variance homogeneity by examining the graphs of the residuals (Montgomery *et al.*, 2012; Quinn et Keough, 2002); standardized abundances were fourth-root transformed, while epiphyte load and soluble sugars were square-root transformed prior to the analyses.

We characterized the nature of each significant interaction effect as either antagonistic, synergistic, additive, or dominant (sensu Côté et al. 2016) using a calculated 95% confidence limit of the expected additive effect (Darling et Côté, 2008). To do so, we measured the response to single stressor compare to no stressor, calculated the expected additive response, then compared the cumulative response to both single stressor and expected additive responses. If the cumulative response was not different from the additive model, we considered there was no interaction and thus the response was classified *additive*. If the cumulative response was lower than the expected additive, it was classified as an *antagonistic* response unless the response was the same as one of the single stressors, then it was classified as a *dominance*. If the response was higher than the expected additive, it was classified as *synergistic*. Finally, if the response was

lower and of opposite response sign, it was classified as *negative synergistic*. See Côté *et al.* (2016) and Galic *et al.* (2018) for further details and examples regarding this terminology.

To examine the effects on epifaunal assemblage structure (based on Bray-Curtis similarities), we ran a permutational multivariate analysis of variance (PERMANOVA; Anderson *et al.*, 2008) with 9999 permutations using the same design described above (3 fixed factors, 2 levels each). Standardized abundance data were pretreated using dispersion weighting (Clarke *et al.*, 2006) by treatment (8 levels, combination of the three factors applied to one plot) in each period and then were transformed by square root (abundance structure) based on the shade plot method (Clarke *et al.*, 2013). The same data were transformed into presence-absence data for the effects on assemblage composition (species identity). We evaluated the contribution of each taxon to the observed similarities/dissimilarities among treatments using a similarity percentage analysis (SIMPER).

Univariate analyses were run using JMP v.11.0, while multivariate analyses were run using PRIMER+PERMANOVA v.7.0.1 (Anderson *et al.*, 2008; Clarke et Gorley, 2015). We used a significance level of $\alpha = 0.05$ for all statistical analyses and marginally significant results were carefully considered.

2.6 Results

The initial average (±SE) density of *Zostera marina* was 664 ± 12 shoot·m^{-2} with an average aboveground biomass of 122.8 ± 3.6 g_{dw}·m^{-2} in early July. We identified a total of 31 taxa, including five species of gastropods, five species of bivalves, seven species

of amphipods, and three species of isopods (see *Annexe B: Table 5.4* for full list). The most abundant species was the periwinkle *Littorina saxatilis*.

2.6.1 Stressors effects on eelgrass

Our experimental treatments (eelgrass shoot density reduction, sediment nutrient enrichment, shading, and the combined treatments) influenced some characteristics of *Z. marina* only in Period 2 (cf. Table 2.1 and *Annexe B: Table 5.5 and 5.6* for results of the other sample periods).

Shading and enrichment treatments showed a significant interaction on eelgrass shoot density (Table 2.1b; Tukey HSD; see Fig. 2.2b). Shading treatment reduced the number of *Z. marina* shoots in plots by 14% in the absence of enrichment (N-S+; Fig. 2.2b) while enrichment increased *Z. marina* density by 18% in the absence of shading (N+S-, Fig. 2.2b). The combined effect (N+S+) was dominated by the effect of shading as the response size was statistically comparable to the effect of shading alone (N-S+, Fig 2.2b).

Density reduction and shading both influenced the *Z. marina* RLE, but they had no significant interaction (Table 2.1a). Density reduction increased RLE, while shading reduced RLE, both by about 20% (Table 2.1a; Fig. 2.2a,e). The interaction type of these two stressors was additive since they canceled each other when they were both present—note the absence of interactions in Table 2.1a and see *Annexe B: Fig. 5.2*.

Table 2.1. Summary of the analyses of variance (ANOVAs) showing the effects of eelgrass shoot density reduction (De), sediment nutrient enrichment (Nu), and shading (Sh) factors on (a) relative leaf elongation rate (day^{-1}; RLE), (b) eelgrass shoot density ($shoot \cdot m^{-2}$; only effects of Nu and Sh), and (c) epiphyte load as chlorophyll *a* concentration ($\mu g_{chl\ a} \cdot g^{-1}_{dw}$) during Period 2 (see 'Methods'). Significant values are shown in **bold**.

	df	*F*-ratio	*p*
a) RLE			
De	1	23.66	**0.0001**
Nu	1	0.45	0.5055
Sh	1	27.73	**0.0001**
De × Nu	1	0.75	0.3925
De × Sh	1	0.01	0.9046
Nu × Sh	1	0.08	0.7824
De × Nu × Sh	1	3.51	0.0702
Residual	32		
b) Eelgrass shoot density			
Nu	1	3.58	0.0768
Sh	1	51.89	**0.0001**
Nu × Sh	1	10.63	**0.0049**
Residual	16		
c) Epiphyte load			
De	1	0.00	0.9837
Nu	1	3.10	0.0877
Sh	1	19.57	**0.0001**
De × Nu	1	0.02	0.8853
De × Sh	1	0.54	0.4668
Nu × Sh	1	0.05	0.8327
De × Nu × Sh	1	0.06	0.8075
Residual	32		

Shading reduced non-structural carbohydrates in shoots and rhizomes by about 39% for starch and 61% for soluble sugars (Table 2.2; Fig. 2.2c,d,g,h; see *Annexe B: Table 5.7 and Fig. 5.2*). Shading and density reduction had two significant interactions for soluble sugars in shoots and starch contents in root-rhizomes (Table 2.2 Reducing eelgrass shoot density marginally increased (Tukey HSD, $p = 0.0845$) soluble sugars in shoots by 44%, but only in the absence of shading (D+S-, Fig. 2.2c).). Shading dominated the effect of eelgrass shoot density reduction as those two stressors together (D+S+) had a response of equal magnitude as shading alone (D-S+, Fig. 2.2c). Shading and density reduction interacted on root-rhizome starch as well, albeit in a negative

synergistic manner: D+S- had the highest concentrations, D+S+ had the lowest (Fig. 2.2h; see *Annexe B: Fig. 5.4d and 5.3*).

The starch concentration in shoots from D-N-S– and D-N+S- treatments (pooled; average ± SE; n = 10) showed very low values, with 0.85 ± 0.1 $mg \cdot g^{-1}_{dw}$ in shoots and 0.27 ± 0.1 $mg \cdot g^{-1}_{dw}$ in rhizomes, respectively. In contrast, average soluble sugar values were 28.7 ± 1.9 $mg \cdot g^{-1}_{dw}$ in shoots and 86.7 ± 11.3 $mg \cdot g^{-1}_{dw}$ in the root-rhizome.

Table 2.2. Summary of the analyses of variance (ANOVAs) showing the effects of eelgrass shoot density reduction (De), sediment nutrient enrichment (Nu), and shading (Sh) factors on the soluble sugar and starch contents of shoots and root-rhizomes in Period 2 (see 'Methods'). Significant values are shown in **bold**.

		Shoots		Root-rhizomes	
	df	***F*-ratio**	*p*	***F*-ratio**	*p*
a) Soluble sugars					
De	1	1.17	0.2869	0.14	0.7132
Nu	1	0.01	0.9268	0.06	0.8086
Sh	1	60.66	**0.0001**	35.90	**0.0001**
De × Nu	1	0.65	0.4261	0.63	0.4323
De × Sh	1	5.80	**0.0220**	3.16	0.0849
Nu × Sh	1	0.11	0.7385	0.01	0.9105
De × Nu × Sh	1	0.14	0.7067	1.29	0.2653
Residual	32				
b) Starch					
De	1	0.62	0.4369	0.01	0.9221
Nu	1	2.14	0.1529	0.29	0.5920
Sh	1	5.58	**0.0244**	3.82	0.0595
De × Nu	1	0.01	0.9111	0.19	0.6700
De × Sh	1	0.19	0.6639	4.22	**0.0481**
Nu × Sh	1	1.89	0.1784	0.06	0.8129
De × Nu × Sh	1	0.99	0.3282	0.02	0.8861
Residual	32				

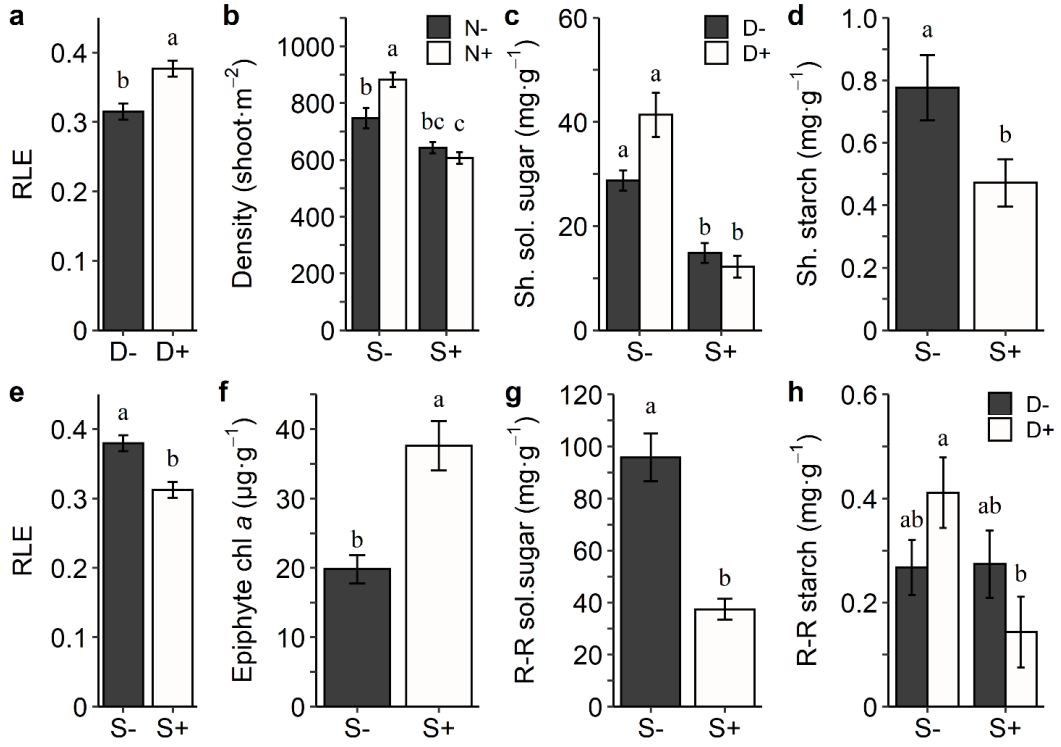

Figure 2.2. Mean (±SE) values of (a, e) eelgrass relative leaf elongation rate (day^{-1}; RLE), (b) eelgrass shoot density, soluble sugars in (c) shoots and (g) root-rhizomes, starch in (d) shoots and (h) root-rhizomes, and (f) epiphyte load on shoots (chlorophyll *a*; µg·g$^{-1}_{dw}$). Values are from Period 2. Gray and white bars are the respective treatments with – stressor absent, + stressor present; D: eelgrass shoot density reduction, N: sediment nutrient enrichment, S: shading. The number of replicates used to obtain the averages was $n = 20$ in a, d, e, f, and g; $n = 10$ in c and h; and $n = 5$ in b. Different letters above bars indicate significant differences ($p < 0.05$, Tukey HSD).

2.6.2 Stressor effect on associated epibenthic communities

Eelgrass shoot density reduction, sediment nutrient enrichment, and shading influenced the invertebrate assemblages in various ways (Table 2.3, 2.4 and Figure 2.3; see *Annexe B: Table 5.8a and Fig. 5.4* for a comparison of the raw abundances). Note that there was a positive correlation between the biomass of *Z. marina* and epifaunal abundance (all periods pooled; $r = 0.530345$; $p < 0.0001$; $n = 120$)). In contrast, the epiphyte load was affected only by shading. The effects of enrichment or shading were only observed in Period 2 (see Table 2.3, 2.4; see *Annexe B: Table 5.5 and 5.6*).

Shading doubled the epiphytic load on the eelgrass shoots (chlorophyll *a*, Table 2.1c; Fig. 2.2f). Epiphytic chlorophyll *b* showed a similar pattern as chlorophyll *a* with a respective increase of 128% and 89% (data not shown). The epiphytic load was not affected by the other treatments.

Standardized abundance and Simpson's diversity were higher in density-reduced plots (D+) than in the density ambient plots (D-) throughout the entire experiment (Table 2.3a,d; Fig. 2.3a,d, showing Period 2). Standardized abundance increased respectively by 80%, 109%, and 25% from Period 1 to Period 3 in the reduced density plots (Fig. 2.3a, showing Period 2). Eelgrass shoot density reduction had no effect on richness (Table 2.3b), but it increased evenness in Period 1 and Period 3 (by 52% and 19% respectively; Table 2.3c, Fig. 2.3c, showing Period 1). Eelgrass shoot density reduction affected the abundance structure of epibenthic assemblages throughout the entire experiment (Table 2.4a, see *Annexe B: Fig. 5.5a,c,e*), but it did not affect their composition (Table 2.4b). Details for those species most affected by our treatments are provided in *Annexe B: Table 5.9-5.13* along with an additional description of the results (see *Annexe B: 5.2.4 Supplementary results: effects of treatments on species*).

Standardized abundance, diversity, and richness were lower in nutrient-enriched plots (N+) than in ambient nutrient plots in Period 2, while they had no effect on evenness (N-; Table 2.3a-d, Fig. 2.3e,b,g). Standardized abundance, diversity, and richness were respectively 23%, 14%, and 22% lower in enriched plots (Fig. 2.3e,b,g). Enrichment influenced the structure and species composition (Table 2.4, see *Annexe B: Fig. 5.5b*). Details of those species that most contributed to the differences in structure between the enrichment treatments are listed in *Annexe B: Table 5.12* along with an additional description of the results (see *Annexe B: 5.2.4 Supplementary results: effects of treatments on species*).

Shading did not influence total abundance in terms of counts or richness (Table 2.3a,b), while it increased evenness by 27% (Table 2.3c, Fig. 2.3f) and diversity by 35% (Table 2.3d, Fig. 2.3h) in Period 2. Shading influenced the abundance structure of assemblages but not in terms of composition (Table 2.4, see *Annexe B: Fig. 5.5d*). Details of those species that most contributed to differences in structure between the shading treatments are listed in *Annexe B: Table 5.13*. Even though shading did not decrease total abundance in counts, it decreased total biomass by about 25% (mean ± SE, S-: 21.4 ± 1.7 and S+: 15.7 ± 1.7; $F_{1,32} = 5.7958$, $p = 0.0220$). Biomass results for all other treatments were, however, comparable to abundance in counts.

Two interactions were significant in Period 2: density reduction × nutrient enrichment on richness (Table 2.3b; Fig. 2.3b) and density reduction × shading on evenness (Table 2.3c; Fig. 2.3f). Nutrient enrichment decreased richness only when combined with the density ambient treatment (D-N+); the combined effect of nutrient enrichment and density reduction (D+N+) was dominated by the density reduction effect (Fig. 2.3b). In a similar way, shading increased evenness only when combined with the density ambient treatment (D-S+); the combined effect of shading and density reduction (D+S+) was antagonistic as both stressors increased evenness. Although their interaction increased evenness, the response was less than the effect of shading but greater than the effect of eelgrass shoot density reduction (Fig. 2.3f). All interacting factors are summarized in Table 2.5.

Table 2.3. Summary of the analyses of variance (ANOVAs) showing the effects of eelgrass shoot density reduction (De), sediment nutrient enrichment (Nu), and shading (Sh) factors on standardized abundance ($N \cdot g^{-1}_{dw}$), richness, Pielou's evenness, and Simpson's diversity index of associated epifauna for all sampling periods. Significant values are shown in **bold**.

		Period 1		Period 2		Period 3	
	df	***F*-ratio**	*p*	***F*-ratio**	*p*	***F*-ratio**	*p*
a) Standardized abundance							
De	1	12.79	**0.0011**	29.95	**0.0001**	4.14	0.0504
Nu	1	0.49	0.4900	4.94	**0.0335**	2.96	0.0950
Sh	1	0.14	0.7139	1.48	0.2326	0.80	0.3784
De × Nu	1	0.02	0.8760	0.26	0.6128	0.46	0.5039
De × Sh	1	3.10	0.0880	0.02	0.8935	0.44	0.5138
Nu × Sh	1	0.86	0.3600	0.09	0.7602	0.01	0.9156
De × Nu × Sh	1	1.36	0.2526	0.42	0.5205	0.92	0.3458
Residual	32						
b) Richness							
De	1	0.14	0.7077	0.45	0.5541	2.63	0.1146
Nu	1	0.14	0.7077	5.31	**0.0279**	3.67	0.0642
Sh	1	0.02	0.3839	1.99	0.1675	0.02	0.8837
De × Nu	1	0.78	0.9004	4.65	**0.0387**	0.02	0.8837
De × Sh	1	1.92	0.1750	0.05	0.8250	0.20	0.6612
Nu × Sh	1	0.78	0.3839	0.27	0.6064	0.54	0.4664
De × Nu × Sh	1	0.14	0.7077	0.01	0.9412	1.76	0.1939
Residual	32						
c) Evenness							
De	1	21.10	**0.0001**	0.61	0.4396	11.50	**0.0019**
Nu	1	0.78	0.3851	0.02	0.8775	0.07	0.7954
Sh	1	0.01	0.9132	21.25	**0.0001**	0.05	0.8219
De × Nu	1	0.19	0.6673	0.46	0.5043	3.50	0.0706
De × Sh	1	0.18	0.6758	6.72	**0.0143**	0.01	0.9355
Nu × Sh	1	0.52	0.4384	1.84	0.1847	1.56	0.2213
De × Nu × Sh	1	0.00	0.9594	0.03	0.8657	2.35	0.1347
Residual	32						
d) Diversity							
De	1	14.78	**0.0005**	4.93	**0.0335**	14.85	**0.0005**
Nu	1	0.17	0.6857	4.87	**0.0346**	0.58	0.4505
Sh	1	0.04	0.8400	23.07	**0.0001**	0.60	0.4443
De × Nu	1	0.00	0.9807	3.64	0.0654	4.09	0.0516
De × Sh	1	1.04	0.3166	3.94	0.0556	0.00	0.9441
Nu × Sh	1	1.58	0.2173	0.32	0.5742	3.11	0.0873
De × Nu × Sh	1	0.00	0.9559	0.18	0.6727	1.49	0.2311
Residual	32						

Table 2.4. Summary of permutational analysis of variance (PERMANOVAs) showing the effects of eelgrass shoot density reduction (De), sediment nutrient enrichment (Nu), and shading (Sh) factors on the structure in standardized abundance ($N \cdot g^{-1}_{dw}$) and composition (transformed into presence-absence) of associated epifauna for all sampling periods. Significant values are shown in **bold**.

		Period 1		Period 2		Period 3	
	df	Pseudo-*F*	*p* perm	Pseudo-*F*	*p* perm	Pseudo-*F*	*p* perm
a) Structure							
De	1	4.07	**0.0020**	5.39	**0.0004**	5.96	**0.0002**
Nu	1	0.37	0.9023	2.64	**0.0262**	1.27	0.2877
Sh	1	0.31	0.9219	3.56	**0.0052**	1.08	0.3922
De × Nu	1	0.20	0.9674	1.15	0.3232	0.62	0.7154
De × Sh	1	1.18	0.3139	1.02	0.3996	1.01	0.4335
Nu × Sh	1	0.87	0.5136	0.37	0.8887	0.98	0.4608
De × Nu × Sh	1	0.69	0.6599	1.29	0.2590	1.16	0.3355
Residual	32						
b) Composition							
De	1	1.92	0.1092	1.27	0.2931	2.43	0.0701
Nu	1	0.11	0.9347	3.14	**0.0239**	1.05	0.3899
Sh	1	0.69	0.6149	2.45	0.0572	1.33	0.2934
De × Nu	1	0.33	0.8441	1.69	0.1668	1.29	0.3167
De × Sh	1	1.44	0.2335	0.83	0.5133	Neg.	
Nu × Sh	1	0.44	0.7755	0.64	0.6352	0.32	0.7775
De × Nu × Sh	1	0.76	0.5759	1.65	0.1795	0.22	0.8304
Residual	32						

Neg.: negative values. 9999 permutations were used.

Table 2.5. Summary of the type of interaction effect among eelgrass shoot density reduction (De), sediment nutrient enrichment (Nu), and shading (Sh) treatments.

	Enrichment (Nu)	**Shading (Sh)**
De	• **Dominance by De** on richness	• **Dominance by Sh** on the soluble sugars of shoots • **Negative synergism** on the starch of the root-rhizome • **Antagonism** on evenness • **Additive** on relative leaf elongation rate
Nu		• **Dominance by Sh** on eelgrass shoot density

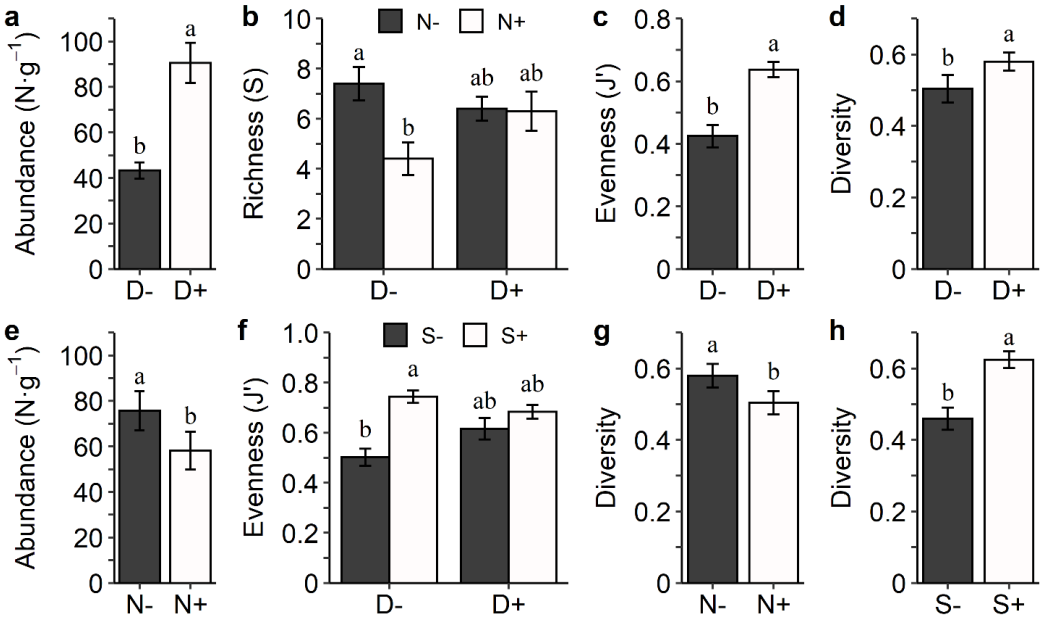

Figure 2.3. Mean (±SE) values of epifaunal (a, e) abundances standardized per shoot dry weight ($N \cdot g^{-1}_{dw}$), (b) species richness, (c, f) Pielou's evenness, (d, g, h) Simpson's diversity. Values are from Period 2 except (c) which is from Period 1. Gray and white bars are the respective treatments with: – stressor absent, + stressor present; D: eelgrass shoot density reduction, N: sediment nutrient enrichment, S: shading. The numbers of replicates used to obtain the averages were $n = 20$ in (a), (c), (d), (e), (g) and (h); $n = 10$ in (b) and (f). Different letters above the bars indicate significant differences ($p < 0.05$).

2.7 Discussion

The aim of this study was to understand how reduced eelgrass density, nutrient enrichment, and decreased light influence eelgrass structure and physiology and the associated faunal assemblages. More importantly, we wanted to explore potential interactions among stressors as they often occur simultaneously. As predicted, shading had the greatest effect on eelgrass. Interestingly, shading reduced plant growth (RLE), reserves of non-structural carbohydrates, and shoot density. Eelgrass shoot density reduction, on the other hand, sustained higher epifaunal densities and increased the

RLE. Sediment nutrient enrichment increased eelgrass shoot density but decreased epifaunal richness, diversity, and total abundance. Nevertheless, we consider that our studied eelgrass bed was resilient to the effects of shading and sediment nutrient enrichment stressors as all measured effects were no longer significantly different five weeks after removing the shading. A reduced eelgrass shoot density continued to have an effect, although our results indicated that the eelgrass was on its way to recovery. Our initial hypotheses were partly confirmed as we saw non-additive interactions, a clear physiological response in eelgrass tissues, and changes in biodiversity related to our induced stressors.

2.7.1 Stressor effects on eelgrass

Of all three main applied stressors, shading most affected eelgrass physiology. Reduced access to light in shaded plots likely reduced the levels of photosynthesis, as shown by decreased values of non-structural carbohydrates—in the form of both sugars and starch—and reduced plant growth (RLE). Previous studies on seagrasses have reported a reduction in non-structural carbohydrates and growth under shading conditions (e.g., Collier *et al.*, 2009; Salo *et al.*, 2015). Our observed 61% reduction in soluble sugars under shading falls within the range (40%–85%) of other studies (Burke *et al.*, 1996; Silva *et al.*, 2013). However, our observed shading effect on starch concentrations in eelgrass, a 39% reduction, is much less common; for example, Burke *et al.* (1996) did not observe any effect of shading on starch concentrations, while Silva *et al.* (2013) measured a decrease in starch only in shoots subjected to 75% shading.

On the other hand, a reduced eelgrass shoot density increased growth and most non-structural carbohydrates under natural light conditions (D+S-). This could be explained by the reduction of self-shading as it is related, among other seagrass characteristics, to shoot density (Enriquez et Pantoja-Reyes, 2005). Other studies have demonstrated an increase in growth due to a reduced shoot density or aboveground biomass (e.g.,

Rattanachot *et al.*, 2016). Although RLE was also higher in eelgrass shoot density-reduced plots under shading (D+S+, see *Annexe B: Fig. 5.2e*), non-structural carbohydrate concentrations were the lowest (not significantly different than D-S+, see *Annexe B: Fig. 5.2a-d and 5.3*). We argue that such decrease in carbohydrates can be attributed not only to shading but also to the lack of a transfer of carbon resources between shoots via the rhizome system; this is induced by the disconnection between the rhizomes, and thus shoots, that occurred when we applied the eelgrass shoot density reduction treatment (Period 0, D+). Burke *et al.* (1996) did not find any effect from the cutting of rhizomes on non-structural carbohydrates under natural light conditions; however, they did not control for the severing of the rhizome under shading, which reduced sugar concentrations. To our knowledge, there are no studies of carbohydrate translocation between ramets in *Z. marina*. Marbà et al. (2006; 2002), however, observed carbon translocation between ramets in eight seagrass species; carbon translocation is therefore quite probable in *Z. marina* as well. In any case, our results indicate that the transfer of resources among shoots may become important under reduced light conditions.

In *Z. marina*, non-structural carbohydrates are usually dominated by soluble sugars (Eriander, 2017; Vichkovitten *et al.*, 2007) and, like other seagrasses, their pool of carbohydrate is mostly constituted of sucrose (e.g., Touchette et Burkholder, 2000; Vichkovitten *et al.*, 2007). Sucrose concentrations are normally higher in rhizomes than in shoots and represent up to 90–100% of soluble sugars (Drew, 1983; Eriander, 2017; Touchette et Burkholder, 2000). In our study, the concentrations of soluble sugars were higher in root-rhizomes, but these concentrations (average range 30–85 $mg \cdot g^{-1}_{dw}$) were much lower than concentrations found in other studies (from 100 to 350 mg·g-1dw in shoots and from 100 to 500 mg·g-1dw in rhizomes; e.g., Drew, 1983; Eriander, 2017; Salo *et al.*, 2015). Similarly, our measured concentrations of starch (< 1 $mg \cdot g^{-1}_{dw}$) were also much lower than levels found in other studies (from 7 to 14 mg·g-1dw in shoots

and rhizomes; e.g., Eriander, 2017; Silva *et al.*, 2013). Such variation in carbohydrate concentrations depends of species, salinity, temperature, season, light exposition, depth, genetics, and the extraction method (Salo *et al.*, 2015; Sorensen *et al.*, 2018; Touchette et Burkholder, 2000). Overall, shoots showed very low starch concentrations (0.5–3%), values which are similar to the 2% measured in rhizomes by Eriander (2017). Starch reserves were slightly higher in shoots than in root-rhizomes, which can be explained by the presence of transient starch stored in shoot chloroplasts during the day for consumption during the night (MacNeill *et al.*, 2017).

We do not know as of yet the seasonality of non-structural carbohydrates at our site. However, other studies have reported higher carbohydrate concentrations in June and September and lower concentrations in winter and July–August (Burke *et al.*, 1996; Touchette et Burkholder, 2007). This suggests that we sampled our shoots when they were at their lowest reserve levels.

Shading reduced eelgrass shoot density, as has been reported by many previous studies on seagrasses (e.g., Collier *et al.*, 2009; Lee et Dunton, 1997; Wong *et al.*, 2019). Shoot loss under shading can occur in as fast as 18 days for *Z. marina* (Backman et Barilotti, 1976). Similarly, a decrease in shoot density and biomass is commonly observed with an increase in water depth (e.g., Middelboe *et al.*, 2003; Olesen *et al.*, 2002). This could indicate a self-thinning mechanism in response to light reduction to diminish self-shading and, in turn, affect habitat complexity and the associated community (see below).

Nutrient enrichment increased shoot density in the absence of shading at our site. An increase in shoot density could be the first response to enrichment in a limiting environment (Short, 1983 and references therein), suggesting that our site may have a

nutrient limitation for eelgrass. Other studies on seagrasses reported opposite effects of enrichment on shoot density; the responses depended on the initial nutrient state (e.g., Orth, 1977; Short, 1983, 1987). Typically, studies report an increased shoot growth in limiting environments (e.g., Bulthuis et Woelkerling, 1981; Lee et Dunton, 2000). Growth (measured as RLE here) was not affected by enrichment in our case. Perhaps our enrichment treatment was too short in duration to increase shoot growth, although long enough to increase shoot density. While enrichment under no shading increased shoot density, enrichment under shading decreased it.

2.7.2 Stressor effect on associated epibenthic communities

Of all main effects, only shading affected epiphyte load. We observed shading to increase epiphytic algae; nevertheless, most studies report a decrease of epiphytic algae under shaded conditions (e.g., Blake et Duffy, 2016; Collier *et al.*, 2009). The increase in epiphytic algae at our site could be explained by the observed concomitant reduction in density of the dominant grazer *Littorina saxatilis* and a reduction in the overall invertebrate biomass, including other grazer species (see below).

Among our applied stressors, a reduced eelgrass shoot density has the greatest effect on assemblage structure, abundance, and diversity of epibenthic macroinvertebrates. Density-reduced plots recorded a higher standardized abundance, evenness, and diversity as well as a different abundance structure. These differences were mainly due to an increase in the standardized abundance (by gram of eelgrass) of periwinkles, isopods, and gammarids in the density-reduced plots. A possible explanation would be that more individuals remained and shared less available space among the leaves of the remaining plants. Part of the mechanism allowing this scenario is the increased light penetration due to less canopy that most likely increased the availability of food items, such as epiphytic algae. Epiphyte load values were not lower despite a greater grazer concentration or higher despite a better access to light. Epiphytes can, in fact, affect the

distribution of epifauna abundance via their trophic role: more epiphytes increase the abundance of grazers, while the abundance of filter feeders remains unchanged (Bologna et Heck, 1999; Gartner *et al.*, 2013). That the relative abundance of the epiphytic grazer *L. vincta* was higher in eelgrass-reduced plots, but not for *Mytilus* spp., supports this idea. Our results highlight the importance of eelgrass as a habitat-forming species even at low density (reduced shoot number) within a meadow to help sustain high epifaunal density and diversity.

Changes in invertebrate assemblages related to higher nutrient concentrations are caused generally by an increase in algae (macroalgae and epiphytic algae), organic matter, and hypoxia (e.g., Gil *et al.*, 2006; Schmidt *et al.*, 2017), a scenario that we did not observe. Nevertheless, in the enriched (N+) plots of Period 2, we observed a lower abundance for two thirds of the species as well as a lower diversity and richness, especially when density was left untouched (D-N+). Indeed, we noted a significant decrease in the abundance of the gastropods *L. saxatilis* and *E. truncata*, and the amphipod *P. holbolli* (see *Annexe B: Table 5.12*) *E. truncata* was absent from some of the enriched plots, while *P. holbolli* was absent in more than half of the enriched plots. This reduction in grazers cannot be easily explained and did not seem to have a positive effect on epiphytic algae as we did not observe a difference in epiphyte load. Possibly, the increase in eelgrass shoot density was enough to intensify self-shading, which could have affected epiphytic algae and the grazer assemblage. We saw no nutrient effect during the last period, and this observation is probably due to the dissolution of the nutrient sticks between Periods 1 and 2 (personal observations) followed by a rapid recovery. With a notable exception, enrichment seemed to affect the distribution of *Mytilus* spp. as there were 50% fewer mussels in the enriched plots in Period 3 ($F_{1,32} = 4.5967$, $p = 0.0397$).

Our results suggest that under conditions of reduced light, changes in epiphytic algae affected the epifaunal assemblages. After 19 days of shading, smaller individuals were found under shading than under the natural light conditions as shown by a decrease in the standardized biomass without an effect on standardized abundance. This reflects a proportional increase of small species under shaded conditions, such as the gastropod *E. truncata*, the isopod *Edotia triloba*, and juvenile gammarids, while the abundance of *Littorina saxatilis* decreased (see *Annexe B: Table 5.13*). The compositional changes in species are also shown by an increase in evenness (and then diversity values) under shading. The reduced abundance of *L. saxatilis* under shading is likely not a direct effect of light attenuation; it may be related to shading causing a decrease in diatoms, the preferred food item of *L. saxatilis* (e.g., Otero-Schmitt *et al.*, 1997), which in turn decreased *L. saxatilis* abundance to trigger an increase in total epiphytic algae. Such an increase in epiphytic algae may have attracted other epifaunal grazer species (see Gil *et al.*, 2006 for results of epifauna change through epiphyte change). Other studies have shown a reduction in faunal total abundance under shading conditions due to a reduction of epiphytic algae or habitat complexity (Edgar et Robertson, 1992; Gartner *et al.*, 2010). In our study, however, we cannot disentangle the direct effect of light reduction from the presence of screens above the plots. The screens could attract or repulse some species as well as alter the interactions among species (e.g., predation), modify water movements, and increase drifting macroalgae such as *Laminaria* spp. in the vicinity of sampled plots, even plots having regular maintenance. Gartner *et al.* (2010) observed more fish under shading treatments in seagrasses, although the fish did not appear to affect the abundance of epifauna directly. Nevertheless, the lack of shading effects during the final period indicates a rapid recovery of the assemblages. Such a rapid recovery of eelgrass bed habitat would be an advantage in turbid events that occur in coastal areas.

2.8 Concluding remarks

Our results suggest that eelgrass beds can be resistant to multiple disturbances and stressors as no effects were observed on measured variables when all our treatments were applied simultaneously (D+N+S+). The studied meadow also showed resilience to multiple stressors as during the study, most observed effects were undetectable at the end of the experiment. The nature of stressors and their interactions varied in their influence on species, suggesting that other stressors, alone or in combination with others, may also affect communities in an unpredictable manner. Thus, further manipulative studies are required to improve our understanding of the effects of multiple stressors on assemblages and habitat-forming species.

Our results indicate that most of the epifaunal assemblage and its diversity are linked to habitat availability and epiphytic algae food resources. Shading affects eelgrass by reducing leaf elongation, non-structural carbohydrate content, and shoot density. Density-reduced plots sustained high epifaunal densities, thereby illustrating the importance of eelgrass as a habitat-forming species. We also observed that the nutrient enrichment of sediments increased shoot density, although it negatively affected epifaunal biodiversity. Most of our treatments did not affect species richness, confirming that complementary metrics (e.g. diversity related indices, univariate and multivariate data, see Cimon et Cusson, 2018) are required to document the effects of stressors on community stability.

Studies involving multiple stressors are scarce (e.g., Cimon et Cusson, 2018; Moreno-Marín *et al.*, 2018), although they are essential to document potential trajectories and types of interaction following multiple disturbances/stressors. Here, we observed additive, antagonistic, and negative synergistic interactions among our treatments,

while most interactions highlighted a dominance by one stressor over another. Our results testify to the importance of field experiments that include multiple disturbance and stressors and their interactions to estimate the effects on community assemblages, as well as the importance of proper testing to ascertain cumulative effects rather than assuming additivity.

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CHAPITRE III
SITE DEPENDENT EFFECTS OF PROXIMITY TO PATCH EDGE AND EELGRASS COMPLEXITY ON EPIFAUNAL COMMUNITIES WITHIN *ZOSTERA MARINA* L. MEADOWS

In preparation

Title: Site dependent effects of proximity to patch edge and eelgrass complexity on epifaunal communities within *Zostera marina* L. meadows

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Keywords: edge effect, foundation species, field experimentation, habitat complexity, manipulative study

3.1 Abstract

Climate change, habitat loss, and fragmentation are driving ecologists to study the relationship between habitat complexity and biodiversity. The response of species assemblages in relation to habitat complexity and seascapes in seagrass meadows remains poorly studied. In a field experiment, we factorially manipulated *Zostera marina* L. complexity using eelgrass shoot density reduction and position within a meadow (interior and edge) at five widely dispersed sites. We evaluated how eelgrass shoot density and position within a meadow (interior or edge) affect abundance structure and biological traits of epifaunal assemblage.

All sites had a higher eelgrass shoot density in the interior of the sites compared to the edge. We found a higher epifaunal species richness at the edges in most sites. Interestingly, in most regions we observed an increase in standardized epifaunal densities, primarily due to small organisms, where eelgrass complexity was reduced without noticeable change in species richness. We obtained slightly different results when using functional diversity and biological traits. Our results suggest that size, feeding habits, and swimming capacities were the most important traits related to changes in habitat structure for epifaunal assemblages. We did not observe a dominant interaction between eelgrass shoot density reduction and position within a meadow.

Instead, the effect of position and eelgrass complexity on epifaunal assemblage diversity and biological traits depends strongly on the specific considered region. Our standardized study suggests that epifaunal species and traits are influenced by ecological drivers other than edge or eelgrass complexity effects and that any directional effect on a given region should not be generalized.

3.2 Introduction

Coastal ecosystems are often dominated by habitat-forming macrophytes, such as seagrasses and macroalgae. Habitat-forming species (or ecosystem engineers sensu Jones *et al.*, 1994) play an essential role in ecosystem functioning, notably by sheltering, protecting, and providing food to numerous organisms (Bertness *et al.*, 1999), and help stabilize communities (Maggi *et al.*, 2009). The loss of habitat-forming species negatively affects the surrounding community by reducing the richness of associated species and epifaunal densities, changing community structure and composition, and altering community recovery from disturbance (Cimon et Cusson, 2018; Herkul et Kotta, 2009; Rueda *et al.*, 2009; Watt et Scrosati, 2013). Seagrasses provide a complex habitat that offers many ecosystem functions and services, e.g., reduce water movement, provide shelter from predation, stabilize sediments, and determine the structure of associated faunal assemblages (Christie *et al.*, 2009; Connolly, 1995; Herkul et Kotta, 2009; Namba et Nakaoka, 2018; Reed et Hovel, 2006). Multiple factors have led to the decline of eelgrass beds worldwide, e.g., coastal development, invasive species, eutrophication, sea-level rise, and increased turbidity (Airoldi et Beck, 2007; Duarte, 2002; Orth *et al.*, 2006; Waycott *et al.*, 2009). These different perturbations can decrease shoot density, increase habitat fragmentation and degradation, and even cause the disappearance of seagrass bed. All these scenarios

produce major modifications in community structure and productivity (Connolly, 1995; Duarte, 2002; Herkul et Kotta, 2009; Reed et Hovel, 2006).

Habitat loss and fragmentation result in decreased habitat complexity, decreased patch size, and increased edge effect at the seascape and local scale (Fahrig, 2003); this in turn can influence species richness and other components of diversity (Airoldi *et al.*, 2008; Fahrig, 2003). Typically, the presence of seagrass or a higher seagrass density and complexity will increase community stability, species richness and abundance, as well as influence assemblage composition, increase the habitat carrying capacity (Calizza *et al.*, 2017 see Chapter II of the present thesis; Cimon *et al.*, submitted; Edgar et Robertson, 1992; Lundquist *et al.*, 2018), and increase the number functional traits (Lefcheck *et al.*, 2017a). It can also enhance protection against predation and solar radiation (Edgar et Robertson, 1992). On the other hand, a reduction in seagrass density can decrease seagrass self-shading, thereby increasing the leaf surface area, shoot weight, growth, and number of leaves (Rattanachot *et al.*, 2016). This, in turn, can increase epifaunal abundance. Indeed, seagrass surface area appears to be more important than shoot density, as Sirota et Hovel (2006) found that shoot surface area was a stronger explanatory variable for epifaunal biomass than shoot density or shoot length. A reduction of seagrass complexity could, for example, decrease abundance and dominance, and increase diversity, as well as alter assemblage composition (Pierri-Daunt et Tanaka, 2014); however, a drastic decline of associated species could occur if change goes beyond a certain habitat complexity threshold (Pittman *et al.*, 2004; Reed et Hovel, 2006). The complete disappearance of seagrass can favor organisms living partly in sediments (Rueda *et al.*, 2009). Epifauna can actively select high-complexity habitats to reduce the success of their predators (Reynolds *et al.*, 2018); however, this predation risk does not always influence epifaunal habitat selection (Tait et Hovel, 2012) nor does habitat complexity always affect predation success (Hovel *et al.*, 2016).

Although habitat loss negatively affects biodiversity, habitat fragmentation can affect biodiversity either positively or negatively (Bell *et al.*, 2001; Fahrig, 2003). Studies of fragmentation effects on associated fauna often report positive, neutral, or negative effects on faunal densities, diversity, functional diversity, and composition (e.g., Arponen et Bostrom, 2012; Healey et Hovel, 2004; Lefcheck *et al.*, 2016). The response may even be species specific (e.g., Tanner, 2005), landscape dependent (Tanner, 2006), or linked more generally to the "quality" of adjacent habitats (Ries *et al.*, 2004).

One consequence of habitat fragmentation is the increase of edges and the perimeter to area ratio. The edges of seagrass beds are affected in various ways. Seagrass structural complexity may be lower at edges (Moore and Hovel 2010), thereby decreasing species richness as higher structural complexity promotes richness (Christie *et al.*, 2009); however, edges often show higher taxonomic richness (Pierri-Daunt et Tanaka, 2014) and faunal abundance (Bologna, 2006; Bologna et Heck, 2002; Warry *et al.*, 2009). Faunal density, species composition, size distribution, and secondary production can differ between the edge and interior of a bed (Bologna, 2006), although the actual sign of the relation depends on multiple processes (Bell *et al.*, 2001). Indeed, epifaunal density and biomass can increase or decrease from edge to interior (Bologna, 2006; Moore et Hovel, 2010), while some groups may be unaffected (Bologna, 2006; Tanner, 2005). Finally, larval settlement is generally greater at edges and in patchy areas, although these habitats are often less suitable for larval survival because of greater disturbance and lower sediment stability (Bostrom *et al.*, 2010). Edges influence predation risk in various ways and edges tend to be risker than interior of patches when shoot density, epibiont biomass and crustacean biomass are lower at the edge (Hovel *et al.*, in preparation).

This study aims to verify the primary and interactive effects of eelgrass shoot density reduction [complexity] and proximity to edges [position] on the structure, biodiversity, and biological traits of epifaunal assemblages. We hypothesized that proximity to patch edge and lower eelgrass complexity will support lower richness and diversity and display distinct assemblage structures relative to the interior or ambient shoot density. We also expected that the addition of proximity to edge with lower structural complexity affects the epifaunal assemblages to an even greater extent. We expected to observe more abundant and more diverse epifaunal assemblages where eelgrass shoot density was high. However, the outcome of these hypotheses may depend strongly on the characteristics of the adjacent habitats (see Ries *et al.*, 2004). We tested our hypotheses within contrasting meadows of *Zostera marina* L. in five different regions. Since associated species across regions are very different and have only few species in common, we used a biological trait approach rather than a higher taxonomic approach. Biological trait analysis (BTA) uses a combination of traits, such as life history, morphological attributes, and behavioral features, to link the species to their ecological function (Bremner *et al.*, 2006b). Even though biological traits are likely less sensitive to habitat perturbations than individual species (Ellis *et al.*, 2017), the use of biological traits is resistant to large-scale biogeographic variations and should improve predictions of changes in ecosystem functioning (Bremner *et al.*, 2003; Wong et Dowd, 2015). Moreover, changing habitat structure and its functional components might have a cascading effect from benthic epifauna to fish (Connolly, 1994) to services to humans. This study should provide a better comprehension of the role of habitat-forming species structure and seascape in shaping epifaunal assemblages in function of their biological traits.

3.3 Methods

A two-way factorial experiment was conducted in summer 2015 in five *Zostera marina* L. meadows located in five widely geographically spread regions (FR: Mediterranean Sea, France; MX: Punta Banda Estuary, Mexico; QU: St. Lawrence Estuary, Quebec, Canada; VA: Chesapeake Bay, Virginia, USA; SF: Bay of San Francisco, California, USA). The sites range in latitude from 31 to 49° N (Table 3.1, see *Annexe C: Table 5.14*). Forty-two plots of 1 × 1 m were established in shallow water (0 to <1 m) at each region (Table 3.1). This design was part of a larger study from the *Zostera* Experimental Network led by K. Hovel, J. Stachowicz, and E. Duffy. Plots were spaced at a minimum of 2 m. The two factors used in the experiment were position within the bed (Position, 2 levels: Edge and Interior) and eelgrass shoot density reduction (Complexity, 3 levels: 0, 50, and 80 % reduction of initial eelgrass shoot density) (6 treatments, $n = 7$). Proximity to edge was studied using natural positions by installing half of the plots along an unvegetated edge of a patch of eelgrass and the other half within the bed at a minimum distance of 3 m between the edge and interior positions. Complexity treatments were randomly applied to plots. Shoot density reduction was applied using quadrats separated in 100 cells of 10 × 10 cm; the number of cells occupied was counted in each plot then 0, 50, or 80% of the occupied cells were randomly cleared of all their eelgrass shoots, including rhizomes and roots. Due to low shoot density in the San Francisco region (SF), density reduction was applied using the number of shoots, i.e., 0, 50, or 80% of the shoots were randomly cleared from the plots (see *Annexe C: Table 5.14*).

Initial eelgrass shoot density was measured with 20-cm-diameter rings (3 estimates/plot; or total number of shoots within the plots in the case of SF). Aboveground biomass was assessed using the dried collected shoots (at 60 °C) from

complexity-reduced plots at the beginning of the experiment extrapolated to the entire plot ($g_{dw} \cdot m^{-2}$). Initial eelgrass shoot density and aboveground biomass were both used to characterize differences between regions and positions before the start of the experiment. Microalgae epibenthic load was estimated using the leaves of three eelgrass shoots scraped with a microscope slide under filtered sea water at the end of the experiment. The water loaded with epiphytes was filtered on pre-weighted GF/F filters then dried at 60 °C to assess epiphytes biomass (microalgae epibenthic biomass per unit eelgrass biomass, hereafter epiphytes; $mg \cdot g^{-1}{}_{dw}$).

Epifaunal collection was made in the center of each plot (n = 42 by region). Sampling was done once every 11 to 31 days after plot set up to allow epifauna to settle and to prevent eelgrass shoot density from increasing (see *Annexe C: Table 5.14*). Abundance and species composition were obtained by collecting underwater the eelgrass and its associated fauna in a 500-µm mesh bag with an opening ~ 20 cm (Duffy *et al.*, 2015). Fauna was separated from shoots in the laboratory by shaking under freshwater. The collected fauna was then sifted through a 500-µm sieve and preserved in 70% ethanol for further sorting. Individuals were identified to the lowest taxonomic level possible then passed through a nested series of sieves (8.0, 5.6, 4.0, 2.8, 2.0, 1.4, 1.0, 0.71, 0.5 mm) to evaluate size distribution. Shoots and other macrophytes were then dried at 60 °C to standardize the epifauna abundance by macrophyte biomass ($N \cdot g^{-1}{}_{macrophyte}$; [epifaunal density]).

Table 3.1. The five regions sampled in the study. Temperature and salinity were measured at low tide. MLLW: mean lower low water. The total richness is the total number of species used in the analysis for the all the samples in that region. No data available at this time where n.d.

Region	Location	Latitude (N)	Longitude	Mean temperature (°C)	Mean salinity (PSU)	Edge depth (m)	Interior depth (m)	Total richness
FR	Bouzigues/Crique de l'Angle, France	43.45	3.66	27.8	34.4	n.d.	n.d.	41
MX	Punta Banda Estuary, Mexico	31.75	-116.63	23	38	-0.40	-0.30	30
QU	Baie-St-Ludger, Quebec, Canada	49.09	-68.32	18	29.5	-0.13	-0.16	20
SF	Pt Molate, San Francisco, CA, USA	37.95	-122.42	17	32	-0.37	-0.59	16
VA	Goodwin Islands, VA, USA	37.22	-76.40	n.d.	n.d.	n.d.	n.d.	16

3.3.1 Biological trait approach

We used a biological trait approach to improve our understanding of species-habitat relationships and to allow a more general comparison between regions. The used biological traits were size, life habits and movement, feeding habits, reproduction dispersal, and larval feeding mode. Each trait was separated into three or four categories (Table 3.2). These traits can reflect responses, such as the ability to escape or resist predation, dispersal and recruitment, growth requirements, and food availability (Beauchard *et al.*, 2017). We avoided using redundant traits as much as possible to prevent giving those traits too much weight. Traits were obtained from web databases (BIOTIC, MarLIN, Polytraits, WoRMS), published literature, feeding and behavioral experiments previously performed by coauthors, and sample processing, i.e., size structure observed in samples. We used appropriate data from related species when information on biological traits was not available at the species level (see species trait list in *Annexe C: Table 5.16*).

We used fuzzy-coded frequency profiles of categories with the constraint that the scores across the categories of a trait sum to 1 (based on method by Chevenet *et al.*, 1994; Wong et Dowd, 2015). Traits were weighted by species abundance, then these abundance-weighted traits were summed over all taxa for each sample to produce a sample-by-trait table. We then calculated the frequency of occurrence of the weighted trait categories (weighted trait occurrence, WTO) (Bremner *et al.*, 2006a). We looked at the overall structure of traits, as well as the structure of individual traits and patterns of each category to detect any effect of our treatments using the WTO.

Table 3.2. Biological traits and categories used to compare the species present in the five regions on a common basis to better measure species-habitat relationships.

Trait	Category	Code
Size	Large; 4.0 to >8.0 cm	La
	Medium; 1.4–4.0 cm	Me
	Small 0.5–1.4 cm	Sm
Life habits and movement	Swimmer	Sw
	Crawler	Cr
	Burrower / Habit related to sediments including refuges	Bu
	Sessile / Attached / Hides in seagrass leaves	Se
Feeding habits	Grazer / Browser	Gr
	Filter / Suspension feeder	Fi
	Deposit feeder / Detritivore	De
	Predator / Scavenger	PS
Reproduction dispersal	Broadcast spawner	Bst
	Brooder	Bro
	Egg case layer	Lay
Larval feeding mode	Lecitotrophic	Le
	Planktotrophic	Pl
	Direct development	Dd

Trait diversity was calculated using a computed species traits distance matrix by region (Gower's distance for fuzzy coded traits) with the 'dist.ktab' function in 'ade4' package (Pavoine *et al.*, 2009; Thioulouse *et al.*, 1997) run in the 'dbFD' function in the 'FD' package of R using Lingoes correction if distances were not Euclidean (Laliberté et Legendre, 2010; Legendre et Anderson, 1999; R Core Team, 2016). The 'dbFD' function allowed us to calculate four indices to describe functional diversity: functional richness (FRic; volume of functional space occupied by a community), functional evenness (FEve; regularity of the distribution of abundance in the functional volume; high = regular), functional divergence (FDiv; divergence in the distribution of abundance in the functional volume; high when abundant species have divergent trait

values) (Villéger *et al.*, 2008), and Rao's quadratic entropy (RaoQ (Q); the mean functional distance between two randomly chosen individuals; Botta-Dukát, 2005; Mouchet *et al.*, 2010; Rao, 1982).

3.3.2 Statistical analysis

All analyses on species were performed on standardized abundances ($N \cdot g^{-1}$ $_{macrophyte}$; [epifaunal density]). To test for a simple or an interactive effect of density reduction and position on total epifaunal density (N g^{-1}), species richness (S), functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), Rao's quadratic entropy (RaoQ), WTO structure, and species redundancy (R = 1 – (RaoQ/Simpson diversity)) (Ricotta *et al.*, 2016), we used permutational (multivariate) analysis of variance (PER-ANOVA/PERMANOVA; Anderson *et al.*, 2008) run with 9999 permutations based on the following design: Region (random) × Position (fixed) × Complexity (fixed). All these indices were highly different between regions even when using biological traits (see Appendix 1: Table S4–S7). Therefore, the regions are difficult to compare directly, and we preferred analyzing our results using an orthogonal design by region using the same two fixed factors (Position and Complexity). Euclidean distances were used as resemblance measure for all analyses. Total epifaunal densities of species were fourth-root transformed, while WTO was square-root transformed prior to analyses. These transformations were determined using to shade-plot method (Clarke *et al.*, 2013). Post hoc comparisons were performed using pairwise *t*-tests within the same analysis. No corrections were applied to the obtained exact permutation *p*-values, following the approach of Anderson et al. (2008).

We used principal component ordination (PCO) with resemblance measures calculated in the 'ade4' package (see above) to visualize species–species resemblance, using their biological traits as well as Euclidean distances for WTO structure. Euclidean distances, which are not the most common distances used for testing and representation when

analyzing fuzzy coded traits, were correlated at 85.2% with the distance matrix calculated by the 'ade4' package. Therefore, we consider the tests and their representations rather equivalent. Statistical analyses and PCO were performed in PRIMER & PERMANOVA v.7 (Anderson *et al.*, 2008; Clarke et Gorley, 2015). We used a significance level of $\alpha = 0.05$ for all statistical tests; however, observed *p*-values close to significance were carefully considered.

3.4 Results

Overall, 117 taxa were identified and used for the analysis, most of them identified at the species level (see the complete species list in *Annexe C: Table 5.15*; total richness by region in Table 3.1). All diversity indices were affected by region (see *Annexe C: Tables 5.17–5.20*). Regions explained 78% of variation for abundance, 64% for richness, and 52% for Simpson diversity (not shown for the latter). We saw no effect of position or complexity outside of the interaction with region; the only two exceptions were that initial shoot density was affected by position with higher densities in the interior (see *Annexe C: Table 5.17*a) and that the size-weighted trait occurrence was affected by complexity (see *Annexe C: Table 5.21*b) with smaller organisms in 80% complexity-reduced plots compared to the ambient plots. We did not find any interaction between position and complexity in the main tests (see *Annexe C: Table 5.17–5.20*). Therefore, results are presented by region (see 'Methods').

3.4.1 Initial eelgrass measures and epiphytic algae

All regions tested together, as well as each region taken separately, showed a significant effect of position on eelgrass shoot density with higher densities at the interior (see *Annexe C: Table 5.17a and 5.21a, Fig. 5.6a*). Eelgrass aboveground biomass was influenced by position in QU, SF, and VA (see *Annexe C: Table 5.21b*,

Fig. 5.6b). Eelgrass biomass was higher at the interior of the bed in QU and SF, while it was higher at the edge in VA.

Microepiphytes were affected by position in MX, QU, and SF, but only SF had differences when considering only the ambient plots (see *Annexe C: Table 5.218c, Fig. 5.6c*). Epiphytes were higher in the interior in MX, while it was higher at the edge in QU. In SF, epiphytes were about three times higher at the edge than the interior.

3.4.2 Total epifaunal densities and species richness

Total epifaunal density was significantly affected by position only in SF (Table 3.3a). Interior epifaunal densities were 63% lower than at edges in SF (Fig. 3.1a). Although not significant, densities tended to be lower at the interior in the other regions, except in QU (Fig. 3.1a). Density reduction–affected densities in three regions (Table 3.3a) were significant in MX and QU (and had a $p = 0.0569$ in VA). Eelgrass complexity-reduced plots had higher epifaunal densities than ambient complexity in QU, but only the 80% density-reduction plots were higher than ambient plots in VA (Fig. 3.1c). In MX, the interaction between position and density reduction was significant (Table 3.1a); the edge of 80% complexity-reduced plots had total densities >40% higher than all other treatments (Fig. 3.1d). Results were comparable to results obtained using raw data, i.e., no standardization per biomass of macrophyte, except in MX and QU where raw abundance showed no significant difference among complexity levels (respectively: Pseudo-$F_{2,36} = 2.5791$, $p = 0.0900$; Pseudo-$F_{2,36} = 0.3947$, $p = 0.6766$) because there was consistently fewer shoots collected in the complexity-reduced treatments; however, the same quantity of epifauna was collected in QU, while there were fewer individuals collected in the complexity–reduced plots in MX, although the amount remained greater than that of ambient plots by gram of shoot (results not shown).

Richness was significantly affected by position on four of the five sites (Table 3.3b). Richness was lower in the interior than the edge in FR, MX, and SF, while it was lower at the edge in VA, and no differences were found in QU. Although position was significant in FR and MX, the richness did not differ among position when considering only the ambient treatment (see *Annexe C: Table 5.30*). We did not observe any effect on species richness of density reduction alone or in interaction with position (Table 3.3b).

Table 3.3. Summary of PER-ANOVAs showing the effects of position (Pos) and complexity (Com) on total density, richness, functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), Rao's quadratic entropy (RaoQ), functional redundancy, and biological weighted trait occurrence structure (PERMANOVA) of standardized species by region. Significant results are shown in **bold**, while results in *italics* indicate that only ambient plots significantly differed from the results here (cf. *Annexe C: Table 5.29*).

		FR		MX		QU		SF		VA	
	df	***Pseudo-F***	***P (perm)***	***Pseudo-F***	***P (perm)***	***Pseudo-F***	***P (perm)***	***Pseudo-F***	***P (perm)***	***Pseudo-F***	***P (perm)***
a) Total densities											
Position	1	0.7147	0.4124	0.5105	0.4883	0.0106	0.9208	29.754	**0.0001**	0.8041	0.3871
Complexity	2	0.6059	0.5558	3.7362	**0.0288**	6.3269	**0.0049**	1.2000	0.3176	3.0705	0.0569
Pos × Com	2	0.2311	0.7952	3.8226	**0.0304**	1.6970	0.1953	1.1164	0.3428	0.4482	0.6445
Residual	36										
b) Species richness											
Position	1	4.3981	***0.0420***	6.7634	***0.0140***	0.1922	0.6605	34.164	**0.0001**	31.314	**0.0001**
Complexity	2	0.8195	0.4508	0.2225	0.7964	0.7687	0.4685	0.2264	0.8005	0.4793	0.6248
Pos × Com	2	1.6102	0.2107	0.6958	0.5037	1.2171	0.3204	1.6819	0.2042	0.3728	0.6957
Residual	36										
c) FRic											
Position	1	4.4093	***0.0449***	4.8553	***0.0319***	0.0867	0.7718	11.889	***0.0011***	6.3317	***0.0141***
Complexity	2	0.7503	0.4821	0.0311	0.9680	0.2034	0.8217	0.2388	0.7958	0.6012	0.5753
Pos × Com	2	1.3424	0.2657	0.1200	0.8875	1.4658	0.2430	0.9641	0.3882	0.2826	0.7662
Residual	36*										
d) FEve											
Position	1	1.1248	*0.2946*	0.3424	0.5578	0.2894	0.5979	10.287	**0.0024**	0.4738	0.4885
Complexity	2	1.8411	0.1677	0.6220	0.5431	5.2062	**0.0093**	0.1602	0.8573	4.2850	**0.0262**
Pos × Com	2	1.5547	0.2318	1.3068	0.2826	1.0372	0.3686	0.9060	0.4119	1.6428	0.2077
Residual	36*										

	df	FR		MX		QU		SF		VA	
		Pseudo-F	*P (perm)*	*Pseudo-F*	*P (perm)*	*Pseudo-F*	*P (perm)*	*Pseudo-F*	*P (perm)*	*Pseudo-F*	*P (perm)*
e) FDiv											
Position	1	1.5772	0.2191	4.4149	***0.0390***	0.5773	0.4463	44.410	**0.0001**	1.8871	0.1795
Complexity	2	0.3851	0.6874	1.1574	0.3295	1.4979	0.2472	0.5928	0.5636	1.0838	0.3466
Pos × Com	2	3.7380	**0.0347**	1.2177	0.3001	0.6523	0.5306	2.0512	0.1439	0.4578	0.6440
Residual	36*										
f) RaoQ											
Position	1	8.5382	***0.0059***	4.1481	***0.0499***	0.3438	0.5607	2.3806	0.1294	5.6609	***0.0229***
Complexity	2	2.1853	0.1291	3.0981	0.0604	5.8031	**0.0062**	0.4935	0.6137	0.4012	0.6814
Pos × Com	2	0.2754	0.7602	0.2350	0.7882	1.3349	0.2753	0.3866	0.6797	1.8868	0.1691
Residual	36										
g) Redundancy											
Position	1	0.0449	0.8375	0.9021	0.3484	8.6219	***0.0038***	67.424	**0.0001**	0.7488	0.4206
Complexity	2	1.6323	0.2061	3.2017	0.0549	0.6992	0.5163	0.5585	0.5766	2.6110	0.0921
Pos × Com	2	0.7471	0.4820	0.4942	0.6084	0.4580	0.6463	1.9669	0.1546	1.8104	0.1892
Residual	36										
h) WTO structure											
Position	1	3.1386	***0.0350***	2.9772	***0.0295***	0.3317	0.7213	50.664	**0.0001**	3.1002	**0.0224**
Complexity	2	2.2391	0.0538	3.5500	**0.0037**	5.0317	**0.0054**	0.7015	0.6137	7.0860	**0.0003**
Pos × Com	2	3.2157	**0.0131**	0.5541	0.7984	1.3868	0.2344	1.3670	0.2330	1.5133	0.1633
Residual	36										

Note: PER-ANOVAs and PERMANOVA were run with 9999 permutations using Euclidean distances. Densities (a) were fourth-root transformed, while WTO (h) were square-root transformed before analysis.

*Residual was 27 for VA and 34 for QU as calculations were not possible for some plots.

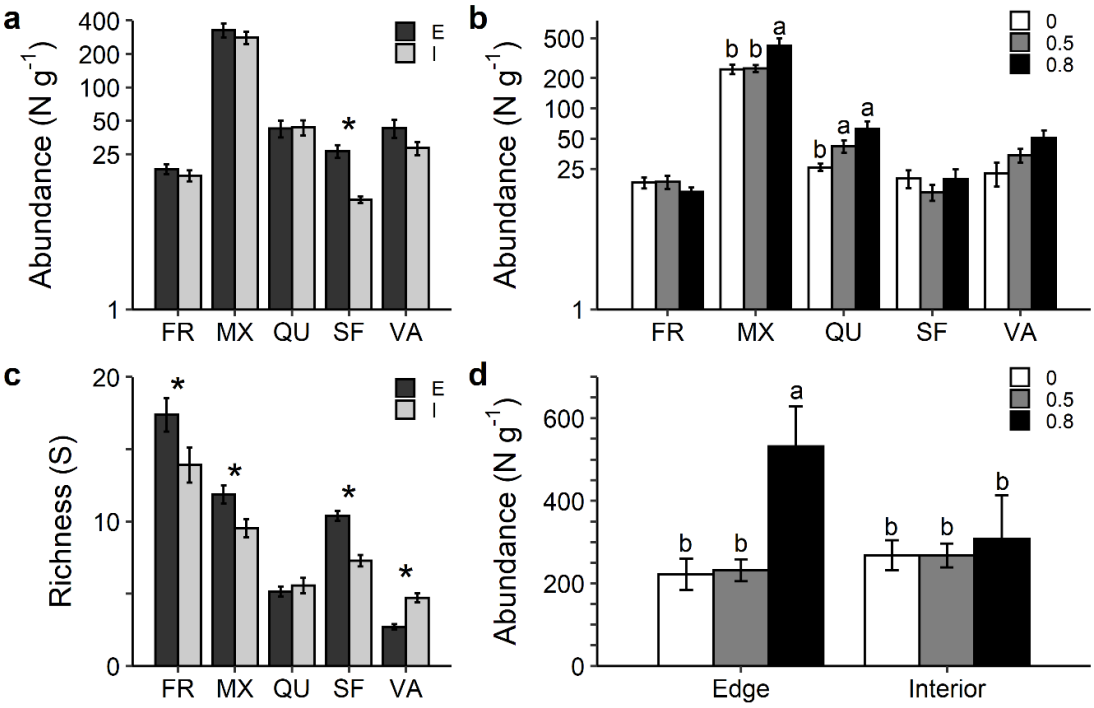

Figure 3.1. Mean (±SE) values of (a, c, d) total epifaunal density ($N \cdot g^{-1}$ $_{macrophyte}$) and (b) species richness. Values show the effect of position (a–b), density reduction (c), and the interaction between position and density reduction for MX region only (d). Bars are the respective treatment with E: Edge; I: Interior; 0: ambient eelgrass shoot density; 0.5: 50% density reduction; 0.8: 80% density reduction. The number of replicates used to obtain the averages was n = 21 in (a and c), n = 14 in (b), and n = 7 in (d).

3.4.3 Functional diversity

We did not find any consistency in results between regions for the functional diversity indices. The overall functional richness (FRic) was influenced significantly by position in four regions, but not by density reduction (Table 3.3c) and showed the same pattern as observed with species richness: lower at the interior than at the edge in FR, MX, and SF, while it was lower at the edge in VA, and no differences were observed in QU.

The functional evenness (FEve) was affected by position in SF and by complexity in QU and VA (Table 3.3d). FEve values were higher at the interior in SF (Figure 3.2a)

while lower in the ambient plots in QU, and lower in the 80% complexity-reduced plots in VA (Figure 3.3a). The functional divergence (FDiv) was higher in the interior in MX and SF (Figure 3.2b).

The Rao's quadratic entropy (RaoQ) values were higher for the edges in FR and MX but lower in the VA region (Figure 3.2c; Table 3.3f). RaoQ was also affected by complexity in QU (Table 3.3f), where it was lower in ambient plots (Figure 3.3b).

Redundancy (R), which evaluates how much community members perform similar functions (Ricotta *et al.*, 2016), was affected by position in SF and QU (Table 3.3g). Redundancy was higher at the edge in SF, while it was lower in QU (Figure 3.2d). Density reduction marginally affected redundancy in MX, where it decreased slightly from ambient conditions to 80% reduced–complexity plots (results not shown).

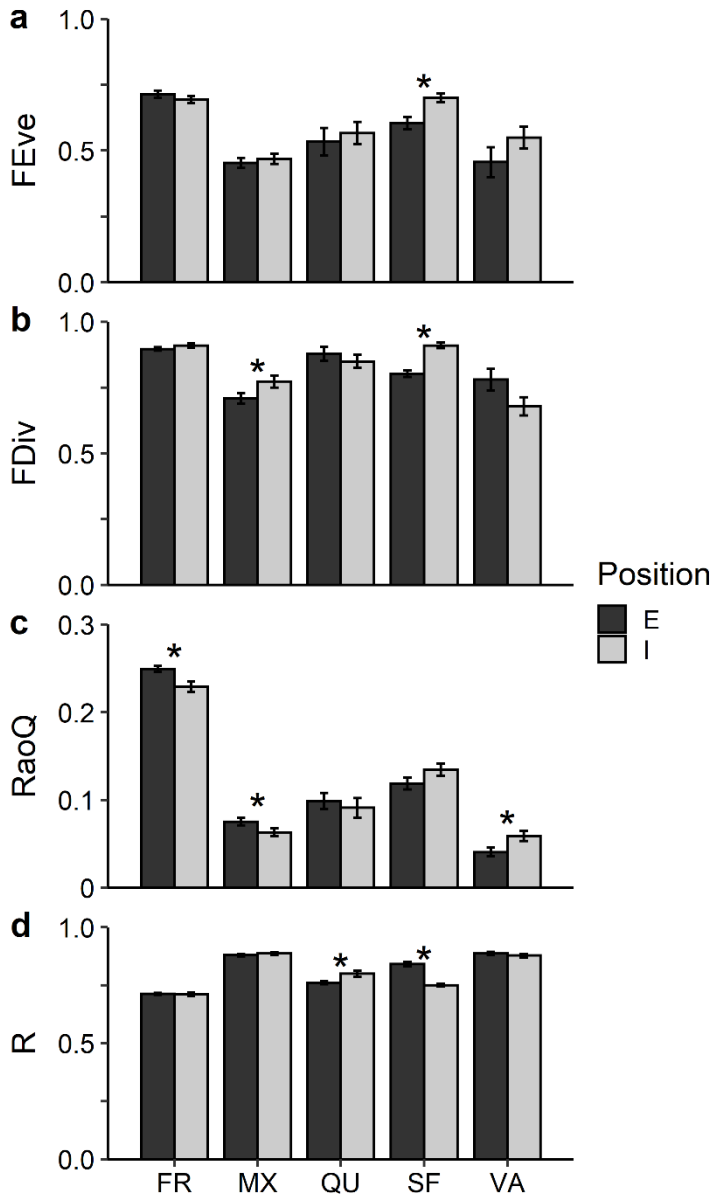

Figure 3.2. Mean (±SE) values of (a) functional evenness and (b) Rao's quadratic entropy. Values show the effect of complexity (a–b). Bars are the respective treatment with 0: ambient eelgrass shoot density; 0.5: 50% density reduction; 0.8: 80% density reduction. The number of replicates used to obtain the averages was $n = 14$ (a–b). Different letters indicate significant differences ($p < 0.05$).

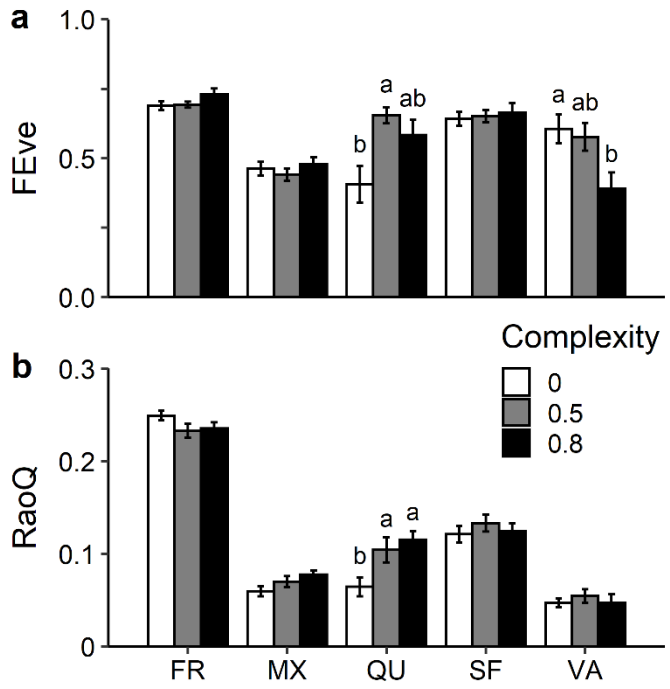

Figure 3.3. Mean (±SE) values of (a) functional evenness and (b) Rao's quadratic entropy. Values are showing effect of complexity (a-b). Bars are the respective treatment with 0: ambient eelgrass shoot density; 0.5: 50% density reduction; 0.8: 80% density reduction. The number of replicates used to obtain the averages was n = 14 (a-b). Different letters indicate significant differences ($p < 0.05$).

3.4.4 Biological traits occurrence structure

The structure of all weighted traits was affected by position or complexity separately (i.e., Region × Position and/or Region × Complexity) except for the size trait where complexity was significant (see *Annexe C: Table 5.20*). Post hoc tests indicated marginally significant differences of size structure with smaller individuals in complexity-reduced plots compared to ambient plots (pairwise tests: $P_{0 \text{ vs } 0.5} = 0.0818$; $P_{0 \text{ vs } 0.8} = 0.0684$; $P_{0.5 \text{ vs } 0.8} = 0.2623$).

Weighted trait occurrence (WTO) structure was affected by position in FR, MX, SF, and VA, while it was affected by complexity in MX, QU, and VA, and by their

interaction in FR (Table 3.3h). When only ambient plots were analyzed for the effect of position, only SF and VA remained with a different WTO structure among positions (Table 3.3h). We refer the reader to Figures 4 and 5 for detailed WTO by trait and region and to Appendix 1 for a detailed description of treatment effects on trait categories (see *Annexe C:* Biological traits occurrence detailed results), statistical analysis (see *Annexe C: Table 5.25-5.29*), detailed WTO by trait and treatment in FR (see *Annexe C: Fig. 5.9*), and PCO of WTO structure by treatment in FR (see *Annexe C: Fig. 5.8*). All used traits were affected by at least one treatment in one region (see *Annexe C: Table 5.31-5.32* for summary of effects).

The traits responsible for the differences between position were specific to each region (Figure 3.6; see *Annexe C: Table 5.31*). In FR, interior plots had less large-sized, swimmer, crawler, and deposit feeders. The interior plots also had more sessile and filter-feeding organisms than edge plots (Figure 3.6b, see *Annexe C: Table 5.31*). In MX, interior plots had fewer deposit feeders, egg laying, and lecithotrophic organisms, while they had more brooding organisms than edge plots (Figure 3.6d, see *Annexe C: Table 5.31*). Most traits were affected by position in SF and differences were sharply oriented (Figure 3.6c); interior plots were characterized by larger crawling, grazing, and egg-laying organisms, while edge plots were characterized by more medium- and small-sized, swimming, sessile, filter-feeding, deposit-feeding, and brooding organisms (Figure 3.6c, see *Annexe C: Table 5.31*). In VA, interior plots had fewer medium-sized organisms, while they also had more small-sized, burrowing, filter feeding, predator/scavenger, broadcast-spawning, and lecithotrophic organisms than edge plots (Figure 3.6a, see *Annexe C: Table 5.31*).

As for position, the traits responsible for the differences between complexity treatments were unique to each region (Figure 3.7; see *Annexe C: Table 5.32*). In MX, most traits were affected by 80% reduced-complexity compared to the ambient-complexity and

50% reduced-complexity plots; 80% reduced-complexity plots had fewer medium-sized, swimming, crawling, and grazing organisms. They also had more sessile, filter-feeding, deposit-feeding, egg-laying, and lecithotrophic organisms (Figure 3.7b; see *Annexe C: Table 5.32*). Most traits were affected by complexity in QU and differences were concentrated on one axis (Figure 3.7c); complexity-reduced plots had fewer medium-sized, crawling, grazing, brooding, and directly developing organisms. They also had more small-sized, burrowing, deposit-feeding, broadcast-spawning, and planktotrophic organisms compared to ambient plots (Figure 3.7c; see *Annexe C: Table 5.32*). In VA, complexity-reduced plots had fewer large- and medium-sized swimming and grazing organisms. They also had more small-sized, crawling, burrowing, filter- and deposit-feeding organisms compared to the ambient plots (Figure 3.7d; see *Annexe C: Table 5.32*).

Specific results by treatment of FR region are found in *Annexe C* (*Table 5.33 and Fig 5.9*). In FR, the effects of complexity occurred mostly in the interior, not at the edge.

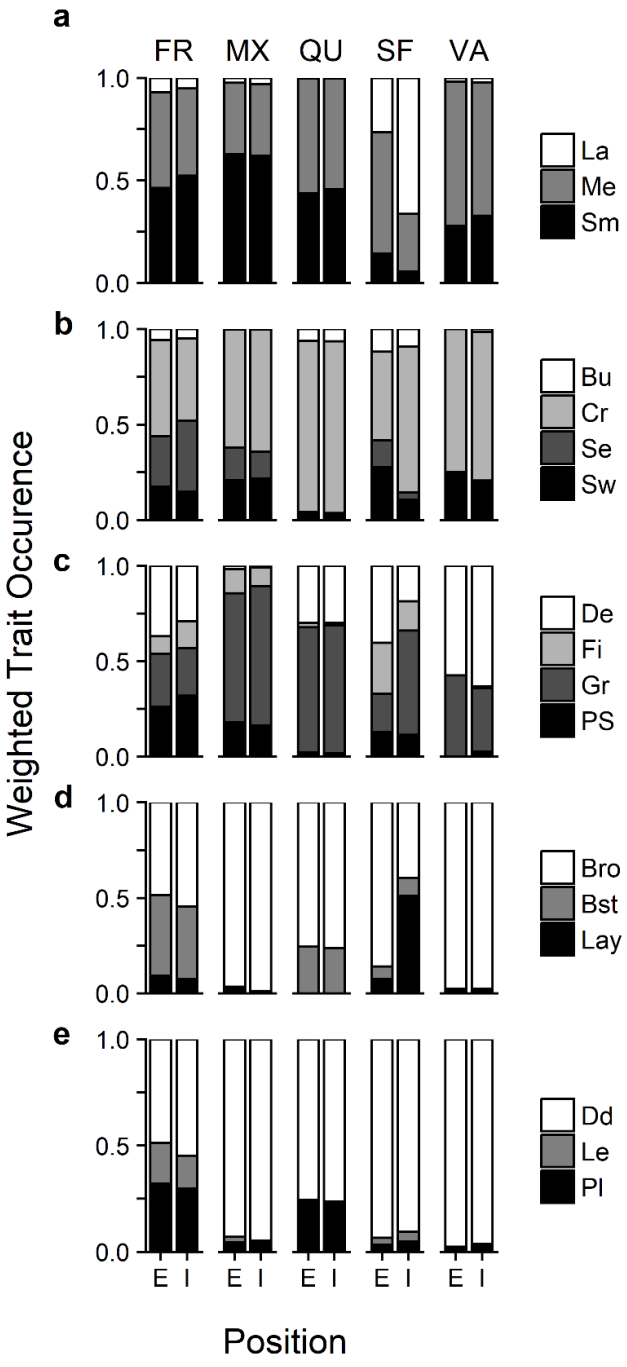

Figure 3.4. Proportions of each category of trait by position in each region showing (a) size, (b) life habits and movement, (c) feeding habits, (d) reproduction dispersal, and (e) larval feeding mode. Please refer to Table 3.1 for decoding trait categories acronyms. Bars are the respective treatment with E: Edge; I: Interior.

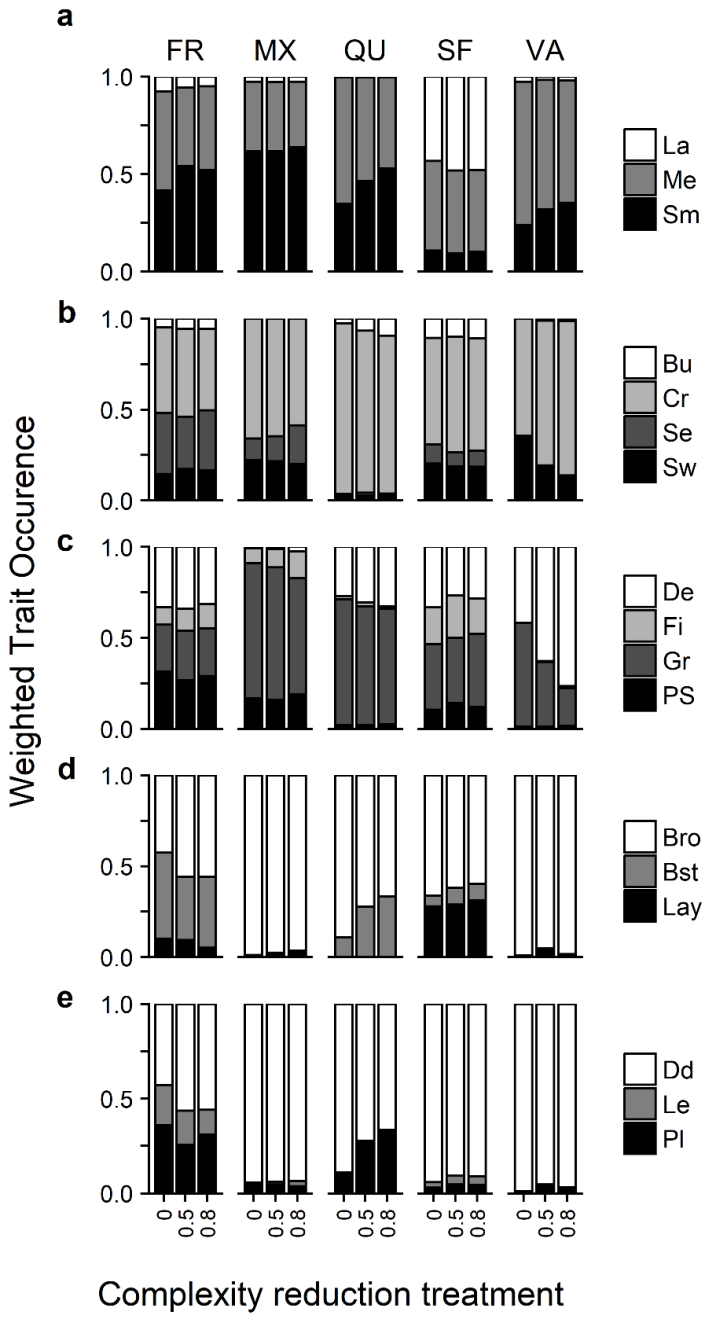

Figure 3.5. Proportions of each category of trait by complexity in each region showing (a) size, (b) life habits and movement, (c) feeding habits, (d) reproduction dispersal, and (e) larval feeding mode. Please refer to Table 3.1 for decoding trait categories acronyms. Bars are the respective treatment with 0: ambient eelgrass shoot density; 0.5: 50% density reduction; 0.8: 80% density reduction.

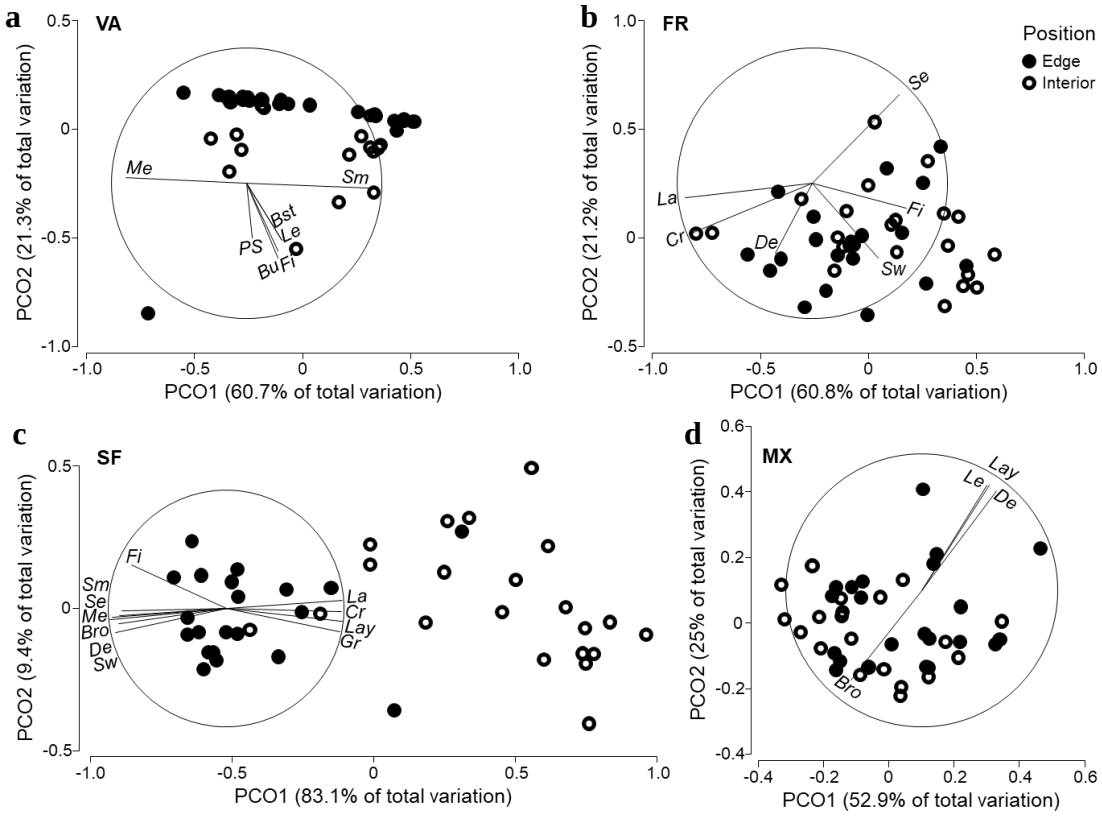

Figure 3.6. Principal coordinate ordinations illustrating the position effect on weighted trait occurrence structure (WTO) of (a) VA, (b) FR, (c) SF, and (d) MX. Values were calculated based on Euclidean distances of the WTO. Vectors are the more responsible traits for differences in position. Please refer to Table 3.1 for decoding trait categories. Only significant vectors were kept ($p < 0.05$).

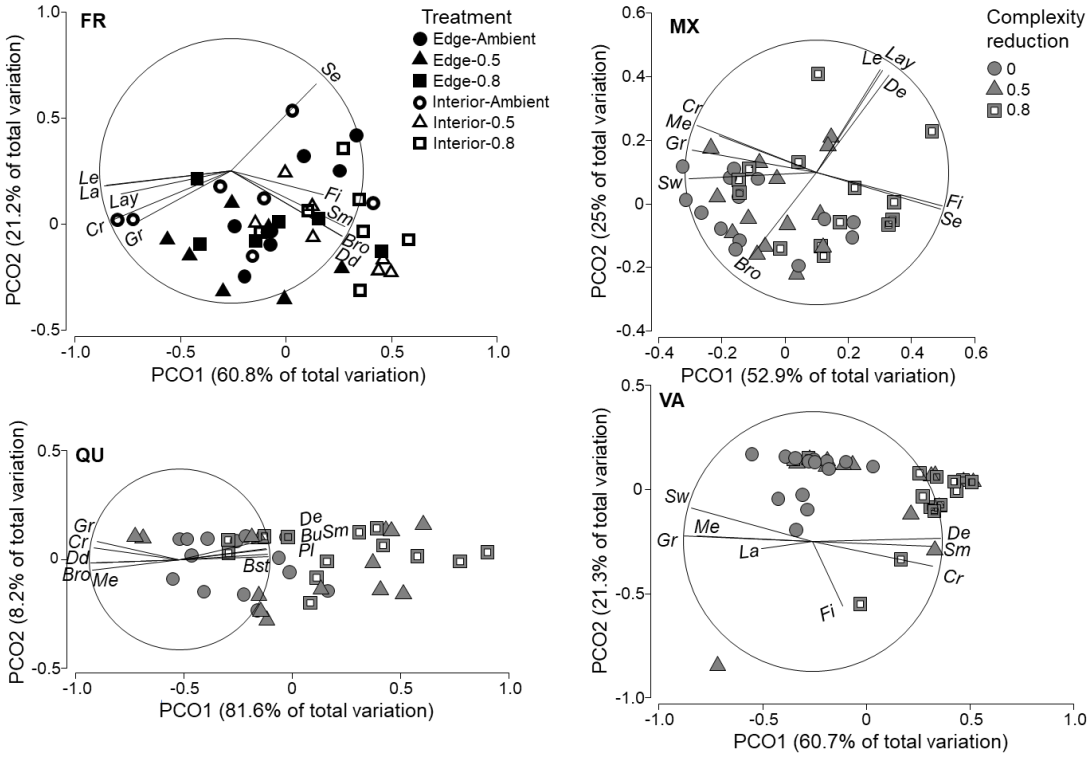

Figure 3.7. Principal coordinate ordinations plots illustrating the effect on weighted trait occurrence structure (WTO) of the interaction of position and complexity in (a) FR and the effect of complexity in (b) MX, (c) QU and (d) VA. Values were calculated based on Euclidean distances of the WTO. Please refer to Table 3.1 for decoding trait categories acronyms. Vectors are the more responsible traits for differences in complexity. Only significant vectors were kept ($p < 0.05$).

3.5 Discussion

The understanding of how position in relation to patch edge and eelgrass structural complexity influence eelgrass and its associated assemblages is important in the context of increased degradation of coastal habitats. The use of a biological-trait approach helps to define if there are generalities in functional diversity and trait occurrence that exist between distant regions marked by various seascape configurations and adjacent habitat characteristics. We found that the effects of edge

and *Zostera marina* complexity on epifaunal assemblage diversity and biological traits depend strongly on the considered region. Such region-dependent effects suggest that other processes drive epifaunal assemblage structure than the eelgrass-related habitat per se or its proximity to the patch edge. We observed weak or no support for our hypotheses, as we observed neither denser nor more diverse assemblages with higher eelgrass structural complexity nor did assemblages increase in diversity or density in the interior of sites. Rather, we measured higher epifaunal densities per shoot when complexity was reduced in most regions. Also, we did not observe much significant interaction between complexity and proximity to edges. Interestingly, compared to common diversity indices, we obtained slightly different results when using functional diversity and biological traits.

3.5.1 Effects on diversity-related indices

We found a greater epifaunal species richness at the edge of our studied meadows. This was often observed along with higher abundances (Bologna et Heck, 2002; Pierri-Daunt et Tanaka, 2014; Warry *et al.*, 2009); however, measuring no difference is also not surprising, as it has been observed several times (e.g., Tanner, 2006). Higher richness at the edge could, for example, result from higher colonization or faunal migration (Bologna et Heck, 2002; Bostrom *et al.*, 2010), but it could also depend on the adjacent habitat and its characteristics as well as the habitat itself and present trophic resources (Ries *et al.*, 2004). With one exception (SF region), epifaunal densities were not higher in the edge plots or only showed some similar, but not significant, trends. Note that natural shoot density was higher in the interior for all regions, as is regularly observed (e.g., Schmidt *et al.*, 2011; Wong et Dowd, 2015), and that the aboveground shoot biomass was inconsistent between positions and across regions.

Epiphytic shoot load was higher at the edge in two regions and higher in the interior in one region. Epiphytic shoot load can play an important trophic role and influence epifaunal distribution (Bologna et Heck, 1999; Gartner *et al.*, 2013). Epiphytes were about 3× more abundant at the edge than at the interior in SF, and this may explain the higher epifaunal densities, richness, species diversity, and evenness at the edge in SF even though edge had lower habitat complexity (both shoot biomass and density). While this was observed in SF, such a relationship was not detected for any of the other four sites, even where epiphytic load differed between positions. Indeed, epiphytes were significantly more abundant at the edge in QU and at the interior in MX, yet neither region showed higher epifaunal densities, richness, or diversity where epiphytes were more abundant. Instead, there were no differences between positions in QU, and species richness was higher at the edge in MX. Moreover, no differences in epiphytes were measured among complexity treatments, while differences in densities or diversity were seen in MX and QU, confirming that other factors, such as habitat structural complexity, are also responsible.

In most regions, we observed an increase in epifaunal densities where complexity was reduced, without noticeable changes in species richness. Epifaunal densities were higher in complexity-reduced plots in QU and VA, while an interaction occurred in MX where only 80%-reduced plots at the edge showed higher densities. Interestingly, the increase in density was primarily due to small organisms, as their proportion was higher in complexity-reduced plots. Reed et Hovel (2006) observed the effects on both epifaunal density and richness and suggested that organisms living in the removed habitat may have moved to the closest remaining shoots, increasing the densities per shoot. In our study, small organisms showed higher densities on remaining shoots probably due to the scale dependency of the perceived habitat heterogeneity (see Wiens, 1976). The lesser proportion of larger organisms within the complexity-reduced plots would suggest that they probably moved to vegetation in the vicinity, as the

reduced habitat would not provide enough resources or protection. However, we lack data to support this explanation and since it was not generally observed, other factors may also drive the species assemblages.

3.5.2 Effects on functional diversity and biological traits

Expecting region-specific effects in our results through use of the usual diversity indices, we sought generalizations involving the functional diversity indices. Also, we did not use functional diversity indices to describe functions per se, but rather to characterize differences among our treatments and detect potential environmental filtering. Functional richness (FRic) showed the exact same response pattern to our treatments as species richness. This may be attributed to the fuzzy-coding method using a variety of scores that produced almost as many unique compositions of functions as the actual species richness. Thus, this method does not add much new information for functional richness between regions. Along the same lines, functional evenness (FEve) had few but inconsistent responses between regions. Our results are close to those of species evenness for the density-reduction treatment but not for the position treatment. So, although species were more evenly distributed at the edge in SF, the separation of traits was more clustered; this is consistent with the higher trait redundancy and lower functional divergence measured at the edge in that region. Interestingly, however, changes in trait separation that occurred in QU and VA were consistent with the changes of dominance in species evenness where traits were less clustered when species were more evenly distributed, thus suggesting a better use of resources among species (e.g., Mason *et al.*, 2005). In contrast, we observed higher divergence (FDiv) in the interior position in MX and SF regions, and greater niche differentiation or lower competition for resources may occur. Also, a lower competition for resources is consistent with the higher FEve, which indicates a more even distribution of traits (interior in SF region).

In most regions, Rao's quadratic entropy (RaoQ) was influenced by position, but these results were not consistent. Generally, species richness and RaoQ indices showed similar responses to position within the meadow (cf. Fig 3.1c and 3.2c) except for the SF region. This latter result could be explained by the opposite effects of FRic and FDiv, that are both part of RaoQ, even though SF also had a difference in richness (Botta-Dukát et Czúcz, 2016). Complexity effect was only observed in QU and was not related to functional richness or diversity, but rather to functional evenness. The use of a different fuzzy-coding method, such as 0 to 3 scores used by most authors, the RaoQ results may have been slightly different. Higher trait diversity (divergence) suggests competitive interactions (Perronne *et al.*, 2017), while lower trait diversity (convergence) suggests the necessity of unique adaptations to establish and persist in a given habitat (Defeo et McLachlan, 2005). According to Ricotta *et al.* (2016), a highly diverse (RaoQ) community is a community at risk to lose functions more easily suggesting that the edge in FR and MX, and the complexity-reduced plots in QU would be likely less persistent through time than their counterpart treatment. Our results indicate that habitat degradation and fragmentation may have an impact on the functioning of assemblages.

Analysis of weighted trait occurrence (WTO) gives information on the distribution of biological traits across regions and allow us to highlight important traits in relation to habitat edge or density reduction. Results suggest that size (small/medium) and feeding habit (grazers/deposit feeders) together with proportion of swimmers are the traits most influenced by the factors considered in this study. Generally, smaller individuals, fewer swimmers and grazers, and more deposit feeders were found in the complexity-reduced plots. Additionally, however, although not observed in all regions, a greater number of swimmers and deposit feeders and fewer filter feeders were observed within edge plots (cf. *Annexe C: Table 5.32-5.33 and section 5.3.1*). Size is highly important as it is related to growth, productivity, the used spatial niche, and trophic interactions

(Andersen *et al.*, 2016; Woodward *et al.*, 2005). Moreover, size increases dispersal capacities as larger and swimming organisms can travel farther and could temporarily stay in habitats of reduced quality. Smaller organisms can be related to more stressed and disturbed habitats as well as other opportunistic traits such as short life span (Pearson et Rosenberg, 1978). Therefore, regions with smaller organisms following eelgrass complexity reduction or position within bed could be more sensitive to such stress. This suggests avoiding massive habitat density reduction. Deposit feeders were more proportionally abundant at the edge or in complexity-reduced plots which could indicate a shift of food resources or indicate a more disturbed environment as it is an opportunistic trait. Nevertheless, other region-dependent effects may suggest that species bearing the same traits will not necessarily react the same way to a perturbation, and that other processes are shaping these biological traits.

3.6 Concluding remarks

The use of the same methodology between widely spread eelgrass meadows that have differing abiotic conditions, biotic interactions, and different adjacent habitats allowed us to provide comparable observation of edge effects or habitat-density reduction. Our study illustrates that edge and reduced-complexity environments within *Zostera* beds cannot be perceived as degraded habitats having a consistent negative effect on epifauna diversity and composition. Indeed, edges generally had higher richness, while a habitat reduced to only 20% of its original complexity continued to sustain a dense, rich, and diverse epifaunal assemblage. Such a finding would not have been obtained using only a specific region; for example, the VA region showed a high reduction in species richness at the edge, which was the opposite response of that observed in other regions (FR, MX, and SF). Our findings also suggest potential trophic-cascade effects as variation in food resources at higher trophic levels are affected differently by

complexity and edges between regions. It is clear from such varied responses between regions that other biological or environmental processes shape local epifaunal assemblages. Neumann *et al.* (2016) evaluated that tidal stress, mud content and salinity were among the most important habitat features influencing functional composition while Wong (2018) was able to identify that community structure and secondary production were influenced by shoot density, temperature, depth, exposure, sediment organic and sand content, and canopy height. We believe that other processes could also be responsible for shaping community such as predation risk (Hovel et al. in submission), productivity profiles, availability of other food sources, currents (strength and orientation), patch size, and the ecological properties (including complimentary properties) of the adjacent habitat.

3.7 Acknowledgments

We thank all lab and field assistants for their precious contributions of time and effort to make this project happen. We thank Dr. M.B. Hay for verifying the English. The project is a research contribution of Québec-Océan. This article is part of the Ph.D. thesis of S.C., who was supported by a scholarship from NSERC (Natural Sciences and Engineering Research Council of Canada, Alexander Graham Bell Canada Graduate Scholarships-Doctoral Program).

CONCLUSION GÉNÉRALE

Les écosystèmes sont façonnés par de nombreuses interactions biologiques et variables environnementales. Les stress environnementaux peuvent se manifester en simultané et leurs effets se cumuler de diverses manières. Ma thèse nous a montré que les stress peuvent effectivement entrer en interaction, mais qu'en fait la majorité du temps il s'agissait plutôt d'une *dominance* de l'effet d'un stress par rapport à un autre. L'interaction entre les stress va varier en fonction de leur identité et du milieu étudié. Aussi, la réponse à un même stress ne sera pas toujours la même. Les deux premiers chapitres de cette thèse montrent les résultats d'expériences *in situ* semblables dans deux milieux différents. Ces deux expériences nous ont révélé que les stress sur les macrophytes structurants pouvaient avoir un important impact sur les communautés associées. Le dernier chapitre offre les résultats d'une même expérience reproduite sur cinq sites distincts dans le but de vérifier si la densité des plants de zostère et la proximité avec la bordure avaient les mêmes effets dans des systèmes différents.

4.1 Retour sur les objectifs et hypothèses

L'objectif principal de cette thèse était d'évaluer les effets simples et cumulés des stress multiples sur les communautés benthiques médiolittorales reliés au rôle des macrophytes structurants. Ainsi, trois expériences *in situ* manipulant les macrophytes structurants ont été réalisées. Deux de ces expériences ont manipulé des stress multiples avec trois stress différents. L'une a été réalisée en milieu rocheux et l'autre dans un herbier marin. La dernière expérience a été répliquée dans cinq herbiers marins éloignés et distincts. Pour le premier chapitre, j'ai manipulé la présence de macrophytes

structurants et de brouteurs clés, ainsi que la concentration des nutriments dans un contexte de résilience à la suite d'une perturbation consistant à la mise à nue des parcelles étudiées. Pour le second, j'ai manipulé la densité de macrophytes structurants, la quantité de lumière et la concentration en nutriments dans les sédiments. Quant au dernier chapitre, j'ai manipulé la densité des macrophytes structurants et la proximité avec la bordure en utilisant notamment une approche par traits biologiques. Les hypothèses principales étaient que les macrophytes et les brouteurs clés jouent un rôle important dans la structure des communautés associées et tamponnent les effets d'un enrichissement ; que la multiplication des stress a un plus grand impact sur les communautés que les stress uniques ou doubles ; que les stress ne seront pas systématiquement *additifs* ou *synergiques* ; et enfin que les macrophytes structurants, quel que soit le milieu étudié, jouent un rôle dominant et équivalent au niveau de leurs communautés associées.

Mes résultats montrent que la présence de macroalgues a facilité la récupération des communautés face à des stress alors que les brouteurs n'ont pas joué de rôle particulier de protection face au stress ou d'accélération de la résilience (chapitre I). La majorité du temps, la multiplication des stress n'a pas eu un plus grand impact sur les communautés à l'exception du stress triple dans le chapitre I pour le pourcentage de dissimilarité et la résilience. Effectivement, le pourcentage de dissimilarité entre les parcelles à stress triple et les références est resté élevé tout au long de l'expérience (Fig. 1.4) et la récupération des parcelles à stress triple n'était toujours pas atteinte à la fin de l'expérience en composantes multivariées (Tableau 1.3). La majorité des stress utilisés pour les trois chapitres n'ont pas montré d'interaction entre eux. Le type d'interaction le plus fréquent entre les divers stress est la *dominance* (répertoriée cinq fois, dont une est très proche d'une synergie positive) et les types suivants ont aussi été observés : une interaction *additive*, deux interactions *synergiques négatives* et une interaction *antagoniste* (Tableau 4.1). À l'exception de l'interaction de type *additif*,

nous n'avions pas prédit les réponses observées. Finalement, les macrophytes structurants jouent effectivement un rôle de premier ordre sur leurs communautés associées, mais ce rôle n'est pas forcément équivalent partout et va dépendre des stress auxquels la communauté fait face. De manière récurrente dans ma thèse, les stress concernant les macrophytes structurants ont causé des effets sur les communautés étudiées et ces effets étaient souvent les plus éloquents. Il est possible que les réponses à ce stress soient toutefois dominées par les effets d'autres stress p. ex. dans le chapitre II, l'effet de l'ombrage a dominé celui de la réduction de densité de zostère sur les sucres solubles des feuilles de zostère. Le chapitre III a permis de mettre en lumière le fait que la réduction en densité de zostère et la proximité avec la bordure d'un herbier n'auront pas toujours le même effet selon le site. Cet effet pourrait même être dépendant de la portion d'un herbier étudié selon l'exposition aux diverses variables biotiques et abiotiques auxquelles elle ferait face.

Les hypothèses spécifiques du premier chapitre ont été partiellement confirmées. La présence des macroalgues a facilité le rétablissement des communautés. Les divers stress ont influencé les indices de diversité, notamment l'enlèvement de la canopée a permis l'établissement d'algues de sous-canopée et a diminué l'abondance des invertébrés associés. La réduction de la présence des brouteurs n'a pas accentué le phénomène d'enlèvement de canopée. Enfin, l'effet cumulé des stress a ralenti la récupération de la communauté associée par plus de trois mois, mais la récupération n'était pas atteinte à la fin de l'expérience.

Les hypothèses spécifiques du second chapitre ont aussi été partiellement confirmées. La densité des zostères est importante pour la structure des assemblages d'invertébrés. La croissance de la zostère a été augmentée par la réduction en densité et diminuée par l'ombrage et leur interaction est *additive*, mais l'enrichissement des sédiments n'a pas influencé la croissance des feuilles de zostère. L'ombrage a occasionné des effets

physiologiques chez la zostère : diminution de la croissance, diminution des glucides non structuraux et diminution de la densité des plants de zostères (probablement associée à une mortalité), l'ombrage n'a pas diminué, mais plutôt doublé la concentration des algues épiphytes, et certains de ces changements ont été atténués en présence de la réduction en densité de zostère (croissance, concentration en amidon dans les rhizomes). Finalement, l'addition des stress n'a pas causé une plus grande dissimilarité dans les assemblages épifauniques, mais chaque stress a eu certains effets distincts.

Tableau 4.1. Résumé des types d'interaction entre les divers stress pour les chapitres I et II : enlèvement de la canopée (Ca), réduction des brouteurs (Gr), enrichissement en nutriments (Nu), réduction en densité (De) et ombrage (Sh). Se référer aux différents chapitres pour les détails. Gris = absence d'effet. Noter que le chapitre III n'a pas présenté d'interaction entre les stress étudiés et qu'il est donc absent de ce tableau.

Chap.	**Additif**	**Dominance**	**Antagonisme**	**Synergie négative**
I		• Ca domine Gr pour la richesse (proche synergie) • Ca domine Nu pour diversité et équitabilité		• Traitement Ca × Nu pour la richesse
II	• De et Sh sur l'élongation des feuilles de zostères	• De domine Nu pour la richesse • Sh domine De pour les sucres solubles • Sh domine Nu sur la densité de zostère	• Sh et Nu sur l'équitabilité	• Sh et De sur l'amidon des rhizomes

Pour terminer, les hypothèses du troisième chapitre ont également été partiellement confirmées. La structure des assemblages a été affectée par la proximité avec la bordure dans chacune des régions et par la densité des zostères dans certaines régions. Nous avons aussi observé des réponses au niveau des traits biologiques, mais les réponses

étaient dépendantes des régions comme pour les indices de diversité au niveau des espèces. Contrairement à l'hypothèse de départ, la richesse était souvent plus élevée à la bordure de l'herbier. Aussi, nos traitements ne nous ont pas permis de déterminer s'il existe un seuil de densité de zostère à partir duquel des caractéristiques symptomatiques d'un assemblage sont observées laissant présager à un écroulement des communautés (point de bascule). En revanche, nous avons vu quelques réponses graduelles entre les traitements de réduction de densités. Finalement, nous n'avons pas mesuré d'interaction ayant des effets cumulatifs de ces deux stress sur les variables étudiées.

4.2 Contributions majeures

4.2.1 La résistance et la résilience

Le chapitre I a permis de déterminer que la résilience des communautés dépend de la nature et du nombre de stress auxquels est assujettie la communauté et que les macrophytes structurants ont un rôle important pour le maintien de cette composante. L'absence de macrophytes structurants et l'addition des stress ont systématiquement allongé le temps de récupération des communautés, de 2 à plus de 4 mois ici. Il est fréquent d'allonger le temps de récupération d'une communauté en absence de macrophytes structurants et en ajoutant des stress, mais les temps de récupération vont varier énormément selon le milieu et les stress (O'Leary *et al.*, 2017). De plus, la récupération complète des communautés n'a pas été atteinte là où les stress étaient triples. Mes résultats, bien qu'attendus, n'avaient jamais encore été démontrés dans une expérience *in situ* et viennent confirmer le rôle stabilisant des macrophytes structurants. Mes résultats sont d'autant plus intéressants puisqu'en étudiant seulement les différents indices univariés ou multivariés, chose faite la plupart du temps dans la littérature, il

n'était pas possible de déterminer que l'addition de stress avait un réel impact sur la stabilité des communautés alors qu'ici on peut l'affirmer.

Les résultats du chapitre II indiquent que l'herbier étudié est relativement robuste face aux stress appliqués dans mon expérience. Effectivement, l'herbier serait résistant aux stress multiples puisqu'aucun effet triple n'a été observé. L'herbier étudié a aussi montré une bonne résilience puisque la majorité des effets observés n'étaient plus détectables à la fin de l'expérience. Ces propriétés sont une excellente nouvelle et n'avaient pas été anticipées ainsi lors du choix et de l'intensité des stress. Il serait donc intéressant de tester des intensités et des durées différentes dans le but de définir un seuil de résistance et de déterminer si la récupération devient plus difficile à partir d'une certaine durée ou intensité d'un stress. Aussi, vu la récupération rapide, davantage de mesures sur les communautés seraient souhaitables pour capturer l'ensemble de la réponse.

4.2.2 Les macrophytes structurants

Les macrophytes structurants ont des effets importants sur leurs communautés associées. Par exemple, l'enlèvement de la canopée macroalgale dans le chapitre I est le stress ayant eu les plus grands impacts sur les espèces associées en modifiant de plusieurs façons les indices de diversité, la structure des communautés et a aussi ralenti voire rendue impossible une récupération. L'absence des macroalgues structurantes a notamment permis l'établissement d'algues éphémères et a diminué l'abondance des invertébrés (voir Schiel et Lilley, 2011 pour des résultats similaires). Il est fréquemment rapporté dans la littérature que lors de la succession en milieu rocheux, des algues éphémères opportunistes s'établissent puis sont remplacées par des macroalgues structurantes (e.g., Korpinen et Jormalainen, 2008; Sousa, 1979). Or, nous n'avons pas observé cela dans le premier chapitre ce qui laisse présager que la succession d'algues éphémères à la suite d'un enlèvement des macroalgues de canopée

n’est pas un passage obligé, et ce, même en situation d’enrichissement ou en présence de brouteurs réduits.

Dans les chapitres II et III, une densité de zostère réduite à seulement 20 % de sa densité initiale était suffisante pour maintenir des assemblages riches, denses et diversifiés. Les résultats du chapitre II suggèrent que les assemblages épifauniques sont fortement liés à la disponibilité de l’habitat, mais aussi à la ressource alimentaire que représentent les algues épiphytes.

Les résultats du chapitre III montrent que les effets de bordure et la diminution de complexité d’habitat n’ont pas forcément des effets négatifs sur la diversité et la composition de l’épifaune. Effectivement, l’hétérogénéité du milieu à l’échelle d’un herbier est importante pour la diversité de l’épifaune ainsi que pour d’autres processus comme le démontrent les effets importants dépendants des sites. La richesse était plus élevée aux bordures des herbiers malgré une plus forte densité de zostères à l’intérieur des herbiers. Aussi, plus d’individus par gramme de zostères ont été retrouvés sur certains des sites là où la densité des zostères était réduite sans changement au niveau de la richesse. L’utilisation des traits biologiques a identifié la taille, les habitudes de consommation et les capacités natatoires comme étant les traits (ou catégories) les plus importants reliés à la complexité d’habitat pour les espèces épifauniques.

Lorsque les macrophytes structurants sont absents ou que leur densité est réduite, les invertébrés qui s’y trouvent sont plus petits. Cette constatation a été constante dans toutes mes expériences (chapitres I, II et III) et serait caractéristique d’habitats perturbés et stressés (Pearson et Rosenberg, 1978).

Sans surprise, les résultats du chapitre II indiquent que l'accès à la lumière est extrêmement important pour la productivité et la survie des macrophytes. Nos résultats démontrent que le transfert des ressources au niveau des rhizomes entre les plants de zostère devient primordial en situation de stress. Effectivement, bien que la croissance des plants de zostères soumis à la fois à l'ombrage et à la réduction de densité de zostère n'ait pas été affectée (additivité des effets sur la lumière disponible), les glucides non structuraux y étaient les plus bas.

4.2.3 Les indices liés à la diversité

Les divers stress utilisés dans cette thèse ont eu des impacts variés sur les variables de diversité étudiées. Ceci indique que des mesures complémentaires à la richesse sont nécessaires pour capter l'ensemble des effets que les stress ont sur les communautés.

Les résultats de cette thèse confirment que la richesse seule est impuissante pour décrire les effets des stress sur les communautés. Effectivement, les communautés associées du traitement d'enrichissement au chapitre I montraient une récupération complète de la richesse après deux mois d'expérience alors que l'identité des espèces présentes était tout autre. Dans le chapitre II, la plupart des traitements n'ont pas affecté la richesse, alors que les autres composantes ont été affectées de façon plus récurrente.

Ma thèse permet donc de recommander davantage de variables que la richesse seule et plus particulièrement l'utilisation d'indices multivariés pour capter les changements les plus subtils. Notamment, une approche par traits biologiques, ou traits fonctionnels dans certains cas, pourrait être avantageuse pour définir les effets de changement d'identité ou d'abondances d'espèces (voir Beauchard *et al.*, 2017; Ricotta et Moretti, 2011; Vinagre *et al.*, 2017). Il serait très hasardeux et réducteur à ne prendre qu'une seule dimension, comme le nombre d'espèces, pour en conclure un quelconque effet.

4.2.4 Les stress et les perturbations

Les résultats obtenus dans cette thèse confirment que les stress auront des effets cumulatifs difficilement prédictibles. L'influence des stress sur les communautés va varier en fonction des espèces, des variables étudiées et du type de stress induits. Leur influence devrait aussi varier en fonction des sites et des processus biotiques et abiotiques qui s'y retrouvent. Les résultats suggèrent donc que d'autres stress auront des effets différents sur les communautés et qu'ils auront des effets cumulatifs non prédictibles.

Cette thèse souligne l'importance des études qui manipulent des stress multiples au niveau de la compréhension des effets qu'ils peuvent avoir sur les communautés. Ce qui est intéressant ici, c'est que la plupart des interactions entre les stress étaient de type dominant et la dominance émanait généralement du stress ayant le plus grand impact. Ceci est une bonne nouvelle en soit puisque les impacts ne sont pas plus grands en cumulant les stress. Cependant, l'absence de synergie positive est sans doute due à l'identité des stress étudiés. Il est important de conserver un certain niveau de précaution de ce côté puisque de dire que les stress n'interagissent que très rarement de façon synergique pourrait minimiser cette possibilité et faire pencher vers des décisions qui pourraient être coûteuses pour les écosystèmes sans connaître le réel type d'interaction.

4.3 Limites de l'étude et perspectives

Le troisième chapitre a bien montré que les effets des macrophytes structurants sur les communautés dépendaient du site étudié. Ces résultats laissent donc présager que les réponses des deux premiers chapitres pourraient être modulées si les mêmes expériences étaient réalisées dans des systèmes différents. Les résultats que nous avons

obtenus sont toutefois très informatifs par rapport aux interactions entre stresseurs et indices de biodiversité. Le chapitre III démontre donc qu'il sera primordial pour les futures études d'évaluer les effets des stress localement, mais aussi à plusieurs endroits. Effectivement, même en utilisant une étude standardisée, nous n'avons pas été en mesure d'obtenir les mêmes résultats partout. Ceci souligne l'attention particulière que les scientifiques doivent porter à l'utilisation de méta-analyses utilisant une multitude d'études non standardisées.

L'utilisation de traits biologiques est de plus en plus fréquente dans la littérature. Cette méthode permet d'approcher les mesures de diversité sous un autre angle qui peut être davantage relié aux fonctions des communautés. Ici, le chapitre III a utilisé l'approche par traits biologiques pour comparer les assemblages sur des points communs et tenter de repérer des patrons récurrents face aux changements de l'habitat. L'approche par traits biologiques est complexe et les réponses obtenues vont varier en fonction des traits choisis. Une approche que nous pourrions toutefois encore réaliser est de vérifier les effets de réduction de densité de zostère et l'effet de bordure sur les brouteurs. Effectivement, nous connaissons le type de nourriture consommée par nos brouteurs. Il pourrait donc être intéressant de vérifier si la composition en brouteurs change selon l'habitat. Ceci pourrait nous informer sur des changements dans la disponibilité des différents types de nourriture et d'en mesurer les effets sur nos propres manipulations entre les sites distants.

Les stress ont plusieurs composantes que cette thèse n'a pas explorées, mais qui seraient intéressantes à combiner à des études futures *in situ* sur les stress multiples. Effectivement, les stress ont plusieurs particularités pouvant influencer les systèmes qui n'ont pas été prises en compte dans cette thèse : le moment (« *timing* ») de leur application, la durée, la fréquence, la variance temporelle et l'intensité (Airoldi, 2000; Airoldi et Cinelli, 1997; Airoldi et Virgilio, 1998; Bertocci *et al.*, 2005). Des

changements au niveau du *timing* des stress pourraient avoir des conséquences considérables au niveau des assemblages. Par exemple, s'ils sont synchronisés avec la reproduction ou le recrutement compte tenu du cycle de vie et du mode reproductif des espèces, ou encore en lien avec la saison de production (Airoldi, 2000; Bertocci *et al.*, 2005; Wong *et al.*, 2019). Ces moments auront d'ailleurs plus de chance d'arriver avec l'augmentation de la fréquence des stress. La variance temporelle des stress se caractérise par le niveau de régularité de leur fréquence. Plus la variance augmente, plus il y a aura des périodes de stress rapprochés, puis de longues périodes sans aucun stress par opposition à des stress survenant à des cycles réguliers. Des changements au niveau de la fréquence et de la variance temporelle des stress pourraient affecter la richesse, la diversité, la structure et la variabilité temporelle des communautés (Benedetti-Cecchi *et al.*, 2006; Bertocci *et al.*, 2005; Butler, 1989; Navarrete, 1996). Ce n'est toutefois pas toujours le cas, par exemple Atalah *et al.* (2007b) n'ont vu aucun effet de la variabilité temporelle et de la séquence d'une perturbation sur la richesse, l'abondance totale et la structure d'une communauté, résultats qu'ils supposent potentiellement liés à colonisation rapide par des propagules disponibles. Les différentes composantes des stress peuvent possiblement avoir des effets interactifs et cela dépend probablement du contexte. Par exemple, certaines études rapportent des effets indépendants de la variance temporelle et de l'intensité des stress (p. ex. Bertocci *et al.*, 2005), tandis que d'autres rapportent des effets interactifs (p. ex. Benedetti-Cecchi *et al.*, 2006), voire les deux selon le contexte (Atalah *et al.*, 2007a).

Les résultats de ma thèse suggèrent que des stress au niveau de l'habitat ayant des effets sur les invertébrés pourraient causer une cascade trophique. Par exemple, un changement au niveau du couvert de macrophytes diminue la taille des individus présents. Ces invertébrés sont potentiellement une ressource alimentaire pour des niveaux trophiques plus élevés ce qui pourrait réduire la capacité de « prédateurs » que

le milieu peut soutenir. Il serait donc intéressant d'évaluer les effets de ces stress à des niveaux trophiques plus élevés.

Les expériences de cette thèse ont, bien sûr, été effectuées à petite échelle (environ un mètre). Effectivement, même si nos parcelles étaient stressées, deux mètres plus loin, de belles communautés non stressées pouvant abriter des espèces diverses et leurs propagules étaient présentes. Des stress appliqués à de plus grandes échelles (même de l'ordre de dizaines de mètres et plus) viendraient changer la présence et la densité des macrophytes structurants, la présence de propagules à proximité et les conditions physiques locales ce qui viendrait notamment affecter la résilience des communautés (O'Leary *et al.*, 2017) bien que ces milieux soient ouverts et certaines propagules pourraient venir de milieux non affectés plus lointains (Crowe *et al.*, 2000; Hawkins *et al.*, 1999). Par exemple, au chapitre I, peut-être que les fucales ne se seraient pas rétablies aussi facilement et que la colonisation par les espèces éphémères deviendrait importante pour la succession. On pourrait croire que dans le chapitre III, les plus grandes espèces s'étant déplacées plus loin n'auraient pas trouvé un habitat adéquat ce qui suggère des effets encore plus élevés sur la cascade trophique. Aussi, les résultats des chapitres II et III pourraient être influencés par l'addition de l'endofaune dans les études. Effectivement, l'endofaune peut représenter une grande partie la production secondaire au niveau des macroinvertébrés (Wong, 2018). Il serait donc intéressant d'inclure l'endofaune dans les études futures.

Ma thèse indique donc que les stress peuvent avoir des effets cumulatifs, que ces effets ne sont pas systématiquement additifs ou synergiques ; que les effets vont dépendre de l'identité des stress et du site étudié ; que naturellement les communautés font preuve de résistance et de résilience aux stress lorsque des milieux intacts sont à proximité et que les stress sont de courte durée ; et qu'un habitat, même à faible densité, peut être riche et diversifié et qu'il vaut la peine de conserver une certaine hétérogénéité de

l'habitat. À la lumière de ces résultats, nous suggérons donc de vérifier les effets des stress sur le moyen et long terme, sur de plus grandes échelles locales et régionales. Il est à noter aussi que la majorité des stress utilisés dans cette thèse ont été sélectionnés pour leur faisabilité en matière de logistique plutôt que pour évaluer les effets directs de stress futurs réalistes. Des études combinant les stress inévitables sont donc nécessaires puisque les effets cumulatifs des stress ne sont pas prévisibles. De plus amples études sur le terrain et en laboratoire sont évidemment nécessaires. J'ajouterai cependant que seules les expériences sur le terrain, quand elles sont possibles, ajoutent le réalisme que les expériences en laboratoire ne peuvent pas livrer. Un bon dosage entre ces approches est souhaitable.

Dans le cadre des changements anticipés dans les milieux marins littoraux, la présence d'espèce structurante devient essentielle au maintien des communautés telles que nous les connaissons. En identifiant localement les stress qui viendraient affecter les macrophytes structurants et les ressources trophiques telles que les algues épiphytes et les invertébrés, une meilleure gestion des écosystèmes est assurée.

4.4 Recommandations

J'émets ici des recommandations pour les biologistes et les gestionnaires des milieux littoraux. Ces recommandations découlent de mes résultats, mais aussi de l'ensemble de mes réflexions émanant de mes études doctorales.

Pour les spécialistes du vivant :

- Répéter les études sur plusieurs sites, étant donné que les effets peuvent être divergents en magnitude et en direction. Bien décrire les habitats adjacents pour vérifier les effets de bordures.
- Conserver un certain niveau d'hétérogénéité et de complexité de structures (feuilles, thalles, racines, etc.) dans les habitats de macrophytes pour soutenir une plus grande diversité en habitats puisque l'hétérogénéité procurera un plus grand nombre de niches ce qui augmentera potentiellement le nombre d'espèces associées.
- Ne jamais se limiter à la richesse pour une mesure de la stabilité/pérennité des écosystèmes ; évaluer la diversité, l'équitabilité, la structure d'abondance et la composition (multivarié), ainsi que les traits biologiques en univarié, mais également en multivarié. Le traitement de ces variables donnera une réponse plus complète de la stabilité des assemblages.
- Effectuer, autant que possible, les expériences sur des parcelles de plus de 1 m^2 dans le but d'obtenir des mécanismes aussi proches que possible du stress testé. Ceci pour diminuer la possibilité de refuges pour certaines espèces et la présence de propagules si ce n'est pas réaliste avec le scénario anticipé.
- Effectuer des études sur plusieurs mois (saisonnalité), voire sur plusieurs années (variance annuelle). Il peut être nécessaire d'étudier des communautés sur le long terme pour être en mesure de déterminer, par exemple, leurs résistance et résilience puisque les stress pourront avoir des effets différents selon leur durée et les saisons.

Pour les gestionnaires de l'environnement :

- Préserver les habitats dominés par les macrophytes structurants puisqu'ils abritent de nombreuses espèces et maintiennent la capacité de résilience des communautés. Ils fournissent une panoplie de services écosystémiques.
- Ne pas se baser uniquement sur le nombre d'espèces pour une idée de la valeur de biodiversité, ou sa dynamique, des communautés biologiques.
- Diminuer autant que possible les stress présents dans un même environnement, car ils peuvent interagir de façon imprévisible. Ainsi, l'ajout d'un nouveau stress dans un environnement n'engendra pas simplement une addition de ses effets obtenus lors d'études effectuées séparément.
- Promouvoir des études incluant les stress multiples dans un habitat particulier qui doit être géré pour connaître le type d'interactions entre stress et leurs répercussions sur le milieu.

ANNEXES

Annexe A – Informations supplémentaires concernant le Chapitre I : Cimon, S. and Cusson, M. 2018. Impact of multiple disturbances and stress on the temporal trajectories and resilience of benthic intertidal communities. Ecosphere 9. doi.org/10.1002/ecs2.2467

Table 5.1. List and classification of taxa found during all sampling periods at Sainte-Flavie, Quebec, Canada. Taxa marked with an asterisk were removed from the canopy-removed plots; taxa marked with a double asterisk were removed from the grazer-reduced plots. Taxa marked with † and ‡ were respectively exclusively or mostly present in Period 9 when destructive sampling occurred (biomass).

Species	Type	Phylum	Class	Order	Family
Algae					
Chordaria flagelliformis	Brown alga	Ochrophyta	Phaeophyceae	Ectocarpales	Chordariaceae
Ectocarpus sp.	Brown alga	Ochrophyta	Phaeophyceae	Ectocarpales	Ectocarpaceae
*Fucus distichus edentatus**	Brown alga	Ochrophyta	Phaeophyceae	Fucales	Fucaceae
*Fucus vesiculosus**	Brown alga	Ochrophyta	Phaeophyceae	Fucales	Fucaceae
Laminaria sp.	Brown alga	Ochrophyta	Phaeophyceae	Laminariales	Alariaceae
Ralfsia fungiformis	Brown alga	Ochrophyta	Phaeophyceae	Ralfsiales	Ralfsiaceae
Petalonia fascia	Brown alga	Ochrophyta	Phaeophyceae	Scytosiphonales	Scytosiphonaceae
Scytosiphon lomentaria	Brown alga	Ochrophyta	Phaeophyceae	Scytosiphonales	Scytosiphonaceae
Stragularia clavata	Brown alga	Ochrophyta	Phaeophyceae	Scytosiphonales	Scytosiphonaceae
Enteromorpha sp.	Green alga	Chlorophyta	Ulvophyceae	Ulvales	Ulvaceae
Ulvaceae	Green alga	Chlorophyta	Ulvophyceae	Ulvales	Ulvaceae
Porphyra sp.	Red alga	Rhodophyta	Bangiophyceae	Bangiales	Bangiaceae
Clathromorphum circumscriptum	Red alga	Rhodophyta	Florideophyceae	Corallinales	Hapalidiaceae
Hildenbrandia rubra	Red alga	Rhodophyta	Florideophyceae	Hildenbrandiales	Hildenbrandiaceae
Invertebrates					
Oligochaeta‡	Animal	Annelida	Oligochaeta		
Polychaeta‡	Animal	Annelida	Polychaeta		
Hediste diversicolor†	Animal	Annelida	Polychaeta	Phyllodocida	Nereididae
Nereis pelagica†	Animal	Annelida	Polychaeta	Phyllodocida	Nereididae
Pholoe minuta†	Animal	Annelida	Polychaeta	Phyllodocida	Pholoidae
Eteone longa†	Animal	Annelida	Polychaeta	Phyllodocida	Phyllodocidae
Pectinaria gouldii†	Animal	Annelida	Polychaeta	Terebellida	Pectinariidae
Amphipoda†	Animal	Arthropoda	Malacostraca	Amphipoda	
*Cancer irroratus***	Animal	Arthropoda	Malacostraca	Decapoda	Cancridae
*Jaera albifrons***‡	Animal	Arthropoda	Malacostraca	Isopoda	Janiridae
Balanus sp.	Animal	Arthropoda	Maxillopoda	Sessilia	Balanidae
Aulactinia stella	Animal	Cnidaria	Anthozoa	Actinaria	Actiniidae
*Strongylocentrotus droebachiensis***	Animal	Echinodermata	Echinoidea	Camarodonta	Strongylocentrotidae
Mya arenaria†	Animal	Mollusca	Bivalvia	Myoida	Myidae
Mytilus spp.	Animal	Mollusca	Bivalvia	Mytiloida	Mytilidae
Macoma balthica†	Animal	Mollusca	Bivalvia	Veneroida	Tellinidae
Margarites sp.**	Animal	Mollusca	Gastropoda	Archaeogastropoda	Margaritidae
*Ecrobia truncata***	Animal	Mollusca	Gastropoda	Littorinimorpha	Hydrobiidae
*Lacuna vincta***	Animal	Mollusca	Gastropoda	Littorinimorpha	Littorinidae
*Littorina littorea***	Animal	Mollusca	Gastropoda	Littorinimorpha	Littorinidae
*Littorina obtusata***	Animal	Mollusca	Gastropoda	Littorinimorpha	Littorinidae
*Littorina saxatilis***	Animal	Mollusca	Gastropoda	Littorinimorpha	Littorinidae
*Skeneopsis planorbis***‡	Animal	Mollusca	Gastropoda	Littorinimorpha	Skeneopsidae
*Testudinalia testudinalis***	Animal	Mollusca	Gastropoda	Patellogastropoda	Lottiidae
Nemerta†	Animal	Nemerta			

Table 5.2. Summary of PERMANOVAs showing the effects of treatment and contrast of canopy (Ca) factor on the structure (in abundance % cover) for the non-manipulated species of the communities for all periods. Significant values are shown in **bold**.

		Period 2		Period 3		Period 4		Period 5	
	df	***Pseudo-F***	*p* (perm)	***Pseudo-F***	*p* (perm)	***Pseudo-F***	*p* (perm)	***Pseudo-F***	*p* (perm)
% Cover									
Treatment	8	1.4745	0.078	1.4855	0.082	1.7940	**0.018**	2.5525	**0.003**
Ca	1	0.6191	0.644	0.6438	0.624	0.8389	0.512	2.8741	**0.028**
Residual	27								
		Period 6		Period 7		Period 8		Period 9	
	df	***Pseudo-F***	*p* (perm)	***Pseudo-F***	*p* (perm)	***Pseudo-F***	*p* (perm)	***Pseudo-F***	*p* (perm)
% Cover									
Treatment	8	1.1198	0.294	1.3349	0.118	2.5597	**0.001**	1.5989	**0.028**
Ca	1	2.1599	0.052	4.2087	**0.003**	4.9599	**0.001**	4.8863	**0.001**
Residual	27								

Table 5.3. Summary of PERMDISP analysis (999 permutations were run) showing the effects of treatment and the three main factors on dispersion of the community structure of non-manipulated species from percent cover for all periods and from biomass at final sampling (Period 9). Significant values are shown in **bold**.

		Period 2		Period 3		Period 4		Period 5	
	df	**F**	***p* (perm)**	**F**	***p* (perm)**	**F**	***p* (perm)**	**F**	***p* (perm)**
% Cover									
Treatment	8	0.8127	0.791	1.1535	0.650	1.2751	0.660	0.1780	2.1733
Residual	27								
Ca	1	2.3770	0.234	5.47e-7	0.999	0.4595	0.564	0.7085	0.564
Gr	1	0.1522	0.759	0.9857	0.382	0.0761	0.832	0.3691	0.563
Nu	1	4.1660	0.102	0.5596	0.528	0.2641	0.675	0.9184	0.396
Residual	30								

		Period 6		Period 7		Period 8		Period 9	
	df	**F**	***p* (perm)**	**F**	***p* (perm)**	**F**	***p* (perm)**	**F**	***p* (perm)**
% Cover									
Treatment	8	1.8232	0.483	3.2912	0.070	6.267	**0.003**	0.7037	0.838
Residual	27								
Ca	1	9.6717	**0.016**	11.309	**0.001**	3.4610	0.094	1.8310	0.242
Gr	1	0.0578	0.851	0.0022	0.972	11.091	**0.008**	1.1087	0.361
Nu	1	1.1531	0.395	0.0905	0.803	1.8916	0.246	0.9904	0.404
Residual	30								

		Period 9	
	df	**F**	***p* (perm)**
Biomass			
Treatment	8	5.2404	**0.028**
Residual	27		
Ca	1	4.5606	**0.001**
Gr	1	0.4256	0.718
Nu	1	1.0883	0.394
Residual	30		

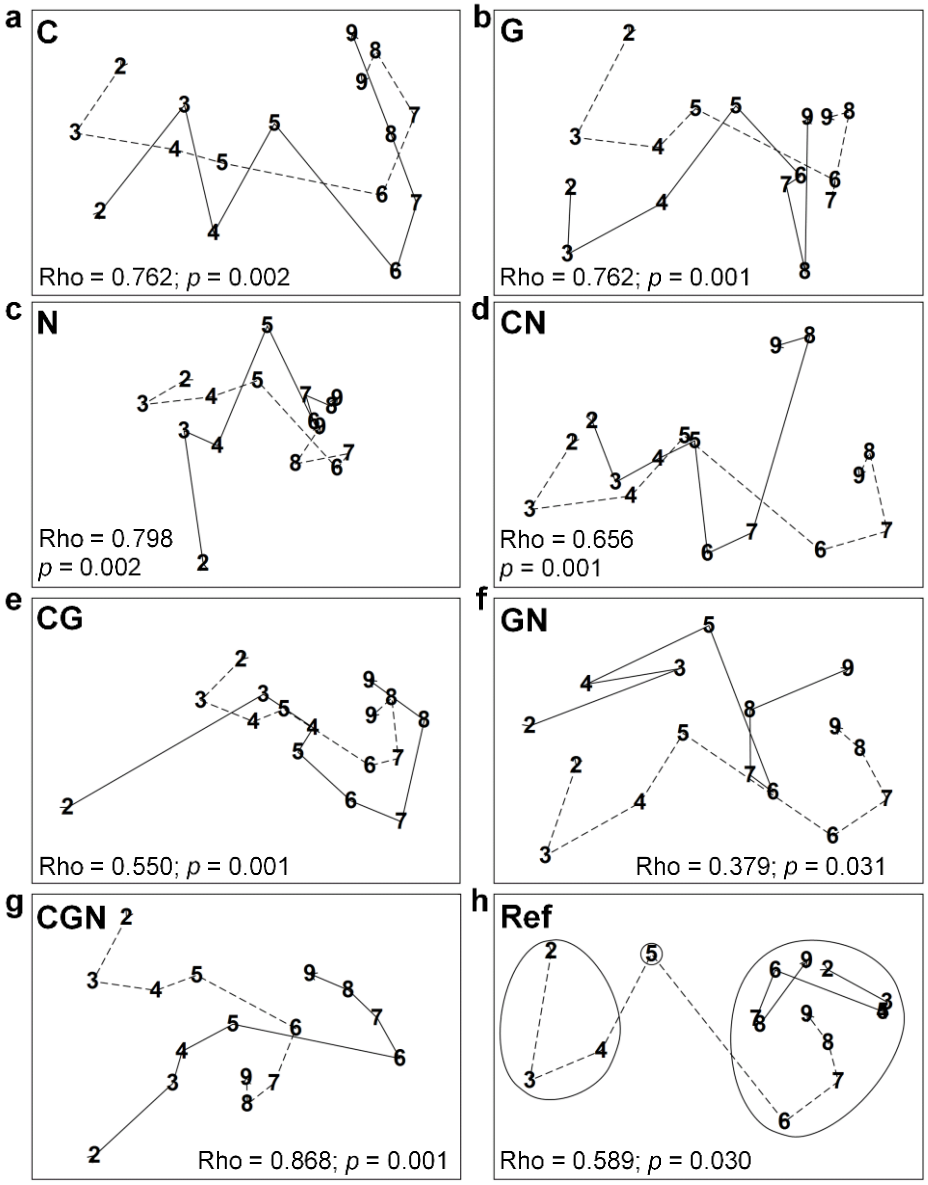

Figure 5.1. Non-metric multidimensional scaling (nMDS) ordinations illustrating average community structure patterns over time for the different treatments (plain line) in comparison with the controls (dashed line) (a–h). Numbers along the lines represent periods. See Fig. 1.1 for treatments and the definitions of C, G, N; the number of letters (1–3; C,G,N) in the treatment labels represents the quantity of stress applied except for Ref, which represents the reference plots. Rho and *p* values have been calculated with Mantel-type tests using Spearman rank. In (h), circles represent a cluster group having an average 60% similarity. Stress from a to h: 0.09, 0.08, 0.13, 0.11, 0.08, 0.11, 0.10, and 0.08, respectively.

Annexe B – Informations supplémentaires concernant le Chapitre II : Cimon, S., Deslauriers, A. and Cusson, M. Multiple stressors and disturbance effects on eelgrass and epifaunal macroinvertebrate assemblage structure.

5.2.2 Taxa found during sampling

Table 5.4 List and classification of taxa found during all sampling periods at Pointe-aux-Outardes, Quebec, Canada.

Species	Type	Phylum	Class	Order	Family
Invertebrates					
Nereis pelagica	Animal	Annelida	Polychaeta	Phyllodocida	Nereididae
Pholoe minuta	Animal	Annelida	Polychaeta	Phyllodocida	Pholoidae
Insect larvae*	Animal	Arthropoda	Insecta		
Calliopius laeviusculus	Animal	Arthropoda	Malacostraca	Amphipoda	Calliopiidae
Crassicorophium bonellii	Animal	Arthropoda	Malacostraca	Amphipoda	Corophiidae
Gammarus lawrencianus	Animal	Arthropoda	Malacostraca	Amphipoda	Gammaridae
Gammarus oceanicus	Animal	Arthropoda	Malacostraca	Amphipoda	Gammaridae
Gammarus spp. juvenile	Animal	Arthropoda	Malacostraca	Amphipoda	Gammaridae
Gammarus tigrinus	Animal	Arthropoda	Malacostraca	Amphipoda	Gammaridae
Phoxocephalus holbolli	Animal	Arthropoda	Malacostraca	Amphipoda	Phoxocephalidae
Pontogeneia inermis	Animal	Arthropoda	Malacostraca	Amphipoda	Pontogeneiidae
Cancer irroratus megalop	Animal	Arthropoda	Malacostraca	Decapoda	Cancridae
Hippolytidae shrimp	Animal	Arthropoda	Malacostraca	Decapoda	Hippolytidae
Edotia triloba	Animal	Arthropoda	Malacostraca	Isopoda	Idoteidae
Idotea phosphorea	Animal	Arthropoda	Malacostraca	Isopoda	Idoteidae
Jaera albifrons	Animal	Arthropoda	Malacostraca	Isopoda	Janiridae
Mysis gaspensis	Animal	Arthropoda	Malacostraca	Mysida	Mysidae
Mysis stenolepsis	Animal	Arthropoda	Malacostraca	Mysida	Mysidae
Mya arenaria	Animal	Mollusca	Bivalvia	Myida	Myidae
Mya truncata	Animal	Mollusca	Bivalvia	Myida	Myidae
Mytilus spp.†	Animal	Mollusca	Bivalvia	Mytiloida	Mytilidae
Mesoderma arctatum	Animal	Mollusca	Bivalvia	Veneroida	Mesodesmatidae
Macoma balthica	Animal	Mollusca	Bivalvia	Veneroida	Tellinidae
Ecrobia truncata	Animal	Mollusca	Gastropoda	Littorinimorpha	Hydrobiidae
Lacuna vincta	Animal	Mollusca	Gastropoda	Littorinimorpha	Littorinidae
Littorina saxatilis	Animal	Mollusca	Gastropoda	Littorinimorpha	Littorinidae
Testudinalia testudinalis	Animal	Mollusca	Gastropoda	Patellogastropoda	Lottiidae
Margarites costalis	Animal	Mollusca	Gastropoda	Trochida	Margaritidae
*Obelia dichotoma**‡	Animal	Cnidaria	Hydrozoa	Leptothecata	Campanulariidae
Vertebrates					
*Cyclopterus lumpus**	Animal	Chordata	Actinopterygii	Scorpaeniformes	Cyclopteridae
Fish larvae*	Animal	Chordata	Actinopterygii		

* Taxa removed from analysis.

† Composed of *Mytilus edulis*, *Mytilus trossolus* and hybrids (see Moreau et al. 2005)

‡ *Obelia dichotoma* was probably discarded while separating eelgrass and animals and was therefore not included in the analysis.

5.2.3 Additional tables

5.2.3.1 Table 5.5 – Eelgrass shoot density for Period 0 and Period 3

Table 5.5. Summary of ANOVA showing the effects of sediment nutrient enrichment (Nu) and shading (Sh) factors on eelgrass shoot density for Period 0 and Period 3. Significant values are shown in **bold**.

		Period 0		Period 3	
	df	***F*-ratio**	*p*	***F*-ratio**	*p*
Eelgrass shoot density					
Nu	1	0.89	0.3592	0.11	0.7437
Sh	1	2.25	0.1532	2.16	0.1613
Nu × Sh	1	0.08	0.7848	1.50	0.2382
Residual	16				

5.2.3.2 Table 5.6 – Epiphytic mass for Period 1

Table 5.6. Summary of ANOVA showing the effects of eelgrass shoot density reduction (De), sediment nutrient enrichment (Nu), and shading (Sh) factors on epiphyte load at Period 1 (dry weight of epiphytes (g) / dry weight of *Z. marina* (g)). Significant values are shown in **bold**.

		Period 1	
	df	***F*-ratio**	*p*
e) Epiphyte load			
De	1	2.35	0.1352
Nu	1	0.81	0.3736
Sh	1	0.00	0.9967
De × Nu	1	3.44	0.0727
De × Sh	1	1.22	0.2775
Nu × Sh	1	3.32	0.0778
De × Nu × Sh	1	0.07	0.7933
Residual	32		

5.2.3.3 Table 5.7 – PERMANOVA of total NSC for Period 2

Table 5.7. Summary of PERMANOVAs showing the effects of eelgrass shoot density reduction (De), sediment nutrient enrichment (Nu), and shading (Sh) factors on normalized soluble sugars and starch for leaves and root-rhizomes separately using Euclidean distances at Period 2. Significant values are shown in **bold**.

	df	Pseudo-*F*	*p* perm
Total non-structural carbohydrates structure			
De	1	0.6340	0.617
Nu	1	0.7696	0.539
Sh	1	17.396	**0.001**
De × Nu	1	0.2254	0.919
De × Sh	1	3.0157	**0.016**
Nu × Sh	1	0.6626	0.590
De × Nu × Sh	1	0.4036	0.807
Residual	32		

Note: 999 permutations were used.

5.2.3.4 Table 5.8 – ANOVAs of raw abundances and eelgrass from epifauna samples

Table 5.8. Summary of ANOVAs showing the effects of eelgrass shoot density reduction (De), sediment nutrient enrichment (Nu), and shading (Sh) factors on raw abundance of epifauna (N) and biomass of *Z. marina* (g_{dw}) collected with epifaunal samples at sampling periods 1 to 3. Raw abundances were log transformed while *Z. marina* biomass were square-root transformed. Significant values are shown in **bold**.

		Period 1		Period 2		Period 3	
	df	***F*-ratio**	*p*	***F*-ratio**	*p*	***F*-ratio**	*p*
a) Raw abundance							
De	1	1.0346	0.3167*	6.4721	**0.0160**	3.2221	0.0821
Nu	1	0.4557	0.5045	3.5277	0.0695*	0.0448	0.8338
Sh	1	0.0000	0.9954	7.9085	**0.0083***	0.0000	0.9954
De × Nu	1	0.6139	0.4391	2.8260	0.1025	2.8788	0.0995
De × Sh	1	5.8750	**0.0212***	1.0199	0.3201	0.0017	0.9678
Nu × Sh	1	2.6126	0.1158	2.1815	0.1495	0.8792	0.3555
De × Nu × Sh	1	0.5166	0.4775	1.1287	0.2960	1.8028	0.1888
Residual	32						
a) *Z. marina* biomass							
De	1	21.392	**0.0001**	5.4348	**0.0262**	9.7571	**0.0038**
Nu	1	2.3672	0.1337	0.4195	0.5218	1.2006	0.2814
Sh	1	0.0824	0.7759	16.210	**0.0003**	0.1505	0.7006
De × Nu	1	1.7538	0.1948	5.3332	**0.0275**	3.7621	0.0613
De × Sh	1	0.5313	0.4714	2.2819	0.1407	0.2428	0.6256
Nu × Sh	1	1.2217	0.2773	2.5104	0.1229	0.0864	0.7707
De × Nu × Sh	1	0.1729	0.6803	4.5186	**0.0413**	3.7908	0.0604
Residual	32						

*Indicates differences in terms of significant results with standardized abundances (see Table 2.3)

5.2.4 Supplementary results: effects of treatments on species

5.2.4.1 Effect of eelgrass shoot density reduction on species

The species that most contributed to the differences in structure between density treatments are listed in Tables 5.9, 5.10, and 5.11; we can observe a decrease in average dissimilarity through time. Two species showed a significant increase in standardized abundance in Period 1 under reduced eelgrass shoot density: the gastropod *Ecrobia truncata* and the isopod *Edotia triloba*. The periwinkle *L. saxatilis* lost its dominance and shared its dominance with another gastropod *Ecrobia truncata* in Period 1.

Four species had a significant increase in their standardized abundance in Period 2 in the reduced-density eelgrass plots: the gastropods *E. truncata, Littorina saxatilis*, and *Lacuna vincta* and the bivalve *Mytilus* spp.

Three species had a significant increase in standardized abundance in Period 3 under conditions of reduced eelgrass shoot density: the isopod *Idotea phosphorea*, and the gastropods *L. vincta* and *E. truncata*. Recruitment of *L. vincta*, which occurred in July–August, was higher in density-reduced plots. We also observed more *Mytilus* spp. in Period 3 compared to other periods; however, we observed no differences in their standardized abundances among the eelgrass shoot density treatments.

5.2.4.2 Shading effect on species

The species that most contributed to the differences in structure between the shading treatments are listed in Supplementary Table 5.13. Four taxa had a significant change of standardized abundance: *L. saxatilis* decreased, while *E. truncata*, *E. triloba*, and juvenile *Gammarus* sp. increased under shading. The higher evenness can be attributed to the decrease of the dominant species, *L. saxatilis*, combined with an increase of other species (notably *E. truncata* and *E triloba)*. Although *L. saxatilis* remained the

dominant species under conditions of shading, the total abundance of all other species was about 25% higher than the abundance of *L. saxatilis*, while *L. saxatilis* had about 40% more individuals than the total abundance of all other species under natural light conditions.

5.2.5 SIMPER tables

5.2.5.1 Table 5.9 – Density reduction in Period 1

Table 5.9. Summary of SIMPER (percentage of similarity) for eelgrass shoot density reduction in Period 1. Table shows species that cumulatively contribute up to 70% to the dissimilarity between treatments. D-: eelgrass shoot density untouched; D+: eelgrass shoot density reduced; Av. nb.: average number (abundance); Av. diss.: average dissimilarity; Diss/SD: dissimilarity divided by standard deviation; Contrib.%: percentage of contribution; Cum.%: cumulated percentage of contribution. Species in **bold** have significant differences (*p*-values provided) of abundance between treatments (*t*-test).

Species	Av. nb. D-	Av. nb. D+	Av. diss.	Diss/SD	Contrib.%	Cum.%
***Ecrobia truncata p* < 0.0001**	**0.48**	**1.37**	6.95	1.44	14.79	14.79
Jaera albifrons	0.57	0.67	5.16	1.17	10.99	25.79
Mytilus spp.	0.42	0.55	4.52	1.10	9.62	35.41
***Edotia triloba p* = 0.0190**	**0.24**	**0.67**	4.49	1.13	9.55	44.96
Idotea phosphorea	0.53	0.38	4.43	1.08	9.44	54.41
Littorina saxatilis	2.50	2.61	3.91	1.23	8.33	62.73
Phoxocephalus holbolli	0.33	0.39	3.47	1.04	7.40	70.13

Note: average dissimilarity between D- and D+ = 46.96

5.2.5.2 Table 5.10 – Density reduction in Period 2

Table 5.10. Summary of SIMPER (percentage of similarity) for eelgrass shoot density reduction in Period 2. Table shows species that cumulatively contribute up to 70% to the dissimilarity between treatments. D-: eelgrass shoot density untouched; D+: eelgrass shoot density reduced; Av. nb.: average number (abundance); Av. diss.: average dissimilarity; Diss/SD: dissimilarity divided by standard deviation; Contrib.%: percentage of contribution; Cum.%: cumulated percentage of contribution. Species in **bold** have significant differences (*p*-values provided) of abundance between treatments (*t*-test).

Species	Av. nb. D-	Av. nb. D+	Av. diss.	Diss/SD	Contrib.%	Cum.%
***Ecrobia truncata* p < 0.0001**	**0.47**	**1.42**	5.04	1.54	13.42	13.42
***Littorina saxatilis* p < 0.0001**	**2.99**	**3.74**	4.69	1.35	12.47	25.89
***Mytilus spp.* p = 0.0176**	**0.30**	**0.77**	3.94	1.10	10.49	36.39
***Lacuna vincta* p = 0.0215**	**2.00**	**2.39**	3.43	1.38	9.13	45.51
Phoxocephalus holbolli	0.46	0.56	3.01	1.20	8.02	53.53
Gammarus oceanicus	0.32	0.41	2.59	0.95	6.90	60.43
Idotea phosphorea	0.32	0.41	2.57	0.94	6.85	67.28
Edotia triloba	0.29	0.45	2.50	1.02	6.66	73.94

Note: average dissimilarity between D- and D+ = 37.57

5.2.5.3 Table 5.11 – Density reduction in Period 3

Table 5.11. Summary of SIMPER (percentage of similarity) for eelgrass shoot density reduction in Period 3. Table shows species that cumulatively contribute up to 70% to the dissimilarity between treatments. D-: eelgrass shoot density untouched; D+: eelgrass shoot density reduced; Av. nb.: average number (abundance); Av. diss.: average dissimilarity; Diss/SD: dissimilarity divided by standard deviation; Contrib.%: percentage of contribution; Cum.%: cumulated percentage of contribution. Species in **bold** have significant differences (*p*-values provided) of abundance between treatments (*t*-test).

Species	Av. nb. D-	Av. nb. D+	Av. diss.	Diss/SD	Contrib.%	Cum.%
***Idotea phosphorea* p < 0.0001**	**0.63**	**1.63**	7.79	1.60	26.15	26.15
***Lacuna vincta* p = 0.0071**	**1.57**	**2.03**	4.73	1.45	15.87	42.02
***Ecrobia truncata* p = 0.0117**	**0.49**	**0.95**	4.38	1.19	14.68	56.70
Mytilus spp.	1.18	1.20	3.83	1.30	12.85	69.56
Littorina saxatilis	2.48	2.52	3.22	1.13	10.82	80.37

Note: average dissimilarity between D- and D+ = 29.80

5.2.5.4 Table 5.12 – Sediment nutrient enrichment in Period 2

Table 5.12. Summary of SIMPER (percentage of similarity) sediment nutrient enrichment in Period 2. Table shows species that cumulatively contribute up to 70% to the dissimilarity between treatments. N-: no nutrients added; N+: nutrients added; Av. nb.: average number (abundance); Av. diss.: average dissimilarity; Diss/SD: dissimilarity divided by standard deviation; Contrib.%: percentage of contribution; Cum.%: cumulated percentage of contribution. Species in **bold** have significant differences (*p*-values provided) of abundance between treatments (*t*-test).

Species	Av. nb. N-	Av. nb. N+	Av. diss.	Diss/SD	Contrib.%	Cum.%
***Littorina saxatilis p*=0.0250**	**3.56**	**3.18**	4.16	1.20	11.38	11.38
***Ecrobia truncata p* = 0.0139**	**1.09**	**0.80**	4.12	1.37	11.27	22.64
Mytilus spp.	0.62	0.45	3.72	1.03	10.19	32.84
***Phoxocephalus holbolli p* = 0.0362**	**0.70**	**0.32**	3.30	1.28	9.03	41.86
Lacuna vincta	2.25	2.14	3.29	1.32	9.02	50.88
Gammarus oceanicus	0.33	0.41	2.59	0.95	7.09	57.97
Idotea phosphorea	0.32	0.41	2.57	0.96	7.04	65.01
Edotia triloba	0.43	0.31	2.49	1.01	6.82	71.83

Note: average dissimilarity between N- and N+ = 36.54

5.2.5.5 Table 5.13 – Shading in Period 2

Table 5.13. Summary of SIMPER (percentage of similarity) for shading in Period 2. Table shows species that cumulatively contribute up to 70% to the dissimilarity between treatments. S-: natural light; S+: shading; Av. nb.: average number (abundance); Av. diss.: average dissimilarity; Diss/SD: dissimilarity divided by standard deviation; Contrib.%: percentage of contribution; Cum.%: cumulated percentage of contribution. Species in **bold** have significant differences (*p*-values provided) of abundance between treatments (*t*-test).

Species	Av. nb. S-	Av. nb. S+	Av. diss.	Diss/SD	Contrib.%	Cum.%
***Ecrobia truncata p* = 0.0232**	**0.73**	**1.15**	4.21	1.39	11.38	11.38
***Littorina saxatilis p* = 0.0319**	**3.55**	**3.19**	4.19	1.20	11.34	22.72
Mytilus spp.	0.70	0.37	3.77	1.10	10.20	32.92
Lacuna vincta	2.03	2.36	3.40	1.33	9.20	42.12
Phoxocephalus holbolli	0.36	0.66	3.11	1.23	8.40	50.52
***Edotia triloba p* = 0.0156**	**0.16**	**0.58**	2.73	1.09	7.38	57.90
Gammarus oceanicus	0.26	0.48	2.68	0.96	7.25	65.15
Idotea phosphorea	0.28	0.45	2.60	0.94	7.04	72.19

Note: Average dissimilarity between S- and S+ = 36.97; *Gammarus* sp. juvenile $p = 0.0044$ (average 0.41 shaded and 0.02 natural light, no transformations).

5.2.6 Supplementary figures

5.2.6.1 Figure 5.2 – Non-structural carbohydrates and RLE (De × Sh)

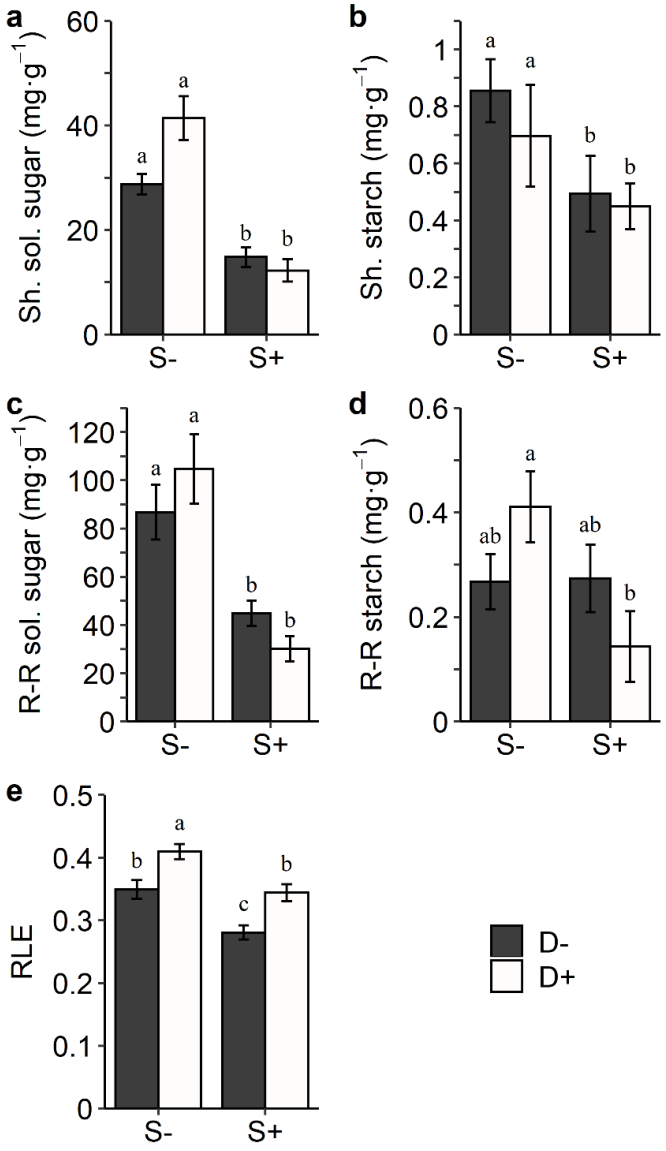

Figure 5.2. Mean (±SE) values of soluble sugars ($mg \cdot g^{-1}_{dw}$) in (a) shoots and (c) root-rhizomes, starch content ($mg \cdot g^{-1}_{dw}$) in (b) shoots and (d) root-rhizomes, and (e) relative leaf elongation. The reported values are from Period 2. Gray and white bars are the respective treatments with D-: eelgrass shoot density untouched; D+: eelgrass shoot density reduced; S-: natural light; S+: shading. The numbers of replicates used to obtain the averages was $n = 10$. Different letters above the bars indicate significant differences ($p < 0.05$, Tukey HSD).

5.2.6.2 Figure 5.3 – PCA of non-structural carbohydrates with links to RLE

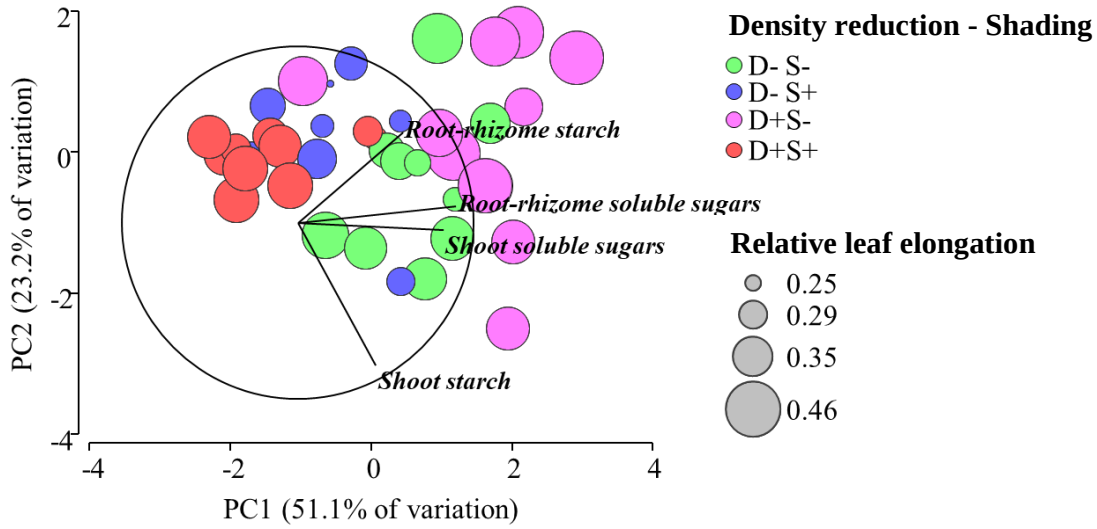

Figure 5.3. Principal component analysis (PCA) plot of normalized non-structural carbohydrates in shoots and root-rhizomes. Values are from Period 2. D-: eelgrass shoot density untouched; D+: eelgrass shoot density reduced; S-: natural light; S+: shading. Each bubble represents a plot. Bubble size is proportional to the relative leaf elongation rate (day^{-1}; RLE).

5.2.6.3 Figure 5.4 – Raw abundance results

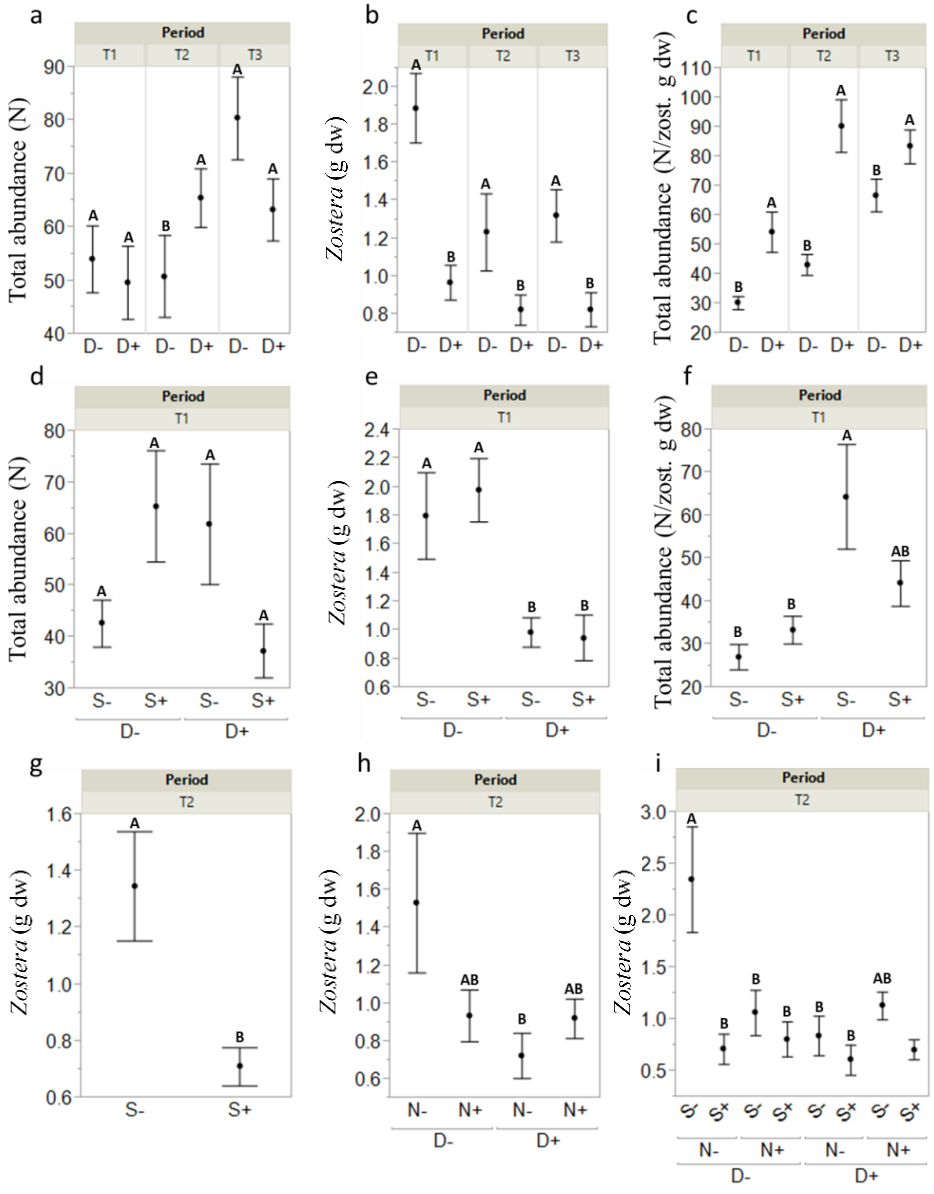

Figure 5.4. Mean (±SE) values of total raw abundance (a, d), biomass of *Zostera marina* from epifaunal samples (b, e, g–i), (c, f) total abundance standardized per shoot dry weight. Values are from Period 1, 2, and 3 in a–c, Period 1 in d–f, and Period 2 in g–i. D-: eelgrass shoot density untouched; D+: eelgrass shoot density reduced; N-: no nutrients added; N+: nutrients added; S-: natural light; S+: shading. The numbers of replicates used to obtain the averages were $n = 20$ in (a–c) and (g); $n = 10$ in (d–f) and (h); $n = 5$ in (i). Different letters above the bars indicate significant differences ($p < 0.05$; Tukey HSD for multiple comparisons).

5.2.6.4 Figure 5.5 – nMDS

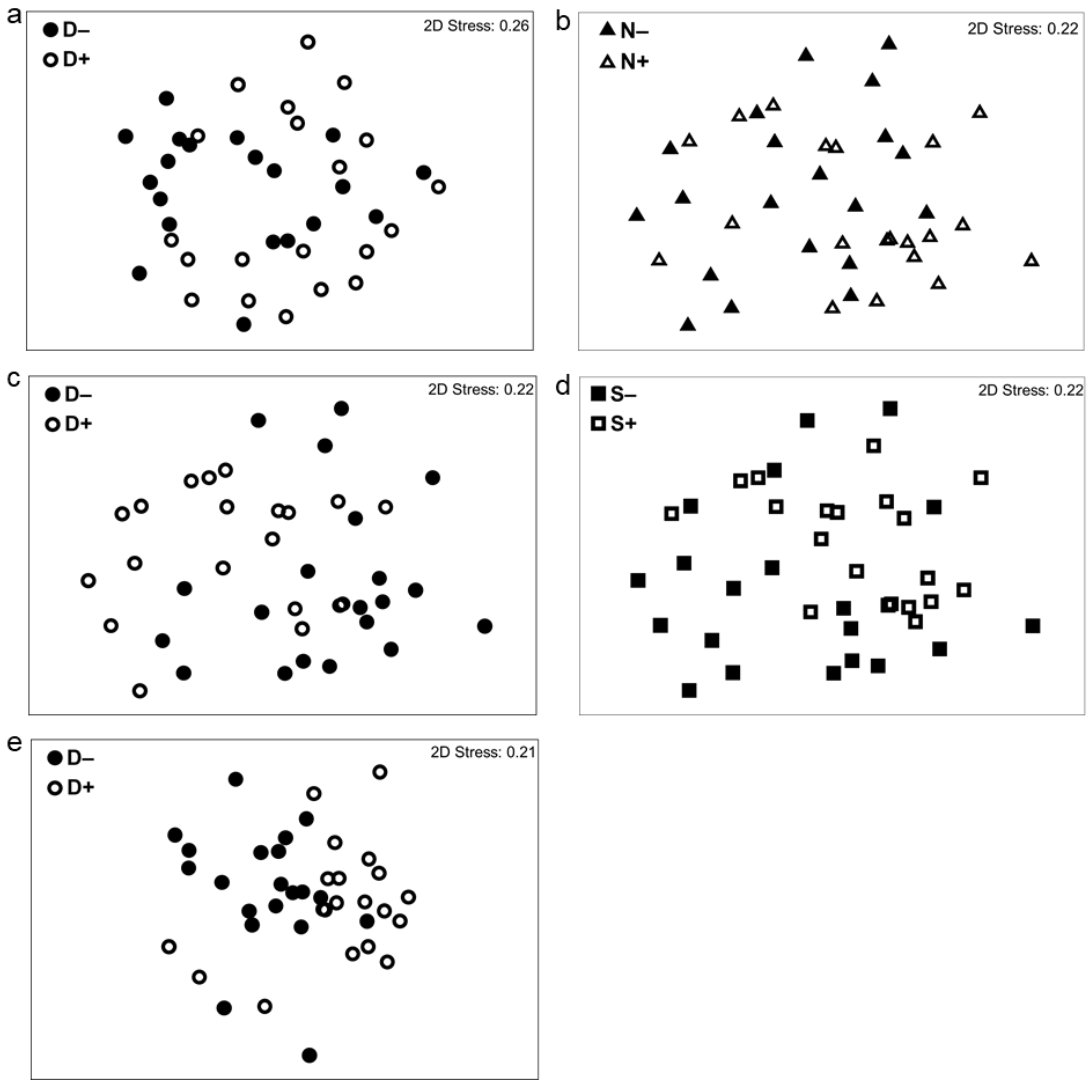

Figure 5.5. Non-metric multidimensional scaling plots illustrating the effect (cf. Table 4 for details) on assemblage structure of (a, c, e) eelgrass shoot density reduction, (b) sediment nutrient enrichment, and (d) shading in Period 1 (a), Period 2 (b–d), and Period 3 (e). Values were calculated based on Bray-Curtis similarities of the dispersion-weighted and square root–transformed standardized abundance of species. Black and white symbols are the respective treatments with - stress absent, + stress present; D: eelgrass shoot density reduction, N: sediment nutrient enrichment, S: shading.

Annexe C – Informations supplémentaires concernant le Chapitre III : Cimon, S., Hovel, K., Boyer, K.E., Duffy, J.E., Hereu, C.M., Jorgensen, P., Kiriakopolos, S., Pierrejean, M., Reynolds, P.L., Rossi, F., Stachowicz, J.J., Ziegler, S.L., Cusson, M. Site-dependent effects of proximity to patch edge and eelgrass complexity on epifaunal communities within *Zostera marina* L. meadows.

5.3.2 Biological traits occurrence detailed results

Trait categories taken apart revealed that most traits were affected by position and complexity depending on the site (Table 5.25–5.29).

5.3.2.1 Size

Medium-sized organisms generally had the highest proportions with some exceptions: MX was dominated by small-sized organisms, while FR and SF showed a change of dominance following position and complexity (Fig. 3.4a). Position had a general, though not significant, effect on medium-sized organisms that tended to occupy a lower proportion in the interior; this was significant in SF and VA (Fig. 3.4a, Table 5.25b). Position did not have a general effect on large- or small-sized organisms.

In FR, there was slightly fewer large-sized organisms in the interior compared to the edges. Small-sized organisms occupied a higher proportion in the interior, while medium-sized organisms had the same proportions at the edge and interior (Fig. 3.4a, Table 5.25). In MX and QU, there were no differences in the distribution of sizes following position (Fig. 3.4a, Table 5.25). In SF, the proportion of large-sized organisms in the interior was more than double that of the edge (Fig. 3.4a, Table 5.25a). The interior was dominated by large-sized organisms followed by medium-sized organisms and a small proportion of small-sized organisms; the edge was dominated by medium-sized organisms followed by large- then small-sized organisms (Fig. 3.4a, Table 5.25). In VA, medium-sized organisms dominated the size proportions (Fig.

3.4a). The edge had more medium-sized and fewer small-sized organisms than the interior (Fig. 3.4a).

The effect of complexity reduction on size depended on the region (Table 5.20), but it also showed a general significant effect on medium-sized organisms that had lower proportions when complexity was reduced (Table 5.20). On the other hand, small-sized organisms had higher proportions where complexity was reduced, and this was significant for FR, QU, and VA (Fig. 3.5a, Table 5.25). The dominant size of organisms changed with complexity in FR and QU (Fig. 3.5a). In FR, medium-sized organisms dominated the proportions of sizes in ambient plots, while small-sized organisms dominated where complexity was reduced (Fig. 3.5a; Table 5.25). Gradual changes occurred in QU with medium-sized taxa dominating ambient plots, and small-sized organisms dominated the 80%-reduced plots (Fig. 3.5a, Table 5.25).

Some sites showed an interaction between position × complexity for large- and small-sized organisms (Table 5.25). MX showed higher proportions of small-sized organisms and lower proportions of medium- and large-sized organisms where complexity was reduced by 80%, but only at the edge (results not shown). FR showed no effect of complexity at the edge, but higher proportions of large- and medium-sized organisms occurred in the interior of ambient plots, while small-sized organisms had higher proportions in complexity-reduced plots (Fig. 5.9).

5.3.2.2 Life habits and movements

Life-habit categories were affected by position or complexity depending on the region (Table 5.20b, 5.23b, 5.26). All sites were dominated by the crawling trait, and our treatments did not influence that dominance (Fig. 3.4b, 3.5b).

Effects of position or complexity were not always consistent among sites for life-habit categories (Table 5.31, 5.32; Fig. 3.4b, 3.5b). Swimmers were generally, though not significantly, more proportionally abundant at the edge, and the difference with the interior was significant for FR and SF (Table 5.31, Fig. 3.4b). The proportion of swimmers was lower where complexity was reduced in MX and VA (Table 5.32, Fig. 3.5b). Crawlers were more proportionally abundant at the edge in FR, while they were more proportionally abundant in the interior in SF (Table 5.31). Reduction in complexity showed lower proportions of crawlers in MX and QU, while they were more proportionally abundant in VA (Fig. 3.5b). There was also an interaction between Site × Position × Complexity for crawlers in FR; complexity reduction increased the proportion of crawlers at the edge of the bed, while it decreased in the interior (Fig. 5.9b). Burrowers showed no general patterns; they were more proportionally abundant in the interior in VA, and they were more proportionally abundant in the complexity-reduced plots in QU and VA (Table 5.31, 5.32; Fig. 3.4b, 3.5b). Sessile organisms showed no general pattern; they were more proportionally abundant in the interior in FR, at the edge in SF, and when complexity was reduced by 80% in MX (Table 5.31, 5.32; Fig. 3.4b, 3.5b).

5.3.2.3 Feeding habits

Feeding-habit categories were affected by position or complexity depending of the region (Table 5.20c, 5.23c, 5.27), and the effect of complexity reduction, when present, was consistent among regions (Table 5.32). The effect on deposit feeders was consistent among regions for position and complexity reduction (Table 5.31-5.32). Grazers were affected by position only in SF where they were proportionally more abundant in the interior and were negatively affected by complexity reduction in MX, QU, and VA (Table 5.31, 5.32; Fig. 3.4c, 3.5c). Filter feeders were proportionally more abundant at the interior in FR and VA; they were more abundant at the edge in SF and positively affected by complexity reduction in MX and VA (Table 5.31, 5.32; Fig. 3.4c,

3.5c). Deposit feeders were more proportionally abundant at the edge in FR, MX, and SF and where complexity was reduced in MX, QU, and VA (Table 5.31, 5.32; Fig. 3.4c, 3.5c Finally, only position had an impact on the predator/scavenger category where it was absent from the edge in VA (Table 5.31, 5.32; Fig. 3.4c, 3.5c).

5.3.2.4 Reproduction dispersal

Reproduction categories were affected by position or complexity, depending of the region (Table 5.20d, 5.23d, 5.28), and were dominated by brooders in all regions (Fig. 3.4d and 3.5d). Position effect had the opposite effect in MX and SF (Fig. 3.4d). Broadcast spawners were affected by position only in VA and were more proportionally abundant in the interior. They were negatively affected by complexity reduction in MX and positively affected in QU (Table 5.31-5.32; Fig. 3.4d, 3.5d). Brooders were proportionally more abundant in the interior in MX and at the edge in SF, while they were more abundant in ambient plots in QU (Table 5.31-5.32; Fig. 3.4d, 3.5d). Egg-case producers were more proportionally abundant at the edge in MX and in the interior in SF. They were more abundant where complexity was reduced in MX (Table 5.31-5.32; Fig. 3.4d, 3.5d).

5.3.2.5 Larval feeding mode

The larval feeding categories were affected by complexity depending on the region (Table 5.20e, 5.23e, 5.29) and were dominated by direct development at all sites (Fig. 3.4e, 3.5e). Position had only an effect in VA where lecithotrophic larvae as well as planktotrophic larvae were absent from the edge, with one exception (Table 5.29, Fig. 3.4e). Complexity reduction showed opposite patterns in FR and QU where the direct-development proportion increased under complexity reduction in FR and decreased in QU, while planktotrophic larvae decreased in FR and increased in QU, and this effect was most important in the interior for the FR site (Table 5.32-5.33; Fig. 3.5e, 5.9e).

5.3.3 Supplementary tables and figures

Table 5.14. Average shoot density ± standard error and above-ground biomass at the beginning of the experiment in each region as well as experiment duration, patchiness of the site, if it is a monospecific meadow or not (other seagrass species mentioned) and approximative size of the meadow.

	Shoot density (shoot/m²)		**Above-ground biomass ($g_{shoot\ dw}/m^2$)**		**Duration (days)**	**Patchiness**	**Monospecific**	**Meadow size (km²)**
Region	**Edge**	**Interior**	**Edge**	**Interior**				
FR	200 ± 15	253 ± 16	256 ± 31	254 ± 39	11	n.d.	n.d.	n.d.
MX	935 ± 41	1169 ± 72	104 ± 8	95 ± 7	22	n.d.	n.d.	n.d.
QU	567 ± 19	691 ± 18	76 ± 6	144 ± 9	13	Continuous	Mono	17
SF	49 ± 3	60 ± 2	40 ± 5	75 ± 5	31	Patchy	n.d.	n.d.
VA	1254 ± 47	1691 ± 59	281 ± 13	235 ± 21	16	Continuous	*Ruppia maritima*	0.0322

Table 5.15. List of taxa collected and used in the analysis as well as regions where they were found.

Phylum	Class	Order	Family	Genus	Species / Taxa	Species label	Region where present
Annelida	**Polychaeta**	**Eunicida**	Lumbrineridae	*Lumbrineris*	*Lumbrineris* sp.	Lumb	FR
Annelida	**Polychaeta**	**Phyllodocida**	Hesionidae	*Oxydromus*	*Oxydromus pallidus*	Oxyd	FR
			Nereididae	*Nereis*	*Nereis pelagica*	Ner.P	QU
			Nereididae	*Nereis*	*Nereis* spp.	Ner.S	VA
			Nereididae	*Platynereis*	*Platynereis bicanaliculata*	Pla.B	MX
			Nereididae	*Platynereis*	*Platynereis dumerilii*	Pla.D	FR
			Phyllodocidae	*Nereiphylla*	*Nereiphylla rubiginosa*	Ner.R	FR
			Polynoidae	*Harmothoe*	*Harmothoe* sp.	Harm	FR
			Polynoidae	*Lepidonotus*	*Lepidonotus squamatus*	Lepi	QU
Annelida	**Polychaeta**	**Polychaeta**	Polychaeta	Polychaeta	Polychaeta	Poly	SF
Annelida	**Polychaeta**	**Sabellida**	Serpulidae	Serpulidae	Serpulidae	Serp	FR
Arthropoda	**Malacostraca**	**Amphipoda**	Ampeliscidae	*Ampelisca*	*Ampelisca brevicornis*	Amp.B	VA
			Ampeliscidae	*Ampelisca*	*Ampelisca* spp.	Amp.S	SF
			Amphilochidea	*Apolochus*	*Apolochus picadurus*	Apol	MX
			Amphipoda	Amphipoda	Unknown Amphipod	U.Amp	SF
			Amphipoda	Amphipoda	Unknown Amphipod A - MX	U.Amp.MX	MX
			Ampithoidae	*Ampithoe*	*Ampithoe longimana*	Amp.L	VA
			Ampithoidae	*Ampithoe*	*Ampithoe plumulosa*	Amp.P	MX
			Ampithoidae	*Ampithoe*	*Ampithoe ramondi*	Amp.R	FR
			Ampithoidae	*Ampithoe*	*Ampithoe valida*	Amp.V	SF
			Ampithoidae	*Cymadusa*	*Cymadusa compta*	Cyma	VA
			Aoridae	*Bemlos*	*Bemlos macromanus*	Beml	MX
			Aoridae	*Grandidierella*	*Grandidierella japonica*	Gran	SF
			Aoridae	*Microdeutopus*	*Microdeutopus algicola*	Mic.Al	FR
			Aoridae	*Microdeutopus*	*Microdeutopus anomalus*	Mic.An	FR
			Aoridae	*Microdeutopus*	*Microdeutopus* sp.	Mic.S	FR
			Aoridae	*Paramicrodeutopus*	*Paramicrodeutopus schmitti*	P.Sch	MX
			Atylidae	*Atylus*	*Atylus massiliensis*	Atyl	FR
			Calliopiidae	*Calliopius*	*Calliopius laeviusculus*	Call	QU
			Caprellidae	*Caprella*	*Caprella californica*	Cap.C	SF, MX

Phylum	Class	Order	Family	Genus	Species / Taxa	Species label	Region where present
			Caprellidae	*Caprella*	*Caprella drepanochir*	Cap.D	SF
			Caprellidae	*Caprella*	*Caprella penantis*	Cap.P	VA
			Caprellidae	Caprellidae	Juvenile caprellid	Juv.C	SF
			Caprellidae	*Phtisica*	*Phtisica marina*	Phti	FR
			Corophiidae	*Corophium*	*Corophium* spp.	Coro	SF, VA, FR
			Corophiidae	*Monocorophium*	*Monocorophium californianum*	Mon.C	SF, MX
			Corophiidae	*Monocorophium*	*Monocorophium insidiosum*	Mon.I	SF
			Dexaminidae	*Paradexamine*	*Paradexamine* spp.	P.Spp	SF
			Gammaridae	*Gammarus*	*Gammarus duebeni*	Gam.B	QU
			Gammaridae	*Gammarus*	*Gammarus insensibilis*	Gam.I	FR
			Gammaridae	*Gammarus*	*Gammarus lawrencianus*	Gam.L	QU
			Gammaridae	*Gammarus*	*Gammarus mucronatus*	Gam.M	VA
			Gammaridae	*Gammarus*	*Gammarus oceanicus*	Gam.O	QU
			Gammaridae	*Gammarus*	*Gammarus* sp. juvenile	Gam.J	QU
			Gammaridae	*Gammarus*	*Gammarus tigrinus*	Gam.T	QU
			Haustoriidae	Haustoriidae	Haustoriidae	Haus	FR
			Hyalidae	*Protohyale*	*Protohyale frequens*	Prot	MX
			Iphimediidae	*Iphimedia*	*Iphimedia vicina*	Iphi	FR
			Ischyroceridae	*Ericthonius*	*Ericthonius brasiliensis*	Eri.B	MX
			Ischyroceridae	*Ericthonius*	*Ericthonius punctatus*	Eri.P	FR
			Ischyroceridae	*Jassa*	*Jassa slatteryi*	Jass	SF
			Lysianassidae	*Lysianassa*	*Lysianassa* sp.	Lysi	FR
			Maeridae	*Elasmopus*	*Elasmopus levis*	Ela.L	VA
			Maeridae	*Elasmopus*	*Elasmopus rapax*	Ela.R	MX
			Maeridae	*Elasmopus*	*Elasmopus* sp.	Ela.S	FR
			Oedicerotidae	*Monoculodes*	*Monoculodes* sp.	Mon.S	QU
			Phoxocephalidae	*Phoxocephalus*	*Phoxocephalus holbolli*	Phox	QU
			Podoceridae	*Podocerus*	*Podocerus brasiliensis*	Podo	MX
			Pontogeneiidae	*Nasageneia*	*Nasageneia quinsana*	Nasa	MX
			Pontogeneiidae	*Pontogeneia*	*Pontogeneia inermis*	Pont	QU
Arthropoda	**Malacostraca**	**Cumacea**	Cumacea	Cumacea	Cumacea	Cuma	MX
Arthropoda	**Malacostraca**	**Decapoda**	Crangonidae	*Crangon*	*Crangon septemspinosa*	Cran	VA
			Decapoda	Decapoda	Decapod larvae A	Deca	MX

Phylum	Class	Order	Family	Genus	Species / Taxa	Species label	Region where present
			Decapoda	Decapoda	Shrimp sp.1	Shri	QU
			Hippolytidae	*Hippolyte*	*Hippolyte californiensis*	Hip.C	MX
			Hippolytidae	*Hippolyte*	*Hippolyte* sp.	Hip.S	VA
			Varunidae	*Hemigrapsus*	*Hemigrapsus oregonensis*	Hemi	MX
Arthropoda	**Malacostraca**	**Isopoda**	Arcturidae	*Arcturinella*	*Arcturinella* sp.	Ar.Sp	FR
			Idoteidae	*Edotia*	*Edotia triloba*	Edot	VA, QU
			Idoteidae	*Erichsonella*	*Erichsonella attenuata*	Eri.A	VA
			Idoteidae	*Erichsonella*	*Erichsonella crenulata*	Eri.C	MX
			Idoteidae	*Idotea*	*Idotea balthica*	Ido.B	VA
			Idoteidae	*Idotea*	*Idotea chelipes*	Ido.C	FR
			Idoteidae	*Idotea*	*Idotea phosphorea*	Ido.P	QU
			Idoteidae	*Pentidotea*	*Pentidotea resecata*	Pent	SF
			Janiridae	*Jaera*	*Jaera albifrons*	Jaer	QU
			Munnidae	*Munna*	*Munna* sp.	Munn	MX
			Paranthuridae	*Califanthura*	*Califanthura squamosissima*	Cali	MX
			Sphaeromatidae	*Dynamene*	*Dynamene bidentata*	Dyna	FR
			Sphaeromatidae	*Lekanesphaera*	*Lekanesphaera hookeri*	Leka	FR
			Sphaeromatidae	*Paracerceis*	*Paracerceis sculpta*	P.Scu	MX
			Sphaeromatidae	*Sphaeroma*	*Sphaeroma serratum*	Sph.J	FR
			Sphaeromatidae	Sphaeromatidae	Sphaeroma juvenile	Sph.S	FR
Arthropoda	**Malacostraca**	**Tanaidacea**	Tanaidacea	Tanaidacea	Tanaidacea	Tana	SF, VA
			Tanaididae	*Tanais*	*Tanais dulongii*	Tan.D	FR
Cnidaria	**Anthozoa**	**Actiniaria**	Actiniidae	*Anemonia*	*Anemonia sulcata*	Anem	FR
Echinodermata	**Asteroidea**	**Valvatida**	Asterinidae	*Asterina*	*Asterina* sp.	Aste	FR
Echinodermata	**Ophiuroidea**	**Ophiurida**	Amphiuridae	*Amphipholis*	*Amphipholis squamata*	Amph	FR
Mollusca	**Bivalvia**	**Cardiida**	Cardiidae	*Parvicardium*	*Parvicardium exiguum*	Parv	FR
			Semelidae	*Abra*	*Abra alba*	Abra	FR
			Tellinidae	*Limecola*	*Limecola balthica*	Lime	QU
Mollusca	**Bivalvia**	**Myida**	Myidae	*Mya*	*Mya arenaria*	MyaA	QU
Mollusca	**Bivalvia**	**Mytilida**	Mytilidae	*Arcuatula*	*Arcuatula senhousia*	Ar.Se	FR
			Mytilidae	*Mytilus*	*Mytilus* spp.	Myti	QU
Mollusca	**Bivalvia**	**Pectinida**	Pectinidae	*Argopecten*	*Argopecten ventricosus*	Argo	MX

Phylum	Class	Order	Family	Genus	Species / Taxa	Species label	Region where present
Mollusca	**Bivalvia**	**Venerida**	Veneridae	*Polititapes*	*Polititapes aureus*	Poli	FR
Mollusca	**Gastropoda**	**Anaspidea**	Aplysiidae	*Phyllaplysia*	*Phyllaplysia taylori*	Phyl	SF
Mollusca	**Gastropoda**	**Archaeogastropoda**	Trochidae	*Jujubinus*	*Jujubinus striatus*	Juju	FR
Mollusca	**Gastropoda**	**Caenogastropoda**	Cerithiidae	*Bittiolum*	*Bittiolum varium*	Bit.V	VA
			Cerithiidae	*Bittium*	*Bittium reticulatum*	Bit.R	FR
			Cerithiidae	*Cerithium*	*Cerithium vulgatum*	Ceri	FR
Mollusca	**Gastropoda**	**Cephalaspidea**	Bullidae	*Bulla*	*Bulla gouldiana*	Bulla	MX
			Cylichnidae	*Acteocina*	*Acteocina inculta*	Acte	MX
Mollusca	**Gastropoda**	**Littorinimorpha**	Assimineidae	*Assiminea*	*Assiminea californica*	Assi	MX
			Calyptraeidae	*Crepidula*	*Crepidula convexa*	Cre.C	MX
			Calyptraeidae	*Crepidula*	*Crepidula fornicata*	Cre.F	VA
			Hydrobiidae	*Ecrobia*	*Ecrobia truncata*	Ecro	QU
			Littorinidae	*Littorina*	*Littorina saxatilis*	Litt	QU
			Rissoidae	*Pusillina*	*Pusillina lineolata*	Pusi	FR
Mollusca	**Gastropoda**	**Neogastropoda**	Columbellidae	*Alia*	*Alia carinata*	Alia	MX
			Cystiscidae	*Gibberula*	*Gibberula miliaria*	Gib.M	FR
			Cystiscidae	*Gibberula*	*Gibbula umbilicalis*	Gib.U	FR
			Nassariidae	*Nassarius*	*Nassarius tiarula*	Nass	MX
			Nassariidae	*Tritia*	*Tritia corniculum*	Trit	FR
Mollusca	**Gastropoda**	**Patellograstropoda**	Lottiidae	*Tectura*	*Tectura depicta*	Tect	MX
Mollusca	**Gastropoda**	**Trochoidea**	Phasianellidae	*Tricolia*	*Tricolia tenuis*	Tric	FR
Platyhelminthes	**Rhabditophora**	**Polycladida**	Stylochoplanidae	*Triplana*	*Triplana viridis*	Trip	MX

Table 5.16. Species × Trait matrix of fuzzy scores of traits used for biological-trait analysis. See trait/categories code in Table 3.2.

		Trait categories																
Species	**Species label**	**La**	**Me**	**Sm**	**Sw**	**Cr**	**Bu**	**Se**	**Gr**	**Fi**	**De**	**PS**	**Bst**	**Bro**	**Lay**	**Le**	**Pl**	**Dd**
Abra alba	Abra	0.4	0.53	0.11	0	0	1	0	0	0.5	0.5	0	1	0	0	0	1	0
Acteocina inculta	Acte	0.1	0.91	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0
Alia carinata	Alia	0.8	0.25	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0
Ampelisca brevicornis	Amp.B	0	0	1	0.5	0.5	0	0	0	0.5	0.5	0	0	1	0	0	0	1
Ampelisca spp.	Amp.S	0	0.38	0.58	0.33	0.33	0	0.34	0	0.5	0.5	0	0	1	0	0	0	1
Amphipholis squamata	Amph	0	0.62	0.38	0	1	0	0	0	0.25	0.5	0.25	0	1	0	0	0	1
Ampithoe longimana	Amp.L	0	0.43	0.57	0.5	0.5	0	0	0.34	0	0.33	0.33	0	1	0	0	0	1
Ampithoe plumulosa	Amp.P	0.1	0.33	0.56	0.25	0.12	0.13	0.50	0.8	0	0.2	0	0	1	0	0	0	1
Ampithoe ramondi	Amp.R	0	0.13	0.87	0.5	0.5	0	0	0.8	0	0.2	0	0	1	0	0	0	1
Ampithoe valida	Amp.V	0.5	0.42	0.09	0.25	0.25	0	0.5	0.8	0	0.2	0	0	1	0	0	0	1
Anemonia sulcata	Anem	0	0.96	0.01	0	0	0	1	0	0	0	1	1	0	0	0	1	0
Apolochus picadurus	Apol	0	0.07	0.93	0.25	0.75	0	0	0.5	0	0	0.5	0	1	0	0	0	1
Arcturinella sp.	Ar.Sp	0	0.38	0.62	0.5	0.5	0	0	0	0	1	0	0	1	0	0	0	1
Arcuatula senhousia	Ar.Se	0.5	0.15	0.38	0	0	0	1	0	1	0	0	1	0	0	0	1	0
Argopecten ventricosus	Argo	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0
Assiminea californica	Assi	0	0.47	0.53	0	1	0	0	0.5	0	0.5	0	0	0	1	1	0	0
Asterina sp.	Aste	0	0	1	0	1	0	0	0	0	0	1	0	0	1	1	0	0
Atylus massiliensis	Atyl	0	0	1	0.5	0.5	0	0	0	0	0	1	0	1	0	0	0	1
Bemlos macromanus	Beml	0	0.2	0.8	0.25	0.45	0.15	0.15	0.67	0.33	0	0	0	1	0	0	0	1
Bittiolum varium	Bit.V	0	0.88	0.13	0	1	0	0	1	0	0	0	0	0	1	0	1	0
Bittium reticulatum	Bit.R	0.2	0.81	0	0	1	0	0	0.5	0	0.5	0	1	0	0	1	0	0
Bulla gouldiana	Bulla	1	0	0	0	1	0	0	0.7	0	0.3	0	0	0	1	1	0	0
Califanthura squamosissima	Cali	0.1	0.79	0.09	0	1	0	0	0	0	0	1	0	1	0	0	0	1
Calliopius laeviusculus	Call	0	0.42	0.58	0.5	0.5	0	0	0	0	0	1	0	1	0	0	0	1
Caprella californica	Cap.C	0.8	0.15	0.1	0.1	0.9	0	0	0	0.4	0	0.6	0	1	0	0	0	1
Caprella drepanochir	Cap.D	0.7	0.33	0	0	1	0	0	0	0.5	0.5	0	0	1	0	0	0	1
Caprella penantis	Cap.P	0	0.58	0.42	0	1	0	0	0	0	1	0	0	1	0	0	0	1
Cerithium vulgatum	Ceri	1	0	0	0	1	0	0	0.5	0	0.5	0	0	0	1	0	0	1
Corophium spp.	Coro	0	0.72	0.27	0.25	0.25	0.25	0.25	0	0.25	0.75	0	0	1	0	0	0	1

		Trait categories															
Species	**Species label**	**La**	**Me**	**Sm**	**Sw**	**Cr**	**Bu**	**Se**	**Gr**	**Fi**	**De**	**PS**	**Bst**	**Bro**	**Lay**	**Le**	**Pl**	**Dd**
Crangon septemspinosa	Cran	0.5	0.5	0	0.33	0.34	0.33	0	0	0	0.5	0.5	0	1	0	0	1	0
Crepidula convexa	Cre.C	0.1	0.64	0.29	0	1	0	0	0	0.5	0.5	0	0	1	0	0	0	1
Crepidula fornicata	Cre.F	0	1	0	0	0.5	0	0.5	0	1	0	0	0	1	0	0	1	0
Cumacea	Cuma	0	0.56	0.44	0.25	0.75	0	0	0.2	0	0.4	0.4	0	1	0	0	0	1
Cymadusa compta	Cyma	0	0	1	0.4	0.4	0	0.2	0.8	0	0.2	0	0	1	0	0	0	1
Decapod larvae A	Deca	0.3	0	0.71	0.5	0.5	0	0	0.1	0	0	0.9	0	1	0	0	1	0
Dynamene bidentata	Dyna	0.3	0.71	0	0.5	0.5	0	0	0.5	0	0.5	0	0	1	0	0	0	1
Ecrobia truncata	Ecro	0	0.06	0.94	0	0.75	0.25	0	0.5	0	0.5	0	1	0	0	0	1	0
Edotia triloba	Edot	0	0.09	0.91	0.1	0.9	0	0	1	0	0	0	0	1	0	0	0	1
Elasmopus levis	Ela.L	0	0.38	0.62	0.5	0.5	0	0	0.6	0	0.2	0.2	0	1	0	0	0	1
Elasmopus rapax	Ela.R	0	1	0	0.25	0.75	0	0	0.7	0	0.1	0.2	0	1	0	0	0	1
Elasmopus sp.	Ela.S	0	0.44	0.56	0.5	0.5	0	0	0.6	0	0.2	0.2	0	1	0	0	0	1
Erichsonella attenuata	Eri.A	0.2	0.59	0.24	0	1	0	0	0.75	0	0.25	0	0	1	0	0	0	1
Erichsonella crenulata	Eri.C	0.7	0.29	0	0	1	0	0	0.9	0	0.1	0	0	1	0	0	0	1
Ericthonius brasiliensis	Eri.B	0	0.24	0.76	0.15	0.25	0	0.60	0.3	0.4	0	0.3	0	1	0	0	0	1
Ericthonius punctatus	Eri.P	0	0	1	0.15	0.25	0	0.60	0.3	0.4	0	0.3	0	1	0	0	0	1
Gammarus duebeni	Gam.B	0	0	1	0.5	0.5	0	0	0.33	0	0.34	0.33	0	1	0	0	0	1
Gammarus insensibilis	Gam.I	0	0.8	0.2	0.5	0.5	0	0	1	0	0	0	0	1	0	0	0	1
Gammarus lawrencianus	Gam.L	0	0.7	0.3	0.5	0.5	0	0	1	0	0	0	0	1	0	0	0	1
Gammarus mucronatus	Gam.M	0	0.74	0.26	0.5	0.5	0	0	0.5	0	0.5	0	0	1	0	0	0	1
Gammarus oceanicus	Gam.O	0	0.8	0.2	0.5	0.5	0	0	0.5	0	0.25	0.25	0	1	0	0	0	1
Gammarus sp. juvenile	Gam.J	0	0	1	0.5	0.5	0	0	0.5	0	0.25	0.25	0	1	0	0	0	1
Gammarus tigrinus	Gam.T	0	0.36	0.64	0.5	0.5	0	0	0.5	0	0.25	0.25	0	1	0	0	0	1
Gibberula miliaria	Gib.M	0	1	0	0	1	0	0	0.5	0	0.5	0	1	0	0	0	1	0
Gibbula umbilicalis	Gib.U	0.2	0.78	0.03	0	1	0	0	0.5	0	0.5	0	1	0	0	0	1	0
Grandidierella japonica	Gran	0	1	0	0.25	0.25	0	0.5	0	0.1	0.9	0	0	1	0	0	0	1
Harmothoe sp.	Harm	0	1	0	0	1	0	0	0	0	0.5	0.5	0	1	0	0	1	0
Haustoriidae	Haus	0	0	1	0.5	0.5	0	0	0	0.25	0.75	0	0	1	0	0	0	1
Hemigrapsus oregonensis	Hemi	0	1	0	0	0.5	0.5	0	0.5	0	0	0.5	0	1	0	0	1	0
Hippolyte californiensis	Hip.C	0.4	0.61	0.01	0.25	0.75	0	0	0.4	0	0	0.6	0	1	0	0	1	0
Hippolyte sp.	Hip.S	0	1	0	0.33	0.34	0.33	0	0.25	0	0	0.75	0	1	0	0	1	0
Idotea balthica	Ido.B	0	0.83	0.13	0.5	0.5	0	0	0.8	0	0.2	0	0	1	0	0	0	1
Idotea chelipes	Ido.C	0	0.5	0.5	0.5	0.5	0	0	0.6	0	0.2	0.2	0	1	0	0	0	1

		Trait categories																
Species	**Species label**	**La**	**Me**	**Sm**	**Sw**	**Cr**	**Bu**	**Se**	**Gr**	**Fi**	**De**	**PS**	**Bst**	**Bro**	**Lay**	**Le**	**Pl**	**Dd**
Idotea phosphorea	Ido.P	0.1	0.4	0.51	0.25	0.75	0	0	0.6	0	0.1	0.3	0	1	0	0	0	1
Iphimedia vicina	Iphi	0	0.1	0.9	0.5	0.5	0	0	0	0	1	0	0	1	0	0	0	1
Jaera albifrons	Jaer	0	0.15	0.85	0.1	0.9	0	0	0.5	0	0.5	0	0	1	0	0	0	1
Jassa slatteryi	Jass	0	0.9	0.05	0.4	0.5	0	0.1	0	0.5	0.25	0.25	0	1	0	0	0	1
Jujubinus striatus	Juju	0.3	0.66	0	0	1	0	0	0.75	0	0.25	0	0	0	1	1	0	0
Juvenile caprellid	Juv.C	0.2	0.59	0.26	0	1	0	0	0	1	0	0	0	1	0	0	0	1
Lekanesphaera hookeri	Leka	0.2	0.69	0.14	0.5	0.5	0	0	0	0	1	0	0	1	0	0	0	1
Lepidonotus squamatus	Lepi	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	1	0
Limecola balthica	Lime	0	0.1	0.9	0	0	1	0	0	0.25	0.75	0	1	0	0	0	1	0
Littorina saxatilis	Litt	0	0.76	0.24	0	1	0	0	0.75	0	0.25	0	0	1	0	0	0	1
Lumbrineris sp.	Lumb	0	0.63	0.37	0	0.5	0.5	0	0	0	0.5	0.5	1	0	0	0	0	1
Lysianassa sp.	Lysi	0	0.42	0.58	0.5	0.5	0	0	0	0	0	1	0	1	0	0	0	1
Microdeutopus algicola	Mic.Al	0	0	1	0.5	0.5	0	0	0.25	0.25	0.5	0	0	1	0	0	0	1
Microdeutopus anomalus	Mic.An	0	0	1	0.5	0.5	0	0	0.25	0.25	0.5	0	0	1	0	0	0	1
Microdeutopus sp.	Mic.S	0	0.01	0.99	0.5	0.5	0	0	0.25	0.25	0.5	0	0	1	0	0	0	1
Monocorophium californianum	Mon.C	0	0.92	0.08	0.15	0.15	0.7	0	0	0.5	0.5	0	0	1	0	0	0	1
Monocorophium insidiosum	Mon.I	0	1	0	0.25	0.25	0.25	0.25	0	0.5	0.5	0	0	1	0	0	0	1
Monoculodes sp.	Mon.S	0	0	1	0.33	0.33	0.34	0	0	0	0	1	0	1	0	0	0	1
Munna sp.	Munn	0	0.04	0.96	0	1	0	0	1	0	0	0	0	1	0	0	0	1
Mya arenaria	MyaA	0	0.67	0.33	0	0	1	0	0	1	0	0	1	0	0	0	1	0
Mytilus spp.	Myti	0	0.57	0.43	0	0.25	0	0.75	0	1	0	0	1	0	0	0	1	0
Nasageneia quinsana	Nasa	0	0.3	0.7	0.25	0.75	0	0	0.5	0	0	0.5	0	1	0	0	0	1
Nassarius tiarula	Nass	0.9	0.07	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0
Nereiphylla rubiginosa	Ner.R	0	0.14	0.86	0	1	0	0	0	0	0	1	1	0	0	0	0	0
Nereis pelagica	Ner.P	0	0	1	0.33	0.34	0.33	0	0	0.33	0.33	0.34	1	0	0	1	0	0
Nereis spp.	Ner.S	0	1	0	0	0	1	0	0	0.5	0	0.5	1	0	0	0	0	0
Oxydromus pallidus	Oxyd	0	0	1	0	0.5	0.5	0	0	0	0.5	0.5	1	0	0	0	0	0
Paracerceis sculpta	P.Scu	0	0.48	0.5	0.25	0.75	0	0	1	0	0	0	0	1	0	0	0	1
Paradexamine spp.	P.Spp	0.1	0.75	0.16	0.5	0.5	0	0	0.5	0	0.5	0	0	1	0	0	0	1
Paramicrodeutopus schmitti	P.Sch	0	1	0	0.15	0.15	0.35	0.35	0	0.5	0.5	0	0	1	0	0	0	1
Parvicardium exiguum	Parv	0.3	0.33	0.37	0	0	0	1	0	1	0	0	1	0	0	0	1	0
Pentidotea resecata	Pent	0.9	0.06	0	0.5	0.5	0	0	0	0	1	0	0	1	0	0	0	1
Phoxocephalus holbolli	Phox	0	0.07	0.93	0.5	0.5	0	0	0.5	0	0.5	0	0	1	0	0	0	1

		Trait categories															
Species	**Species label**	**La**	**Me**	**Sm**	**Sw**	**Cr**	**Bu**	**Se**	**Gr**	**Fi**	**De**	**PS**	**Bst**	**Bro**	**Lay**	**Le**	**Pl**	**Dd**
Phtisica marina	Phti	0	0	1	0	1	0	0	0.33	0	0.33	0.34	0	1	0	0	0	1
Phyllaplysia taylori	Phyl	0.9	0.11	0.01	0	1	0	0	1	0	0	0	0	0	1	0	0	1
Platynereis bicanaliculata	Pla.B	0	0.67	0.33	0.2	0.2	0.2	0.40	0.8	0	0.2	0	1	0	0	0	1	0
Platynereis dumerilii	Pla.D	0	0.22	0.77	0.5	0.5	0	0	0	0	1	0	1	0	0	0	1	0
Podocerus brasiliensis	Podo	0	0.43	0.57	0.2	0.5	0	0.30	0.2	0.8	0	0	0	1	0	0	0	1
Polititapes aureus	Poli	0.9	0	0.09	0	0	0	1	0	1	0	0	1	0	0	0	1	0
Polychaeta	Poly	0.7	0.27	0.04	0	0.5	0.5	0	0	0.5	0	0.5	0	0	1	0	0	0
Pontogeneia inermis	Pont	0	0	1	0.5	0.5	0	0	0	0	0	1	0	1	0	0	0	1
Protohyale frequens	Prot	0	0.38	0.62	0.25	0.75	0	0	1	0	0	0	0	1	0	0	0	1
Pusillina lineolata	Pusi	0	0.88	0.11	0	1	0	0	0.5	0	0.5	0	1	0	0	0	1	0
Serpulidae	Serp	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Shrimp sp.1	Shri	0	1	0	0.33	0.34	0.33	0	0.33	0	0.33	0.34	0	1	0	0	1	0
Sphaeroma juvenile	Sph.J	0	0.2	0.8	0.5	0.5	0	0	0	0	0	0	0	1	0	0	0	1
Sphaeroma serratum	Sph.S	0.3	0.33	0.33	0.5	0.5	0	0	0	0	1	0	0	1	0	0	0	1
Tanaidacea	Tana	0.1	0.86	0.04	0.33	0.34	0.33	0	0	0.25	0.75	0	0	1	0	0	0	1
Tanais dulongii	Tan.D	0	0.02	0.98	0.33	0.34	0.33	0	0	0	1	0	0	1	0	0	0	1
Tectura depicta	Tect	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0
Tricolia tenuis	Tric	0	0.86	0.1	0	1	0	0	0.75	0	0.25	0	1	0	0	1	0	0
Triplana viridis	Trip	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0
Tritia corniculum	Trit	0.5	0.44	0.06	0	1	0	0	0	0	0	1	0	0	1	0	1	0
Unknown Amphipod	U.Amp	0	0.5	0.46	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0	1	0	0	0	1
Unknown Amphipod A - MX	U.Amp.MX	0	0	1	0.33	0.33	0.15	0.19	0.25	0.25	0.25	0.25	0	1	0	0	0	1

Table 5.17. Summary of PER-ANOVAs showing the effects of region (Reg), position (Pos), and complexity (Com) on shoot density, aboveground shoot biomass, and the epiphytic load on shoots. Significant results are shown in **bold.**

	All regions		
	df	***Pseudo-F***	*P (perm)*
a) Shoot density			
Region	4	595.65	**0.0001**
Position	1	26.489	**0.0111**
Complexity	2	0.0600	0.9482
Region × Pos	4	1.2634	0.2883
Region × Com	8	0.7158	0.6819
Pos × Com	2	2.9102	0.1080
Reg × Pos × Com	8	0.4712	0.8779
Residual	180		
b) Above-ground shoot biomass			
Region	4	109.87	**0.0001**
Position	1	0.7780	0.4170
Region × Pos	4	13.221	**0.0001**
Residual	220		
c) Epiphytic microalgae load			
Region	4	129.67	**0.0001**
Position	1	0.7316	0.4832
Complexity	2	2.6030	0.1414
Region × Pos	4	42.405	**0.0001**
Region × Com	8	0.6182	0.7604
Pos × Com	2	3.9786	0.0597
Reg × Pos × Com	8	0.6126	0.7685
Residual	180		

Note: PER-ANOVAs were run with 9999 permutations using Euclidean distances. Shoot densities (a) and biomass (b) were fourth-root transformed, while epiphytes (c) were square-root transformed before analysis. Complexity factor does not appear in (b) because shoots were not collected in the ambient plots.

Table 5.18. Summary of PER-ANOVAs (a–e) and PERMANOVAs (f–g) showing the effects of region (Reg), position (Pos), and complexity (Com) on standardized abundance, species richness, Pielou evenness, Simpson diversity, species assemblage structure, and composition. Significant results are shown in **bold**.

	All regions				All regions		
	df	***Pseudo-F***	*P (perm)*		**df**	***Pseudo-F***	*P (perm)*
a) Standardized abundance				**d) Diversity 1-lam'**			
Region	4	213.51	**0.0001**	Region	4	58.181	**0.0001**
Position	1	3.6063	0.1331	Position	1	0.8330	0.4074
Complexity	2	3.6343	0.0750	Complexity	2	0.7099	0.5207
Region × Pos	4	2.1853	0.0716	Region × Pos	4	2.7505	**0.0270**
Region × Com	8	2.2571	**0.0254**	Region × Com	8	1.9536	0.0542
Pos × Com	2	0.6806	0.5433	Pos × Com	2	2.4347	0.1462
Reg × Pos × Com	8	1.9446	0.0580	Reg × Pos × Com	8	1.1561	0.3296
Residual	180			Residual	180		
b) Richness*				**e) Structure**			
Region	4	102.20	**0.0001**	Region	4	142.19	**0.0001**
Position	1	1.5627	0.2825	Position	1	1.0175	0.4818
Complexity	2	0.2708	0.7971	Complexity	2	0.9749	0.5441
Region × Pos	4	6.3927	**0.0002**	Region × Pos	4	6.0644	**0.0001**
Region × Com	8	0.7694	0.6323	Region × Com	8	1.6041	**0.0001**
Pos × Com	2	1.7567	0.2337	Pos × Com	2	0.9896	0.4842
Reg × Pos × Com	8	1.1923	0.3059	Reg × Pos × Com	8	1.0682	0.2258
Residual	180			Residual	180		
c) Evenness				**f) Composition**			
Region	4	35.677	**0.0001**	Region	4	247.72	**0.0001**
Position	1	2.4377	0.1961	Position	1	1.0682	0.4565
Complexity	2	0.1502	0.8720	Complexity	2	0.9823	0.5185
Region × Pos	4	1.9073	0.1148	Region × Pos	4	4.1710	**0.0001**
Region × Com	8	4.5405	**0.0002**	Region × Com	8	0.8049	0.9289
Pos × Com	2	2.6740	0.1271	Pos × Com	2	1.0056	0.4696
Reg × Pos × Com	8	0.9535	0.4747	Reg × Pos × Com	8	0.9183	0.7186
Residual	180			Residual	180		

Note: PER-ANOVAs were run with 9999 permutations using Euclidean distances, while PERMANOVAs were performed using Bray-Curtis dissimilarities. Data were pretreated with dispersion weighting by Region x Treatment in (f). Abundance were square-root transformed in (a) and (f) while they were transformed into presence/absence in (g).

*The Margalef index gives comparable results as well as ES(15).

Table 5.19. Summary of PER-ANOVAs and PERMANOVA showing the effects of region (Reg), position (Pos), and complexity (Com) on functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), Rao's quadratic entropy (RaoQ), functional redundancy, and biological-weighted trait occurrence multivariate structure of standardized species. Significant results are shown in **bold**.

	All regions				All regions		
	df	***Pseudo-F***	*P (perm)*		**df**	***Pseudo-F***	*P (perm)*
a) FRic				**d) RaoQ**			
Region	4	125.19	**0.0001**	Region	4	273.86	**0.0001**
Position	1	8.6585	0.0626	Position	1	0.0235	0.9303
Complexity	2	1.3759	0.3238	Complexity	2	1.1513	0.3812
Region × Pos	4	1.1364	0.3692	Region × Pos	4	3.6056	**0.0070**
Region × Com	8	0.7845	0.5879	Region × Com	8	2.9624	**0.0043**
Pos × Com	2	Neg.		Pos × Com	2	2.2517	0.1698
Reg × Pos × Com	8	1.3294	0.2812	Reg × Pos × Com	8	0.7709	0.6261
Residual	180			Residual	180		
b) FEve				**e) Redundancy**			
Region	4	27.591	**0.0001**	Region	4	209.99	**0.0001**
Position	1	3.9351	0.1164	Position	1	0.2222	0.6955
Complexity	2	0.1975	0.8333	Complexity	2	1.9992	0.1926
Region × Pos	4	1.3021	0.2973	Region × Pos	4	23.241	**0.0001**
Region × Com	8	4.8575	**0.0002**	Region × Com	8	1.1253	0.3541
Pos × Com	2	0.8186	0.4829	Pos × Com	2	1.4849	0.2987
Reg × Pos × Com	8	1.5819	0.1681	Reg × Pos × Com	8	1.0027	0.4350
Residual	180			Residual	180		
c) FDiv				**f) WTO structure**			
Region	4	31.191	**0.0001**	Region	4	165.02	**0.0001**
Position	1	Neg.		Position	1	0.7541	0.5496
Complexity	2	0.7592	0.4942	Complexity	2	1.1649	0.3607
Region × Pos	4	6.5562	**0.0002**	Region × Pos	4	14.685	**0.0001**
Region × Com	8	1.5979	0.1621	Region × Com	8	3.5254	**0.0001**
Pos × Com	2	0.8130	0.4650	Pos × Com	2	1.4605	0.2159
Reg × Pos × Com	8	1.0455	0.4141	Reg × Pos × Com	8	1.5975	**0.0082**
Residual	180			Residual	180		

Note: PER-ANOVAs (a-f) and PERMANOVA (g) were run with 9999 permutations using Euclidean distances. WTO (f) were square-root transformed before analysis.

Table 5.20. Summary of PERMANOVAs showing the effects of region (Reg), position (Pos), and complexity (Com) on the structure of each trait. Significant results are shown in **bold.**

Occurrence structure	All regions				All regions		
	df	***Pseudo-F***	**df**		**df**	***Pseudo-F***	*P (perm)*
a) Size				**d) Reproduction**			
Region	4	278.34	**0.0001**	Region	4	140.16	**0.0001**
Position	1	1.0534	0.4791	Position	1	0.5655	0.5439
Complexity	2	4.7560	**0.0325**	Complexity	2	0.6835	0.5941
Region × Pos	4	25.539	**0.0001**	Region × Pos	4	23.181	**0.0001**
Region × Com	8	2.0417	**0.0107**	Region × Com	8	3.0023	**0.0001**
Pos × Com	2	1.0407	0.4070	Pos × Com	2	2.2562	0.1103
Reg × Pos × Com	8	2.1434	**0.0061**	Reg × Pos × Com	8	1.5108	0.0883
Residual	180			Residual	180		
b) Life habits				**e) Larval feeding**			
Region	4	165.48	**0.0001**	Region	4	102.24	**0.0001**
Position	1	0.8946	0.5128	Position	1	0.2515	0.7774
Complexity	2	0.8753	0.5918	Complexity	2	0.4151	0.7764
Region × Pos	4	13.701	**0.0001**	Region × Pos	4	1.5490	0.1368
Region × Com	8	4.3910	**0.0001**	Region × Com	8	3.4554	**0.0001**
Pos × Com	2	0.9974	0.4225	Pos × Com	2	1.1832	0.3561
Reg × Pos × Com	8	1.2825	0.1777	Reg × Pos × Com	8	2.0746	**0.0080**
Residual	180			Residual	180		
c) Feeding habits							
Region	4	196.88	**0.0001**				
Position	1	0.7843	0.5027				
Complexity	2	1.5100	0.2984				
Region × Pos	4	13.467	**0.0001**				
Region × Com	8	4.2218	**0.0001**				
Pos × Com	2	1.5501	0.2288				
Reg × Pos × Com	8	1.2147	0.2320				
Residual	180						

Note: PERMANOVAs were run with 9999 permutations using Euclidean distances. Data were square-root transformed before analysis.

Table 5.21. Summary of post hoc tests of PER-ANOVAs and PERMANOVA showing pairwise tests regarding complexity treatment on total densities, functional evenness (FEve), Rao's quadratic entropy (RaoQ), and biological-weighted trait occurrence multivariate structure of standardized species by region. Significant results are shown in **bold**, while light grey shading indicates zones where complexity had no effect on these variables.

	FR		MX		QU		SF		VA	
	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)
a) Total densities										
Complexity										
100% vs 50%			0.3713	0.7281	2.1859	**0.0414**				
100% vs 80%			2.1861	**0.0374**	3.5907	**0.0006**				
50% vs 80%			2.1300	**0.0403**	1.5275	0.1457				
b) Species' richness										
c) FRic										
d) FEve										
Complexity										
100% vs 50%					3.3935	**0.0035**			0.4144	0.6095
100% vs 80%					2.1111	0.0509			2.7788	**0.0281**
50% vs 80%					0.8293	0.4323			2.2424	0.0547
e) FDiv										
f) RaoQ										
Complexity										
100% vs 50%					2.3697	**0.0269**				
100% vs 80%					3.5794	**0.0021**				
50% vs 80%					0.6981	0.4977				
g) Redundancy										
h) WTO structure										
Complexity										
100% vs 50%			0.9336	0.4480	2.1022	**0.0309**			2.4275	**0.0020**
100% vs 80%			2.4777	**0.0032**	3.4235	**0.0002**			4.4988	**0.0001**
50% vs 80%			1.7728	**0.0269**	1.0214	0.3156			1.1842	0.2224

Note: PER-ANOVAs (a–f) and PERMANOVA (h) were run with 9999 permutations using Euclidean distances. Abundance (a) and WTO (h) were square-root transformed before analysis.

Table 5.22. Summary of PER-ANOVAs showing the effects of position (Pos) and complexity (Com) on shoot density, aboveground shoot biomass, and epiphytic load on shoots by region. Significant results are shown in **bold**; results in *italics* indicates that ambient plots only show different degrees of significance compared to the results of 'Position' below (see light grey 'Ambient only').

		FR		MX		QU		SF		VA	
	df	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)
a) Shoot density											
Position	1	4.9161	**0.0332**	4.2991	**0.0431**	11.586	**0.0016**	4.8475	**0.0327**	14.899	**0.0008**
Complexity	2	0.9948	0.3787	0.7698	0.4684	0.3905	0.6800	0.3263	0.7315	0.0653	0.9396
Pos × Com	2	0.2411	0.7936	1.0079	0.3699	0.2158	0.8066	1.8546	0.1699	0.2482	0.7802
Residual	36										
b) Above-ground shoot biomass											
Position	1	0.0196	0.8840	0.9886	0.3239	45.111	**0.0001**	27.405	**0.0001**	4.5754	**0.0335**
Residual	vary										
c) Epiphytic microalgae load											
Position	1	2.3214	0.1417	9.4419	***0.0038***	6.8295	***0.0094***	78.969	**0.0001**	1.6816	0.2023
Ambient only	1	2.1884	0.1667	2.1284	*0.1727*	1.8799	*0.1970*	67.089	**0.0004**	4.1536	0.0736
Complexity	2	2.7236	0.0781	0.3084	0.7334	0.6773	0.5299	0.8480	0.4292	0.6362	0.5331
Pos × Com	2	0.5085	0.6140	0.7763	0.4629	0.6197	0.5641	1.2983	0.2907	0.7747	0.4613
Residual	36										

Note: PER-ANOVAs were run with 9999 permutations using Euclidean distances. Shoot densities (a) and biomass (b) were fourth-root transformed, while epiphytes (c) were square-root transformed before analysis. Complexity factor does not appear in (b) because shoots were not collected in the ambient plots. Residual degrees of freedom in (b) vary from 11 in FR to 49–54 at other sites.

Table 5.23. Summary of PER-ANOVAs showing the effects of position (Pos) and complexity (Com) on the structure of each trait as well as the effect of position using ambient plots only by region. Significant results are shown in **bold**, while *italics* indicate that ambient plots only show different degrees of significance compared to the results of 'Position' below (see light grey 'Ambient only').

Occurrence structure		FR		MX		QU		SF		VA	
	df	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)
a) Size											
Position	1	2.4089	0.1191	0.9845	0.3373	0.2733	0.6353	78.627	**0.0001**	4.5015	***0.0298***
Ambient only	1	2.5331	0.1186	1.3246	0.2938	0.5173	0.4892	29.450	**0.0001**	1.1608	*0.3069*
Complexity	2	3.1074	**0.0492**	0.8484	0.4670	6.5820	**0.0036**	0.4862	0.6729	8.0449	**0.0008**
Pos × Com	2	3.8965	**0.0240**	3.5980	**0.0239**	1.5743	0.2112	1.2782	0.2816	0.7156	0.5281
Residual	36										
b) Life habits											
Position	1	6.0721	***0.0053***	1.3781	0.2429	0.3661	0.7565	50.748	**0.0001**	2.7576	0.0811
Ambient only	1	0.8261	*0.4048*	0.3894	0.5255	0.4399	0.7259	17.754	**0.0008**	0.1136	0.9305
Complexity	2	0.5579	0.7019	4.1834	**0.0230**	4.6172	**0.0022**	0.5443	0.7050	11.188	**0.0002**
Pos × Com	2	2.9913	**0.0252**	0.1677	0.8763	1.1153	0.3556	0.8045	0.5167	0.8945	0.4466
Residual	36										
c) Feeding habits											
Position	1	5.7450	***0.0035***	3.4974	**0.0387**	1.0050	0.3734	37.958	**0.0001**	4.0361	***0.0312***
Ambient only	1	0.6419	*0.5010*	0.7283	0.4331	0.3418	0.7363	18.727	**0.0013**	2.4530	*0.1084*
Complexity	2	0.5872	0.7194	4.6198	**0.0042**	1.0463	0.3971	0.8944	0.4636	10.758	**0.0001**
Pos × Com	2	2.7230	**0.0252**	0.2048	0.9514	0.8154	0.5323	1.1072	0.3394	1.4315	0.2365
Residual	36										
d) Reproduction											
Position	1	1.7790	0.1749	5.1330	***0.0113***	0.2299	0.6599	59.718	**0.0001**	1.4523	0.2348
Ambient only	1	1.3669	0.2742	2.6901	*0.0842*	0.0227	0.8954	30.985	**0.0005**	4.0368	0.1889
Complexity	2	3.8654	**0.0088**	2.6565	**0.0484**	5.8704	**0.0069**	0.5872	0.6496	0.6263	0.6869
Pos × Com	2	3.1162	**0.0278**	0.4015	0.7960	1.3691	0.2613	1.9933	0.1098	1.6406	0.1583
Residual	36										
e) Larval feeding											
Position	1	1.1981	0.2854	3.1077	0.0513	0.2041	0.7639	2.1263	0.1566	2.5378	0.0942
Ambient only	1	1.8996	0.1823	2.054	0.1369	0.1135	0.8548	0.0089	0.9741	7.0533	0.0726
Complexity	2	2.5982	0.0535	2.4995	0.0554	5.2356	**0.0081**	1.2703	0.2982	0.4782	0.7447
Pos × Com	2	3.3725	**0.0252**	0.9715	0.4231	1.6353	0.1882	0.6981	0.5049	2.4670	**0.0470**
Residual	36										

Note: PER-ANOVAs were run with 9999 permutations using Euclidean distances. Data were square-root transformed before analysis.

Table 5.24. Summary of PER-ANOVAs and PERMANOVAs showing the effects of position (Pos) and complexity (Com) on (a) Pielou evenness, (b) Simpsons diversity (1-λ'), (c) abundance structure, and (d) composition of each trait, as well as the effect of position using ambient plots only by region. Significant results are shown in **bold**, while *italics* indicate that ambient plots only show different degrees of significance compared to the results of 'Position' below.

		FR		MX		QU		SF		VA	
	df	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)
a) Evenness											
Position	1	20.799	***0.0001***	1.0036	0.3232	1.2478	0.2717	7.6384	***0.0100***	0.4464	0.4987
Complexity	2	1.0013	0.3746	1.4677	0.2405	6.5324	**0.0041**	0.5826	0.5659	4.1300	**0.0264**
Pos × Com	2	0.1820	0.8361	0.4322	0.6507	1.9125	0.1626	0.2708	0.7633	1.5153	0.2353
Residual	36*										
b) Diversity 1-λ'											
Position	1	12.276	***0.0010***	6.8082	***0.0117***	0.2428	0.6197	8.6743	***0.0043***	0.8693	0.3676
Complexity	2	0.0790	0.9267	1.3815	0.2690	4.5582	**0.0213**	0.9240	0.4094	1.1364	0.3423
Pos × Com	2	1.7150	0.1937	0.1925	0.8367	2.1348	0.1310	0.5254	0.5982	1.6308	0.2152
Residual	36*										
c) Structure											
Position	1	2.2636	***0.0190***	4.7491	***0.0001***	2.5718	***0.0144***	26.215	**0.0001**	3.5587	**0.0007**
Complexity	2	0.7177	0.8201	2.1338	**0.0029**	1.5705	0.0921	0.6970	0.7780	2.3202	**0.0054**
Pos × Com	2	1.0999	0.3290	1.7732	**0.0185**	0.8915	0.5701	0.8837	0.5871	0.8403	0.6286
Residual	36										
d) Composition											
Position	1	1.5388	0.1714	5.6010	***0.0002***	2.6919	***0.0241***	9.6773	**0.0001**	6.0772	**0.0002**
Complexity	2	0.4418	0.9342	2.1035	**0.0272**	0.5142	0.8550	0.9311	0.5047	0.5802	0.7812
Pos × Com	2	0.9547	0.4903	1.5230	0.1313	0.5405	0.8374	0.7451	0.6393	1.1007	0.3907
Residual	36										

Note: PER-ANOVAs were run with 9999 permutations using Euclidean distances, while Bray-Curtis dissimilarities were used for PERMANOVAs. Densities were fourth-root transformed before analysis.

*Residual was 35 for VA and QU as calculations were not possible for one plot.

Table 5.25. Summary of PER-ANOVAs showing the effects of position (Pos) and complexity (Com) on each category of the size trait by region. Significant results are shown in **bold**, while *italics* indicate that ambient plots only show different degrees of significance compare to the results of 'Position' below (see light grey 'Ambient only').

Occurrence Size		FR		MX		QU		SF		VA	
	df	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)
a) Large											
Position	1	5.1069	***0.0293***	1.0597	0.3160	0.9341	0.3368	89.788	**0.0001**	0.4638	0.5186
Ambient only	1	1.3054	*0.2766*	1.7354	0.2152	2.1751	0.1212	40.715	**0.0004**	0.4751	0.5110
Complexity	2	2.1997	0.1289	0.2266	0.8056	0.1112	0.8969	0.6427	0.5295	3.2483	**0.0411**
Pos × Com	2	5.0875	**0.0105**	4.1672	**0.0221**	0.7856	0.4720	1.2328	0.3109	1.5892	0.2197
Residual	36										
b) Medium											
Position	1	1.8223	0.1825	0.2858	0.5910	0.2859	0.6079	75.424	**0.0001**	6.1692	***0.0187***
Ambient only	1	2.3902	0.1452	0.1811	0.6720	0.4417	0.5123	26.341	**0.0016**	1.7718	*0.2148*
Complexity	2	3.4583	**0.0426**	3.8239	**0.0297**	6.6319	**0.0033**	0.3924	0.6803	9.4219	**0.0002**
Pos × Com	2	2.5731	0.0895	0.4449	0.6508	1.5822	0.2196	0.6925	0.5120	0.3262	0.7250
Residual	36										
c) Small											
Position	1	1.5092	0.2213	1.1743	0.2873	0.2147	0.6453	56.073	**0.0001**	5.3273	***0.0233***
Ambient only	1	3.6668	0.0809	0.1991	0.7454	0.3643	0.5437	15.057	**0.0046**	1.1868	*0.3045*
Complexity	2	3.2814	**0.0482**	2.4755	0.0990	6.9848	**0.0029**	0.2676	0.7734	9.2530	**0.0008**
Pos × Com	2	4.3913	**0.0187**	2.5977	0.0835	1.6216	0.2099	2.5665	0.0868	0.5476	0.5745
Residual	36										

Note: PER-ANOVAs were run with 9999 permutations using Euclidean distances. WTO were square-root transformed prior to analysis.

Table 5.26. Summary of PER-ANOVAs showing the effects of position (Pos) and complexity (Com) on each category of the life-habits and movement trait by region. Significant results are shown in **bold**, while *italics* indicate that ambient plots only show different degrees of significance compare to the results of 'Position' below (see light grey 'Ambient only').

Occurrence Life habits		FR		MX		QU		SF		VA	
	df	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)
a) Swimmer											
Position	1	6.1441	**0.0191**	2.6900	0.1094	0.1331	0.7273	74.237	**0.0001**	1.0576	0.3083
Ambient only	1	6.0935	**0.0322**	0.3142	0.5773	0.8649	0.3756	35.682	**0.0005**	0.0206	0.8830
Complexity	2	1.8029	0.1777	5.1255	**0.0107**	1.7482	0.1814	0.4543	0.6441	13.742	**0.0004**
Pos × Com	2	1.5436	0.2264	0.5230	0.6002	2.6570	0.0830	0.4407	0.6466	0.7327	0.4903
Residual	36										
b) Crawler											
Position	1	4.2933	***0.0434***	0.8218	0.3667	0.0662	0.8053	71.071	**0.0001**	0.7567	0.3924
Ambient only	1	0.6119	*0.4434*	0.0741	0.7182	0.2023	0.6332	27.424	**0.0010**	0.0000	0.9990
Complexity	2	0.2483	0.7837	4.1137	**0.0262**	5.8088	**0.0077**	0.8065	0.4629	12.463	**0.0001**
Pos × Com	2	3.8848	**0.0320**	0.3143	0.7250	1.6092	0.2131	1.3046	0.2870	0.4285	0.6532
Residual	36										
c) Burrower											
Position	1	0.7593	0.3942	0.0038	0.9444	0.1518	0.7013	3.4791	0.0679	10.654	***0.0023***
Ambient only	1	2.0184	0.1730	2.0812	0.2212	0.0936	0.7658	2.1731	0.1589	n.d.	*n.d.*
Complexity	2	0.0945	0.9105	0.2097	0.8127	7.3753	**0.0025**	0.1274	0.8829	2.4599	0.0978
Pos × Com	2	0.2722	0.7717	1.5644	0.2232	1.2348	0.3049	0.4798	0.6240	1.7662	0.1900
Residual	36										
d) Sessile											
Position	1	10.260	***0.0025***	1.4859	0.2328	0.8610	0.3615	58.286	**0.0001**	1.2757	0.2767
Ambient only	1	0.0689	*0.8030*	0.4002	0.5193	0.4995	0.4983	18.220	**0.0039**	n.d.	n.d.
Complexity	2	0.7164	0.5008	4.3244	**0.0222**	1.6644	0.2028	0.7904	0.4739	1.1794	0.3458
Pos × Com	2	4.1297	**0.0229**	0.0776	0.9294	0.0579	0.9403	1.0258	0.3692	1.6033	0.2235
Residual	36										

Note: PER-ANOVAs were run with 9999 permutations using Euclidean distances. WTO was square-root transformed prior to analysis.
n.d.: no data – the analysis could not be performed.

Table 5.27. Summary of PER-ANOVAs showing the effects of position (Pos) and complexity (Com) on each category of the feeding-habits trait by region. Significant results are shown in **bold**, while *italics* indicate that ambient plots only show different degrees of significance compare to the results of 'Position' below (see light grey 'Ambient only').

Occurrence Feeding habits		FR		MX		QU		SF		VA	
	df	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)
a) Grazer											
Position	1	0.9282	0.3374	2.9981	0.0928	0.9089	0.3471	51.891	**0.0001**	1.4742	0.2316
Ambient only	1	1.6614	0.2198	0.4126	0.5054	0.0000	0.9969	25.510	**0.0013**	0.1925	0.6756
Complexity	2	0.1734	0.8422	5.2797	**0.0099**	4.0839	**0.0255**	0.2931	0.7511	13.976	**0.0001**
Pos × Com	2	3.4972	**0.0406**	0.3941	0.6733	0.8763	0.4230	1.5532	0.2271	1.3928	0.2667
Residual	36										
b) Filter											
Position	1	9.6803	***0.0039***	2.4020	0.1342	1.0048	0.3232	25.717	**0.0001**	12.573	**0.0006**
Ambient only	1	0.3027	*0.5973*	0.7152	0.4101	0.1508	0.7097	15.677	**0.0025**	n.d.	n.d.
Complexity	2	1.4822	0.2431	4.4942	**0.0206**	0.2667	0.7672	1.0292	0.3658	4.9430	**0.0099**
Pos × Com	2	4.8975	**0.0128**	0.0044	0.9965	0.0787	0.9243	1.6144	0.2143	3.8244	**0.0309**
Residual	36										
c) Deposit											
Position	1	13.624	***0.0012***	9.9964	***0.0025***	0.0130	0.9110	44.029	**0.0001**	1.3394	0.2656
Ambient only	1	1.2228	*0.2974*	3.4338	*0.0918*	0.0182	0.8959	14.159	**0.0025**	0.2225	0.6556
Complexity	2	0.3787	0.6929	7.5934	**0.0021**	4.5722	**0.0179**	1.4899	0.2467	10.302	**0.0007**
Pos × Com	2	1.3945	0.2608	0.5891	0.5574	0.6436	0.5320	0.2079	0.8199	1.5625	0.2240
Residual	36										
d) Pred/Scav											
Position	1	3.5529	0.0696	1.5115	0.2318	1.4156	0.2389	1.8901	0.1773	19.133	**0.0004**
Ambient only	1	0.0243	0.8793	0.1978	0.6540	0.6016	0.4499	4.3939	0.0589	8.5491	**0.0199**
Complexity	2	0.4027	0.6616	1.7482	0.1950	0.5243	0.6028	1.2841	0.2835	0.4329	0.6511
Pos × Com	2	1.2847	0.2931	0.2187	0.8022	2.2930	0.1126	0.9067	0.4073	0.0928	0.9098
Residual	36										

Note: PER-ANOVAs were run with 9999 permutations using Euclidean distances. WTO was square-root transformed prior to analysis.

Table 5.28. Summary of PER-ANOVAs showing the effects of position (Pos) and complexity (Com) on each category of the reproduction dispersal trait by region. Significant results are shown in **bold**, while *italics* indicate that ambient plots only show different degrees of significance compare to the results of 'Position' below (see light grey 'Ambient only').

Occurrence Reproduction		FR		MX		QU		SF		VA	
	df	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)
a) Broadcast											
Position	1	2.0635	0.1633	0.7186	0.4008	0.3001	0.5828	2.1128	0.1590	7.0569	**0.0100**
Ambient only	1	0.2179	0.6473	2.8071	0.1096	0.0127	0.9157	0.0077	0.9382	n.d.	n.d.
Complexity	2	5.2739	**0.0097**	0.8958	0.4136	5.8694	**0.0063**	1.2685	0.2937	2.3240	0.1119
Pos × Com	2	1.4424	0.2475	0.7696	0.4719	1.5305	0.2344	0.7195	0.4979	1.9493	0.1539
Residual	36										
b) Brooder											
Position	1	1.4049	0.2434	9.0877	**0.0045**	0.0170	0.8973	63.533	**0.0001**	0.0200	0.9683
Ambient only	1	2.4787	0.1561	9.8189	**0.0078**	0.1015	0.7644	25.999	**0.0007**	3.0705	0.1045
Complexity	2	5.4286	**0.0099**	3.4365	**0.0381**	5.8733	**0.0043**	0.5112	0.6065	0.9083	0.4978
Pos × Com	2	4.5333	**0.0157**	0.7219	0.4946	0.8793	0.4249	1.8832	0.1672	0.9311	0.5028
Residual	36										
c) Lays egg case											
Position	1	1.8384	0.1873	7.1370	***0.0112***	Cat. ab.	Cat. ab.	81.801	**0.0001**	0.3162	0.6320
Ambient only	1	1.1533	0.3013	2.5525	*0.1225*	Cat. ab.	Cat. ab.	49.673	**0.0004**	4.0513	0.0609
Complexity	2	2.5733	0.0861	3.4732	**0.0437**	Cat. ab.	Cat. ab.	0.3432	0.7153	0.1872	0.9001
Pos × Com	2	3.1307	0.0545	0.2203	0.8013	Cat. ab.	Cat. ab.	2.5900	0.0877	1.6617	0.1911
Residual	36										

Note: PER-ANOVAs were run with 9999 permutations using Euclidean distances. WTO was square-root transformed prior to analysis.

Table 5.29. Summary of PER-ANOVAs showing the effects of position (Pos) and complexity (Com) on each category of the larval feeding mode trait by region. Significant results are shown in **bold**, while *italics* indicate that ambient plots only show different degrees of significance compare to the results of 'Position' below (see light grey 'Ambient only').

Occurrence Larval feeding		FR		MX		QU		SF		VA	
	df	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)
a) Lecitotrophic											
Position	1	1.2317	0.2729	5.9718	***0.0213***	0.5799	0.4662	2.1128	0.1638	*7.0569*	***0.0101***
Ambient only	1	2.1236	0.1739	4.1359	*0.0667*	0.5788	0.4635	0.0077	0.9368	*n.d.*	*n.d.*
Complexity	2	1.4487	0.2521	3.4832	**0.0426**	0.2153	0.8111	1.2685	0.2983	2.3240	0.1122
Pos × Com	2	3.7540	**0.0289**	0.0214	0.9786	2.8644	0.0680	0.7195	0.4894	1.9493	0.1627
Residual	36										
b) Planktotrophic											
Position	1	0.6989	0.4092	0.0244	0.8711	0.2152	0.6429	2.1128	0.1564	1.9187	*0.1829*
Ambient only	1	0.6308	0.4349	0.8077	0.4590	0.0260	0.8688	0.0077	0.9407	7.0836	***0.0205***
Complexity	2	4.1142	**0.0259**	1.5628	0.2232	5.7011	**0.0066**	1.2685	0.2943	0.0800	0.9421
Pos × Com	2	0.5512	0.5857	2.0323	0.1454	1.7374	0.1980	0.7195	0.5012	2.6966	0.0571
Residual	36										
c) Direct											
Position	1	1.5275	0.2249	2.6931	0.1071	0.0211	0.8887	2.2819	0.1386	0.0865	0.8640
Ambient only	1	2.3653	0.1654	2.0902	0.1720	0.1015	0.7661	0.0324	0.8742	n.d.	n.d.
Complexity	2	5.4100	**0.0072**	0.1663	0.8399	5.8252	**0.0065**	1.2912	0.2895	0.6585	0.6478
Pos × Com	2	4.5368	**0.0175**	0.4282	0.6620	0.8373	0.4382	0.4517	0.6466	1.4584	0.2249
Residual	36										

Note: PER-ANOVAs were run with 9999 permutations using Euclidean distances. WTO was square-root transformed prior to analysis.

Table 5.30. Summary of PER-ANOVAs showing the effects of position, using only ambient plots, on total density, species richness, functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), Rao's quadratic entropy (RaoQ), functional redundancy, and biological-weighted trait occurrence structure (PERMANOVA) of standardized species by region. Significant results are shown in **bold**.

		FR		MX		QU		SF		VA	
	df	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)	Pseudo-*F*	*P* (perm)
a) Total density											
Position	1	0.9593	0.3331	0.9120	0.3854	0.3173	0.5757	16.466	**0.0021**	0.1102	0.7549
Residual	12										
b) Species richness											
Position	1	0.0022	1.0000	1.8145	0.2436	2.3102	0.1865	8.7339	**0.0187**	19.267	**0.0060**
Residual	12										
c) FRic											
Position	1	0.0011	0.9729	2.6406	0.0949	0.6461	0.4237	2.9314	0.0972	2.4662	0.1868
Residual	12*										
d) FEve											
Position	1	5.5006	**0.0407**	2.3689	0.1550	1.0887	0.3223	6.8019	**0.0168**	0.0031	0.9646
Residual	12*										
e) FDiv											
Position	1	0.0104	0.9310	3.0412	0.1068	n.d.	n.d.	30.095	**0.0021**	1.1877	0.3117
Residual	12*										
f) RaoQ											
Position	1	2.0069	0.1788	2.1860	0.1675	0.0054	0.9398	2.8375	0.1277	2.7799	0.1127
Residual	12										
g) Redundancy											
Position	1	0.0680	0.7982	1.3368	0.2619	3.5611	0.0801	66.763	**0.0004**	1.8684	0.1949
Residual	12										
h) WTO structure											
Position	1	1.3513	0.2588	0.9660	0.3599	0.2498	0.8923	22.849	**0.0005**	2.8066	**0.0360**
Residual	12										

Note: PER-ANOVAs and PERMANOVA were run with 9999 permutations using Euclidean distances. Densities (a) were fourth-root transformed, while WTO (h) was square-root transformed before analysis.

*Residual was 8 for VA and 11 for QU as calculations were not possible for some plots.

n.d.: no data – the analysis could not be performed.

Table 5.31. Summary of PER-ANOVAs positive or negative effect of position on the structure of each category of trait. Positive effects are highlighted in green, negative effects are highlighted in red, and nonsignificant results are in light grey. Categories are the respective treatment with E: Edge; I: Interior. Legend for traits can be found at Table 3.2. Regions are as in Table 3.1.

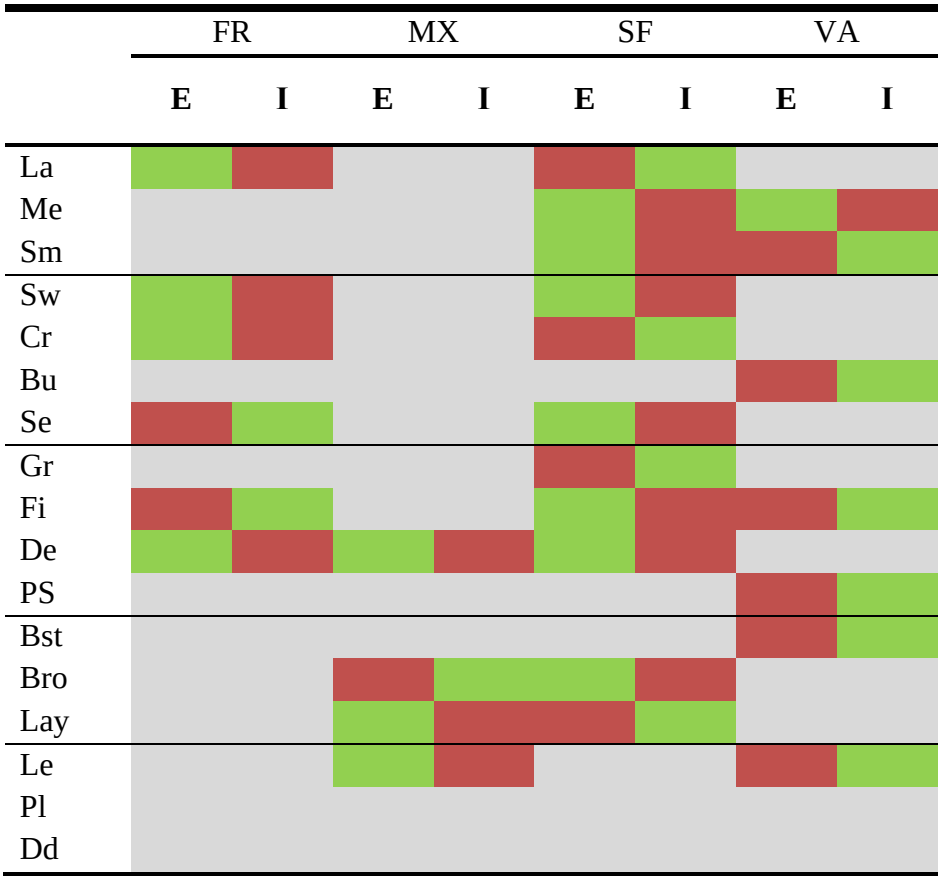

Table 5.32. Summary of PER-ANOVAs positive or negative effect of complexity on the structure of each category of trait. Positive effects are highlighted in green, negative effects are highlighted in red, and nonsignificant results are light grey. One marginally significant result is in light green and red. Categories are the respective treatment with 0: ambient eelgrass shoot density; 0.5: 50% complexity-reduced; 0.8: 80% complexity-reduced. Legend for traits can be found at Table 3.2. Regions are as in Table 3.1.

Table 5.33. Summary of PER-ANOVAs positive or negative effect of treatment on the structure of each category of trait. Positive effects are highlighted in green, negative effects are highlighted in red and nonsignificant results are light grey. Marginally significant or not significant with all highlighted treatment result is in light green or red. Categories are the respective treatment with E: Edge; I: Interior; 0: ambient eelgrass shoot density; 0.5: 50% complexity-reduced; 0.8: 80% complexity-reduced. Legend for traits can be found at Table 3.2. FR are as in Table 3.1.

	FR					
	E			**I**		
	Amb.	**0.5**	**0.8**	**Amb.**	**0.5**	**0.8**
La						
Me						
Sm						
Sw						
Cr						
Bu						
Se						
Gr						
Fi						
De						
PS						
Bst						
Bro						
Lay						
Le						
Pl						
Dd						

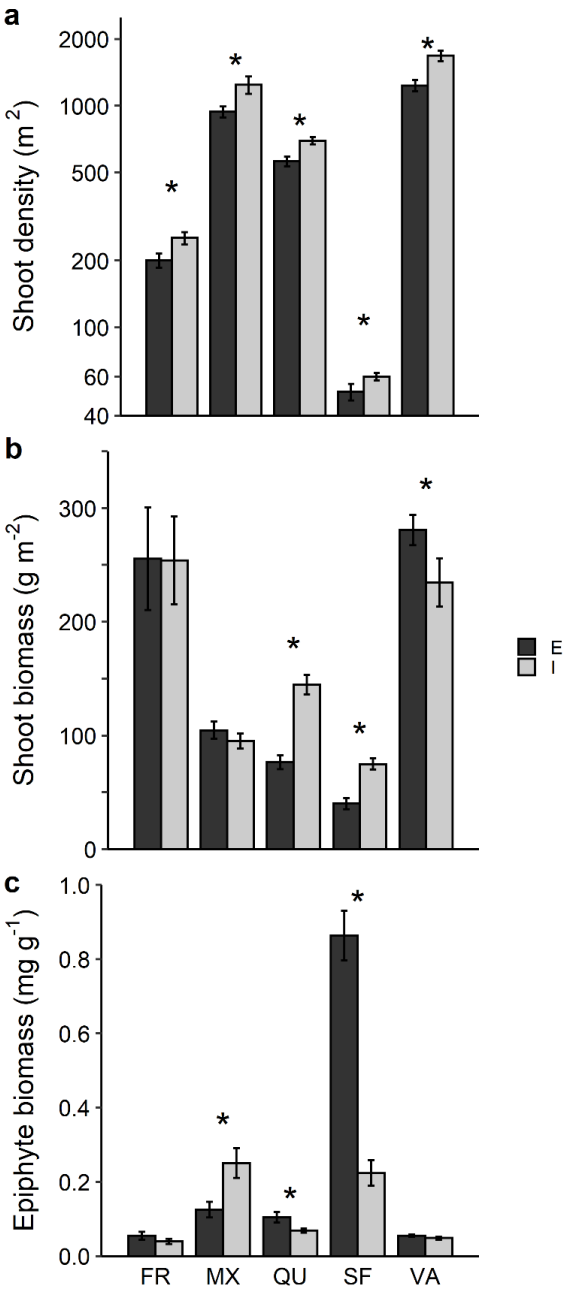

Figure 5.6. Mean (±SE) values of (a) eelgrass shoot density (N m^{-2}), (b) eelgrass shoot biomass (g m^{-2}), and (c) epiphyte load biomass (mg $g^{-1}_{shoot\ dw}$). Values are showing effect of position. Bars are the respective treatment with E: Edge; I: Interior. The number of replicates used to obtain the averages was n = 21 in (a and c), n = 28 in (b) but n = 5 in interior and n = 13 in edge in FR, n = 26 in edge in SF and n = 23 in interior in VA.

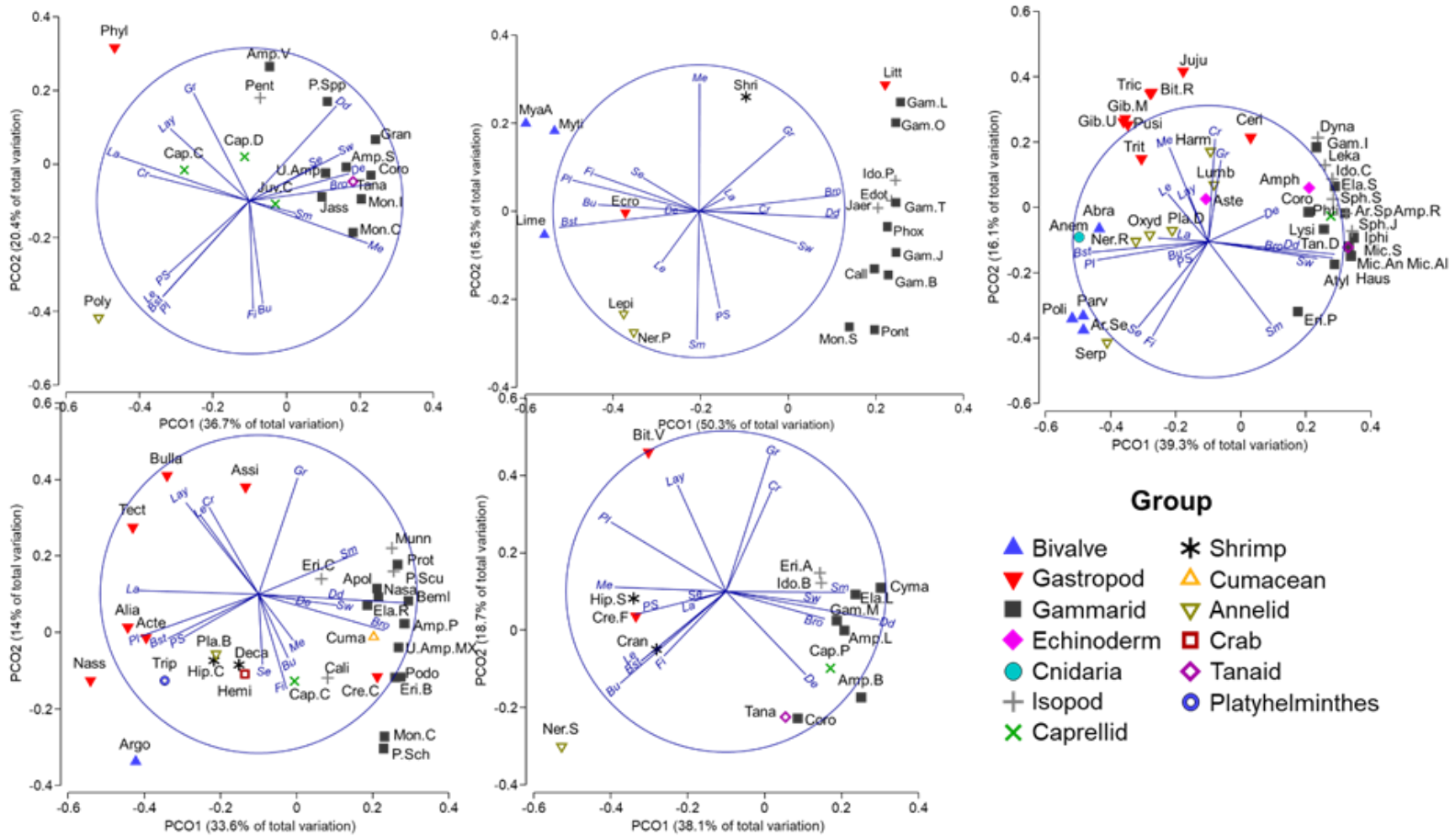

Figure 5.7. Principal coordinate ordinations illustrating the distances among species using their biological traits by region. Values were calculated based on fuzzy calculated Gower's distances using 'dist.ktab' in the 'ade4' R package. All trait categories are illustrated with vectors. Refer to Table 2 of the main text for decoding the trait categories and refer to Table S2 for decoding the species.

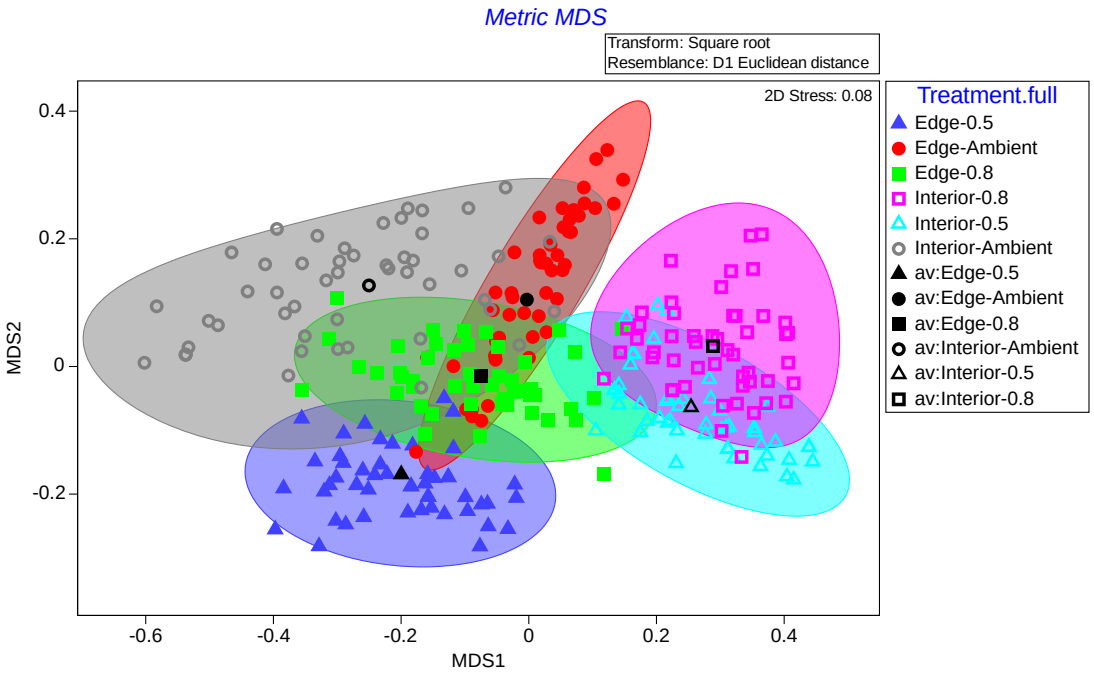

Figure 5.8. Metric multidimensional scaling (mMDS) of the estimated 95% region of bootstrap averages ($n = 50$) from replicates (Euclidean distances; square-root transformed WTO) of treatments (position × complexity) in France (FR; see Table 3.3h). Bootstrapping performed in $m = 4$ dimensional mMDS space.

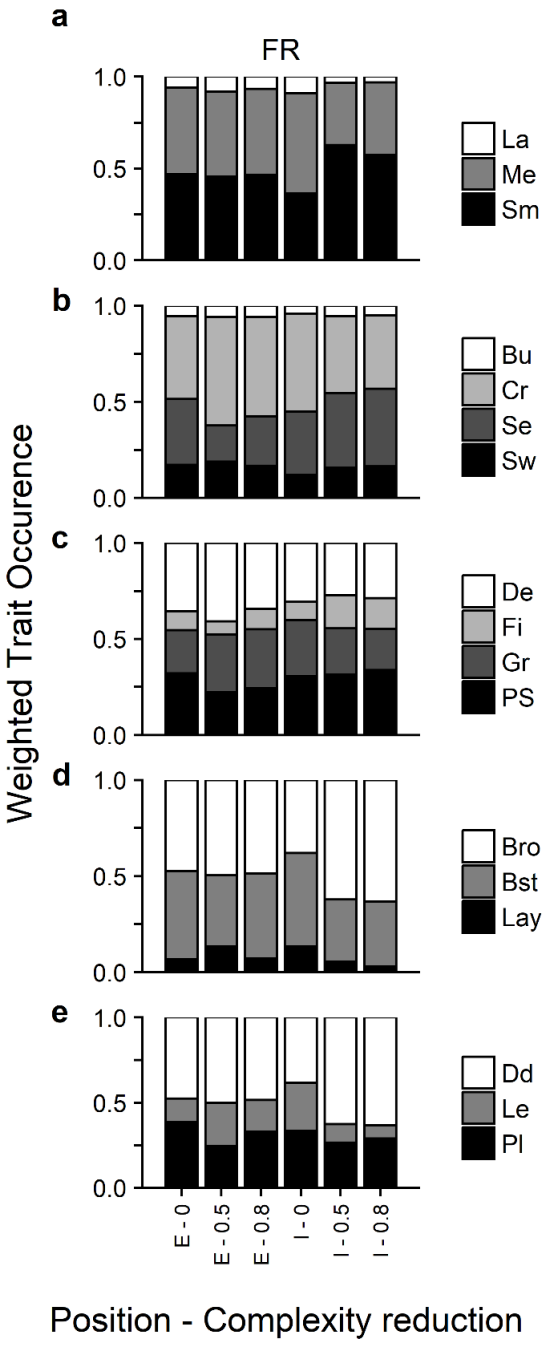

Figure 5.9. Proportions of each category of trait by treatment (position and complexity) for France (FR) region showing (a) size, (b) life habit, (c) feeding habit, (d) reproduction mode, and (e) larval feeding mode. Please refer to Table 1 for decoding-trait categories. Bars are the respective treatment with E: Edge; I: Interior; 0: ambient eelgrass shoot density; 0.5: 50% complexity-reduced; 0.8: 80% complexity-reduced.

REFERENCES

Agardy, T., Alder, J., Dayton, P., Curran, S., Kitchingman, A., Wilson, M., Catenazzi, A., Restrepo, J., Birkeland, C., Blaber, S., Saifullah, S., Branch, G., Boersma, D., Nixon, S., Dugan, P., Davidson, N. et Vörösmarty, C. (2005). Chapter 19 Coastal systems. Dans Baker, J., Casasola, P. M., Lugo, A., Rodriguez, A. S. et Ling Tang, L. D. (dir.), *Ecosystems and human well-being: Current state and trends*. Washington, DC. : Island Press.

Airoldi, L. (2000). Responses of algae with different life histories to temporal and spatial variability of disturbance in subtidal reefs. *Marine Ecology Progress Series, 195*, 81-92.

Airoldi, L., Balata, D. et Beck, M.W. (2008). The gray zone: Relationships between habitat loss and marine diversity and their applications in conservation. *Journal of Experimental Marine Biology and Ecology, 366*(1–2), 8-15.

Airoldi, L. et Beck, M.W. (2007). Loss, status and trends for coastal marine habitats of Europe. *Oceanography and Marine Biology, 45*, 345-405.

Airoldi, L. et Cinelli, F. (1997). Effects of sedimentation on subtidal macroalgal assemblages: An experimental study from a Mediterranean rocky shore. *Journal of Experimental Marine Biology and Ecology, 215*(2), 269-288.

Airoldi, L. et Virgilio, M. (1998). Responses of turf-forming algae to spatial variations in the deposition of sediments. *Marine Ecology Progress Series, 165*, 271-282.

Alestra, T. et Schiel, D.R. (2014). Effects of opportunistic algae on the early life history of a habitat-forming fucoid: influence of temperature, nutrient enrichment and grazing pressure. *Marine Ecology Progress Series*, *508*, 105-115.

Allison, G. (2004). The influence of species diversity and stress intensity on community resistance and resilience. *Ecological Monographs, 74*(1), 117-134.

Andersen, K.H., Berge, T., Gonçalves, R.J., Hartvig, M., Heuschele, J., Hylander, S., Jacobsen, N.S., Lindemann, C., Martens, E.A., Neuheimer, A.B., Olsson, K., Palacz, A., Prowe, A.E.F., Sainmont, J., Traving, S.J., Visser, A.W., Wadhwa, N. et Kiørboe, T. (2016). Characteristic sizes of life in the oceans, from bacteria to whales. *Annual Review of Marine Science, 8*(1), 217-241.

Anderson, M.J., Gorley, R.N. et Clarke, K.R. (2008). *PERMANOVA+ for PRIMER: Guide to software and statistical methods*. Plymouth : PRIMER-E.

Anderson, M.J. et Underwood, A.J. (1997). Effects of gastropod grazers on recruitment and succession of an estuarine assemblage: A multivariate and univariate approach. *Oecologia, 109*(3), 442-453.

Aquilino, K.M. et Stachowicz, J.J. (2012). Seaweed richness and herbivory increase rate of community recovery from disturbance. *Ecology, 93*(4), 879-890.

Archambault, D. et Bourget, E. (1983). Importance of the routine of clearing on the structure and succession of intertidal rocky communities in a subarctic environment. *Canadian Journal of Fisheries and Aquatic Sciences, 40*(8), 1278-1292.

Arevalo, R., Pinedo, S. et Ballesteros, E. (2007). Changes in the composition and structure of Mediterranean rocky-shore communities following a gradient of nutrient enrichment: Descriptive study and test of proposed methods to assess water quality regarding macroalgae. *Marine Pollution Bulletin, 55*(1-6), 104-113.

Arponen, H. et Bostrom, C. (2012). Responses of mobile epifauna to small-scale seagrass patchiness: is fragmentation important? *Hydrobiologia, 680*(1), 1-10.

Atalah, J., Anderson, M.J. et Costello, M.J. (2007a). Temporal variability and intensity of grazing: a mesocosm experiment. *Marine Ecology Progress Series, 341*, 15-24.

Atalah, J. et Crowe, T.P. (2010). Combined effects of nutrient enrichment, sedimentation and grazer loss on rock pool assemblages. *Journal of Experimental Marine Biology and Ecology, 388*(1-2), 51-57.

Atalah, J., Otto, S.A., Anderson, M.J., Costello, M.J., Lenz, M. et Wahl, M. (2007b). Temporal variance of disturbance did not affect diversity and structure of a marine fouling community in north-eastern New Zealand. *Marine Biology, 153*(2), 199-211.

Backman, T.W. et Barilotti, D.C. (1976). Irradiance reduction: Effects on standing crops of the eelgrass *Zostera marina* in a coastal lagoon. *Marine Biology, 34*(1), 33-40.

Baggett, L.P., Heck, K.L., Frankovich, T.A., Armitage, A.R. et Fourqurean, J.W. (2010). Nutrient enrichment, grazer identity, and their effects on epiphytic algal

assemblages: field experiments in subtropical turtlegrass *Thalassia testudinum* meadows. *Marine Ecology Progress Series, 406*, 33-45.

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C. et Silliman, B.R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs, 81*(2), 169-193.

Beauchard, O., Veríssimo, H., Queirós, A.M. et Herman, P.M.J. (2017). The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. *Ecological Indicators, 76*, 81-96.

Bell, S.S., Brooks, R.A., Robbins, B.D., Fonseca, M.S. et Hall, M.O. (2001). Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. *Biological Conservation, 100*(1), 115-123.

Benedetti-Cecchi, L., Bertocci, I., Vaselli, S. et Maggi, E. (2006). Temporal variance reverses the impact of high mean intensity of stress in climate change experiments. *Ecology, 87*(10), 2489-2499.

Benedetti-Cecchi, L., Pannacciulli, F., Bulleri, F., Moschella, P.S., Airoldi, L., Relini, G. et Cinelli, F. (2001). Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. *Marine Ecology-Progress Series, 214*, 137-150.

Bergeron, P. et Bourget, E. (1984). Effet du froid et des glaces sur les peuplements intertidaux des régions nordiques, particulièrement dans l'estuaire du Saint-Laurent. *Océanis, 10*(3), 279-304.

Bergeron, P. et Bourget, E. (1986). Shore topography and spatial partitioning of crevice refuges by sessile epibenthos in an ice disturbed environment. *Marine Ecology Progress Series, 28*, 129-145.

Bertness, M.D., Leonard, G.H., Levine, J.M., Schmidt, P.R. et Ingraham, A.O. (1999). Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology, 80*(8), 2711-2726.

Bertocci, I., Domínguez Godino, J., Freitas, C., Incera, M., Araújo, R., Bio, A., Arenas, F., Sousa-Pinto, I., Reis, P.A. et Domínguez, R. (2015). The regime of climate-related disturbance and nutrient enrichment modulate macroalgal invasions in rockpools. *Biological invasions., 17*(1), 133-147.

Bertocci, I., Godino, J.A.D., Freitas, C., Incera, M., Bio, A. et Dominguez, R. (2017). Compounded perturbations in coastal areas: contrasting responses to nutrient

enrichment and the regime of storm-related disturbance depend on life-history traits. *Functional Ecology, 31*(5), 1122-1134.

Bertocci, I., Maggi, E., Vaselli, S. et Benedetti-Cecchi, L. (2005). Contrasting effects of mean intensity and temporal variation of disturbance on a rocky seashore. *Ecology, 86*(8), 2061-2067.

Blake, R.E. et Duffy, J.E. (2010). Grazer diversity affects resistance to multiple stressors in an experimental seagrass ecosystem. *Oikos, 119*(10), 1625-1635.

Blake, R.E. et Duffy, J.E. (2012). Changes in biodiversity and environmental stressors influence community structure of an experimental eelgrass *Zostera marina* system. *Marine Ecology Progress Series, 470*, 41-54.

Blake, R.E. et Duffy, J.E. (2016). Influence of environmental stressors and grazer immigration on ecosystem properties of an experimental eelgrass community. *Journal of Experimental Marine Biology and Ecology, 480*, 45-53.

Boaventura, D., Alexander, M., Della Santina, P., Smith, N.D., Re, P., da Fonseca, L.C. et Hawkins, S.J. (2002). The effects of grazing on the distribution and composition of low-shore algal communities on the central coast of Portugal and on the southern coast of Britain. *Journal of Experimental Marine Biology and Ecology, 267*(2), 185-206.

Bokn, T.L., Duarte, C.M., Pedersen, M.F., Marba, N., Moy, F.E., Barron, C., Bjerkeng, B., Borum, J., Christie, H., Engelbert, S., Fotel, F.L., Hoell, E.E., Karez, R., Kersting, K., Kraufvelin, P., Lindblad, C., Olsen, M., Sanderud, K.A., Sommer, U. et Sorensen, K. (2003). The response of experimental rocky shore communities to nutrient additions. *Ecosystems, 6*(6), 577-594.

Bologna, P.A.X. (2006). Assessing within habitat variability in plant demography, faunal density, and secondary production in an eelgrass (*Zostera marina* L.) bed. *Journal of Experimental Marine Biology and Ecology, 329*(1), 122-134.

Bologna, P.A.X. et Heck, K.L. (1999). Macrofaunal associations with seagrass epiphytes - Relative importance of trophic and structural characteristics. *Journal of Experimental Marine Biology and Ecology, 242*(1), 21-39.

Bologna, P.A.X. et Heck, K.L. (2002). Impact of habitat edges on density and secondary production of seagrass-associated fauna. *Estuaries, 25*(5), 1033-1044.

Bostrom, C. et Bonsdorff, E. (2000). Zoobenthic community establishment and habitat complexity - the importance of seagrass shoot-density, morphology and physical

disturbance for faunal recruitment. *Marine Ecology Progress Series, 205*, 123-138.

Bostrom, C., Tornroos, A. et Bonsdorff, E. (2010). Invertebrate dispersal and habitat heterogeneity: Expression of biological traits in a seagrass landscape. *Journal of Experimental Marine Biology and Ecology, 390*(2), 106-117.

Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science, 16*(5), 533-540.

Botta-Dukát, Z. et Czúcz, B. (2016). Testing the ability of functional diversity indices to detect trait convergence and divergence using individual-based simulation. *Methods in Ecology and Evolution, 7*(1), 114-126.

Bracken, M.E.S. et Nielsen, K.J. (2004). Diversity of intertidal macroalgae increases with nitrogen loading by invertebrates. *Ecology, 85*(10), 2828-2836.

Bremner, J., Rogers, S.I. et Frid, C.L.J. (2003). Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. *Marine Ecology Progress Series, 254*, 11-25.

Bremner, J., Rogers, S.I. et Frid, C.L.J. (2006a). Matching biological traits to environmental conditions in marine benthic ecosystems. *Journal of Marine Systems, 60*(3), 302-316.

Bremner, J., Rogers, S.I. et Frid, C.L.J. (2006b). Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecological Indicators, 6*(3), 609-622.

Brey, T., Müller-Wiegmann, C., Zittier, Z.M.C. et Hagen, W. (2010). Body composition in aquatic organisms — A global data bank of relationships between mass, elemental composition and energy content. *Journal of Sea Research, 64*(3), 334-340.

Bulleri, F., Benedetti-Cecchi, L., Cusson, M., Maggi, E., Arenas, F., Aspden, R., Bertocci, I., Crowe, T.P., Davoult, D., Eriksson, B.K., Fraschetti, S., Gollety, C., Griffin, J.N., Jenkins, S.R., Kotta, J., Kraufvelin, P., Molis, M., Pinto, I.S., Terlizzi, A., Valdivia, N. et Paterson, D.M. (2012a). Temporal stability of European rocky shore assemblages: variation across a latitudinal gradient and the role of habitat-formers. *Oikos, 121*(11), 1801-1809.

Bulleri, F., Russell, B.D. et Connell, S.D. (2012b). Context-dependency in the effects of nutrient loading and consumers on the availability of space in marine rocky environments. *Plos One, 7*(3).

Bulthuis, D.A. et Woelkerling, W.J. (1981). Effects of in situ nitrogen and phosphorus enrichment of the sediments on the seagrass *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog in Western Port, Victoria, Australia. *Journal of Experimental Marine Biology and Ecology, 53*(2), 193-207.

Burke, M.K., Dennison, W.C. et Moore, K.A. (1996). Non-structural carbohydrate reserves of eelgrass *Zostera marina*. *Marine Ecology Progress Series, 137*, 195-201.

Burkepile, D.E. et Hay, M.E. (2006). Herbivore vs. nutrient control of marine primary producers: Context-dependent effects. *Ecology*, *87*(12), 3128-3139.

Burkholder, J.M., Tomasko, D.A. et Touchette, B.W. (2007). Seagrasses and eutrophication. *Journal of Experimental Marine Biology and Ecology, 350*(1-2), 46-72.

Butler, M.J. (1989). Community responses to variable predation: Field studies with sunfish and freshwater macroinvertebrates. *Ecological Monographs, 59*(3), 311-328.

Calizza, E., Costantini, M.L., Careddu, G. et Rossi, L. (2017). Effect of habitat degradation on competition, carrying capacity, and species assemblage stability. *Ecology and Evolution, 7*(15), 5784-5796.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. et Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature, 486*(7401), 59-67.

Cardoso, P.G., Raffaelli, D., Lillebo, A.I., Verdelhos, T. et Pardal, M.A. (2008). The impact of extreme flooding events and anthropogenic stressors on the macrobenthic communities' dynamics. *Estuarine Coastal and Shelf Science, 76*(3), 553-565.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. et Diaz, S. (2000). Consequences of changing biodiversity. *Nature, 405*(6783), 234-242.

Chevenet, F., Doledec, S. et Chessel, D. (1994). A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology, 31*(3), 295-309.

Chow, P.S. et Landhäusser, S.M. (2004). A method for routine measurements of total sugar and starch content in woody plant tissues. *Tree Physiology, 24*(10), 1129-1136.

Christie, H., Norderhaug, K.M. et Fredriksen, S. (2009). Macrophytes as habitat for fauna. *Marine Ecology Progress Series, 396*, 221-233.

Cimon, S. et Cusson, M. (2018). Impact of multiple disturbances and stress on the temporal trajectories and resilience of benthic intertidal communities. *Ecosphere*, *9*(10), e02467.

Cimon, S., Cusson, M. et Deslauriers, A. (submitted). Multiple stressors and disturbance effects on eelgrass and epifaunal macroinvertebrate assemblage structure.

Clarke, K.R. (1990). Comparisons of dominance curves. *Journal of Experimental Marine Biology and Ecology, 138*(1), 143-157.

Clarke, K.R., Chapman, M.G., Somerfield, P.J. et Needham, H.R. (2006). Dispersion-based weighting of species counts in assemblage analyses. *Marine Ecology Progress Series, 320*, 11-27.

Clarke, K.R. et Gorley, R.N. (2015). *PRIMER v7: User Manual/Tutorial.* Plymouth : PRIMER-E.

Clarke, K.R., Gorley, R.N., Somerfield, P.J. et Warwick, R.M. (2014). *Changes in marine communities: An approach to statistical analysis and interpretation 3rd edition*. Plymouth, UK : PRIMER-E Ltd.

Clarke, K.R., Tweedley, J.R. et Valesini, F.J. (2013). Simple shade plots aid better long-term choices of data pre-treatment in multivariate assemblage studies. *Journal of the Marine Biological Association of the United Kingdom, 94*(1), 1-16.

Cloern, J.E., Abreu, P.C., Carstensen, J., Chauvaud, L., Elmgren, R., Grall, J., Greening, H., Johansson, J.O.R., Kahru, M., Sherwood, E.T., Xu, J. et Yin, K.D. (2016). Human activities and climate variability drive fast-paced change across the world's estuarine-coastal ecosystems. *Global Change Biology, 22*(2), 513-529.

Collier, C.J., Lavery, P.S., Ralph, P.J. et Masini, R.J. (2009). Shade-induced response and recovery of the seagrass *Posidonia sinuosa*. *Journal of Experimental Marine Biology and Ecology, 370*(1-2), 89-103.

Connolly, R.M. (1994). Removal of seagrass canopy - effects on small fish and their prey. *Journal of Experimental Marine Biology and Ecology, 184*(1), 99-110.

Connolly, R.M. (1995). Effects of removal of seagrass canopy on assemblages of small, motile invertebrates. *Marine Ecology Progress Series, 118*(1-3), 129-137.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P. et van den Belt, M. (1997). The value of the world's ecosystem services and natural capital. *Nature, 387*(6630), 253-260.

Côté, I.M., Darling, E.S. et Brown, C.J. (2016). Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B-Biological Sciences, 283*(1824).

Crain, C.M., Kroeker, K. et Halpern, B.S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters, 11*(12), 1304-1315.

Crowe, T.P., Bracken, M.E.S. et O'Connor, N.E. (2012). Reality check: Issues of scale and abstraction in biodiversity research, and potential solutions. Dans DM, P., RJ, A. et M, S. (dir.), *Marine biodiversity futures and ecosystem functioning: Frameworks, methodologies and integration* (p. 185-200). Oxford, UK : Oxford University Press.

Crowe, T.P., Thompson, R.C., Bray, S. et Hawkins, S.J. (2000). Impacts of anthropogenic stress on rocky intertidal communities. *Journal of Aquatic Ecosystem Stress and Recovery, 7*(4), 273-297.

Cusson, M., Crowe, T.P., Araujo, R., Arenas, F., Aspden, R., Bulleri, F., Davoult, D., Dyson, K., Fraschetti, S., Herkul, K., Hubas, C., Jenkins, S., Kotta, J., Kraufvelin, P., Migne, A., Molis, M., Mulholland, O., Noel, L.M.L.J., Paterson, D.M., Saunders, J., Somerfield, P.J., Sousa-Pinto, I., Spilmont, N., Terlizzi, A. et Benedetti-Cecchi, L. (2015). Relationships between biodiversity and the stability of marine ecosystems: Comparisons at a European scale using meta-analysis. *Journal of Sea Research, 98*, 5-14.

Daily, G.C. (1997). Chapter 1 Introduction: What are ecosystems services? Dans Daily, G. C. (dir.), *Nature's services. Societal dependance on natural ecosystems* (p. 1-10). Washington, D.C., USA : Island Press.

Darling, E.S. et Côté, I.M. (2008). Quantifying the evidence for ecological synergies. *Ecology Letters*, *11*(12), 1278-1286.

Dayton, P.K. (1972). *Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica*. Kansas, Allen Press. United States. P : Lawrence.

de Mazancourt, C., Isbell, F., Larocque, A., Berendse, F., De Luca, E., Grace, J.B., Haegeman, B., Polley, H.W., Roscher, C., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B.J. et Loreau, M. (2013). Predicting ecosystem stability from community composition and biodiversity. *Ecology Letters*, *16*(5), 617-625.

Defeo, O. et McLachlan, A. (2005). Patterns, processes and regulatory mechanisms in sandy beach macrofauna: A multi-scale analysis. *Marine Ecology-progress Series - MAR ECOL-PROGR SER*, *295*, 1-20.

DesJarlais, C., Allard, M., Bélanger, D., Blondlot, A., Bouffard, A., Bourque, A., Chaumont, D., Gosselin, P., Houle, D., Larrivée, C., Lease, N., Pham, A.T., Roy, R., Savard, J.-P., Turcotte, R. et Villeneuve, C. (2010). *Ouranos. Savoir s'adapter aux changements climatiques*. Montréal.

Deslauriers, A., Fournier, M.-P., Cartenì, F. et Mackay, J. (2018). Phenological shifts in conifer species stressed by spruce budworm defoliation. *Tree Physiology*, *39*(4), 590-605.

Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E. et Thomson, D. (1998). The statistical inevitability of stability-diversity relationships in community ecology. *American Naturalist*, *151*(3), 264-276.

Donohue, I., Hillebrand, H., Montoya, J.M., Petchey, O.L., Pimm, S.L., Fowler, M.S., Healy, K., Jackson, A.L., Lurgi, M., McClean, D., O'Connor, N.E., O'Gorman, E.J. et Yang, Q. (2016). Navigating the complexity of ecological stability. *Ecology Letters*, *19*(9), 1172-1185.

Donohue, I., Petchey, O.L., Montoya, J.M., Jackson, A.L., McNally, L., Viana, M., Healy, K., Lurgi, M., O'Connor, N.E. et Emmerson, M.C. (2013). On the dimensionality of ecological stability. *Ecology Letters*, *16*(4), 421-429.

Drake, L.A., Dobbs, F.C. et Zimmerman, R.C. (2003). Effects of epiphyte load on optical properties and photosynthetic potential of the seagrasses *Thalassia testudinum* Banks ex König and *Zostera marina* L. *Limnology and Oceanography*, *48*(1, part 2), 456-463.

Drew, E.A. (1983). Sugars, cytolitols and seagrass phylogeny. *Aquatic Botany, 15*(4), 387-408.

Duarte, C.M. (2002). The future of seagrass meadows. *Environmental Conservation, 29*(2), 192-206.

Duarte, C.M., Borja, A., Carstensen, J., Elliott, M., Krause-Jensen, D. et Marba, N. (2015). Paradigms in the recovery of estuarine and coastal ecosystems. *Estuaries and Coasts, 38*(4), 1202-1212.

Duffy, E.J., Richardson, P.J. et Canuel, E.A. (2003). Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecology Letters, 6*(7), 637-645.

Duffy, J.E. (2006). Biodiversity and the functioning of seagrass ecosystems. *Marine Ecology Progress Series, 311*, 233-250.

Duffy, J.E., Reynolds, P.L., Bostrom, C., Coyer, J.A., Cusson, M., Donadi, S., Douglass, J.G., Eklof, J.S., Engelen, A.H., Eriksson, B.K., Fredriksen, S., Gamfeldt, L., Gustafsson, C., Hoarau, G., Hori, M., Hovel, K., Iken, K., Lefcheck, J.S., Moksnes, P.O., Nakaoka, M., O'Connor, M.I., Olsen, J.L., Richardson, J.P., Ruesink, J.L., Sotka, E.E., Thormar, J., Whalen, M.A. et Stachowicz, J.J. (2015). Biodiversity mediates top-down control in eelgrass ecosystems: a global comparative-experimental approach. *Ecology Letters, 18*(7), 696-705.

Edgar, G.J. (1990). The use of the size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. *Journal of Experimental Marine Biology and Ecology, 137*(3), 195-214.

Edgar, G.J. et Robertson, A.I. (1992). The influence of seagrass structure on the distribution and abundance of mobile epifauna: pattern and process in a Western Australian *Amphibolis* bed. *Journal of Experimental Marine Biology and Ecology, 160*(1), 13-31.

Eklof, J.S., McMahon, K. et Lavery, P.S. (2009). Effects of multiple disturbances in seagrass meadows: shading decreases resilience to grazing. *Marine and Freshwater Research, 60*(12), 1317-1327.

Ellis, J.I., Clark, D., Atalah, J., Jiang, W., Taiapa, C., Patterson, M., Sinner, J. et Hewitt, J. (2017). Multiple stressor effects on marine infauna: responses of estuarine taxa and functional traits to sedimentation, nutrient and metal loading. *Scientific Reports, 7*.

Elmqvist, T., Folke, C., Nystrom, M., Peterson, G., Bengtsson, J., Walker, B. et Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment, 1*(9), 488-494.

Enriquez, S. et Pantoja-Reyes, N.I. (2005). Form-function analysis of the effect of canopy morphology on leaf self-shading in the seagrass *Thalassia testudinum*. *Oecologia, 145*(2), 235-243.

Eriander, L. (2017). Light requirements for successful restoration of eelgrass (*Zostera marina* L.) in a high latitude environment - Acclimatization, growth and carbohydrate storage. *Journal of Experimental Marine Biology and Ecology, 496*, 37-48.

Eriksson, B.K., Ljunggren, L., Sandstrom, A., Johansson, G., Mattila, J., Rubach, A., Raberg, S. et Snickars, M. (2009). Declines in predatory fish promote bloom-forming macroalgae. *Ecological Applications, 19*(8), 1975-1988.

Eriksson, B.K., Rubach, A. et Hillebrand, H. (2006). Biotic habitat complexity controls species diversity and nutrient effects on net biomass production. *Ecology, 87*(1), 246-254.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics, 34*(1), 487-515.

Fokeera-Wahedally, S.B.M. et Bhikajee, M. (2005). The effects of in situ shading on the growth of a seagrass, *Syringodium isoetifolium. Estuarine, Coastal and Shelf Science, 64*(2–3), 149-155.

Fowler, D., Coyle, M., Skiba, U., Sutton, M.A., Cape, J.N., Reis, S., Sheppard, L.J., Jenkins, A., Grizzetti, B., Galloway, J.N., Vitousek, P., Leach, A., Bouwman, A.F., Butterbach-Bahl, K., Dentener, F., Stevenson, D., Amann, M. et Voss, M. (2013). The global nitrogen cycle in the twenty-first century. *Philosophical Transactions of the Royal Society B-Biological Sciences, 368*(1621).

Fradette, P. et Bourget, E. (1980). Ecology of benthic epifauna of the estuary and gulf of St-Lawrence: factors influencing their distribution and abundance on buoys. *Canadian Journal of Fisheries and Aquatic Sciences, 37*, 979-999.

Freidenburg, T.L., Menge, B.A., Halpin, P.M., Webster, M. et Sutton-Grier, A. (2007). Cross-scale variation in top-down and bottom-up control of algal abundance. *Journal of Experimental Marine Biology and Ecology, 347*(1-2), 8-29.

Galic, N., Sullivan, L.L., Grimm, V. et Forbes, V.E. (2018). When things don't add up: quantifying impacts of multiple stressors from individual metabolism to ecosystem processing. *Ecology Letters, 21*(4), 568-577.

Gamfeldt, L., Lefcheck, J.S., Byrnes, J.E.K., Cardinale, B.J., Duffy, J.E. et Griffin, J.N. (2015). Marine biodiversity and ecosystem functioning: what's known and what's next? *Oikos, 124*(3), 252-265.

Gartner, A., Lavery, P.S., McMahon, K., Brearley, A. et Barwick, H. (2010). Light reductions drive macroinvertebrate changes in *Amphibolis griffithii* seagrass habitat. *Marine Ecology Progress Series, 401*, 87-100.

Gartner, A., Tuya, F., Lavery, P.S. et McMahon, K. (2013). Habitat preferences of macroinvertebrate fauna among seagrasses with varying structural forms. *Journal of Experimental Marine Biology and Ecology, 439*, 143-151.

Gil, M., Armitage, A.R. et Fourqurean, J.W. (2006). Nutrient impacts on epifaunal density and species composition in a subtropical seagrass bed. *Hydrobiologia, 569*(1), 437-447.

Gilbert, D., Chabot, D., Archambault, A., Rondeau, B. et Hébert, H. (2007). Appauvrissement en oxygène dans les eaux profondes du Saint-Laurent marin - Causes possibles et impacts écologiques. *Le naturaliste canadien, 131*(1), 67-75.

Goodman, D. (1975). The theory of diversity-stability relationships in ecology. *The Quarterly Review of Biology, 50*(3), 237-266.

Grant, C. et Provencher, L. (2007). *Caractérisation de l'habitat et de la faune des herbiers de Zostera marina (L.) de la péninsule de Manicouagan (Québec)*. (Rapport technique canadien des sciences halieutiques et aquatiques1488-545XN° 2772 2772).

Grime, J.P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist, 111*(982), 1169-1194.

Grimm, V. et Wissel, C. (1997). Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia, 109*(3), 323-334.

Guerry, A.D. (2008). Interactive effects of grazing and enrichment on diversity; conceptual implications of a rocky intertidal experiment. *Oikos, 117*(8), 1185-1196.

Gustafsson, C. et Bostrom, C. (2011). Biodiversity influences ecosystem functioning in aquatic angiosperm communities. *Oikos, 120*(7), 1037-1046.

Gustafsson, C. et Bostrom, C. (2013). Influence of neighboring plants on shading stress resistance and recovery of eelgrass, *Zostera marina* L. *Plos One, 8*(5).

Halpern, B.S., Frazier, M., Potapenko, J., Casey, K.S., Koenig, K., Longo, C., Lowndes, J.S., Rockwood, R.C., Selig, E.R., Selkoe, K.A. et Walbridge, S. (2015). Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nature Communications, 6*, 7615.

Halpern, B.S., Selkoe, K.A., Micheli, F. et Kappel, C.V. (2007). Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. *Conservation Biology, 21*(5), 1301-1315.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R. et Watson, R. (2008). A global map of human impact on marine ecosystems. *Science, 319*(5865), 948-952.

Harley, C.D.G., Anderson, K.M., Demes, K.W., Jorve, J.P., Kordas, R.L., Coyle, T.A. et Graham, M.H. (2012). Effects of climate change on global seaweed communities. *Journal of Phycology, 48*, 1064-1078.

Hauxwell, J., Cebrian, J. et Valiela, I. (2003). Eelgrass *Zostera marina* loss in temperate estuaries: relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. *Marine Ecology Progress Series, 247*, 59-73.

Hawkins, S.J., Allen, J.R. et Bray, S. (1999). Restoration of temperate marine and coastal ecosystems: nudging nature. *Aquatic Conservation: Marine and Freshwater Ecosystems, 9*(1), 23-46.

Hawkins, S.J. et Hartnoll, R.G. (1983). Grazing of intertidal algae by marine-invertebrates. *Oceanography and Marine Biology, 21*, 195-282.

Hawkins, S.J., Sugden, H.E., Mieszkowska, N., Moore, P.J., Poloczanska, E., Leaper, R., Herbert, R.J.H., Genner, M.J., Moschella, P.S., Thompson, R.C., Jenkins, S.R., Southward, A.J. et Burrows, M.T. (2009). Consequences of climate-driven biodiversity changes for ecosystem functioning of North European rocky shores. *Marine Ecology Progress Series, 396*, 245-259.

Healey, D. et Hovel, K.A. (2004). Seagrass bed patchiness: effects on epifaunal communities in San Diego Bay, USA. *Journal of Experimental Marine Biology and Ecology, 313*(1), 155-174.

Heck, K.L., Hays, G. et Orth, R.J. (2003). Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series, 253*, 123-136.

Hemminga, M.A. et Duarte, C.M. (2000). *Seagrass ecology*. Cambridge, UK : Cambridge University Press.

Herkul, K. et Kotta, J. (2009). Effects of eelgrass (*Zostera marina*) canopy removal and sediment addition on sediment characteristics and benthic communities in the Northern Baltic Sea. *Marine Ecology-an Evolutionary Perspective, 30*, 74-82.

Hillebrand, H., Bennett, D.M. et Cadotte, M.W. (2008). Consequences of dominance: A review of evenness effects on local and regional ecosystem processes. *Ecology, 89*(6), 1510-1520.

Holling, C.S. (1973). Resilience and Stability of Ecological Systems. *Annual Review of Ecology and Systematics, 4*, 1-23.

Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L. et O'Connor, M.I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature, 486*(7401), 105-109.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J. et Wardle, D.A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs, 75*(1), 3-35.

Hovel, K. et Fonseca, M.S. (2005). Influence of seagrass landscape structure on the juvenile blue crab habitat-survival function. *Marine Ecology Progress Series, 300*, 179-191.

Hovel, K.A., Duffy, J.E., Stachowicz, J.J., Reynolds, P., Bostrom, C., Boyer, K.E., Cimon, S., Cusson, M., Fodrie, J., Gagnon, K., Hereu, C.M., Hori, M., Jorgensen, P., Kruschel, C., Lee, K.S., O'Connor, N.E., Nakaoka, M., Tomas, F., Rossi, F. et Ruesink, J.L. (in preparation). Effects of eelgrass patch edges on predation risk are influenced by habitat features bu not habitat degradation.

Hovel, K.A., Warneke, A.M., Virtue-Hilborn, S.P. et Sanchez, A.E. (2016). Mesopredator foraging success in eelgrass (*Zostera marina* L.): Relative effects of epiphytes, shoot density, and prey abundance. *Journal of Experimental Marine Biology and Ecology, 474*, 142-147.

Howarth, R.W. (1988). Nutrient limitation of net primary production in marine ecosystems. *Annual Review of Ecology and Systematics, 19*, 89-110.

Hughes, A.R., Bando, K.J., Rodriguez, L.F. et Williams, S.L. (2004). Relative effects of grazers and nutrients on seagrasses: a meta-analysis approach. *Marine Ecology Progress Series, 282*, 87-99.

Ingrisch, J. et Bahn, M. (2018). Towards a comparable quantification of resilience. *Trends in Ecology & Evolution, 33*(4), 251-259.

IPCC. (2014). *Climate change 2014: Synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovermmental Panel on Climate Change*. Dans [Core Writing Team, R. K. P. a. L. A. et (eds.)], M. (dir.). Geneva, Switzerland : IPCC.

Jaschinski, S. et Sommer, U. (2008). Top-down and bottom-up control in an eelgrass-epiphyte system. *Oikos, 117*(5), 754-762.

Jenkins, S.R., Hawkins, S.J. et Norton, T.A. (1999). Direct and indirect effects of a macroalgal canopy and limpet grazing in structuring a sheltered inter-tidal community. *Marine Ecology Progress Series, 188*, 81-92.

Jiang, L. et Pu, Z. (2009). Different effects of species diversity on temporal stability in single-trophic and multitrophic communities. *American Naturalist, 174*(5), 651-659.

Jochum, M., Schneider, F.D., Crowe, T.P., Brose, U. et O'Gorman, E.J. (2012). Climate-induced changes in bottom-up and top-down processes independently alter a marine ecosystem. *Philosophical Transactions of the Royal Society B-Biological Sciences, 367*(1605), 2962-2970.

Jones, C.G., Lawton, J.H. et Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos, 69*(3), 373-386.

Joseph, L. et Cusson, M. (2015). Resistance of benthic intertidal communities to multiple disturbances and stresses. *Marine Ecology Progress Series, 534*, 49-64.

Korpinen, S. et Jormalainen, V. (2008). Grazing and nutrients reduce recruitment success of *Fucus vesiculosus* L. (Fucales : Phaeophyceae). *Estuarine Coastal and Shelf Science, 78*(2), 437-444.

Korpinen, S., Jormalainen, V. et Honkanen, T. (2007). Effects of nutrients, herbivory, and depth on the macroalgal community in the rocky sublittoral. *Ecology, 88*(4), 839-852.

Kraufvelin, P. (2007). Responses to nutrient enrichment, wave action and disturbance in rocky shore communities. *Aquatic Botany, 87*(4), 262-274.

Laliberté, E. et Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology, 91*(1), 299-305.

Lange, K., Liess, A., Piggott, J.J., Townsend, C.R. et Matthaei, C.D. (2011). Light, nutrients and grazing interact to determine stream diatom community composition and functional group structure. *Freshwater Biology, 56*(2), 264-278.

Lee, K.S. et Dunton, K.H. (1997). Effect of in situ light reduction on the maintenance, growth and partitioning of carbon resources in *Thalassia testudinum* banks ex König. *Journal of Experimental Marine Biology and Ecology, 210*(1), 53-73.

Lee, K.S. et Dunton, K.H. (2000). Effects of nitrogen enrichment on biomass allocation, growth, and leaf morphology of the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series, 196*, 39-48.

Lefcheck, J.S., Marion, S.R., Lombana, A.V. et Orth, R.J. (2016). Faunal communities are invariant to fragmentation in experimental seagrass landscapes. *Plos One, 11*(5), e0156550.

Lefcheck, J.S., Marion, S.R. et Orth, R.J. (2017a). Restored eelgrass (*Zostera marina* L.) as a refuge for epifaunal biodiversity in mid-western Atlantic coastal bays. *Estuaries and Coasts, 40*(1), 200-212.

Lefcheck, J.S., Wilcox, D.J., Murphy, R.R., Marion, S.R. et Orth, R.J. (2017b). Multiple stressors threaten the imperiled coastal foundation species eelgrass (*Zostera marina*) in Chesapeake Bay, USA. *Global Change Biology, 23*(9), 3474-3483.

Legendre, P. et Anderson, M.J. (1999). Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs, 69*(1), 1-24.

Lehman, C.L. et Tilman, D. (2000). Biodiversity, Stability, and Productivity in Competitive Communities. *The American Naturalist, 156*(5), 534-552.

Lemieux, J. et Cusson, M. (2014). Effects of habitat-forming species richness, evenness, identity, and abundance on benthic intertidal community establishment and productivity. *Plos One, 9*(10), e109261.

Leoni, V., Vela, A., Pasqualini, V., Pergent-Martini, C. et Pergent, G. (2008). Effects of experimental reduction of light and nutrient enrichments (N and P) on seagrasses: a review. *Aquatic Conservation-Marine and Freshwater Ecosystems, 18*(2), 202-220.

Loreau, M. (2000). Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos, 91*(1), 3-17.

Loreau, M. et de Mazancourt, C. (2013). Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology Letters, 16*, 106-115.

Loreau, M. et Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature, 412*(6842), 72-76.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. et Wardle, D.A. (2001). Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science, 294*(5543), 804-808.

Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H. et Jackson, J.B.C. (2006). Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science, 312*(5781), 1806-1809.

Lotze, H.K., Worm, B. et Sommer, U. (2000). Propagule banks, herbivory and nutrient supply control population development and dominance patterns in macroalgal blooms. *Oikos, 89*(1), 46-58.

Lotze, H.K., Worm, B. et Sommer, U. (2001). Strong bottom-up and top-down control of early life stages of macroalgae. *Limnology and Oceanography, 46*(4), 749-757.

Lubchenco, J. (1983). Littorina and Fucus: effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology, 64*(5), 1116-1123.

Lundquist, C.J., Jones, T.C., Parkes, S.M. et Bulmer, R.H. (2018). Changes in benthic community structure and sediment characteristics after natural recolonisation of the seagrass *Zostera muelleri*. *Scientific Reports, 8*, 13250.

Lyons, D.A., Benedetti-Cecchi, L. et Vinebrooke, R.D. (2015). Modifiers of impacts on marine ecosytems: disturbance regimes, multiple stressors and receiving environments. Dans Crowe, T. P. et Frid, C. L. J. (dir.), *Marine ecosystems: Human impacts on biodiversity, functioning and services*. Cambridge, UK : Cambridge University Press.

Macarthur, R. (1955). Fluctuations of animal populations, and a measure of community stability. *Ecology, 36*(3), 533-536.

MacNeill, G.J., Mehrpouyan, S., Minow, M.A.A., Patterson, J.A., Tetlow, I.J. et Emes, M.J. (2017). Starch as a source, starch as a sink: the bifunctional role of starch in carbon allocation. *Journal of experimental botany, 68*(16), 4433-4453.

Maggi, E., Bertocci, I., Vaselli, S. et Benedetti-Cecchi, L. (2009). Effects of changes in number, identity and abundance of habitat-forming species on assemblages of rocky seashores. *Marine Ecology Progress Series, 381*, 39-49.

Marbà, N., Hemminga, M.A. et Duarte, C.M. (2006). Resource translocation within seagrass clones: allometric scaling to plant size and productivity. *Oecologia, 150*(3), 362-372.

Marbà, N., Hemminga, M.A., Mateo, M.A., Duarte, C.M., Mass, Y.E.M., Terrados, J. et Gacia, E. (2002). Carbon and nitrogen translocation between seagrass ramets. *Marine Ecology Progress Series, 226*, 287-300.

Mason, N.W.H., Mouillot, D., Lee, W.G. et Wilson, J.B. (2005). Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos, 111*(1), 112-118.

May, R.M. (1973). *Stability and complexity in model ecosystems*. Princeton, New Jersey : Princeton University Press.

McCann, K.S. (2000). The diversity-stability debate. *Nature, 405*(6783), 228-233.

McKindsey, C.W. et Bourget, E. (2001). Diversity of a northern rocky intertidal community: The influence of body size and succession. *Ecology, 82*(12), 3462-3478.

Middelboe, A.L., Sand-Jensen, K. et Krause-Jensen, D. (2003). Spatial and interannual variations with depth in eelgrass populations. *Journal of Experimental Marine Biology and Ecology, 291*(1), 1-15.

Montgomery, D.C. (2012). *Design and analysis of experiments, Eight edition*. United States : John Wiley & Sons, Inc.

Montgomery, D.C., Peck, E.A. et Vining, G.G. (2012). *Introduction to linear regression analysis 5th edition*. Hoboken, New Jersey : John Wiley & Sons, Inc.

Moore, E.C. et Hovel, K.A. (2010). Relative influence of habitat complexity and proximity to patch edges on seagrass epifaunal communities. *Oikos, 119*(8), 1299-1311.

Moreau, V., Tremblay, R. et Bourget, E. (2005). Distribution of *Mytilus edulis* and *M. trossolus* on the Gaspé coast in relation to spatial scale. *Journal of Shellfish Research, 24*(2), 545-551.

Moreno-Marín, F., Brun, F.G. et Pedersen, M.F. (2018). Additive response to multiple environmental stressors in the seagrass *Zostera marina* L. *Limnology and Oceanography, 63*(4), 1528-1544.

Mouchet, M.A., Villéger, S., Mason, N.W.H. et Mouillot, D. (2010). Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology, 24*(4), 867-876.

Namba, M. et Nakaoka, M. (2018). Spatial patterns and predictor variables vary among different types of primary producers and consumers in eelgrass (*Zostera marina*) beds. *Plos One, 13*(8), e0201791.

Navarrete, S.A. (1996). Variable predation: Effects of whelks on a mid-intertidal successional community. *Ecological Monographs, 66*(3), 301-321.

Neumann, H., Diekmann, R. et Kroncke, I. (2016). Functional composition of epifauna in the south-eastern North Sea in relation to habitat characteristics and fishing effort. *Estuarine Coastal and Shelf Science, 169*, 182-194.

O'Leary, J.K., Micheli, F., Airoldi, L., Boch, C., De Leo, G., Elahi, R., Ferretti, F., Graham, N.A.J., Litvin, S.Y., Low, N.H., Lummis, S., Nickols, K.J. et Wong, J. (2017). The resilience of marine ecosystems to climatic disturbances. *Bioscience, 67*(3), 208-220.

Olesen, B., Enriquez, S., Duarte, C.M. et Sand-Jensen, K. (2002). Depth-acclimation of photosynthesis, morphology and demography of *Posidonia oceanica* and *Cymodocea nodosa* in the Spanish Mediterranean Sea. *Marine Ecology Progress Series, 236*, 89-97.

Olesen, B. et Sand-Jensen, K. (1994). Patch dynamics of eelgrass *Zostera marina*. *Marine Ecology Progress Series, 106*(1-2), 147-156.

Oliveira, J.P., Bertocci, I., Weber, G.M. et Sousa-Pinto, I. (2011). Type and timing of disturbance modify trajectories of recovery of rockpool assemblages at Aguda (NW Portugal). *Journal of Experimental Marine Biology and Ecology, 399*(2), 135-141.

Oliveira, J.P., Sousa-Pinto, I., Weber, G.M. et Bertocci, I. (2014). Interplay of experimental harvesting and climate-related disturbance on benthic assemblages of rocky seashores. *Marine Ecology Progress Series, 495*, 131-142.

Orth, R.J. (1977). Effect of nutrient enrichment on growth of the eelgrass *Zostera marina* in the Chesapeake Bay, Virginia, USA. *Marine Biology, 44*(2), 187-194.

Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M. et Williams, S.L. (2006). A global crisis for seagrass ecosystems. *Bioscience, 56*(12), 987-996.

Orth, R.J., Heck, K.L. et Vanmontfrans, J. (1984). Faunal communities in seagrass beds - a review of the influence of plant structure and prey characteristics on predator prey relationships. *Estuaries, 7*(4A), 339-350.

Otero-Schmitt, J., Cruz, R., Garcia, C. et Rolán-Alvarez, E. (1997). Feeding strategy and habitat choice in *Littorina saxatilis* (Gastropoda: Prosobranchia) and their role in the origin and maintenance of a sympatric polymorphism. *Ophelia, 46*, 205-216.

Paine, R.T. (1969). A note on trophic complexity and community stability. *American Naturalist, 103*(929), 91-93.

Parsons, T.R., Maita, Y. et Lalli, C.M. (1984). 4.1 - Determination of chlorophylls and total carotenoids: Spectrophotometric method. Dans Parsons, T. R., Maita, Y. et Lalli, C. M. (dir.), *A manual of chemical & biological methods for seawater analysis* (p. 101-104). Amsterdam : Pergamon.

Pavoine, S., Vallet, J., Dufour, A.B., Gachet, S. et Daniel, H. (2009). On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos, 118*(3), 391-402.

Pearson, T.H. et Rosenberg, R. (1978). Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology, 16*, 229-311.

Perronne, R., Munoz, F., Borgy, B., Reboud, X. et Gaba, S. (2017). How to design trait-based analyses of community assembly mechanisms: Insights and guidelines from a literature review. *Perspectives in Plant Ecology, Evolution and Systematics, 25*, 29-44.

Pierri-Daunt, A.B. et Tanaka, M.O. (2014). Assessing habitat fragmentation on marine epifaunal macroinvertebrate communities: an experimental approach. *Landscape Ecology, 29*(1), 17-28.

Piggott, J.J., Townsend, C.R. et Matthaei, C.D. (2015). Reconceptualizing synergism and antagonism among multiple stressors. *Ecology and Evolution, 5*(7), 1538-1547.

Pimm, S.L. (1984). The complexity and stability of ecosystems. *Nature, 307*(5949), 321-326.

Pittman, S.J., McAlpine, C.A. et Pittman, K.M. (2004). Linking fish and prawns to their environment: a hierarchical landscape approach. *Marine Ecology Progress Series, 283*, 233-254.

Quinn, G.P. et Keough, M.J. (2002). *Experimental design and data analysis for biologists*. Cambridge, UK : Cambridge University Press.

Ralph, P.J., Durako, M.J., Enriquez, S., Collier, C.J. et Doblin, M.A. (2007). Impact of light limitation on seagrasses. *Journal of Experimental Marine Biology and Ecology, 350*(1-2), 176-193.

Rao, C.R. (1982). Diversity and dissimilarity coefficients: A unified approach. *Theoretical Population Biology, 21*(1), 24-43.

Rattanachot, E., Short, F.T. et Prathep, A. (2016). *Enhalus acoroides* responses to experimental shoot density reductions in Haad Chao Mai National Park, Trang Province, Thailand. *Marine Ecology-an Evolutionary Perspective, 37*(2), 411-418.

Reed, B.J. et Hovel, K.A. (2006). Seagrass habitat disturbance: how loss and fragmentation of eelgrass *Zostera marina* influences epifaunal abundance and diversity. *Marine Ecology Progress Series, 326*, 133-143.

Reynolds, P.L., Richardson, J.P. et Duffy, J.E. (2014). Field experimental evidence that grazers mediate transition between microalgal and seagrass dominance. *Limnology and Oceanography, 59*(3), 1053-1064.

Reynolds, P.L., Stachowicz, J.J., Hovel, K., Boström, C., Boyer, K., Cusson, M., Eklöf, J.S., Engel, F.G., Engelen, A.H., Eriksson, B.K., Fodrie, F.J., Griffin, J.N., Hereu, C.M., Hori, M., Hanley, T.C., Ivanov, M., Jorgensen, P., Kruschel, C., Lee, K.S., McGlathery, K., Moksnes, P.O., Nakaoka, M., O'Connor, M.I., O'Connor, N.E., Orth, R.J., Rossi, F., Ruesink, J., Sotka, E.E., Thormar, J., Tomas, F., Unsworth, R.K.F., Whalen, M.A. et Duffy, J.E. (2018). Latitude, temperature, and habitat complexity predict predation pressure in eelgrass beds across the Northern Hemisphere. *Ecology, 99*(1), 29-35.

Ricotta, C., de Bello, F., Moretti, M., Caccianiga, M., Cerabolini, B.E.L., Pavoine, S. et Peres-Neto, P. (2016). Measuring the functional redundancy of biological communities: a quantitative guide. *Methods in Ecology and Evolution, 7*(11), 1386-1395.

Ricotta, C. et Moretti, M. (2011). CWM and Rao's quadratic diversity: a unified framework for functional ecology. *Oecologia, 167*(1), 181-188.

Ries, L., Fletcher, R.J., Battin, J. et Sisk, T.D. (2004). Ecological responses to habitat edges: Mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics, 35*(1), 491-522.

Rooney, N. et McCann, K.S. (2012). Integrating food web diversity, structure and stability. *Trends in Ecology & Evolution, 27*(1), 40-46.

Rueda, J.L., Marina, P., Urra, J. et Salas, C. (2009). Changes in the composition and structure of a molluscan assemblage due to eelgrass loss in southern Spain (Alboran Sea). *Journal of the Marine Biological Association of the United Kingdom, 89*(7), 1319-1330.

Ruesink, J.L., Fitzpatrick, J.P., Dumbauld, B.R., Hacker, S.D., Trimble, A.C., Wagner, E.L. et Wisehart, L.M. (2012). Life history and morphological shifts in an intertidal seagrass following multiple disturbances. *Journal of Experimental Marine Biology and Ecology, 424*, 25-31.

Ruiz, J.M. et Romero, J. (2001). Effects of in situ experimental shading on the Mediterranean seagrass *Posidonia oceanica*. *Marine Ecology Progress Series, 215*, 107-120.

Salo, T., Reusch, T.B.H. et Bostrom, C. (2015). Genotype-specific responses to light stress in eelgrass *Zostera marina*, a marine foundation plant. *Marine Ecology Progress Series, 519*, 129-140.

Sand-Jensen, K.A.J. (1977). Effect of epiphytes on eelgrass photosynthesis. *Aquatic Botany, 3*, 55-63.

Savard, J.-P., Bernatchez, P., Morneau, F., Saucier, F., Gagnon, P., Senneville, S., Fraser, C. et Jolivet, Y. (2008). *Étude de la sensibilité des côtes et de la vulnérabilité des communautés du golfe du Saint-Laurent aux impacts des changements climatiques*. Montréal : Ouranos.

Schiel, D.R. et Lilley, S.A. (2007). Gradients of disturbance to an algal canopy and the modification of an intertidal community. *Marine Ecology Progress Series, 339*, 1-11.

Schiel, D.R. et Lilley, S.A. (2011). Impacts and negative feedbacks in community recovery over eight years following removal of habitat-forming macroalgae. *Journal of Experimental Marine Biology and Ecology, 407*(1), 108-115.

Schindler, D.E., Armstrong, J.B. et Reed, T.E. (2015). The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment, 13*(5), 257-263.

Schmidt, A.L., Coll, M. et Lotze, H.K. (2017). Regional-scale differences in eutrophication effects on eelgrass-associated (*Zostera marina*) macrofauna. *Estuaries and Coasts, 40*(4), 1096-1112.

Schmidt, A.L., Coll, M., Romanuk, T.N. et Lotze, H.K. (2011). Ecosystem structure and services in eelgrass *Zostera marina* and rockweed *Ascophyllum nodosum* habitats. *Marine Ecology Progress Series, 437*, 51-68.

Short, F.T. (1983). The seagrass, *Zostera Marina* L.: Plant morphology and bed structure in relation to sediment ammonium in Izembek Lagoon, Alaska. *Aquatic Botany, 16*(2), 149-161.

Short, F.T. (1987). Effects of sediment nutrients on seagrasses: Literature review and mesocosm experiment. *Aquatic Botany, 27*(1), 41-57.

Short, F.T., Burdick, D.M. et Kaldy, J.E. (1995). Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. *Limnology and Oceanography, 40*(4), 740-749.

Short, F.T. et Neckles, H.A. (1999). The effects of global climate change on seagrasses. *Aquatic Botany, 63*(3-4), 169-196.

Short, F.T. et Wyllie-Echeverria, S. (1996). Natural and human-induced disturbance of seagrasses. *Environmental Conservation, 23*(1), 17-27.

Silva, J., Barrote, I., Costa, M.M., Albano, S. et Santos, R. (2013). Physiological responses of *Zostera marina* and *Cymodocea nodosa* to light-limitation stress. *Plos One, 8*(11), e81058.

Sirota, L. et Hovel, K.A. (2006). Simulated eelgrass *Zostera marina* structural complexity: effects of shoot length, shoot density, and surface area on the epifaunal community of San Diego Bay, California, USA. *Marine Ecology Progress Series, 326*, 115-131.

Sorensen, S.T., Campbell, M.L., Duke, E. et Manley-Harris, M. (2018). A standard, analytical protocol for the quantitation of non-structural carbohydrates in seagrasses that permits inter-laboratory comparison. *Aquatic Botany, 151*, 71-79.

Sousa, W.P. (1979). Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs, 49*(3), 227-254.

Sousa, W.P. (1984). The role of disturbance in natural communities. *Annual Review of Ecology and Systematics, 15*, 353-391.

Stachowicz, J.J., Bruno, J.F. et Duffy, J.E. (2007). Understanding the effects of marine biodiversity on communities and ecosystems. *Annual Review of Ecology, Evolution, and Systematics, 38*(1), 739-766.

Stachowicz, J.J., Fried, H., Osman, R.W. et Whitlatch, R.B. (2002). Biodiversity, invasion resistance, and marine ecosystem function: Reconciling pattern and process. *Ecology, 83*(9), 2575-2590.

Statzner, B., Bis, B., Dolédec, S. et Usseglio-Polatera, P. (2001). Perspectives for biomonitoring at large spatial scales: a unified measure for the functional composition of invertebrate communities in European running waters. *Basic and Applied Ecology, 2*(1), 73-85.

Stoner, E.W., Yeager, L.A., Sweatman, J.L., Sebilian, S.S. et Layman, C.A. (2014). Modification of a seagrass community by benthic jellyfish blooms and nutrient enrichment. *Journal of Experimental Marine Biology and Ecology, 461*, 185-192.

Strain, E.M.A., Thomson, R.J., Micheli, F., Mancuso, F.P. et Airoldi, L. (2014). Identifying the interacting roles of stressors in driving the global loss of canopy-forming to mat-forming algae in marine ecosystems. *Global Change Biology, 20*(11), 3300-3312.

Tait, K.J. et Hovel, K.A. (2012). Do predation risk and food availability modify prey and mesopredator microhabitat selection in eelgrass (*Zostera marina*) habitat? *Journal of Experimental Marine Biology and Ecology, 426*, 60-67.

Tanner, J.E. (2005). Edge effects on fauna in fragmented seagrass meadows. *Austral Ecology, 30*(2), 210-218.

Tanner, J.E. (2006). Landscape ecology of interactions between seagrass and mobile epifauna: The matrix matters. *Estuarine Coastal and Shelf Science, 68*(3-4), 404-412.

Team, R.C. (2016). *R: A language and environment for statistical computing*. Vienna, Austria : R Foundation for Statistical Computing. Récupéré de https://www.R-project.org/

Thibodeau, B., de Vernal, A. et Mucci, A. (2006). Recent eutrophication and consequent hypoxia in the bottom waters of the Lower St. Lawrence Estuary: Micropaleontological and geochemical evidence. *Marine Geology, 231*(1–4), 37-50.

Thioulouse, J., Chessel, D., Dole´dec, S. et Olivier, J.-M. (1997). ADE-4: a multivariate analysis and graphical display software. *Statistics and Computing, 7*(1), 75-83.

Tilman, D. (1996). Biodiversity: Population versus ecosystem stability. *Ecology, 77*(2), 350-363.

Tilman, D., Reich, P.B. et Knops, J.M.H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature, 441*(7093), 629-632.

Touchette, B.W. et Burkholder, J.M. (2000). Overview of the physiological ecology of carbon metabolism in seagrasses. *Journal of Experimental Marine Biology and Ecology, 250*(1), 169-205.

Touchette, B.W. et Burkholder, J.M. (2007). Carbon and nitrogen metabolism in the seagrass, *Zostera marina* L.: Environmental control of enzymes involved in carbon allocation and nitrogen assimilation. *Journal of Experimental Marine Biology and Ecology, 350*(1-2), 216-233.

Tuya, F., Viera-Rodriguez, M.A., Guedes, R., Espino, F., Haroun, R. et Terrados, J. (2013). Seagrass responses to nutrient enrichment depend on clonal integration, but not flow-on effects on associated biota. *Marine Ecology Progress Series, 490*, 23-35.

Underwood, A.J. (1989). The analysis of stress in natural populations. *Biological Journal of the Linnean Society, 37*(1-2), 51-78.

Usseglio-Polatera, P., Bournaud, M., Richoux, P. et Tachet, H. (2000). Biomonitoring through biological traits of benthic macroinvertebrates: how to use species trait databases? *Hydrobiologia, 422*(0), 153-162.

Valdivia, N. et Molis, M. (2009). Observational evidence of a negative biodiversity–stability relationship in intertidal epibenthic communities. *Aquatic Biology, 4*(3), 263-271.

Valentine, J.F. et Duffy, J.E. (2006). The central role of grazing in seagrass ecology. Dans Lakrum, A. W. D., Orth, R. J. et Duarte, C. M. (dir.), *Seagrasses: biology, ecology and conservation* (p. 463-501). Netherlands : Springer Netherlands.

van Katwijk, M.M., Bos, A.R., Hermus, D.C.R. et Suykerbuyk, W. (2010). Sediment modification by seagrass beds: Muddification and sandification induced by plant cover and environmental conditions. *Estuarine, Coastal and Shelf Science, 89*(2), 175-181.

van Lent, F., Verschuure, J.M. et van Veghel, M.L.J. (1995). Comparative study on populations of *Zostera marina* L. (eelgrass): in situ nitrogen enrichment and light manipulation. *Journal of Experimental Marine Biology and Ecology, 185*(1), 55-76.

vanKatwijk, M.M., Vergeer, L.H.T., Schmitz, G.H.W. et Roelofs, J.G.M. (1997). Ammonium toxicity in eelgrass *Zostera marina*. *Marine Ecology Progress Series, 157*, 159-173.

Vaz-Pinto, F., Olabarria, C. et Arenas, F. (2013). Role of top-down and bottom-up forces on the invasibility of intertidal macroalgal assemblages. *Journal of Sea Research, 76*, 178-186.

Vichkovitten, T., Holmer, M. et Frederiksen Morten, S. (2007). Spatial and temporal changes in non-structural carbohydrate reserves in eelgrass (*Zostera marina* L.) in Danish coastal waters. *Botanica Marina, 50*(2), 75-87.

Villéger, S., Mason, N.W.H. et Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology, 89*(8), 2290-2301.

Vinagre, P.A., Veríssimo, H., Pais-Costa, A.J., Hawkins, S.J., Borja, Á., Marques, J.C. et Neto, J.M. (2017). Do structural and functional attributes show concordant responses to disturbance? Evidence from rocky shore macroinvertebrate communities. *Ecological Indicators, 75*(Supplement C), 57-72.

Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W., Schlesinger, W.H. et Tilman, D.G. (1997a). Human alterations of the global nitrogen cycle: sources and consequences. *Ecological Applications, 7*(3), 737-750.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. et Melillo, J.M. (1997b). Human Domination of Earth's Ecosystems. *Science, 277*, 494-499.

Warry, F.Y., Hindell, J.S., Macreadie, P.I., Jenkins, G.P. et Connolly, R.M. (2009). Integrating edge effects into studies of habitat fragmentation: a test using meiofauna in seagrass. *Oecologia, 159*(4), 883-892.

Warwick, R.M. (1986). A new method for detecting pollution effects on marine macrobenthic communities. *Marine Biology, 92*(4), 557-562.

Warwick, R.M. et Clarke, K.R. (1993). Increased variability as a symptom of stress in marine communities. *Journal of Experimental Marine Biology and Ecology, 172*(1-2), 215-226.

Watt, C.A. et Scrosati, R.A. (2013). Bioengineer effects on understory species richness, diversity, and composition change along an environmental stress gradient: Experimental and mensurative evidence. *Estuarine Coastal and Shelf Science, 123*, 10-18.

Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T. et Williams, S.L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America, 106*(30), 12377-12381.

Wiens, J.A. (1976). Population responses to patchy environments. *Annual Review of Ecology and Systematics, 7*, 81-120.

Wong, M.C. (2018). Secondary production of macrobenthic communities in seagrass (*Zostera marina*, eelgrass) beds and bare soft sediments across differing environmental conditions in Atlantic Canada. *Estuaries and Coasts*, *41*(2), 536-548.

Wong, M.C. et Dowd, M. (2015). Patterns in taxonomic and functional diversity of macrobenthic invertebrates across seagrass habitats: a case study in Atlantic Canada. *Estuaries and Coasts*, *38*(6), 2323-2336.

Wong, M.C., Griffiths, G. et Vercaemer, B. (2019). Seasonal response and recovery of eelgrass (*Zostera marina*) to short-serm reductions in light availability. *Estuaries and Coasts*, doi.org/10.1007/s12237-12019-00664-12235.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. et Warren, P.H. (2005). Body size in ecological networks. *Trends in Ecology & Evolution*, *20*(7), 402-409.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J. et Watson, R. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science, 314*(5800), 787-790.

Worm, B. et Lotze, H.K. (2006). Effects of eutrophication, grazing, and algal blooms on rocky shores. *Limnology and Oceanography, 51*(1), 569-579.

Worm, B., Lotze, H.K., Hillebrand, H. et Sommer, U. (2002). Consumer versus resource control of species diversity and ecosystem functioning. *Nature*, *417*(6891), 848-851.

Worm, B., Reusch, T.B.H. et Lotze, H.K. (2000). In situ nutrient enrichment: Methods for marine benthic ecology. *International Review of Hydrobiology, 85*(2-3), 359-375.

Yachi, S. et Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America, 96*(4), 1463-1468.

York, P.H., Gruber, R.K., Hill, R., Ralph, P.J., Booth, D.J. et Macreadie, P.I. (2013). Physiological and morphological responses of the temperate seagrass *Zostera*

muelleri to multiple stressors: Investigating the interactive effects of light and temperature. *Plos One, 8*(10), e76377.