



**Effet des herbiers marins sur les communautés de
macroinvertébrés de l'écosystème marin du Saint-Laurent**

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**Mémoire présenté à l'Université du Québec à Chicoutimi en vue de l'obtention du
grade de Maître ès sciences (M.Sc.) en Ressources Renouvelables**

Québec, Canada

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RÉSUMÉ

Les écosystèmes côtiers sont très affectés par les changements globaux et les activités humaines, pourtant ce sont des écosystèmes productifs qui nous rendent de nombreux services écosystémiques. Les herbiers marins sont constitués d'espèces structurantes comme les zostères (*Zostera marina* L.) qui offrent habitat, protection et nourriture, favorable à de nombreux organismes marins qui interviennent dans de nombreux processus de flux de matières dans les réseaux trophiques, telle que la bioturbation. La modification de la structure des communautés macrobenthiques peut fortement altérer le fonctionnement des écosystèmes côtiers et détériorer la stabilité des écosystèmes aquatiques existants. L'espèce de macrophyte marine la plus commune en Atlantique, *Z. marina*, fait face à de nombreuses perturbations et voit sa superficie diminuer drastiquement à travers le monde. Toutefois, une augmentation de la superficie des herbiers de cette espèce dans le Saint-Laurent marin a été observée sans qu'il y ait d'étude qui détaille leurs effets à diverses échelles sur les communautés macrobenthiques associées. Aussi, les données concernant les structures de communauté dans les herbiers sont peu souvent comparées à celles des habitats non végétalisés adjacents. Cette étude a pour objectif d'évaluer l'effet des herbiers sur les communautés de macrobenthos dans le Saint-Laurent en (1) caractérisant l'effet de la présence de zostères sur le profil de biodiversité et sur la structure des communautés endofauniques, en (2) vérifiant si ces effets sont dépendants des échelles locales (100 ms) et régionales (100 kms) et en (3) cernant mieux le rôle des variables sédimentaires et de la structure même des zostères sur la structure des communautés endofauniques. Pour cela, nous avons échantillonné les habitats de zostères et de sédiments nus dans trois régions du Saint-Laurent marin. Dans chacun des habitats, des échantillons d'endofaune et de sédiments ont été prélevés. Des échantillons d'épifaunes, ainsi que des mesures de biomasse et densité de plants ont été effectuées dans les habitats de zostères. Les résultats montrent que la présence de l'herbier avait un effet sur l'abondance, la richesse et la diversité taxonomique et la structure d'abondance seulement lorsque les deux compartiments épi- et endofaune étaient pris en compte ensemble. Aucune différence dans les variables de biodiversité n'a été observée pour l'endofaune, cependant les habitats abritaient des communautés différentes. Des différences significatives de la structure et composition des communautés ont été observées entre les habitats et les régions. L'effet de la région semblait être plus forte que celui de l'habitat et toutes les caractéristiques mesurées de l'habitat avaient une influence significative sur la structure des communautés. Nos résultats montrent l'importance de la prise en considération des échelles spatiales et des compartiments de biodiversité dans le cadre de gestion et conservation des habitats côtiers. Ces résultats pourront également servir de base pour l'état initial de l'habitat ou de données de comparaison avec d'autres projets similaires.

Mots clés : Estuaire et golfe du Saint-Laurent • échelles spatiales (locale et régionale) • *Zostera marina* • macrobenthos • diversité • structure de communauté

ABSTRACT

Coastal ecosystems are one of the most productive ecosystems on Earth, providing critical ecosystem services. They are severely affected and threatened by global changes and human activities. Seagrasses consist of structuring species which provide habitat, protection, and food, to many marine organisms. Changing the structure of macrobenthic communities can strongly alter the functioning of coastal ecosystems and deteriorate the stability of existing aquatic ecosystems. The most common species of seagrass in the Atlantic, *Z. marina*, is facing major disturbances and its area drastically decreases throughout the world. However, an increase in the surface of seagrass beds in the marine St. Lawrence has been observed without any study detailing their effects at various scales on the associated macrobenthic communities. Data on community structures in seagrass beds are rarely compared to those in adjacent unvegetated habitats. My study aims to assess the effect of seagrass beds on macrobenthos communities in the St. Lawrence, by (1) characterizing the effect of seagrass on the biodiversity profile and on the structure communities, (2) to verify whether these effects are dependent on local (100 ms) and regional (100 kms) scales and (3) to better understand the role of sedimentary variables and the very structure of seagrass on the structure of infaunal communities. We sampled eelgrass and bare sediment habitats in three regions of the marine St. Lawrence. In each habitat, infauna and sediment samples were collected. Samples of epifauna, as well as measurements of plant biomass and density were measured in seagrass habitats. My results show that the presence seagrass influence abundance, taxonomic richness and diversity and the structure of abundance only when the two compartments epi- and infauna were considered together. We observe no differences in biodiversity variables for infauna, however the habitats harbored different communities. Significant differences in community structure and composition were observed between habitats and regions. Region scale effects appear to be stronger than that of habitat, and all measured habitat characteristics have a significant influence on community structure. Our results show the importance of considering spatial scales and biodiversity compartments in the management and conservation of coastal habitats. These results can also serve as a basis for the initial state of the habitat or data for comparison with other similar projects.

Key words: St. Lawrence Gulf and estuary • spatial variation • *Zostera marina* • Macrobenthos • Biodiversity • Community structure

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LISTE DES ABRÉVIATIONS

SE ; erreur standard
SI ; Sept-Iles
MA ; Manicouagan
IV ; Isle-verte
OC ; Carbone organique
PER-ANOVA ; analyse de variance par permutations
PERMANOVA ; analyse multivariée des variances par permutations
PCO ; Analyse en coordonnées principales
dbRDA ; Analyse de redondance basée sur la distance
± ; plus ou moins
°C ; degré Celsius
SE ; erreur type
MACO ; *Macoma balthica*
MYA ; *Mya arenaria*
NER ; *Alitta virens*
ETEO ; *Eteone longa*
HETER ; *Heteroastus filiformis*
LITT ; *Littorina* spp
LITR ; *Littorina littorea*
MGAS ; *Mysis gaspensis*
GOCEA ; *Gammarus oceanicus*
MUSS ; *Mytilus edulis*
IDOT ; *Idotea balthica*
PYGO ; *Pygospio elegans*
SPIO ; *Spio filicornis*
JAER ; *Jaera albifrons*
MICRON ; *Micronephtys noetena*

REMERCIEMENTS

Je voudrais dans un premier temps remercier, mon directeur de mémoire Mathieu Cusson, professeur chercheur à l'université de Québec à Chicoutimi, et Pascal Bernatchez, professeur chercheur à l'université de Québec à Rimouski, de m'avoir donné la chance de réaliser ce projet. De même, merci à Fanny Noisette et Maxime Paré d'avoir accepté de faire partie de mon jury d'évaluation.

Je remercie également toute l'équipe pédagogique de l'UQAC, dont Mireille Boulianne et Pascal Tremblay, pour m'avoir accompagné lors de mes contrats d'aide pédagogique, ainsi que les intervenants professionnels responsables de ma formation pour avoir assuré la partie théorique de celle-ci.

J'adresse mes sincères remerciements à tous les professeurs, en particulier Pr Christian Nozais, intervenants et toutes les personnes qui par leurs paroles, leurs écrits, leurs conseils et leurs critiques ont guidé mes réflexions et ont accepté de me rencontrer et de répondre à mes questions durant mes recherches. Pour ces diverses expériences, je remercie le Réseau Québec Maritime sans qui rien de tout cela n'aurait été possible.

Je remercie tout particulièrement mes collègues et amies Sonia Moron et Paola Ayala, pour leur patience à mes nombreuses questions, leur encouragement et leur soutien tout au long de ce parcours. Merci à ma fidèle assistante de terrain et laboratoire, Rachel Maillot, pour sa constante bonne humeur et son travail acharné, ainsi que Stéphanie Cimon pour ses connaissances du terrain, et Théo Chateaugiron pour son aide dans ma campagne d'échantillonnage. Un merci également à mes assistantes de laboratoire, Laurence Bisson, Jean-Simon Boulianne, Julia Martel et Carol-Ann Patenaude pour leur merveilleux travail.

Pour finir, j'aimerais remercier notre Groupe de Soutien des Apprentis Chercheurs Non Anonymes (Anthony et Manon) et mes amis (Estelle, Léa, Cécilia, Lucas, Alexandre, Caroline, Lona, Sirine, Marie, Soazic et Claudio) pour les beaux moments, leurs soutien, tolérance et conseils précieux. Dernier merci, à ma famille qui a toujours été présente pour me guider dans mes choix ainsi que me soutenir dans les moments difficiles.

INTRODUCTION GÉNÉRALE

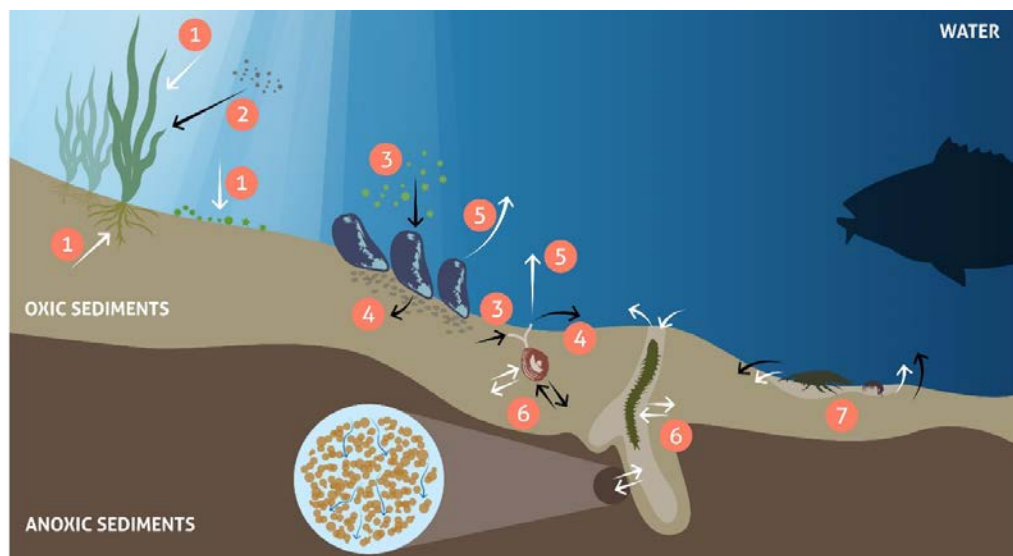
1.1 Anthropisation et détérioration des écosystèmes côtiers

Depuis le début de l'industrialisation, la détérioration (par ex. la perte de biodiversité et de services, la diminution de l'état de santé) des écosystèmes est en constante augmentation. Il reste peu d'endroits sur Terre où les impacts négatifs causés par les humains ne sont pas visibles. Ceci est d'autant plus vrai sur les écosystèmes côtiers marins, où plus de 40% de la population mondiale habite à moins de 100 km des côtes (Halpern *et al.*, 2008 ; SEDAC, 2007). Les conséquences des changements climatiques tels que l'élévation du niveau de la mer, de la température, et l'augmentation de l'intensité et de la fréquence des événements extrêmes, ainsi que la hausse des activités humaines entraînent des répercussions néfastes sur la qualité des eaux notamment par les rejets agricoles et municipaux, mais également par l'exploitation des terres, l'urbanisation côtière et les activités aquatiques récréatives et commerciales (Cloern *et al.*, 2016 ; Ralph *et al.*, 2006). À ce jour, environ 50% des marais salés, 35% des mangroves, 30% des récifs coralliens, 29% des herbiers marins et 16% des vasières ont été perdus ou dégradés dans le monde (Campbell *et al.*, 2022 ; MEA, 2005 ; Murray *et al.*, 2019 ; Orth *et al.*, 2006a ; Valiela *et al.*, 2001 ; Waycott *et al.*, 2009). Malgré ces chiffres alarmants, certains écosystèmes regagnent du terrain, notamment en Europe et aux États-Unis où l'amélioration de la qualité de l'eau et les mesures de restauration et de protection ont permis, par exemple, à certains herbiers marins de croître (de los Santos *et al.*, 2019 ; Lefcheck *et al.*, 2018 ; Vaudrey *et al.*, 2010). En outre, la détérioration de ces habitats ou leur accroissement modifient leurs fonctions et les services écosystémiques qui y sont associés (Barbier *et al.*, 2011a ; Carr *et al.*, 2012 ; Costanza *et al.*, 2014 ; Horton *et al.*, 2018).

1.2 Les écosystèmes marins côtiers : fonctions et services

Les milieux sédimentaires non végétalisés représentent une très grande partie des milieux intertidaux, notamment les grands estrans meubles et les vasières qui couvrent environ 124 286 à 131 821 km² de la surface du globe (Murray *et al.*, 2019). Le processus de

bioturbation, très courant dans les milieux sédimentaires, est un processus par lequel les organismes vivants redistribuent les particules et les solutés dans les sédiments par leurs activités mécaniques (fouissage, terriers) y compris les activités de remaniement des sédiments et de ventilation des terriers (bioirrigation, bioturbation), et améliorent les flux sédiment-eau de solutés (Figure 1; Kristensen *et al.*, 2012). Ensemble, tous ces processus affectent les conditions physiques et chimiques à l'interface sédiment-eau, et influencent fortement la répartition et la dégradation de la matière organique (Aller, 1982 ; Canuel et Hardison, 2016). L'abondance et la diversité de ces organismes ont donc un effet direct sur la disponibilité de matières organiques et la nourriture pour d'autres organismes (Braeckman *et al.*, 2011 ; Gray, 1974). On notera que si ces milieux ne supportent qu'une très faible biomasse de producteurs primaires (par exemple les microorganismes photosynthétiques tels que les diatomées, les cyanobactéries, et les chlorophycées), la productivité des milieux sédimentaires est néanmoins importante (jusqu'à $390 \text{ g C m}^{-2} \text{ an}^{-1}$) et comparable à celle des herbiers marins (Guarini *et al.*, 2000 ; Hope *et al.*, 2020 ; Lebreton *et al.*, 2019). La production secondaire dans ces milieux est aussi élevée et est dépendante de la structure de l'environnement global (par ex. la température, la profondeur, l'exposition aux vagues, le taux de matière organique dans les sédiments; Wong, 2018).



© Ehrnsten E, Sun X, Humborg C, Norkko A, Savchuk OP, Slomp CP, Timmermann K and Gustafsson BG (2020) Understanding Environmental Changes in Temperate Coastal Seas: Linking Models of Benthic Fauna to Carbon and Nutrient Fluxes. *Front. Mar. Sci.* 7:450. (Creative Commons Attribution License)

Figure 1. Principaux processus liés à la végétation et à la faune contrôlant les flux biogéochimiques benthiques. Flèches blanches : flux de solutés, flèches noires : flux de particules. Production primaire : absorption de nutriments et de CO₂ et libération d'oxygène (1), amélioration de la sédimentation et de la stabilisation des sédiments par les producteurs primaires benthiques (2), absorption de nourriture (3), égestion/biodéposition des matières fécales (4), excrétion de nutriments et respiration (5), et la bioturbation, y compris la bioirrigation (6) et le mélange des sédiments (7). (tiré de Ehrnsten *et al.*, 2020)

Les milieux végétalisés, quant à eux, ne représentent qu'une faible fraction des écosystèmes côtiers, parmi eux, on y trouve les herbiers marins répartis dans le monde entier, des régions tropicales aux régions subarctiques et recouvrent approximativement 160 387 à 266 562 km² du globe (Hemminga et Duarte, 2000 ; McKenzie *et al.*, 2020). Ces derniers sont composés d'angiospermes monocotylédones principalement adaptées à la vie en eaux claires, peu profondes, et à un courant relativement faible, tels que ceux qui sont rencontrés dans les estuaires, les baies et les autres zones côtières. En colonisant les habitats de sédiments nus, les herbiers sont considérés comme des espèces fondatrices, mais aussi ingénieuses car elles influencent les interactions physiques et biochimiques de leur environnement. À travers leurs fonctions, ces étendues de prairies marines supportent de nombreux services écosystémiques, tels que la stabilisation des sédiments, la protection des côtes, ou bien le stockage du carbone (Arkema *et al.*, 2013 ; Barbier *et al.*, 2011a ; Duarte *et al.*, 2013 ; MEA, 2005). Tout d'abord, ils modifient la structure physique du substrat meuble des sites colonisés, stabilisent la surface des substrats, ralentissent l'énergie de différents phénomènes

hydrodynamiques par la friction exercée par leurs feuilles, permettant aux particules en suspension, organiques ou inorganiques, de progressivement s'accumuler à la surface (Hansen et Reidenbach, 2012 ; Shepard *et al.*, 2011a). Ceci change les caractéristiques de la surface du substrat qui acquiert plus de particules fines et grâce à des conditions anoxiques du sédiment le stockage de la matière organique y est favorisé, ce qui en font des puits de carbone importants (Kennedy *et al.*, 2010 ; Marbà *et al.*, 2015 ; Röhr *et al.*, 2018 ; van Katwijk *et al.*, 2010). Les herbiers contribuent aussi aux flux biogéochimiques avec une production primaire nette moyenne (en considérant feuilles, rhizomes et racines, matières sèches (DW)) d'environ 1 012 g DW m⁻² an⁻¹, équivalent à 404 g C m⁻² an⁻¹ ou 14,8 tonnes de CO₂ ha an⁻¹ (Figure 1 Duarte et Chiscano, 1999).

La présence dans les herbiers d'un feuillage dense hors du sédiment atténue les vagues et fournit une protection contre les prédateurs. Ainsi, cet habitat constitue un lieu propice à la reproduction pour de nombreuses espèces de poissons et invertébrés, telles que les crevettes (Heck *et al.*, 2003), en plus d'être une source en nourriture pour les organismes qui y trouvent refuge (Barbier *et al.*, 2011a). Les surfaces foliaires offrent également un substrat physique additionnel pour des espèces épiphytiques, comme les moules. Beaucoup de ces espèces y trouvent un refuge et une source de nourriture (diatomées photosynthétiques sur les feuilles; Moncreiff et Sullivan, 2001). Les petits invertébrés brouteurs, tels que les crustacés et les gastéropodes, se nourrissent d'épiphytes et, ce faisant, peuvent aider à garder les herbiers feuilles propres, ce qui favorise la captation de la lumière et leur croissance (Jernakoff et Nielsen, 1997). Ils sont à leur tour consommés par les plus gros crustacés, poissons et oiseaux et constituent des liens importants dans le réseau trophique côtier. Enfin, les feuilles mortes des herbiers ont aussi un rôle dans les écosystèmes côtiers, car elles se décomposent sur les sédiments ou sont rejetées sur les plages, soutenant une communauté diversifiée de décomposeurs qui prospèrent sur le matériel en décomposition (Peduzzi et Herndl, 1991). Certaines de ces feuilles vivantes et mortes sont emportées vers d'autres zones du littoral, alimentant ainsi les organismes des écosystèmes adjacents (Thresher *et al.*, 1992). Les

herbiers abritent donc une grande biodiversité en jouant des rôles importants d'aire de nourrissage, frayère et protection qui favorisent le développement de nombreuses espèces benthiques.

1.3 Importance de la biodiversité

Les macroinvertébrés benthiques sont largement distribués dans tous les types de masses d'eau et sont souvent utilisés comme espèces modèles dans de nombreuses études, car elles ont une mobilité relativement faible, une abondance généralement élevée, et une grande diversité d'espèces (Lancaster et Downes, 2013). Les communautés macrobenthiques peuvent être divisées en plusieurs compartiments dont deux principales sont l'endofaune et l'épifaune. L'endofaune fait référence aux organismes vivants dans le substrat en s'enfouissant ou en construisant des tubes ou des terriers. L'épifaune désigne l'ensemble des invertébrés, sessiles ou mobiles, qui vivent à la surface du substrat, notamment sur les feuilles des herbiers. La biodiversité des espèces présentes composant une communauté peut être mesurée grâce à divers indices biologiques. La richesse spécifique, c'est-à-dire le nombre d'espèces présentes dans l'habitat à une échelle donnée, est la mesure la plus communément utilisée pour quantifier la biodiversité en raison de sa simplicité conceptuelle et à être quantifié (Hamilton, 2005). Or, la diversité taxonomique des espèces est constituée en réalité de trois composantes : le nombre d'espèces (richesse), les abondances relatives des individus au sein des espèces (équité), et la disparité (ou l'identité, responsable de la composition des communautés). Ces composantes sont liées à la stabilité et à la fonction de l'écosystème (Holling, 1973 ; Hooper *et al.*, 2005). La relation entre la biodiversité et le fonctionnement des écosystèmes a été largement étudié, il est généralement admis que plus la richesse spécifique est grande et plus les fonctions de l'écosystème augmentent jusqu'à saturation (Hooper *et al.*, 2005 ; van der Plas, 2019). Ainsi, lorsqu'elles sont mises à l'échelle de l'écosystème, des changements dans la biodiversité peuvent altérer considérablement le fonctionnement et la stabilité des écosystèmes côtiers (Ehrnsten *et al.*, 2020). L'altération des fonctions des écosystèmes, et donc de leurs services associés, a poussé les écologistes à examiner la

relation entre la biodiversité et le fonctionnement des écosystèmes. Cette relation doit cependant être étudiée à plusieurs échelles spatiales, puisqu'il existe divers facteurs environnementaux opérant à ces échelles affectant potentiellement la composition de la communauté (Altermatt, 2013 ; Heino *et al.*, 2015).

1.4 État d'un habitat végétalisé particulier (*Zostera marina* L.) et variations spatiales

Depuis les années 1970, les herbiers marins à l'échelle du globe présentent des signes de déclin dont les principales causes sont la perte d'habitat et la pollution des eaux côtières (Short *et al.*, 2011 ; Waycott *et al.*, 2009). En 2006, Waycott *et al.* (2009) ont estimé qu'un tiers de la superficie des herbiers mondiaux connus avait complètement disparu depuis la fin du XIX^e siècle, principalement en raison du développement côtier et de la dégradation de la qualité de l'eau. En 2016, cette perte de superficie représentait près de 20% de la superficie occupée par les herbiers marins à l'échelle globale en 1880 (Dunic *et al.*, 2021). Le rythme de ce déclin s'est accéléré depuis la seconde moitié du 20^e siècle, passant d'une perte de 0,9% par an en 1940 à 7% en 1990 respectivement, soit une perte sept fois plus élevée en seulement 50 ans (Waycott *et al.*, 2009). *Z. marina* est l'espèce macrophyte marine la plus largement distribuée au monde et constitue l'espèce dominante dans l'Atlantique Nord-Ouest (Short *et al.*, 2007 ; Short et Short, 2003). Sur les côtes Atlantique canadiennes, *Z. marina* forme des herbiers quasi monospécifiques et assure à elle seule plusieurs services écosystémiques. Elle a été classée comme une espèce d'importance écologique dans l'est du Canada (DFO, 2009) puisqu'elle abrite une forte diversité de macrobenthos qui sert également à soutenir une grande biodiversité, des invertébrés aux mammifères en passant par les poissons, dont des espèces exploitées (Figure 2). Malgré un déclin mondial observé dans la superficie de *Z. marina*, l'étendue des herbiers de l'écosystème marin du Saint-Laurent a quant à elle fortement augmentée au cours des dernières décennies, dont 20 800 ha ont été cartographiés dans le système du Saint-Laurent (ECCC, 2020 ; Jobin *et al.*, 2021). Certains changements environnementaux, comme la hausse des températures et la montée des eaux, pourront aussi entraîner un déplacement des herbiers côtiers sud vers le nord (Wilson et Lotze, 2019). Des

événements météorologiques extrêmes, ou encore, des perturbations humaines, notamment l'eutrophisation, le dragage ou le remblayage peuvent également aboutir à des modifications de la structure de l'herbier (Erftemeijer et Lewis, 2007 ; Orth *et al.*, 2006a).

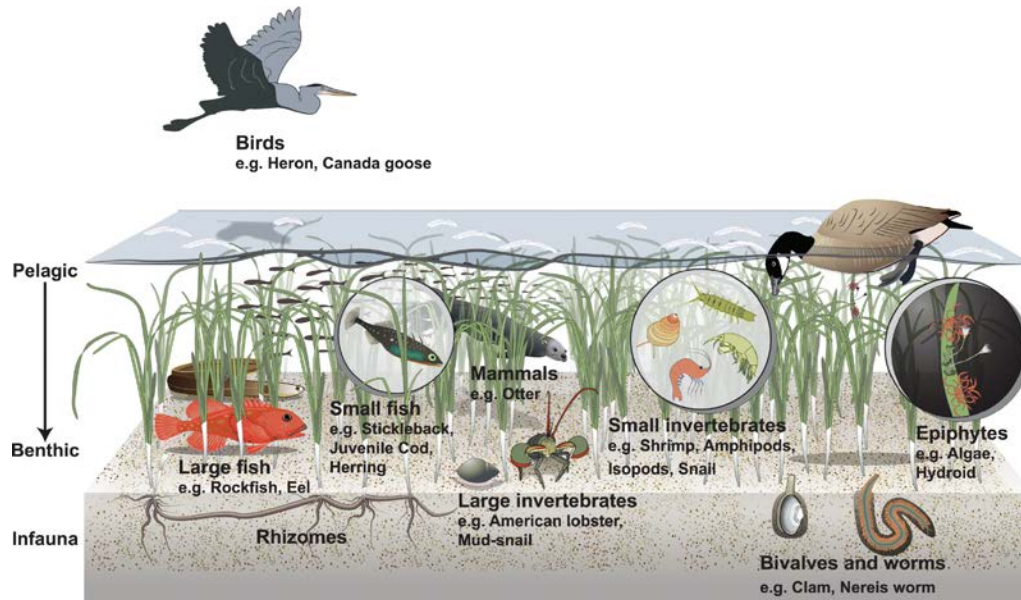


Figure 2. Illustration généralisée d'un herbier de zostères canadien avec des assemblages d'espèces simplifiés, y compris des assemblages épiphytes, de petits invertébrés mobiles, de petits poissons pélagiques et benthiques, de plus gros poissons et invertébrés benthiques, une endofaune sédimentaire, ainsi que des mammifères et des oiseaux (Murphy *et al.*, 2021). (Open access)

La morphologie et structure physiques des herbiers sont influencés par divers facteurs biotiques et abiotiques créant un paysage allant de grandes prairies continues à des herbiers fortement fragmentés ou épars (Frederiksen *et al.*, 2004). Sur de grandes échelles spatiales, des différences dans la structure des herbiers (ex. la densité des plants, le nombre, la longueur et la largeur des feuilles) entraînent des paysages variés et, éventuellement, des variations dans les caractéristiques de l'habitat ainsi que sur la structure des communautés (Grilo *et al.*, 2011 ; Robbins et Bell, 1994). Par exemple, la pression de prédation est plus élevée dans un herbier fragmenté ou à faible densité de plants, car la mobilité des prédateurs y est facilitée (Johnson et Jr, 2006). Si cela s'avère exact pour des sites de l'estuaire maritime du Québec (Manicouagan), une étude sur les herbiers de l'hémisphère nord montre que, généralement, c'est au centre des herbiers où la prédation est plus intense (Hovel *et al.* 2021). Des variations de la structure de l'herbier à de plus petites échelles peuvent directement ou indirectement

influencer la richesse spécifique et l'abondance des macroinvertébrés associés (Githaiga *et al.*, 2019 ; Mannino et Montagna, 1997). L'accroissement de la complexité structurale ou la quantité de plantes disponibles entraînent généralement une augmentation du nombre d'espèces et de leur abondance (Attrill *et al.*, 2000 ; Hovel *et al.*, 2002). Par exemple, la réduction du nombre de plants ou de feuilles de l'herbier diminue l'abondance de l'épifaune mobile (Edgar et Robertson, 1992). L'augmentation de la superficie totale de la surface foliaire disponible peut accroître la quantité d'épiphytes qui servent de source de nourriture à plusieurs invertébrés; influençant indirectement les assemblages de brouteurs associés à l'habitat (van Montfrans *et al.*, 1984). Pour finir, les différences dans l'architecture des plantes exercent une influence indirecte sur les communautés en ralentissant le mouvement de l'eau et en stabilisant le substrat (Hewitt *et al.*, 1997). La morphologie des herbiers varie donc à des échelles locales (quelques mètres) et régionales (plusieurs kilomètres) entraînant des répercussions sur la structure des communautés macrobenthiques. Habituellement, plus l'étendue spatiale de la région étudiée est grande plus les facteurs spatiaux gagnent en importance (Cottenie, 2005). La similarité des structures de communauté décroît alors avec la distance étant donné que les conditions environnementales varient davantage avec la distance géographique (Soininen *et al.*, 2007).

1.5 Objectifs et hypothèses de travail

De nombreuses lacunes subsistent dans notre compréhension de la relation de *Z. marina* sur les communautés macrobenthiques à différentes échelles spatiales, considérant l'épi- et l'endofaune séparément. Ceci est particulièrement vrai dans l'estuaire et le nord du Saint-Laurent, où les données concernant les structures de communauté dans ces herbiers se font rares ainsi que celles des habitats non végétalisés adjacents. L'augmentation de l'étendue des herbiers de l'écosystème marin du Saint-Laurent contredit la tendance mondiale, il est donc important de regarder la relation qu'il existe entre les herbiers marins et les communautés benthiques associées. Il s'agit là d'un manque important à combler afin d'assurer la mise en place de stratégies de conservation efficaces ciblées pour le Saint-Laurent marin. Les résultats

de ces objectifs permettront d'acquérir des connaissances qui seront utiles aux gestionnaires afin de focaliser les efforts de conservation. Mon étude a donc pour objectif global d'évaluer l'effet des herbiers sur les caractéristiques de leur habitat et des communautés macrobenthiques associées. Mes objectifs spécifiques sont (1) de caractériser l'effet de la présence de zostères sur le profil de biodiversité et sur la structure des communautés, (2) de vérifier si ces effets sont dépendants des échelles locales (100 ms) et régionales (100 kms) et (3) d'évaluer le rôle des variables sédimentaires et de la structure même des zostères sur la structure des communautés d'endofaune. Ces résultats permettront de connaître la valeur ajoutée d'un herbier comparativement à un sable nu. Puisque la zostère augmente la complexité des habitats et fournit des ressources alimentaires nous nous attendons à une (i) richesse et diversité taxonomique ainsi qu'une densité plus élevée de l'épi- et l'endobenthos dans les habitats végétalisés (*Zostera marina* L.) que dans les habitats non végétalisés (sédiments nus), ainsi qu'une (ii) diminution de la similarité entre communautés macrobenthiques locales selon la distance géographique.

Eelgrass effects on epifaunal and infaunal associated communities in the St. Lawrence marine ecosystem, Quebec, Canada

INTRODUCTION

Eelgrass beds are considered some of the most productive and valuable ecosystems on Earth (Barbier *et al.*, 2011b; Hogarth, 2015). As a foundation species, they provide critical ecological functions (Cullen-Unsworth *et al.*, 2013; Short *et al.*, 2007). Their tridimensional structure reduces wave energy, increase local sedimentation (Hansen *et al.*, 2012; Shepard *et al.*, 2011b), increase carbon accumulation (Röhr *et al.*, 2018), and provides refuges and food to diverse associated community (Duffy, 2006; Gartner *et al.*, 2013; Herkül *et al.*, 2016). Eelgrass meadows suffered major global decline since 1980 with about 20% (~110 km² yr⁻¹) of their surface area lost worldwide (Orth *et al.*, 2006b; Turschwell *et al.*, 2021; Waycott *et al.*, 2009), and a 65% surface loss in major bays and coastal seas in Europe, North America and Australia (Lotze, 2006). Such loss is mostly due to increase in natural disturbances (e.g., heat stress, grazing, disease, hurricanes; Hughes *et al.*, 2018; James *et al.*, 2020; Shields *et al.*, 2019) and anthropogenic stresses (e.g., pollution, infrastructure development, eutrophication, dredging, increase in sediment and nutrient loading; Heuvel *et al.*, 2019; Montefalcone *et al.*, 2019; Short *et al.*, 2011). In Canada, the eelgrass *Zostera marina* L. are dominant in the Northwest Atlantic (Green and Short, 2003; Short *et al.*, 2007). In the Gulf of St. Lawrence, stressors such as land alteration, nutrient loading, and shellfish aquaculture affected eelgrass beds the most (Murphy *et al.*, 2019). However, the beds showed important increases in surface for the last decade, especially in the Gulf of St. Lawrence (Murphy *et al.*, 2021). More studies are yet to come to define more precisely by which ecological mechanisms may explain such increase.

Seagrasses are considered as foundation species; they modify the environment and facilitate the settlement of multiple species by providing food and shelter. To characterize the effect of eelgrass on the associated benthic invertebrate communities, several studies used

adjacent bare sediment for comparison. They have shown that greater diversity metrics were seen within the meadow compared to adjacent bare habitats (Barnes, 2013, 2017; Fredriksen *et al.*, 2010; Lee *et al.*, 2001). In Japan Coast, Nakamura and Sano (2005) found that abundance of macrobenthos, particularly errant polychaetes, was greater in eelgrass habitat than adjacent sediment but with no difference in biomass of organisms. In Atlantic Canada, Wong and Dowd (2015) found that species richness of infauna and epifauna and diversity increased from bare sediment to interior eelgrass beds (from 8 to 12 and from 0.6 to 0.8 respectively). Magni *et al.* (2017) described a richer and more diverse infaunal community in eelgrass meadows than in adjacent bare sediment. Field observation and experimentation shown that increased belowground complexity enhanced infauna abundances and richness but not biomass in comparison to bare sediment (González-Ortiz *et al.*, 2016). However, Barrio Froján *et al.* (2009) found that although both habitats had distinct macrobenthos infaunal assemblages, there were no differences in diversity metrics. Multiple explanations are possible for these variations and may be ranged from habitat structural complexity to food availability and trophic interactions (Attrill *et al.*, 2000; Orth *et al.*, 1984; York *et al.*, 2012).

Most studies comparing the eelgrass effect were however limited to a single site or only vegetated habitat at a site or region (Barnes, 2013; Wong et Dowd, 2015). Community composition differs between locations partly due to local characteristics of the eelgrass bed. Within eelgrass ecosystems, meadows can be highly heterogeneous, and habitat factors such as shoot density, patch size, edges, gaps and corridors influence associated faunal communities (Attrill *et al.*, 2000; York *et al.*, 2018). Indeed, van Houte-Howes *et al.* (2004) observed significant variation in macroinvertebrate community composition among locations throughout the sites within an estuary. Barnes and Barnes (2014) found that the macrobenthos assemblage in eelgrass and in bare sediment at four different locations were more similar to each other than either were to those of the equivalent habitat types at other nearby localities. Considering that habitat have a numerous different structure (e.g. length and shoot density, sediment composition) it is important to consider more than one spatial scale to cover the heterogeneity of the landscape and understand the processes that contribute to the variability

of macro invertebrate compositions (Edgar et Barrett, 2002). As such, comparison at a larger scale (e.g. >100 km) that encompasses broad environmental conditions would help identify the mechanisms and the most important scale by which the eelgrass structure and shape its associated community. Such information would be valuable to local management agencies for conservation to identify relevant geographical scales to focus management measures.

We sampled various eelgrass (*Zostera marina* L.) beds and adjacent sediment at various spatial scales to test their effect on associated community. Precisely, we evaluated the effect of local (100 ms) versus regional (100 kms) variation on community diversity profiles as well as assessed which environmental drivers were structuring these communities. We compared the associated community according to their biological compartment (epibenthos and/or infauna). To differentiate the effect of each habitat structure on macrobenthos communities, we considered both compartment of epifauna and infauna together and independently. We predict that eelgrass presence will strongly affect both epi- and infauna community structure will increase abundance, and taxa richness and diversity but not biomass when compared to bare sediment. For a given eelgrass/bare sediment habitat, we expect that differences in diversity variables profiles among regions will be greater than within regions (the further away, the more dissimilarity between community will be).

MATERIALS AND METHODS

2.1 Study sites

We sampled intertidal habitats in three regions (Sept-Îles (SI), Manicouagan (MA) and Isle-Verte (IV)), separated by up to 325 km, located on the northern and southern shore estuary and northern part of the Gulf of St. Lawrence (Quebec, Canada; Figure 3.3). The St. Lawrence ecosystem is considered subarctic with summer water temperature and salinity range from 4–16°C and 23–30 PSU, respectively. All sites were sampled between mid-July and early September 2019 during spring tides periods; SI sites were sampled from July 16th to 20th, MA sites from July 30th to August 5th and IV sites from August 30th to September 3rd. Environmental parameters including salinity (PSU), conductivity, and dissolved oxygen (mg L⁻¹) using a

portable field probe (YSI Environmental; YSI EC300; pH100; YSI 550A). Water temperature was also measured while sampling but not considered in the analyses, due to its high daily variability. Differences were observed in salinity among regions with highest value in SI (29 PSU) than IV (27 PSU) and MA (25 PSU). The tidal regime is dominated by semi-diurnal tides with an average of 3.5 m in tidal range (see <https://www.tides.gc.ca/>). We selected these three regions by the presence of exceptionally large eelgrass (*Zostera marina* L.) beds, in increasing surfaces in the last decades, ranging from 1 500 to 3 000 ha (Araújo *et al.* unpublished data). They are accessible from shore as mainly situated in the intertidal fringe (from depth 0.7 m below sea level to 0.2 m above). We selected these three regions by the presence of exceptionally large eelgrass (*Zostera marina* L.) beds, in increasing surfaces in the last decades, ranging from 1 500 to 3 000 ha (Araújo *et al.* unpublished data).

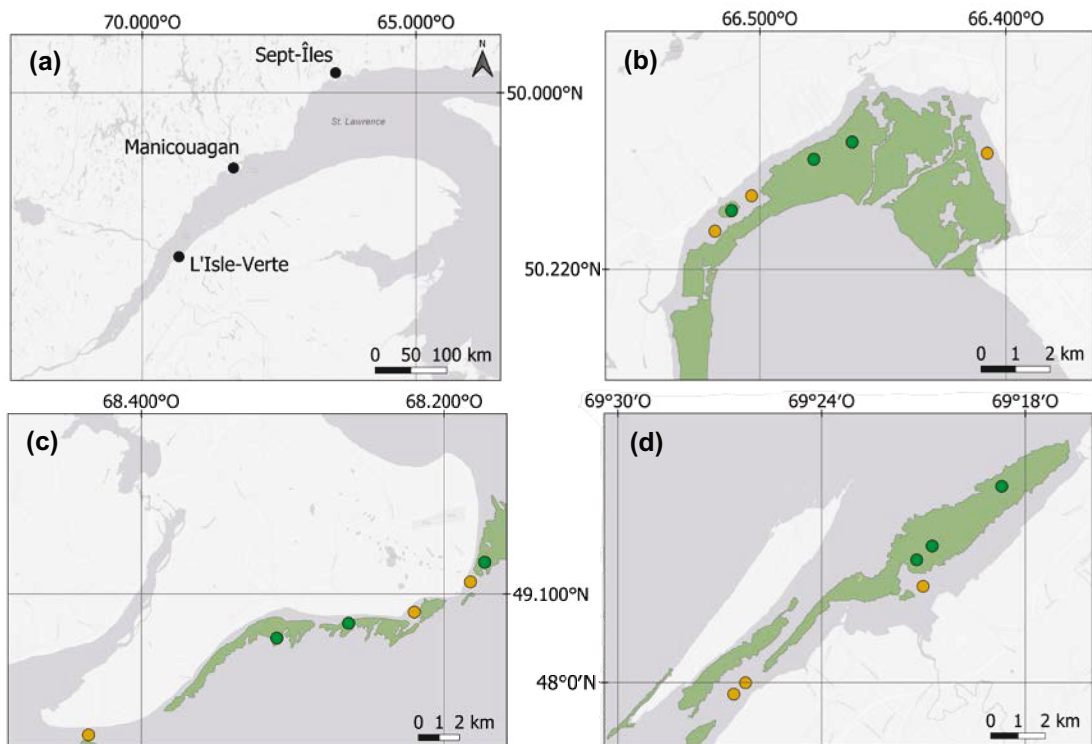


Figure 3. Maps showing the location of the three regions (a) and study sites in (b) Sept-Îles, (c) Manicouagan and (d) Isle-Verte. Eelgrass beds and bare sediment sampled sites are represented by green and yellow dots respectively. Green area represents eelgrass approximate habitat.

In each region, we sampled three vegetated (within *Z. marina* beds) and three unvegetated (bare sediment or with very low eelgrass density) sites. We defined the location of these two habitats using historical satellite images (1985-2017, images from Landsat 4-8 between June and October) where the eelgrass meadow was constantly either not detected (bare sediment) or present (vegetated) since 1984 (Araújo *et al.* manuscript in preparation). In each region numerous areas of the two habitats were defined, through a series of steps (scene cropping, image segmentation, polygon classification and verification; see Araújo *et al.* in preparation materials and methods section for more details). We identified several areas for their large size and accessibility, from which we randomly selected three areas of each habitat in each region. We positioned the sampling sites near the middle of the selected areas to avoid edge effect.

2.2 Collection and laboratory processing

In both habitats, we counted *Z. marina* shoot density as the number of shoots counted in nine haphazardly positioned quadrats (0.04 m² per quadrat). For each eelgrass habitat site, we collected the above- and belowground biomass with three core samplers (20 cm diameter and 20 cm depth). The collected shoots were separated at the meristem with scissors, rinsed on site and placed on ice for transportation to the laboratory where leaves and rhizomes were then gently cleaned of epibionts and detritus by hand under running freshwater. We selected and measured the longest leaf from 15 random shoots to estimate the canopy height. All plant materials were dried at 60°C until constant mass (24 to 48 hrs) and weighted to obtain biomass (± 0.0001 g). Epifauna, defined as animals living on eelgrass, were collected using a 500 μ m mesh bag (18 cm diameter) on top of the blades and cut at the meristem, at low tide when water was still present.

In both eelgrass and sedimentary sites, we collected the benthic infauna, defined as animals living in the sediment, using five corers (cylindrical PVC corer, 10 cm diameter and 20 cm depth) haphazardly positioned with at least 1 m apart. The samples were pre-sieved in the field using a bucket with a 500 μ m bottom mesh and its content were preserved in labelled sample jars with 4% buffered formaldehyde. In the laboratory, we rinsed the samples over 500

μm mesh and we identified the infauna samples to the lowest possible taxonomic level (usually species) using general taxonomic references (Dnestrovskaya et Jirkov, 2010; Jirkov et Leontovich, 2013; Pocklington, 1989). The organisms were counted and weighed (± 0.0001 g) by taxa. In each sample, we also weighed the eelgrass roots, when present. For logistic reasons, some samples were conserved in alcohol weighting and a conversion factor of 1.2 was applied to each obtained biomass (Brey, 1986; Ricciardi et Bourget, 1998). We estimated the diversity profile variables in each sample with total abundance (N) and total biomass (B) with the sum of all number or biomass of individuals and taxa richness (S) and we used the biomass structure data to calculate Shannon diversity index (H') and Pielou evenness (J').

We collected two to four cores (acrylic core sampler, 5 cm diameter and 25 cm depth) for sediment analyses in two sites of each habitat. Each sediment core was divided into five sections of 5 cm (0-5 cm; 5-10 cm; 10-15 cm; 15-20 cm; 20-25 cm) and kept at -20°C (dark) until analysis. Part of the sections were used for grain sizes (one replicate) using an analysis particle size analyzer (LS 13320, Beckman Coulter, Indianapolis, United States) and separated into five sizes: clay ($< 1.88 \mu\text{m}$), silt ($1.88\text{-}58.9 \mu\text{m}$), fine sand ($58.9\text{-}240 \mu\text{m}$), medium sand ($240\text{-}516 \mu\text{m}$), and coarse sand ($516\text{-}2000 \mu\text{m}$). Organic carbon content (two replicate; %OC) were measured with an isotope ratio mass spectrometer (IRMS: Thermo Fisher Delta V Plus; Combustion: Vario PYRO cube de Elementar).

2.3 Data analysis

We tested effect of region (fixed, three levels), habitat (fixed, two levels), or site (nested in the interaction region*habitat, random, three levels per region) and interactions on salinity, habitat characteristics (AG and BG biomass, shoot density, canopy height, grain size, sediment $\delta^{13}\text{C}$) and diversity profile variables (N , B , S , H' and J') with an univariate permutational analysis of variance (PER-ANOVA; Anderson *et al.*, 2008; Clarke et Gorley, 2015), with 9999 permutations. Prior to the multivariate analyses we normalized the environmental data, log transformed all habitat characteristics, and log transformed the macrobenthos biomass and abundance variable to reduce the heteroscedasticity identified by graphical examination of the

residuals (Montgomery *et al.*, 2012; Quinn et Keough, 2002). If significant factor effects were found, we used pairwise post-hoc permutational *t* tests (9999 runs) to identify differences. When the number of permutations were lower than 35 (as in Reg*Hab interaction in some tests) a Monte-Carlo procedure were used to obtain *P* value (Anderson *et al.*, 2008).

We explored differences in macroinfaunal community composition and structure using the same mentioned factorial design with a multivariate permutational analysis of variance (PERMANOVA) applied on a Bray-Curtis similarity matrix using biomass data. Macrobenthos biomass data were log transformed prior to analyses (according to shade plot method; Clarke *et al.*, 2013) to damper very dominant taxa. Similarly, pairwise post-hoc *t* tests were also used as described above. We used Principal Coordinate Analysis (PCO) plot to illustrate macrofaunal community structure. We identified the taxa that mostly contributed to the similarity with a SIMPER analysis (Clarke, 1993). We identified which habitat characteristics (salinity, AG and BG biomass, shoot density, canopy height, grain size, sediment $\delta^{13}C$, all normalized) were linked to observed infaunal community abundance structure using DistLM analyses and visualized with dbRDA plots (Clarke *et al.*, 2014). Prior to analyses, we removed some measured variables (AG and BG biomass), or some sediment size categories were merged as they were highly correlated ($r > 0.8$) with others. Only results with infaunal community are shown due to the incorporation of sediment related variables. For 'ALL', analyses were conducted on the level of SITE with three replicates as we merged the 5 replicates of both infauna and epifauna together.

All statistical analyses and multivariate graphs were performed in PRIMER+PERMANOVA (version 7) and univariate graphs were done in R (version 3.3.1). We used a significance level of $\alpha = 0.05$ for all statistical analyses, and marginally significant results were carefully considered. We named the analyses/results that used combined epi- and infauna data with the term 'ALL', those that used separately epifauna or infauna with 'EPIFAUNA' and 'INFAUNA' respectively.

RESULTS

3.1. Eelgrass and sediment habitat characteristics

3.1.1. Eelgrass bed structure

We observed strong variation within sites in above- and belowground biomass and canopy height values but not among the studied regions (Table 1). Indeed, the factor site significantly explained up to 37%, 44% and 31% of variations within studied regions, respectively. Although canopy height in SI region was, on average, 3-fold less than in IV and MA (113 ± 32 mm, 325 ± 122 mm, and 342 ± 144 mm respectively; Figure S1), differences among regions were not significant (p -value = 0.121). Since adjacent sediment habitat sites were chosen using satellite images some scarce shoots were sometime present but, as expected, shoot density was much higher in eelgrass bed habitat than the adjacent bare sediment (735 ± 56 nb. m² and 70 ± 97 nb. m² respectively; Figure S1), with the highest and lowest density in SI and IV regions respectively (Table 1). Eelgrass structure differed between the region of IV and SI when all structural variables were considered ($t_{1,24} = 2.37$; $p = 0.025$).

Table 1. Summary of PER-ANOVAs showing the effects of region (Reg), habitat (Hab), site (nested in Reg*Hab) on *Zostera* (a) aboveground biomass, (b) belowground biomass, (c) canopy height, and (d) shoot density. Significant values are shown in bold. V% stands for estimate of variance components.

Source of variation	df	MS	Pseudo-F	p-value	V%
(a) Aboveground biomass					
Reg	2	1.411	1.46	0.291	18
Site(Reg)	6	0.966	3.02	0.020	37
Res	18	0.320			45
Total	26				
(b) Belowground biomass					
Reg	2	0.600	1.46	0.296	19
Site(Reg)	6	0.412	5.27	0.003	44
Res	18	7.8E ⁻²			37
Total	26				
(c) Canopy height					
Reg	2	289.780	3.76	0.121	33
Site(Reg)	5	88.885	11.42	< 0.001	31
Res	96	7.787			35
Total	103				
(d) Shoot density					
Reg	2	14.928	2.68	0.108	12
Hab	1	191.150	34.30	< 0.001	44
Reg*hab	2	4.504	0.81	0.480	0
Site(Reg*hab)	12	5.573	2.07	0.042	16
Res	36	2.696			28
Total	53				

3.1.2. Sedimentary composition

We found significant differences in sediment characteristics among regions (Table 2). Generally, the sediments in *Z. marina* meadows of MA and SI region contained a higher percentage of organic carbon (%OC) than in adjacent sediment ($t_{1,14} = 3.70$, $p = 0.022$ and $t_{1,14} = 8.49$, $p = 0.002$, respectively) but not for Isle-Verte region ($t_{1,14} = 0.72$, $p = 0.521$; Figure S2, Table S3 [Figure S2](#)). At SI, we found the highest proportion of fine sediments with high value percentages of OC, clay, and silt (Figure S2).

Table 2. Summary of PERMANOVA showing the effects of region, habitat on multivariate response of sedimentary characteristics using percentage of organic carbon content, clay, silt, very fine, fine, medium, coarse, and very coarse sand. Significant values are shown in bold. V% stands for estimate of variance components.

Source of variation	df	MS	Pseudo-F	p-value	%V
Reg	2	6294.50	17.57	0.008	60
Hab	1	239.14	0.67	0.497	0
Reg*Hab	2	449.63	1.26	0.337	11
Res	6	358.27			29
Total	11				

3.2. Eelgrass effect on macrofaunal diversity variables

A total of 7,821 individuals were sorted out, identified, and classified into 37 taxa (Table S4) from four phyla: Mollusca (65.9%), Annelida (22.2%), Arthropoda (11.1%) and Nematoda (0,8%). Taxa richness values of ALL macrobenthos did not show significant differences among regions but were different between habitats (Table 3). Taxa richness was highest in the eelgrass beds of Sept-Îles (27 taxa), followed by Manicouagan (24 taxa) and Isle-Verte (21 taxa). The eelgrass habitat of each region supported twice as many macrobenthic taxa than the bare sediment (Table 3, Figure 4A), however, no difference was observed between habitats when only infauna was considered. No patterns were observed for community evenness values for ALL macrofauna, INFAUNA or EPIFAUNA across regions and habitat (Table 3). Total abundance of macrofauna was significantly higher in eelgrass than in sediment habitat (Figure 4B) regardless of the regions that only showed marginal differences (Table 3). However, infaunal abundances were higher in the sediment habitat of IV and eelgrass habitat of MA regions (Figure 4C). Although mean biomass of infauna was always higher in sediment habitats than eelgrass habitats for each region, no significant difference was found between habitats.

No significant differences were found when considering all macrofauna for mean biomass. Infaunal biomass was significantly lower in SI than both other regions (Figure 4D). For all macrofauna, the region of SI and the eelgrass habitat supported highest diversity values (Figure 4E, F). Conversely, infaunal diversity was significantly different between habitats within region as sediment showed a higher diversity value than in eelgrass for both IV and SI (Figure 4G). None of the diversity variables from epifauna showed significant differences among regions.

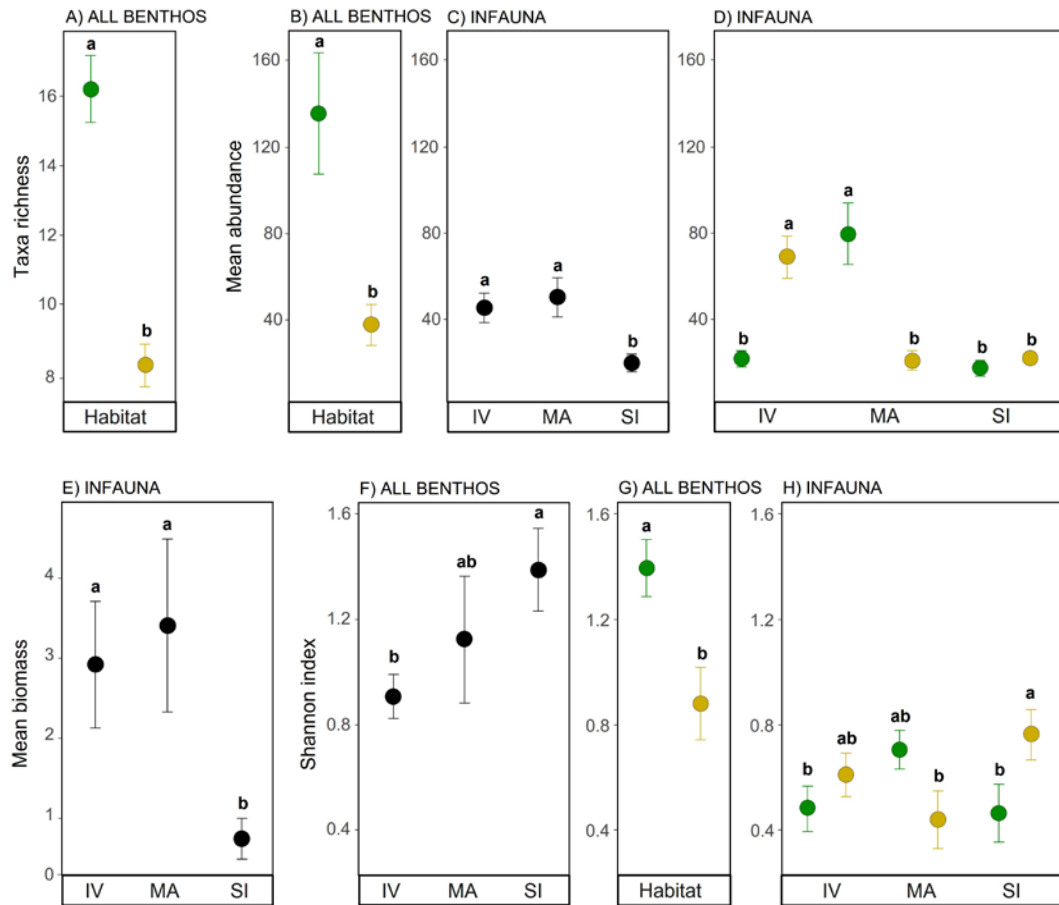


Figure 4. Average (\pm se) of (A) taxa richness, (B, C, D) abundance (per core), (D) biomass (g) and (E, F and G) Shannon diversity index between habitats (yellow and green dot represents sediment and eelgrass habitats respectively), among regions (IV, MA and SI represents Isle-Verte, Manicouagan, and Sept-Iles regions respectively). All variables are per sample. 'ALL' refers to both benthic compartment (epifauna and infauna) while 'INFAUNA' refers to only that compartment. The different letters indicate a significant result.

Table 3. Summary of PER-ANOVAs showing the effects of region, habitat, and site on (a) taxa richness, (b) evenness, (c) total abundance, (d) total biomass, and (e) Shannon. Significant values are in bold. V% stands for estimate of variance components.

Source of variation	<i>All</i>				<i>Infauna</i>				<i>Epifauna</i>			
	df	Pseudo-F	p-value	%V	df	Pseudo-F	p-value	%V	df	Pseudo-F	p-value	%V
(a) Taxa richness												
Reg	2	0.97	0.407	0	2	0.38	0.687	0	2	0.05	0.953	0
Hab	1	42.94	< 0.001	68	1	1.03	0.323	3	-	-	-	-
Reg*Hab	2	0.07	0.932	0	2	0.63	0.550	0	-	-	-	-
Site(Reg*Hab)	-	-	-	-	12	4.77	0.001	45	6	3.60	0.008	42
Residual	12			32	72			52	36			58
Total	17				89				44			
(b) Pielou's evenness												
Reg	2	1.53	0.251	23	2	0.45	0.646	0	2	2.67	0.160	24
Hab	1	0.42	0.592	0	1	1.79	0.206	9	-	-	-	-
Reg*Hab	2	0.14	0.925	0	2	2.68	0.111	22	-	-	-	-
Site(Reg*Hab)	-	-	-	-	12	1.43	0.174	16	6	1.68	0.154	21
Residual	12			77	72			54	36			55
Total	17				89				44			
(c) Total abundance												
Reg	2	3.46	<u>0.063</u>	17	2	5.58	0.023	17	2	1.36	0.31	18
Hab	1	16.62	0.001	35	1	0.01	0.924	0	-	-	-	-
Reg*Hab	2	2.98	0.089	22	2	14.75	< 0.001	41	-	-	-	-
Site(Reg*Hab)	-	-	-	-	12	2.31	0.015	14	6	14.27	< 0.001	51
Residual	12			27	72			28	36			31
Total	17				89				44			
(d) Total biomass												
Reg	2	1.53	0.247	23	2	3.88	0.048	23	2	3.11	0.094	31
Hab	1	0.42	0.601	0	1	1.94	0.192	11	-	-	-	-
Reg*Hab	2	0.14	0.920	0	2	0.41	0.672	0	-	-	-	-
Site(Reg*Hab)	-	-	-	-	12	3.52	< 0.001	28	6	5.71	< 0.001	34
Residual	12			77	72			39	36			35
Total	17				89				44			
(e) Shannon index												
Reg	2	3.91	0.050	20	2	0.27	0.760	0	2	2.24	0.221	24
Hab	1	13.30	0.004	33	1	0.51	0.481	0	-	-	-	-
Reg*Hab	2	2.46	0.128	20	2	4.91	0.026	33	-	-	-	-
Site(Reg*Hab)	-	-	-	-	12	0.96	0.500	0	6	3.16	0.015	30
Residual	12			28	72			67	36			46
Total	17				89				44			

3.3. Eelgrass effect on community structure and composition

With some exception, all components of community structure and composition were similarly affected by region, habitat, and their interaction (Table 4, Figure 5). Among results, community structure of ALL (epifauna and infauna) showed differences between *Z. marina* meadow and bare sediment, but not when only infauna alone is considered (Table 4). A significant effect of habitat was, however, observed for infaunal community composition, explaining a small (10%) proportion of the variation (Table 4B). Region showed a strong influence for both infauna and epifauna community components, with very different communities in SI region (Figure 5). Analyses based on abundance structure (by count) depicted similar results (not shown). The region of SI had the most exclusive taxa (Figure S5). The taxa that contributed the most to the dissimilarity across regions and habitats of infauna communities were *Macoma balthica* (MACO), *Mya arenaria* (MYA), *Alitta virens* (NER), *Eteone longa* (ETEO), and *Heteromastus filiformis* (Table S6).

Table 4. Summary of PERMANOVAs showing the effects of *region, habitat, site* (nested in *Reg*Hab*) on the community structure and the composition (presence/absence) on a) all macrobenthos and for its components of B) Infauna and C) Epifauna. Significant values are in bold. V% stands for estimate of variance components.

Source of variation	Community structure					Community composition			
	df	MS	Pseudo-F	p-value	%V	MS	Pseudo-F	p-value	%V
A) All									
Reg	2	3566	6.245	< 0.001	23	3961	11.884	< 0.001	34
Hab	1	8608	15.074	< 0.001	31	8369	25.108	< 0.001	41
Reg*Hab	2	1940	3.397	< 0.001	22	223	0.668	0.658	0
Residual	12	571			25	333			25
Total	17				100				100
B) Infauna									
Reg	2	22048	7.425	< 0.001	27	26912	9.873	< 0.001	34
Hab	1	2792	0.940	0.473	0	6241	2.289	0.045	10
Reg*Hab	2	7666	2.582	0.023	19	1462	0.536	0.860	0
Site(Reg*Hab)	12	2969	3.235	< 0.001	22	2726	3.741	< 0.001	24
Residual	72	918			32	729			32
Total	89				100	89			100
C) Epifauna									
Reg	2	14005	6,299	0.003	39	12348	6,686	0.004	39
Site(Reg*Hab)	12	2223	3,372	< 0.001	25	1847	2,795	< 0.001	23
Residual	36	659			36	661			38
Total	44				100				100

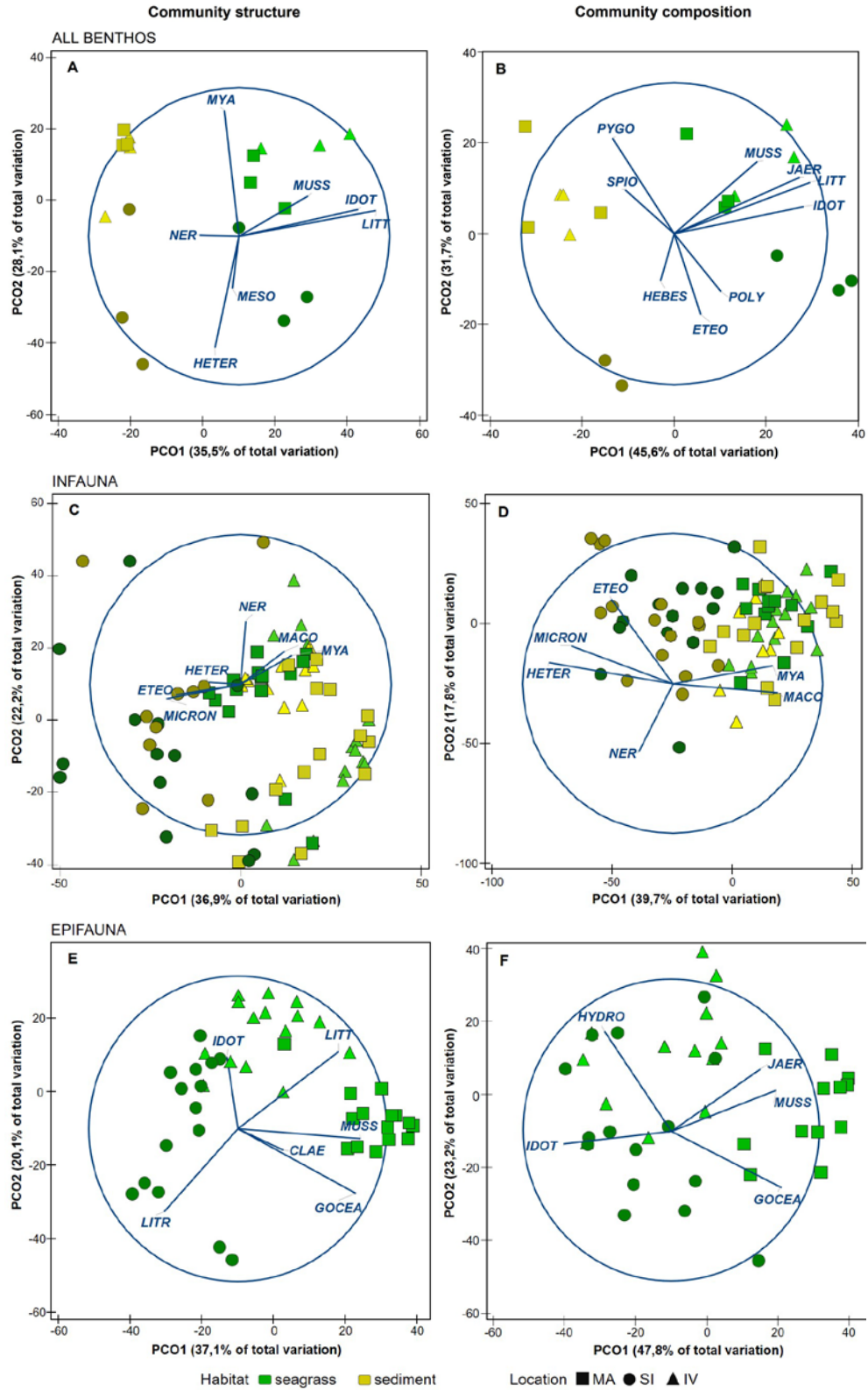


Figure 5. Principal Coordinate Analysis (PCO) plots (Bray-Curtis resemblance based on taxonomic biomass) of community structure (left) and composition (right) of (A) all macrobenthos, (B) infauna and (C) epifauna across the three studied regions and the two surveyed habitats. Vectors length represents Pearson correlation with abundance of important taxa identified from SIMPER analyses. See Table S6 for taxa abbreviation.

3.4. Link between environmental characteristics and community structure

For both analyses using either all macrofauna or infauna only, AG, BL and canopy height were not considered in these analyses as they no data were taken for bare sediment habitat. All environmental variables (density, grain size, salinity and %C) were retained in the best model that explained the community structure across samples (Table S7, Table S8). The environmental variables explained up to 58% of the variability in community structure for ALL macrobenthos while up to 44% for the infauna compartment. The benthic community seen in SI region drives most of the pattern with high proportion of silt and clay or higher salinity or shoots density seen in that region (Figure 6A, B). Shoot density was less significant when only infauna is considered but were kept in the best model (Figure 6B, Table S8).

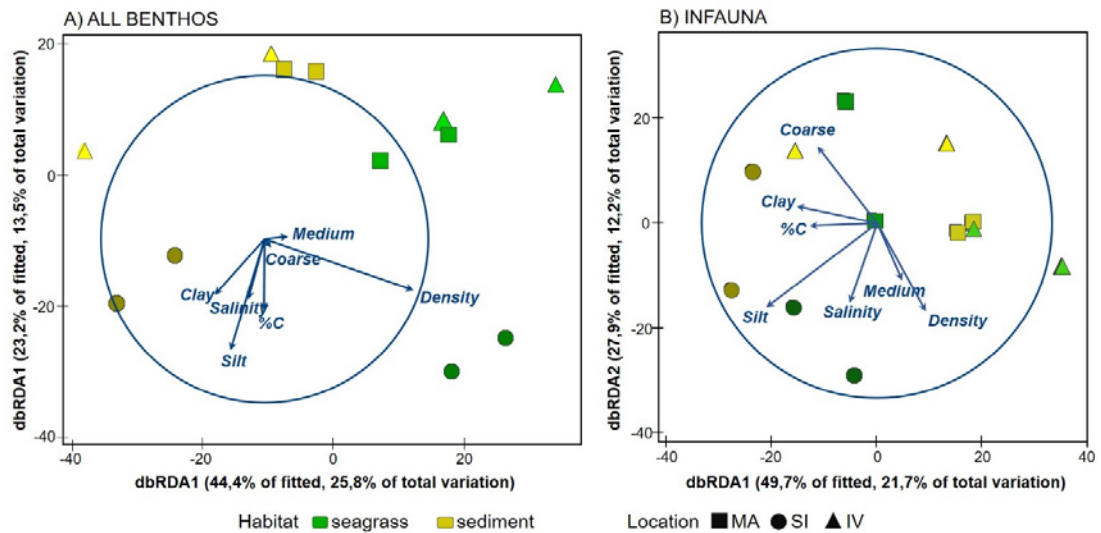


Figure 6. Distance based redundancy analysis (dbRDA) plots of (A) all macrobenthos and (B) infauna samples based on Bray–Curtis distance matrices. Vectors length represents Pearson correlation with variables retained in the DistLM model.

DISCUSSION

Our study examined the effect of eelgrass meadows on macrobenthic communities with a comparison between adjacent unvegetated sediment habitat at local and regional scales. As expected, eelgrass presence modifies and affects positively diversity indices of macrobenthic communities, this prediction, however, could not be supported when only infauna was considered. Small scale (sites ≤ 1 km) was important for the diversity profile variables, notably

on taxa richness and abundance. Such small-scale variations are mostly due to both difference in sediment characteristics and meadow structure, as they can modulate the abundances within associated communities. Larger scale (regions 150-300 km) was more important in shaping either epifauna and infaunal community structure and composition than local scale in each habitat. Overall, the eelgrass had strong positive net effect on diversity related variables, adding several taxa to the community that would not be present otherwise. Such effect, however, may depend on the biological compartment considered as we showed that any observed effect of eelgrass was less obvious when infauna only was considered. Which was a logical result as epifaunal communities were only sampled in seagrass habitat. This study provides not only new insights of scaling effect of macrofauna communities across sediment habitats and eelgrass beds but also the need to separate the effects of both epi- and infauna compartment to the whole macrobenthic community.

Effect of eelgrass on the macroinvertebrate community

We observed a higher abundance of organisms (136 ± 86 vs 37 ± 30 ind. per sample), and taxonomic richness (16 ± 3 vs. 8 ± 2 taxa) in the eelgrass meadow than in nearby bare sediment habitat. While direct comparison between studies remains difficult due to differences in sampling methodology (core and sieve size), eelgrass bed structure (biomass, shoot density), habitat location (intertidal, subtidal) and characteristics (such as hydrodynamics, exposition to wave, disturbance from human activities), many studies have shown a positive effect of eelgrass canopy on macroinvertebrate species diversity, abundance, and biomass compared to adjacent bare habitats (Barnes, 2017; Edgar et Barrett, 2002; Fredriksen *et al.*, 2010; Magni *et al.*, 2017). As such, Barnes and Barnes (2012) observed an increased abundance of macrobenthos by a factor of 2.5 and twice as many species in the seagrass than the adjacent sandflat. They explained this increase because of the physical presence of seagrass itself allowing greater habitat complexity and sediment stability. In our study, it seems that this pattern is mainly explained by the addition of taxa considered here as epifauna to the whole assemblage.

As foundation species, macrophytes add structural complexity with their morphological structure which has been shown to increase biodiversity and determine faunal composition (Duffy, 2006; Loke et Todd, 2016; Qiu *et al.*, 2019). For example, increase in habitat complexity, such as increasing shoot density or higher seagrass cover, has been shown to enhance both diversity and density of epifauna (Reed et Hovel, 2006; Sirota et Hovel, 2006). First, structural complexity of vegetated habitats provided by eelgrass create shelters and refuges and offers greater protection from predation (Dudgeon et Petraitis, 2005; Duffy, 2006; Orth *et al.*, 1984; Stachowicz et Byrnes, 2006). Reynolds *et al* (2018) observed over an ocean-based scale that predation declined with higher shoot density both among and within sites with generally low predation pressure in the St. Lawrence marine estuary but with meadow edges of higher predation risk (Hovel *et al.*, 2021). Among the 18 taxa found in the eelgrass beds across our regions many were mobile, either scavengers or detritivores, that may seek refuges from the predators by hiding in the leaves. Second, the eelgrass leaves considerably enhance the surface for micro- and macroalgae, such as epiphytes, that are an important source of food for many epifaunal invertebrates (Stoner, 1980; Thomsen *et al.*, 2018; van Montfrans *et al.*, 1984). Generally, an increase in biomass and diversity of algal resources resulted in higher epifaunal densities and greater species richness (Dean et Connell, 1987). The availability of epiphytes on eelgrass leaves is one of the main determinants of epifaunal community structure (Duffy *et al.*, 2015). Within a given meadow, eelgrass characteristics that influence associated faunal communities can be heterogeneous. Attrill *et al.* (2000) results suggested that within an eelgrass bed the composition of the associated macroinvertebrate community is not determined by the structural complexity attributes, but by the amount of plant available. For example, multiple short leaves would provide the same amount of available plant than fewer long leaves but would confer different levels of complexity for the macrobenthos. Thus, increasing plant biomass does not necessarily reflect increasing complexity, but does provide a larger surface area (Attrill *et al.*, 2000).

Increased abundance and richness of associated fauna in eelgrass bed compared to bare sediment were not observed for the infauna compartment in our results. Although eelgrass

habitats have traditionally been considered as biodiversity hotspots in sedimentary shores seascape (Hyman *et al.*, 2019; Morrison *et al.*, 2014), few studies did not support the evidence of increased infaunal diversity and abundance in eelgrass beds compared to unvegetated habitats (Alsaffar *et al.*, 2020; Barrio Froján *et al.*, 2009). While the presence of eelgrass did not influence the infaunal community abundance structure, it did explain a small proportion of the variation in the community composition. Thus, additional or different species were found in the eelgrass habitat, but their abundances and/or biomass were too weak to have an impact on the community structure. Alsaffar *et al.* (2020) found similar results where benthic infaunal density and number of taxa did not vary significantly among habitats. We were expecting infaunal diversity and abundance to be affected with the presence of *Z. marina* by adding belowground structural complexity with root system and more sediment stability (González-Ortiz *et al.*, 2016). In our study, we found that all the environmental variables were important in shaping both ALL and infauna communities. The shoot density, proportion of silt, clay and percentage of organic carbon seemed to contribute the most in ALL macrobenthos (Table S6). Even though shoot density was present in our models for infaunal communities, its contribution was less important than for EPIFAUNA. The proportion of silt and clay had the highest effect, which was also explained as a significant part of the macrofauna composition in other studies (Alsaffar *et al.*, 2020; Boyé *et al.*, 2017).

While there was no infaunal taxa strictly associated to the bare sediment habitat, relatively few (one third) infaunal taxa were associated exclusively with eelgrass beds which tripled when epifaunal taxa were included (from 6 to 18; Figure S5). These differences were mostly explained by the addition of mobile mesograzers taxa, such as *Gammarus oceanicus*, *Littorina* spp. or *Hydrobia minuta* that feed on epiphyte on eelgrass leaves (Table S4). Wong et Dowd (2015) found similar results when comparing both epi- and infaunal diversity in bare sediment and seagrass beds in Nova Scotia, Canada. They explained that both epi- and infaunal taxonomic diversity (species number, Margalef and Simpson's indices) increased from bare sediments to the bed interior, due to a prevalence of filter feeders in the bare habitat and grazers in the eelgrass bed interior. By separating the biodiversity into epi- and infauna

compartments, we can identify whether the mechanism of adding abundance or complexity by eelgrass is responsible for the increase in diversity or the effects on composition.

Spatial scale variability of habitat structure and macroinvertebrate community

We observed a strong effect of region and sites in most of our results from epifauna and infauna taken separately. Either epi- or infaunal communities of both habitats were often more different among samples within a few metres than between sites few kilometres apart. Such small scale (within meter) variation is often observed in species composition and overall abundance of the macrofauna (Barnes, 2017; Hewitt *et al.*, 2005; Underwood et Chapman, 1996). Local conditions, such as hydrodynamics, can have a strong influence on plant characteristics (e.g. shoot density, below and aboveground biomass) and surface sediment structure (Fonseca et Bell, 1998; Hansen et Reidenbach, 2012; Schmidt *et al.*, 2012), high heterogeneous sites within each habitat is common. For example, eelgrass bed exposed to wave exposure usually exhibit responses in high belowground biomass to increase their stability (Frederiksen *et al.*, 2004). In our study, Manicouagan sites are the most wave exposed (facing the sea), conversely Sept-Îles (inside a large bay) and Isle-Verte (with an island protecting the coast) sites are more sheltered. Such variation in the belowground biomass, however, was not seen among our studied regions as they supported similar belowground biomass values. Other characteristics such as the size and uniformity of the meadow (Bell *et al.*, 2001; Bowden *et al.*, 2001), shoot density and biomass (Webster *et al.*, 1998), predation (Boström et Mattila, 1999) and environmental conditions (Hovel *et al.*, 2002; Turner *et al.*, 1999), can locally create different seascapes and shape communities at local scale. Community structures within eelgrass beds can change along summer, as well as some eelgrass characteristics (maximum leave length, density, etc.). No noticeable changes in bed phenology were observed at the three studied regions during sampled dates in summer. As such, temporal and spatial effects cannot be separated but we do consider temporal effects to be negligible in comparison of spatial effects. Moreover, in the St. Lawrence system, scouring by sea ice can enhance such heterogeneity within the eelgrass, by ripping off large amount of shoot in a continuous meadow and creating tidal pools of various shapes and sizes (Conlan *et*

al., 1998 ; Pascal *et al.*, 2020). It is interesting, however, that none of the eelgrass structure were showing regional effects except some observed trends with density and canopy height which both varied mostly among sites within habitats (Table 1).

Being situated in a bay on the north of the St. Lawrence Gulf, the environmental conditions of Sept-Îles sites were very different from the other regions. The highest proportion of organic carbon content in both habitats observed in the sites within the bay which could be explained by a reduced hydrodynamic and lower currents and an increase in fine sediment fractions (e.g., silt and clay). The presence of a large saltmarsh around the bay may also contribute to the high proportion of organic carbon in SI sediments. Some studies showed that when current flow and waves are reduced, the loss of organic carbon in the sediments from resuspension decrease (Dahl *et al.*, 2018; Samper-Villarreal *et al.*, 2016). Dahl *et al.*, (2016) also found that higher organic carbon content was strongly related to a higher proportion of fine grain size, like mud. Sept-Îles region also supported a different macrobenthic communities. The infaunal communities of both habitats of Sept-Îles differed greatly from Manicouagan and Isle-Verte, while the communities of the two latter were more similar. Sept-Îles region supported the highest number of infaunal taxa not seen in the two other regions, such as *Heteromastus filiformis* and *Micronephtys noetena*, suggesting that particular sedimentary condition in the bay influenced its macrobenthos community. It is well established that the organic matter and sediment grain size are of great importance for the community structure (Boström *et al.*, 2006; Gray, 1974; Lundquist *et al.*, 2018).

Concluding remarks. Eelgrass meadows provide essential structure, functions, and ecosystem services to the coastal environment and their associated macroinfaunal communities are important indicators of ecosystem health. Our findings support that eelgrass meadows promote diversity of sedimentary habitat. However, our results also highlighted the need to consider, in attempting to measure any seagrasses effects on its associated macrobenthos, into account different sampling locations at various small (m to km) as well as large (> 200 km) scales. One that use only sites within one region may end up with different

results as suggested by the variability we obtained, notably with contrasting results across regions with infaunal abundances or other significant interaction between region and habitat factors seen. Such results suggest that differences in regional or local eelgrass bed structure (e.g., above- and below ground eelgrass biomass, density, canopy height, etc.) and sedimentary characteristics (%OM, granulometric fractions) profile may explain observed community composition and are important to be included in regional-scale assessments of eelgrass beds. By considering the benthic compartments (epifauna/infauna) separately, it allowed us to understand the mechanism by which the eelgrass is important for the diversity profile of sedimentary shores. Thus, we could state that the eelgrass meadows from the St. Lawrence marine systems attract additional species by increasing its aboveground complexity that provides both food provision via additional substrate surfaces for several herbivores and refuge for scavengers or detritivores. More precise observations are needed, however, to disentangle by which mechanisms (e.g., complexity, density, food provisioning) the eelgrass, as a foundation species, regulate the macrobenthic community and habitat ecosystem services in the St. Lawrence marine system. In the context of replacement of bare sediment habitats by more eelgrass bed as seen in the St. Lawrence systems in the last decade, such information along with ours would be useful for conservation and management purposes.

CONCLUSION

Mon mémoire a été réalisé dans le but d'acquérir des connaissances sur les structures des communautés benthiques dans les habitats sédimentaires et en présence d'herbiers marins dans l'estuaire et le golfe du Saint-Laurent. En effet, de nombreuses lacunes existent dans notre compréhension de l'effet de la présence de *Zostera marina* L. sur les communautés macrobenthiques associées considérant les compartiments d'épi- et d'endofaune séparément. Ceci est particulièrement vrai dans l'estuaire et le nord du Saint-Laurent, où les données cohérentes concernant les structures de communauté dans les habitats végétalisés et non végétalisés sont limitées. De plus, contrairement à la tendance mondiale, la surface totale des herbiers du Saint-Laurent a augmenté depuis les dernières décennies, ce qui rend son étude d'autant plus intéressante. D'après la littérature, il existe un paradigme selon lequel la présence de zostères marines augmenterait la diversité et l'abondance des espèces associées (Morrison *et al.*, 2014). Les mécanismes à travers lesquels cette augmentation se produit peuvent aller d'un ajout de complexité de l'habitat par les feuilles, à un changement d'hydrodynamique en passant par la création d'un refuge et d'un ajout de ressources alimentaires.

Nos résultats ont montré qu'il existe bien une augmentation de la richesse et diversité taxonomique, et d'abondance dans les herbiers marins lorsque la totalité du macrobenthos est considérée. D'ailleurs, cette observation n'est vraie que lorsque les deux compartiments de la macrofaune sont pris en compte. Aussi, si l'on considère seulement le compartiment endofaunique, les effets sont beaucoup moins apparents et il ne semble pas y avoir d'effet de la zostère sur la richesse taxonomique. Nous observons néanmoins un changement dans la composition des communautés entre les habitats de zostères et les habitats de sédiments nus. Les communautés semblent donc abriter quelques nouvelles espèces dont l'ajout n'influence pas la structure d'abondance des communautés; il s'agit donc d'espèces rares. Nous nous attendions à avoir des effets dépendamment des échelles locales (100 ms) et régionales (100 kms). Ceci a été vérifié puisqu'il existe une grande variabilité locale dans les paramètres des communautés, et ce par rapport au niveau régional. La région de Sept-Îles en a été un bon exemple, étant située dans le golfe, c'est la région qui différerait le plus en termes de salinité,

variables morphologiques (densité et longueur des plants) et sédimentaires (taille des grains et contenu en carbone organique). C'était également la région ayant une structure de communauté différente des autres régions, notamment de la région de l'Isle-Verte, et le plus d'espèces endofauniques exclusives. La variabilité des réponses dans les trois régions ne nous a pas permis de démêler la contribution relative de chaque facteur pour expliquer le schéma de réponse des communautés macrobenthiques. Mes résultats sont représentatifs d'un environnement complexe ; étant donné l'hétérogénéité des habitats et des régions, ainsi que les différentes réponses selon les compartiments de macrobenthos, il est nécessaire de considérer plusieurs échelles spatiales et populations de macrobenthos lors de projets de caractérisation.

Le projet présente cependant quelques limites. Dans un premier temps, il aurait été judicieux d'échantillonner la colonne d'eau au-dessus du sédiment dans ces habitats pour mieux cerner les disparités entre les deux habitats, ainsi que de voir le réel ajout de l'herbier sur les communautés. De plus, pour de futurs échantillons, il serait préférable d'associer plus directement l'échantillon d'épifaune à celui de l'endofaune ; c'est-à-dire de prendre les échantillons exactement l'un au-dessus de l'autre. Ceci permettrait de voir l'effet de site lorsque la communauté est étudiée dans sa totalité (en combinant l'épifaune et l'endofaune dans un seul échantillon et non à l'échelle du site). Dans un second temps, il serait intéressant d'avoir intégré d'autres variables biotiques et abiotiques, telles que la biomasse d'épiphyte (pouvant expliquer davantage les communautés épibenthiques) ou encore la concentration en métaux lourds et en nutriments, notamment l'azote contenu dans les sédiments (malgré qu'il ne semble pas y avoir d'effet des nutriments sur les communautés à des sites de Manicouagan; M. Cusson, données non publiées). En effet, certaines études ont révélé l'effet de ces différents facteurs sur la structure et la composition en macrobenthos dans les habitats côtiers. Des données environnementales comme la hauteur d'eau, l'exposition aux vagues, ou la turbidité pourraient également être importantes à mesurer puisqu'elles influencent la structure de l'herbier, et donc des communautés. D'autres projets pourraient démêler davantage les différences subtiles qu'il existe entre les habitats du Saint-Laurent. Puisque nous avons

observé des réponses différentes selon les régions, nous suggérons d'étudier plusieurs autres régions afin de réaliser un portrait plus précis des variabilités régionales. Dans notre étude, nous n'avons pas été en mesure d'échantillonner les trois régions en même temps pour des raisons logistiques. Nous croyons tout de même que l'espacement dans le temps des échantillonnages des trois régions (mi-juillet à la fin août et début septembre) n'a pas créé un biais important et que la variation observée est surtout spatiale. Il existe une phénologie (longueur des feuilles, densité, etc.) certaine dans les herbiers du Saint-Laurent, mais les changements sont principalement observés à la fin du printemps (mai-juin). Ces caractéristiques restent toutefois stables aux mois de juillet et août (Léger-Daigle *et al.*; données non publiées). Un rééchantillonnage dans les mêmes régions en même temps et répété pourrait cependant aider à démêler les effets temporels et spatiaux sur les communautés benthiques.

Les projets de conservation devront également considérer leur région comme étant distincte et d'appliquer, au besoin, des protocoles adaptés au contexte de l'objectif de travail ainsi que de la région. De plus, il serait intéressant de regarder la diversité fonctionnelle (p. ex. : prédateur-proie, type d'alimentation, type de déplacement), afin de donner plus de clés pour la conservation des habitats. En effet, l'ajout d'espèces n'est pas toujours synonyme avec ajout de fonction et cet aspect devrait être considéré dans les efforts de restauration et conservation. Ce qui nous amène au point de comparer les herbiers connus avec les herbiers restaurés dans le Saint-Laurent afin de savoir si ceux-ci abritent des structures de communautés similaires. Ainsi, nos résultats montrent l'importance de la prise en considération des échelles spatiales et des compartiments de biodiversité dans le cadre de gestion et conservation des habitats côtiers. Ces résultats pourront également servir de base pour la caractérisation d'un état initial de l'habitat ou de données de comparaison avec d'autres projets similaires. Les herbiers sont indéniablement des habitats sensibles à protéger, notamment par leur support à de nombreuses espèces, mais également par leur rôle de puits de carbone contre les changements climatiques.

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ANNEXES

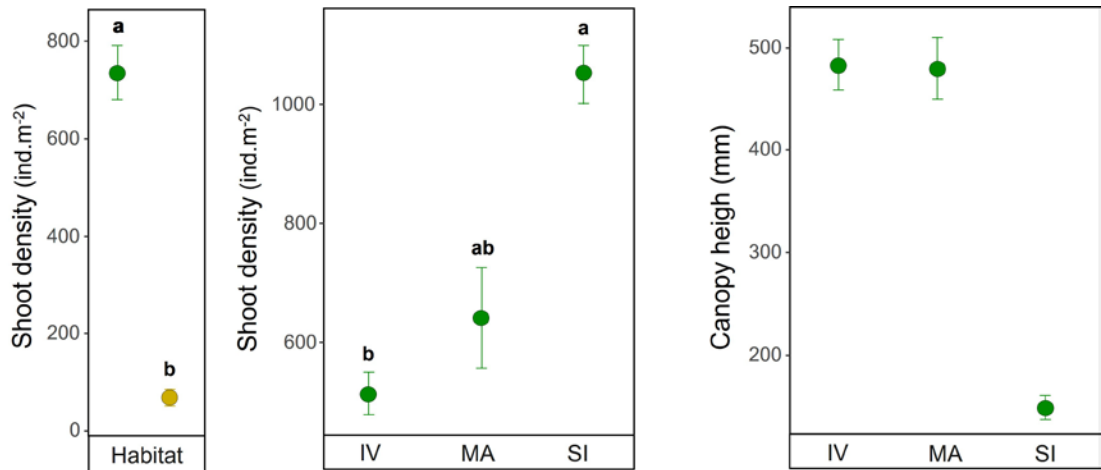


Figure S1. Average (\pm se shoot density (ind. m⁻²) between habitats (yellow and green dot represents sediment and eelgrass habitats respectively) and canopy height (cm) among regions or across regions (IV, MA and SI represents Isle-Verte, Manicouagan, and Sept-Iles regions respectively). The different letters indicate a significant result.

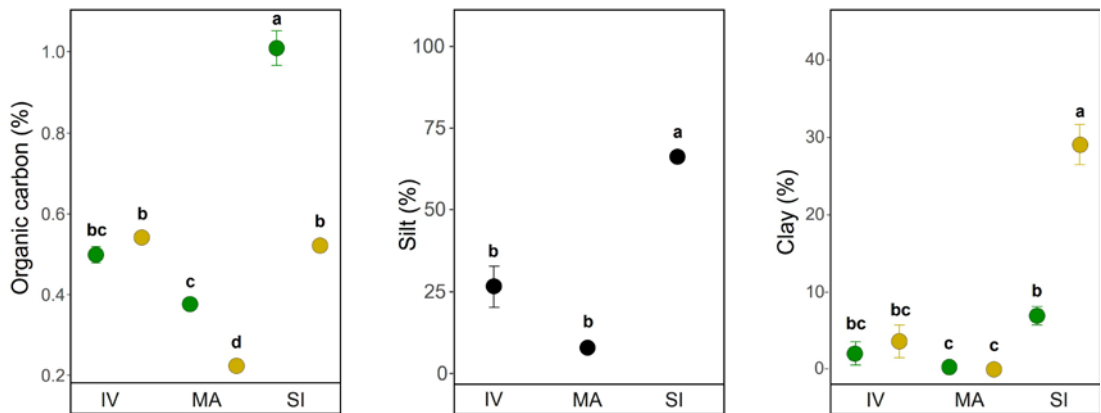


Figure S2. Average (\pm se) percentage of organic carbon content, silt, and clay between habitats (yellow and green dot represents sediment and eelgrass habitats respectively), among regions (IV, MA and SI represents Isle-Verte, Manicouagan, and Sept-Iles regions respectively). The different letters indicate a significant result.

Table S3. Summary of PER-ANOVAs showing the effects of region, and habitat on percentage of (a) organic carbon, (b) silt, (c) clay. (d) fine sand, (e) medium sand and (f) coarse sand. Significant values are in bold. V% stands for estimate of variance components.

Source of variation	df	MSq	Pseudo-F	p	%V
(a) %OC					
Reg	2	1.101	25.917	0.003	38
Hab	1	0.602	13.840	0.012	23
Reg*Hab	2	0.3715	5.667	0.02	24
Res	6	2.50 ^e -17			15
Total	11				
(b) clay					
Reg	2	393,590	29.250	0.006	36
Hab	1	191,500	14,232	0,016	20
Reg*Hab	2	158,350	11,768	0,009	31
Res	6	13,456			13
Total	11				
(c) Silt					
Reg	2	3618,7	18,105	0,013	67
Hab	1	18,118	9,065E-2	0,765	0
Reg*Hab	2	65,220	0,326	0,740	0
Res	6	199,870			33
Total	11				
(d) Fine Sand					
Reg	2	1525,9	17,079	0,012	55
Hab	1	1,8703	2,0934E-2	0,892	0
Reg*Hab	2	161,98	1,813	0,244	18
Res	6	89,346			27
Total	11				
(e) Medium					
Reg	2	220,52	16,362	0,010	66
Hab	1	9,4076	0,69804	0,442	0
Reg*Hab	2	5,4413	0,40375	0,691	0
Res	6	13,477			34
Total	11				
(f) Coarse					
Reg	2	107,14	36,5	0,007	50
Hab	1	13,241	4,5107	0,079	13
Reg*Hab	2	11,282	3,8434	0,083	20
Res	6	2,9354			17
Total	11				

Table S4. Total abundance (\pm se) of each taxa according to the region and habitat. Strictly epifauna are shown with (*)

Taxa	Sept-Îles		Manicouagan		Isle-verte	
	Sediment	Eelgrass	Sediment	Eelgrass	Sediment	Eelgrass
Mollusca						
<i>Macoma balthica</i>	16	23	95	294	452	73
<i>Mesodesma arctatum</i>	3	0	0	16	0	0
<i>Mya arenaria</i>	6	2	18	37	140	76
<i>Mytilus</i> spp*	-	1	-	64	-	32
<i>Hydrobia minuta</i> *	-	11	-	0	-	52
<i>Littorina</i> spp*†	-	542	-	1421	-	1716
<i>Littorina obtusata</i> *	-	13	-	4	-	3
<i>Littorina littorea</i> *	-	20	-	0	-	8
Annelida						
<i>Alitta virens</i>	50	34	36	117	257	54
<i>Capitella capitata</i>	0	16	59	282	16	22
<i>Eteone longa</i>	13	19	8	9	5	2
<i>Fabricia stellaris</i>	1	1	0	0	0	0
<i>Glycera</i> spp.	1	2	0	1	0	0
<i>Harmothoe imbricata</i>	1	1	0	0	0	0
<i>Heteromastus filiformis</i>	93	118	0	0	0	0
<i>Micronephtys noetena</i>	131	4	0	0	0	0
<i>Microphthalmus aberrans</i>	0	1	0	0	0	0
<i>Neoamphritite figulus</i>	0	1	0	0	0	0
<i>Nephtys caeca</i>	0	0	0	0	0	1
<i>Parexogone hebes</i>	2	0	2	21	1	1
<i>Pholoe minuta</i>	0	2	0	2	0	0
<i>Polydora</i> spp.	17	36	1	4	91	51
<i>Pygospio elegans</i>	0	1	41	23	64	10
<i>Spio filicornis</i>	0	0	27	3	0	0
Arthropoda						
<i>Edotea triloba</i>	0	0	0	0	0	4
<i>Idotea balthica</i>	1	46	0	22	0	57
<i>Jaera albifrons</i>	0	6	1	428	0	38
<i>Chiridotea tuftsii</i> *	-	20	-	2	-	0
<i>Gammarus oceanicus</i> *	-	7	-	179	-	3
<i>Calliopius laeviusculus</i> *	-	5	-	52	-	1
<i>Crangon septemspinosa</i> *	-	2	-	0	-	2
<i>Mysis gaspensis</i> *	-	9	-	0	-	3
<i>Cumacea</i> *	-	0	-	2	-	0
<i>Copepoda</i> *	-	1	-	1	-	0
Nemertea	0	0	0	1	0	0
Nematoda	0	0	26	21	5	0
Total	334	944	314	3006	1031	2209

† *L. obtusata* excluded. Abbreviations used: MACO: *Macoma balthica* ; MYA: *Mya arenaria* ; NER: *Alitta virens* ; ETEO: *Eteone longa* ; HETER: *Heteromastus filiformis* ; LITT: *Littorina* spp ; LITR: *Littorina littorea* ; MGAS: *Mysis gaspensis* ; GOCEA: *Gammarus oceanicus* ; MUSS: *Mytilus edulis* ; IDOT: *Idotea balthica* ; PYGO: *Pygospio elegans* ; SPIO: *Spio filicornis* ; JAER: *Jaera albifrons* ; MICRON: *Micronephtys noetena*.

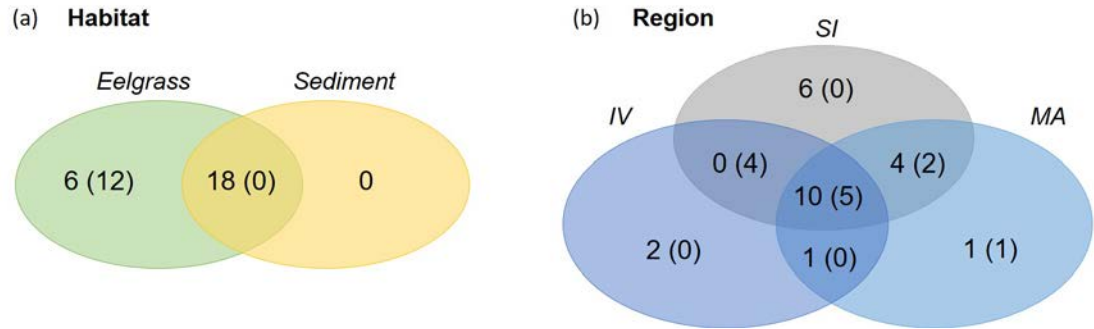


Figure S5. Venn diagram illustrating the numbers of shared and exclusive taxa of infauna for Habitat (a) and Region (b). The number in parenthesis represents the strictly epifauna taxa.

Table S6. Contribution of average biomass of the main macrobenthos taxa to the similarity (70.0 % cut-off; one-way SIMPER) of each habitat within region (average infauna similarity in brackets).

Group IVG - 65.3 (59.1)					
Species	Av.Biom	Av.Sim	Sim/SD	Contrib%	Cum.%
LITT	6.72	17.57	10.88	26.89	26.89
MYA	7.05	16.63	6.37	25.45	52.35
MACO	4.11	10.14	10.92	15.53	67.87
IDOT	3.79	8.94	5.20	13.69	81.56
Group IVY - 76.1 (74.3)					
Species	Av.Biom	Av.Sim	Sim/SD	Contrib%	Cum.%
MACO	7.35	33.10	14.86	43.51	43.51
NER	5.49	24.91	4.59	32.75	76.26
Group MAG - 69.4 (63.5)					
Species	Av.Biom	Av.Sim	Sim/SD	Contrib%	Cum.%
NER	6.37	12.70	29.59	18.30	18.30
LITT	6.62	12.68	9.50	18.27	36.57
MACO	6.22	11.93	6.83	17.19	53.76
GOCEA	5.16	9.54	12.89	13.75	67.51
MUSS	4.92	7.30	1.25	10.52	78.03
Group MAY - 75.6 (54.8)					
Species	Av.Biom	Av.Sim	Sim/SD	Contrib%	Cum.%
MACO	6.30	29.56	7.94	39.11	39.11
MYA	7.04	28.03	37.57	37.08	76.19
Group SIG - 60.7 (37.4)					
Species	Av.Biom	Av.Sim	Sim/SD	Contrib%	Cum.%
MACO	5.15	13.39	19.92	22.07	22.07
LITT	4.19	10.67	14.30	17.59	39.67
NER	3.18	7.68	8.13	12.67	52.34
LITR	3.40	6.77	1.71	11.16	63.49
MGAS	2.07	5.81	19.14	9.58	73.07
Group SIY - 58.5 (46.9)					
Species	Av.Biom	Av.Sim	Sim/SD	Contrib%	Cum.%
MACO	4.91	17.28	3.01	29.56	29.56
NER	4.41	14.34	14.86	24.54	54.10
HETER	3.67	13.98	11.55	23.93	78.03

Note: *Macoma balthica* (MACO), *Mya arenaria* (MYA), *Alitta virens* (NER), *Eteone longa* (ETEO), *Heteroastus filiformis* (HETER), *Littorina* spp. (LITT), *Littorina litorea* (LITR), *Mysis gaspensis* (MGAS), *Gammarus oceanicus* (GOCEA), *Mytilus edulis* (MUSS), and *Idotea balthica* (IDOT).

Table S7. Distance-based multivariate multiple regression (DistLM; procedure Best, selection by AICc) on the relation of environmental variables (%Organic content (OC), Shoot density, Salinity and relative proportion of Clay, Silt, medium and Coarse sand) to the macrobenthos (**ALL**) community structure (log transformed, Bray-Curtis). A) Marginal tests of significant variables ($p < 0.05$) using one variable at a time are shown. Prop. is the proportion of variability explained by the respective variable. B) Overall best solution models with k variable at a time. AICc = Akaike information criterion corrected for small sample size.

DistLM marginal test					
	Variable	SS (trace)	Pseudo-F	P	Prop
1	%OC	12718	7.013	< 0.001	0.108
2	Clay	15450	8.746	< 0.001	0.131
3	Silt	15045	8.483	< 0.001	0.128
4	Medium sand	9616	5.150	< 0.001	0.082
5	Coarse sand	9960	5.352	< 0.001	0.085
6	Shoot density	24784	15.436	< 0.001	0.210
7	Salinity	10654	5.761	< 0.001	0.090

Overall best solution					
AICc	R ²	RSS	k	Selections	ΔAICc
421.64	0.581	49412	7	All	0
422.44	0.556	52350	6	1; 3-7	0.80
422.53	0.555	52429	6	1-6	0.89
423.80	0.526	55894	5	1;3-6	2.16

Table S8. Distance-based multivariate multiple regression (DistLM; procedure Best, selection by AICc) on the relation of environmental variables (%Organic content (OC), Shoot density, Salinity and relative proportion of Clay, Silt, medium and Coarse sand) to the infaunal community structure (log transformed, Bray-Curtis). A) Marginal tests of significant variables ($p < 0.05$) using one variable at a time are shown. Prop. is the proportion of variability explained by the respective variable. B) Overall best solution models with k variable at a time. AICc = Akaike information criteria corrected for small sample size.

DistLM marginal test					
	Variable	SS (trace)	Pseudo-F	P	Prop
1	%OC	7848	5.103	< 0.001	0.081
2	Clay	12064	8.233	< 0.001	0.124
3	Silt	15198	10.769	< 0.001	0.157
4	Medium sand	7845	5.101	< 0.001	0.081
5	Coarse sand	3748	2.330	0.046	0.039
6	Shoot density	3626	2.251	0.050	0.037
7	Salinity	8516	5.578	< 0.001	0.088

Overall best solution					
AICc	R ²	RSS	k	Selections	ΔAICc
427.72	0.437	54682	7	All	0
428.02	0.408	57452	6	1; 3-7	0.30
428.23	0.406	57654	6	1-6	0.51
428.84	0.374	60798	5	3-7	1.12

Table S9. Average Bray-Curtis dissimilarity (%) of the macrofauna biomass (ALL) among habitat within region based on SIMPER results (average dissimilarity of infaunal community compartment in brackets).

Average dissimilarity (%)					
	IVG	IVY	MAG	MAY	SIG
IVG	-	-	-	-	-
IVY	59 (47)	-	-	-	-
MAG	50 (54)	56 (36)	-	-	-
MAY	59 (50)	32 (45)	59 (50)	-	-
SIG	51 (73)	62 (62)	58 (63)	64 (70)	-
SIY	74 (75)	49 (61)	63 (61)	54 (72)	57 (59)