UQAC
Université du Québec
à Chicoutimi

EFFETS DES RÉGIMES DE GLACES CÔTIÈRES SUR LES COMMUNAUTÉS BENTHIQUES MÉDIOLITTORALES DE L'ESTUAIRE MARITIME DU SAINT-LAURENT

par Mathis Bernard

Mémoire présenté à l'Université du Québec à Chicoutimi en vue de l'obtention du grade de maîtrise ès sciences (M. Sc.) en Ressources renouvelables (Ressources biologiques)

Québec, Canada

RÉSUMÉ

Les espèces fondatrices, telles que les zostères (*Zostera marina* L.), les macroalgues et les moules (*Mytilus* spp.), soutiennent une forte biodiversité et jouent un rôle essentiel dans la structure des communautés des écosystèmes médiolittoraux. En créant des habitats offrant refuge contre la prédation et la dessiccation, ainsi que des zones d'alimentation et de reproduction, elles constituent des composantes clés du fonctionnement écologique de ces milieux. En région subarctique, particulièrement dans l'Estuaire maritime du Saint-Laurent, ces espèces sont fortement influencées par les régimes de glace côtière se formant durant l'hiver. L'accumulation de glace le long du littoral forme un pied de glace, une structure fixée à la côte qui protège les habitats médiolittoraux des perturbations physiques et thermiques causées par les vagues, les tempêtes et les basses températures. Toutefois, dans un contexte de changements climatiques, les conditions de formation et de stabilité du pied de glace sont en importante modification. La diminution du recouvrement et de son épaisseur réduit progressivement son rôle protecteur et favorise une augmentation des perturbations hivernales sur les communautés côtières. Cette étude vise à déterminer l'effet des régimes de glace, soit des conditions protégées par un pied de glace ou exposées aux perturbations hivernales en son absence, sur le recouvrement des trois espèces fondatrices, ainsi qu'à évaluer les conséquences de ces perturbations sur la biodiversité et la structure des communautés associées. À l'aide de relevés photographiques réalisés par drones et caméra, le recouvrement des zostères, des macroalgues et des moules a été comparé entre un site protégé par un pied de glace et deux sites exposés aux perturbations hivernales. Ces relevés ont également permis de caractériser l'état des communautés benthiques selon trois statuts de substrat : Stable (maintien du recouvrement des espèces fondatrices), Abrasé (perte totale du recouvrement après l'hiver) et Référence (absence naturelle d'espèces fondatrices avant et après la saison hivernale). Les résultats montrent que les communautés situées dans le site protégé par un pied de glace ont subi de faibles pertes de recouvrement après l'hiver, soit environ 1 % pour les macroalgues et 10 % pour les moules. À l'inverse, les sites exposés aux perturbations hivernales ont connu une diminution beaucoup plus marquée du recouvrement, avec une perte moyenne d'environ 25 % pour les moules, atteignant jusqu'à 46 % en marge des bancs. Les herbiers de zostère présents dans les secteurs exposés ont également enregistré une réduction moyenne de leur recouvrement d'environ 20 %. Ces changements ont entraîné des modifications importantes dans la biodiversité et la structure des communautés associées, particulièrement dans les bancs de moules, où une diminution d'environ 50 % de la richesse spécifique a été observée. Les communautés associées aux herbiers de zostère et aux assemblages macroalgaux ont toutefois présenté des perturbations moins marquées de la structure de communauté à la suite des perturbations hivernales. Le maintien d'espèces secondaires, notamment de moules associées aux rhizomes des zostères arrachées, ainsi que le développement post-hivernal de l'algue filamenteuse *Ulothrix flacca* dans les zones Abrasées, ont favorisé la présence des espèces associées et limité les changements observés dans la biodiversité locale. Ces résultats mettent en évidence l'importance du pied de glace dans la dynamique des espèces fondatrices, mais également le rôle des mécanismes de résistance et de persistance des espèces dans le maintien de la biodiversité des écosystèmes côtiers subarctiques.

Mots clés : Régimes de glace ; Abrasion ; Perturbation hivernale ; Espèces fondatrices ; Macrophytes ; Bancs de moules ; Biodiversité ; Structure de communauté ; Estuaire maritime du Saint-Laurent.

ABSTRACT

Foundation species such as eelgrass (*Zostera marina* L.), macroalgae, and mussels (*Mytilus* spp.) support high biodiversity and play a key role in structuring communities within midlittoral ecosystems. By creating habitats that provide refuge from predation and desiccation, as well as feeding and reproductive areas, these species constitute essential components of the ecological functioning of these environments. In subarctic regions, particularly within the maritime estuary of the St. Lawrence, these species are strongly influenced by coastal ice regimes that develop during winter. The accumulation of ice along the shoreline forms an icefoot, a structure attached to the coast that protects midlittoral habitats from physical and thermal disturbances caused by waves, storms, and low temperatures. However, in the context of climate change, the formation and stability of the icefoot are undergoing major transformations. The reduction in its extent and thickness is progressively weakening its protective role and increasing winter disturbances affecting coastal communities. This study aimed to determine the effect of ice regimes, namely conditions protected by an icefoot or exposed to winter disturbances in its absence, on the cover of the three foundation species, while also evaluating the consequences of these disturbances on biodiversity and the structure of associated communities. Using drone and camera survey, the cover of eelgrass, macroalgae, and mussels was compared between a site protected by an icefoot and two sites exposed to winter disturbances. These surveys also made it possible to characterize benthic community conditions according to three substrate states: Stable (maintenance of foundation species cover), Abraded (complete loss of cover), and Reference (natural absence of foundation species before and after the winter season). The results showed that communities located at the site protected by an icefoot experienced only minor losses in cover following winter, with reductions of approximately 1% for macroalgae and 10% for mussels. In contrast, sites exposed to winter disturbances experienced much greater declines in cover, with an average loss of approximately 25% for mussels, reaching up to 46% along mussel bed margins. Eelgrass beds located in exposed sectors also showed an average reduction in cover of approximately 20%. These changes resulted in major modifications to biodiversity and the structure of associated communities, particularly within mussel beds, where a decline of approximately 50% in species richness was observed. Communities associated with eelgrass beds and macroalgal assemblages nevertheless exhibited less pronounced alterations in community structure following winter disturbances. The persistence of secondary species, notably mussels associated with uprooted eelgrass rhizomes, together with the post-winter development of the filamentous alga *Ulothrix flacca* within abraded areas, contributed to maintaining associated species and limiting changes in local biodiversity. These results highlight the importance of the icefoot in the dynamics of foundation species, while also emphasizing the role of resilience and species persistence mechanisms in maintaining biodiversity within subarctic coastal ecosystems.

Keywords: Ice regimes; Ice abrasion; Winter disturbance; Foundation species; Macrophytes; Mussel beds; Biodiversity; Community structure; St. Lawrence marine Estuary.

TABLE DES MATIÈRES

LISTE DES TABLES

LISTE DES FIGURES

LISTE DES ABRÉVIATIONS

EMSL : Estuaire maritime du Saint-Laurent
SLME : St. Lawrence marine estuary
PM : Pointe-Mistassini
QF : Quai Franquelin
AP : Anse à la Peinture
WW : Wet weight

DÉDICACE

« De loin, la plus grande menace pour l'océan,
Et donc pour nous-mêmes,
Est l'ignorance.
Mais nous pouvons faire quelque chose à ce sujet. »

Sylvia A. Earle

REMERCIEMENTS

Je souhaite exprimer ma sincère reconnaissance envers Mathieu Cusson, mon directeur de recherche. Depuis le début de cette recherche, il a su porter un regard critique, mais toujours bienveillant. Ses conseils, son aide et nos nombreuses rencontres m'ont permis de développer considérablement mes compétences et d'acquérir énormément d'assurance et d'autonomie. Je garderai toujours en tête nos sorties sur le terrain. Un grand merci pour tes encouragements !

Je tiens également à remercier mon codirecteur de recherche, Christian Nozais. Nos discussions à Rimouski et lors des congrès m'ont permis d'avoir de nouvelles perspectives sur ma recherche et d'avoir confiance en mon travail. Merci pour tes conseils et ton engagement dans la rédaction de ce mémoire.

Un merci tout particulier aux membres de mon jury d'évaluation de mémoire, Vincent Lecours et Ladd Johnson, pour leurs précieux conseils, leurs commentaires constructifs et leurs encouragements à la suite de cette évaluation.

Je remercie également les professeurs Pascal Bernatchez et Simon Bélanger, ainsi que toute l'équipe du laboratoire de Dynamique et de Gestion Intégrée des Zones Côtières de l'UQAR. Vous qui avez effectué de nombreux vols de drone pendant plusieurs semaines sur la Côte-Nord et qui vous êtes montrés des plus bienveillants, enthousiastes et aidants durant mon passage dans votre laboratoire, merci.

Je souhaite aussi souligner le soutien précieux de certaines personnes, dont Greta Capelli, qui a su rendre ce projet plus léger et les moments difficiles plus supportables. Tu as su m'épauler, me faire rire et surtout me motiver jour après jour, soir après soir. Je te serai toujours reconnaissant et te souhaite tout le meilleur pour la réussite de ton doctorat. On se retrouve très bientôt !

Merci également à toutes les personnes avec qui j'ai passé du temps sur le terrain et en laboratoire. Merci à Léna Delga pour ton aide au début de ma maîtrise. Merci à Étienne Lecointe pour tes encouragements et ton accompagnement sur la Côte-Nord, sous la pluie, la neige et surtout en pleine canicule ! Je remercie également Shuaishuai Li pour ton aide précieuse sur le terrain, thank you !

Bien sûr, un immense merci à Noah Fruytier et Marie Celhaiguibel pour tous les bons moments passés ensemble durant mon dernier été de terrain. Vous avez été d'une aide et d'un encouragement remarquables. Je vous suis reconnaissant et j'ai hâte de collaborer avec chacune d'entre vous à l'avenir. Je remercie également Émilie Hebert et Erwann Falquero pour leur aide dans l'analyse des données en laboratoire.

Je tiens également à remercier mes « colocs à terre », avec qui j'ai partagé d'innombrables moments mémorables durant ces deux années à Chicoutimi. Merci pour votre soutien

constant et pour toute l'entraide dont nous avons faire preuve au fil du temps. Je suis convaincu que chacun de vous accomplira de grandes choses dans la suite de son parcours.
Enfin, je souhaite exprimer ma gratitude à toutes les personnes qui m'ont accompagné durant ma maîtrise, m'ont soutenu et offert de précieux conseils. Un merci tout particulier à mes parents, ma famille et mes amis, dont les encouragements et la présence, même à plus de 5 000 km, m'ont porté tout au long de ce parcours. Vous avez aussi contribué à la réalisation de cette recherche !

AVANT-PROPOS

Ce mémoire comporte une introduction générale en français, deux chapitres sous forme d'article scientifique en anglais et une conclusion générale en français. Les articles présentent les résultats de l'étude menée pour ce mémoire et dont je serai le premier auteur, mon superviseur et mes co-superviseurs seront les coauteurs. Les résultats présents dans ce mémoire ont fait l'objet de communications scientifiques lors des congrès nationaux et internationaux suivants :

- **Bernard M.**, Nozais C., Bernatchez P., Cusson M (2026). *Under Ice: From Protection to Abrasion - Effects on Macroalgae and Mussel beds.* Affiche. 54th Annual Benthic Ecology Meeting Society. Virginia Beach, VA (USA). 2 mars 2026.

- **Bernard M.**, Nozais C., Bernatchez P., Cusson M. (2026). *Communautés médiolittorales face à des hivers imprévisibles: influence des glaces côtières*. Présentation orale. Réunion scientifique annuelle de Québec-Océan 2026. Rivière-du-Loup, QC (Canada). 4 février 2026.

- **Bernard M.**, Nozais C., Bélanger S., Bernatchez P., Cusson M. (2025). *De la protection à l'abrasion : effet des glaces sur les habitats côtiers*. Affiche. Forum littoral en commun - Restauration des écosystèmes côtiers, Baie-Comeau, QC (Canada). 5 novembre 2025.

- Cusson M., Susini C., Cimon S., **Bernard M.**, Bélanger S., Bernatchez P., Thériault V., Nozais C. (2025). *From scouring to recovery : macroalgal community resilience in ice-disturbed coastal ecosystem.* Présentation orale. European Marine Biology Symposium. Bodø, (Norvège). 8 juillet 2025.

- **Bernard M.**, Nozais C., Bélanger S., Bernatchez P., Cusson M. (2025). *Effets des régimes de glaces sur les communautés benthiques intertidales de l'estuaire maritime du Saint-Laurent*. Affiche. Réunion scientifique annuelle de Québec-Océan 2025. Rivière-du-Loup, QC (Canada). 26 février 2025.

INTRODUCTION GÉNÉRALE

Les milieux côtiers

Situés à l'interface entre les écosystèmes terrestres et marins, les milieux côtiers jouent un rôle écologique crucial. S'étendant sur environ 1 634 701 kilomètres de côtes à l'échelle mondiale (Burke *et al.* 2001), ces milieux soutiennent plus d'un quart de la population humaine vivant à moins de 50 km de la côte (Cosby *et al.* 2024). Composés de nombreux habitats tels que les marais salés, les herbiers de zostère, les récifs coralliens et bien d'autres, cette zone représente une des plus importantes sur la planète en fournissant des zones de refuge (Duffy 2006), d'alimentation (Orth *et al.* 2006) et de reproduction pour de nombreuses espèces terrestres et aquatiques (Beck *et al.* 2001). Ces écosystèmes comptent ainsi parmi les systèmes naturels les plus productifs et les plus diversifiés sur Terre (Barbier *et al.* 2011). Cette richesse d'habitats fournit une multitude de services écosystémiques essentiels aux populations humaines (Costanza *et al.* 1997) en protégeant les côtes contre l'érosion et les tempêtes (Möller *et al.* 2014; Spalding *et al.* 2014), régulant des cycles biogéochimiques (Duarte et Cebrian 1996), mais également en soutenant les pêcheries et l'aquaculture (Beck *et al.* 2001). En outre, les milieux côtiers offrent des bénéfices culturels et récréatifs, contribuant ainsi à la qualité de vie et à l'économie locale (Costanza *et al.* 1997) et sont indispensables au bon maintien des activités humaines.

Les milieux côtiers figurent toutefois parmi les environnements les plus perturbés, caractérisés par une forte variabilité environnementale et soumis à de multiples facteurs de stress, tant physiques que biologiques (Menge et Sutherland 1987; Harley *et al.* 2006). Les fluctuations de température (Helmuth *et al.* 2002), les variations de salinité (Telesh *et al.* 2013), ainsi que les cycles de marée contribuent à générer des conditions environnementales

particulièrement dynamiques et changeantes (Raffaelli et Hawkins 1999). À cette variabilité naturelle se superposent également plusieurs pressions d'origine anthropique, notamment les changements climatiques (Harley *et al.* 2006), la montée du niveau de la mer (Nicholls 2004; Cazenave et Cozannet 2014), ainsi que la pollution et l'intensification des activités humaines dans les zones littorales (Vitousek *et al.* 1997; Halpern *et al.* 2008).

Au sein de ces milieux côtiers, les écosystèmes médiolittoraux figurent parmi les habitats les plus dynamiques et les plus contraignants pour les organismes marins (Connell 1972; Denny et Wethey 2001). Située entre les niveaux de marée haute et de marée basse, la zone médiolittorale est soumise à des cycles répétés d'immersion et d'émersion, entraînant des variations de température, d'humidité et d'exposition à l'air (Colman 1933; Stephenson et Stephenson 1949; Schiel *et al.* 2004). Les organismes occupant ces habitats doivent ainsi développer diverses stratégies physiologiques et écologiques afin de tolérer des conditions environnementales souvent extrêmes, marquées notamment par la dessiccation, de fortes variations thermiques et d'importantes contraintes hydrodynamiques générées par les vagues et les courants (Davison et Pearson 1996; Helmuth *et al.* 2006). Malgré ces contraintes, les écosystèmes médiolittoraux supportent une grande diversité d'organismes et présentent des structures de communautés complexes (Bruno *et al.* 2003; Lemieux et Cusson 2014). La distribution et l'abondance des espèces dans ces milieux sont influencées par une combinaison de facteurs biotiques et abiotiques, incluant les gradients environnementaux, la compétition et la prédation (Menge et Sutherland 1987; Joseph et Cusson 2015; Cimon et Cusson 2018; Cimon *et al.* 2021). Dans de nombreux systèmes côtiers, certaines espèces exercent un rôle important et favorisent l'établissement d'autres organismes. Ces espèces, appelées espèces fondatrices, contribuent fortement à l'organisation et au fonctionnement des communautés benthiques (Stachowicz 2001).

Les espèces fondatrices

Par définition, les espèces fondatrices sont des organismes capables de transformer physiquement leur milieu et de modifier les conditions écologiques locales, créant ainsi des habitats propices à l'établissement et au maintien d'une forte diversité d'espèces associées (Jones *et al.* 1994; Angelini *et al.* 2011). En augmentant la complexité structurelle du milieu, elles peuvent atténuer certains stress environnementaux et offrir des refuges contre la prédation (Orth *et al.* 1984; Watt et Scrosati 2013). Dans les environnements médiolittoraux des régions tempérées et subarctiques, les principales espèces fondatrices incluent notamment les macroalgues, les moules et les zostères (*Zostera marina* Linnaeus, 1753). Leur présence favorise la diversité biologique locale et soutient de nombreuses fonctions écologiques essentielles (Attrill *et al.* 2000; Borthagaray et Carranza 2007; Gollety *et al.* 2011). En se développant en canopées, en agrégats denses ou en vastes herbiers, ces organismes augmentent la complexité physique de l'habitat et modifient les conditions environnementales à fine échelle. Leur présence peut notamment atténuer l'effet des vagues et des courants, réduire les risques de dessiccation, stabiliser les sédiments et favoriser l'accumulation locale de matière organique (Kautsky et Evans 1987; Davison et Pearson 1996; Bertness *et al.* 1999; Hemminga et Duarte 2000; Gutiérrez *et al.* 2003; Duarte *et al.* 2005; Boller et Carrington 2006; Röhr *et al.* 2018). Ces structures biogéniques offrent également des refuges, des surfaces de fixation et des zones d'alimentation pour de nombreuses espèces animales et végétales, soutenant ainsi une biodiversité souvent plus élevée que dans les habitats non structurés (Orth *et al.* 1984; Beck *et al.* 2001; Heck *et al.* 2003; Norling et Kautsky 2007; Wikström et Kautsky 2007; Watt et Scrosati 2013; Arribas *et al.* 2014). Par leurs effets sur les conditions du milieu et sur les interactions entre espèces,

les espèces fondatrices jouent donc un rôle central dans la productivité, la stabilité et le fonctionnement global des communautés benthiques côtières (Connolly 1995; Orth *et al.* 2006; Waycott *et al.* 2009; Lemieux et Cusson 2014; Ørberg *et al.* 2018).

Perturbations hivernales

Dans les régions tempérées froides, subarctiques et arctiques, les conditions hivernales représentent une source majeure de perturbations pour les communautés médiolittorales (Ellis et Wilce 1961; Pugh et Davenport 1997). Aux hautes latitudes, durant la période hivernale, comprise entre la fin novembre et début avril, une baisse marquée des températures caractéristiques favorise la formation de glace de mer (Saucier *et al.* 2003). L'accumulation de cette glace le long du littoral entraîne la formation d'un pied de glace de bas estran, une structure fixée au rivage qui se développe sur la zone médiolittorale et qui, lorsqu'elle est présente, est en continuité avec la banquise côtière adjacente (Dionne 1973). Cette formation de glace influence fortement les conditions physiques du médiolittoral en modifiant l'exposition des organismes benthiques aux contraintes mécaniques et thermiques durant la saison hivernale (Braby 2007; Scrosati et Eckersley 2007; Scrosati 2022). Le pied de glace agit ainsi comme une barrière protectrice entre les glaces dérivantes et le substrat médiolittoral, limitant l'intensité des perturbations (Forbes et Taylor 1994; Barnes 1999). Lorsque cette structure est stable et persistante durant la période hivernale, elle favorise le maintien des communautés sous-jacentes (Anderson 1983). À l'inverse, lorsque le pied de glace est absent ou instable, les habitats benthiques peuvent être directement exposés à l'action abrasive des glaces mobiles transportées par les courants de marée ou les tempêtes, entraînant des perturbations physiques importantes (Archambault et Bourget 1983; McCook et Chapman 1991; Cusson et Bourget 2005). La diminution de la fonction protectrice du pied

de glace peut également entraîner une augmentation du stress thermique (Scrosati et Eckersley 2007). Les hivers rigoureux des régions tempérées froides et subarctiques, pouvant atteindre des températures avoisinant les -40°C, peuvent alors directement impacter les communautés médiolittorales non protégées par le pied de glace, particulièrement lors des périodes de basse marée (Braby 2007). Durant plusieurs heures d'émersion, les macrophytes, les moules et d'autres invertébrés benthiques sont ainsi soumis à des conditions thermiques extrêmes et à un stress physiologique important, susceptibles d'entraîner une mortalité élevée (Murphy et Johnson 1980; Robertson et Mann 1984; Pearson et Davison 1993; Boroda *et al.* 2020). Ainsi, l'absence de protection par un pied de glace durant la période hivernale, dans des environnements soumis à de grandes perturbations, peut entraîner une abrasion du substrat, arracher les organismes fixés et provoquer des modifications importantes de la structure des communautés benthiques (Peck *et al.* 1999; Bertocci *et al.* 2005; Petzold *et al.* 2014).

Le Saint-Laurent marin subarctique

Présent entre deux régions biogéographiques distinctes, telles que la région subarctique et la région de transition boréale/subarctique **(Fig. 1)**, l'estuaire maritime du Saint-Laurent (EMSL) est caractérisé en hiver par la formation de glace de mer le long des côtes (Saucier *et al.* 2003). Dans un contexte de changements climatiques, les régimes de glace côtière dans l'EMSL sont en pleine transformation. Au cours de l'hiver 2017, il a été observé que la durée d'englacement durant la période hivernale avait diminué de 5 semaines comparativement à la période climatique de 1981-2010 (Senneville *et al.* 2014; Galbraith *et al.* 2018). En 2024, il a été reporté que l'épaisseur de glace dans le système a perdu plus de 20 cm par rapport aux années 1991-2007 (Galbraith *et al.* 2025). Couplé à ces observations, Bandet *et al.* (2020)

ont montré qu'une augmentation du nombre de tempêtes et de leur intensité sera à prévoir pour les années à venir. Ces modifications pourraient altérer profondément le rôle protecteur du pied de glace et, par conséquent, la dynamique des communautés benthiques médiolittorales. Dans ce contexte, comprendre comment les différents régimes de glace influencent les espèces fondatrices et les communautés associées devient essentiel pour mieux anticiper l'évolution future des écosystèmes côtiers tempérés froids, subarctiques et arctiques.

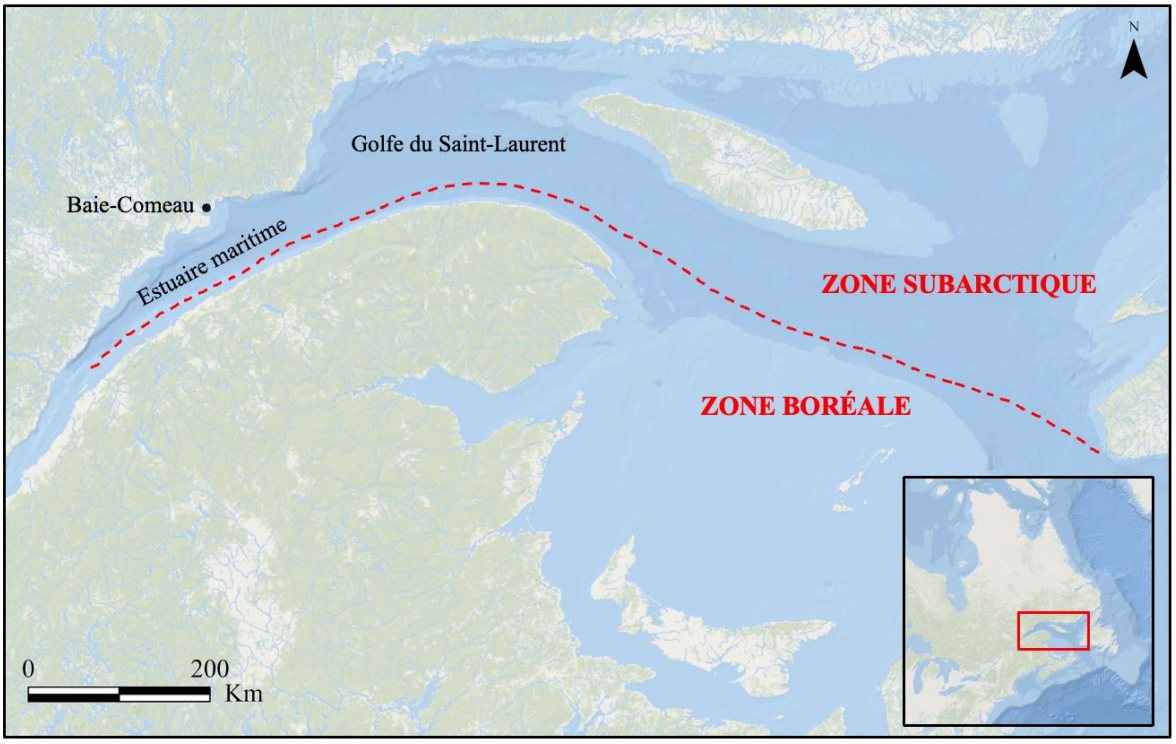


Figure 1. Carte des zones biogéographiques boréale et subarctique du Saint-Laurent marin, incluant l'estuaire maritime et le golfe du Saint-Laurent.

Objectifs et structure du mémoire

L'objectif général de mon mémoire de maîtrise est de caractériser l'effet des régimes de glace sur les communautés benthiques médiolittorales de l'Estuaire maritime du Saint-Laurent,

notamment les habitats dominés par les macroalgues, les bancs de moules et les herbiers de zostère. Trois sous-objectifs seront développés dans les deux chapitres qui composent ce mémoire de maîtrise, afin de mieux comprendre l'influence des différents régimes de glace sur les espèces fondatrices et leurs communautés associées. Ces objectifs sont les suivants :

i) Quantifier les variations de recouvrement de trois espèces fondatrices avant et après la saison hivernale;

ii) Évaluer l'impact des variations de recouvrement sur la biodiversité et la structure des espèces associées aux espèces fondatrices;

iii) Comparer l'influence des deux régimes de glace contrastés, soit la présence d'un pied de glace protecteur et son absence, entraînant une exposition accrue aux glaces dérivantes, sur les habitats de macroalgues, de moules et de zostères marines.

Afin de mieux comprendre les impacts hivernaux sur ces différents habitats, et considérant les différences méthodologiques associées à leur échantillonnage et à leur analyse, le mémoire a été structuré en deux chapitres sous forme d'articles scientifiques. Le premier chapitre évalue l'impact des régimes de glace sur les habitats médiolittoraux dominés par les macroalgues et les bancs de moules. Le second chapitre porte sur l'effet de l'absence d'un pied de glace protecteur sur les herbiers de zostère médiolittoraux, en mettant l'accent sur les modifications de leur structure et des communautés benthiques associées.

Préliminairement à cette étude, nous avons observé que l'absence de pied de glace affectait fortement le substrat médiolittoral, entraînant des pertes massives de nombreux bivalves ainsi qu'une diminution importante du recouvrement des macrophytes marins. À la lumière de ces

observations (aussi, voir le texte de la méthodologie pour les termes « Abrasé », « Stable » et « Référence » employés ci-dessous), les hypothèses suivantes ont été émises :

i) Les anomalies de recouvrement des espèces fondatrices seront plus élevées en absence d'un pied de glace protecteur.

ii) Les communautés des zones Abrasées seront davantage similaires aux zones de Référence qu'à celles des zones dites Stables.

iii) Les sites Exposés après la saison hivernale présenteront une biodiversité et une structure des communautés associées différentes de celles observées dans les sites Protégés.

L'EMSL constitue un site d'étude particulièrement propice pour tester ces hypothèses puisqu'on y observe à la fois des zones protégées et exposées, ainsi qu'une forte abondance de macrophytes et de bancs coquilliers le long du littoral. Afin de répondre à nos objectifs, des analyses d'images satellitaires ont d'abord été réalisées afin de distinguer deux régimes de glace contrastés, correspondant à des zones Protégées par un couvert de glace côtière et à d'autres zones Exposées, sans pied de glace. Un suivi photographique des trois principales espèces fondatrices de l'EMSL a ensuite été réalisé avant et après la saison hivernale 2024-2025. Ces observations ont permis de quantifier les modifications du recouvrement de chacune des espèces fondatrices après l'hiver selon le régime de glace, puis de définir trois statuts de substrat : Stables, Abrasées et Référence. Des échantillonnages biologiques ont ensuite été réalisés dans chacun de ces habitats afin de caractériser les communautés associées en fonction du statut du substrat et du régime de glace.

CHAPITRE I
EFFECTS OF COASTAL SEA ICE ON INTERTIDAL BENTHIC COMMUNITIES IN THE ST. LAWRENCE MARINE SYSTEM

1.1. Introduction

The coastal zone is a dynamic interface where terrestrial, marine, and atmospheric systems interact (Gattuso *et al.* 1998). Considered among the most productive environments worldwide, the coastal marine ecosystems are structured by foundation species, including canopy-forming macroalgae, mussels, and eelgrass (Dayton 1971; Stachowicz 2001). These ecosystem engineers play a key role in structuring habitat and sustaining high biological richness and diversity by providing attachment surfaces, refuges from predation, and food resources for numerous associated species (Bruno *et al.* 2003; Nicholls 2004; Barbier *et al.* 2011). By modifying local environmental conditions, they also mitigate desiccation stress, particularly intense during emersion periods (Bertness *et al.* 1999). The presence of foundation species such as macroalgae and mussels is essential for maintaining the productivity and ecological functioning of intertidal communities (Hardwick-Witman and Mathieson 1983; Suchanek 1985; Everett 1994; Jones *et al.* 1994; Lafferty and Suchanek 2016). However, in cold-temperate environments, this ecological role is strongly modulated by winter disturbances (including winter storms, ice scour, low temperatures, ect. ; Bergeron and Bourget 1984; Bergeron and Bourget 1986; Scrosati and Heaven 2006). In the Northern Hemisphere, especially in subarctic regions, sea ice forms during the winter season and melts in early spring (Saucier *et al.* 2003). Along coastlines, sea ice can take different forms, notably landfast ice and intertidal icefoots. Terminology describing these coastal ice formations varies among authors (Dionne 1973). Following Dionne (1973) description of the

lower intertidal icefoot, the term *icefoot* is used throughout this study to describe the shore-attached coastal ice formation that develops over the intertidal zone and, when present, remains continuous with adjacent landfast ice. This ice formation plays a major role in maintaining the underlying intertidal benthic communities (Anderson 1983). It provides two main types of protection (Scrosati 2022). During low tide, when organisms become exposed to the air, the icefoot acts as a thermal insulator, maintaining temperatures near -5 °C beneath it even when air temperatures drop to -40 °C (Braby 2007; Scrosati and Eckersley 2007; Scrosati 2022; Gill *et al.* 2024). The icefoot also functions as a mechanical shield, reducing physical disturbance by acting as a barrier against wave action, storms, and especially ice scour affecting intertidal benthic communities (Forbes and Taylor 1994; Barnes 1999; Gutt 2001). It further limits sediment transport and contributes to reducing coastal erosion caused by winter storms (Barnhart *et al.* 2014). The icefoot is therefore particularly important in subarctic and cold-temperate regions, where harsh winter conditions may strongly structure intertidal communities. Climate change is reducing both the occurrence and stability of coastal sea ice (Senneville *et al.* 2014). In the St. Lawrence Estuary and Gulf, Galbraith *et al.* (2018) reported a decrease in the ice season of approximately 5 weeks in 2017 relative to the 1981–2010 climatological period. Consistent with this decline in ice duration, coastal sea-ice thickness in the estuary decreased by more than 20 cm in 2024 compared with the 1991–2020 baseline (Galbraith *et al.* 2025). These observations highlight an ongoing shift in regional ice regimes. The reduction and destabilization of coastal ice cover increase the exposure of intertidal communities to intense physical disturbances (Johnson 2007; Barnhart *et al.* 2014). When icefoot protection weakens or disappears, wave dislodgement (Denny 1995; Carrington *et al.* 2009), spring breakup (Gutt 2001) and direct ice scour become dominant disturbance agents (Archambault and Bourget 1983; Scrosati and Eckersley 2007).

These disturbances processes can remove large portions of intertidal organisms including foundation species (Peck *et al.* 1999; Petzold *et al.* 2014). As these foundation species support local biodiversity, their loss can propagate through associated community, altering community composition and spatial organization (Dayton 1971; Bertocci *et al.* 2005; Largaespada *et al.* 2012; Lemieux and Cusson 2014; Cimon and Cusson 2018). In parallel, the absence of an icefoot markedly increases thermal stress on intertidal assemblages (Murphy and Johnson 1980). While foundation species and their associated species exhibit some degree of cold tolerance, tissue damage generally occurs at temperatures below approximately −10 °C (Pearson and Davison 1993; Gutt 2001; Boroda *et al.* 2020). Icefoot loss at low tide exposes organisms directly to colder and more variable air temperatures, increasing freezing injury and winter mortality (Carrington *et al.* 2009). The transition from protected to ice-free winter conditions shift intertidal ecosystems from environments primarily buffered against atmospheric forcing to systems increasingly controlled by both mechanical disturbance and extreme thermal stress. To better anticipate the ecological consequences of ongoing climatic change, it is necessary to understand how modifications in winter ice conditions influence the structure of intertidal ecosystems.

To our knowledge, the positive effects of coastal winter ice (e.g., thermal protection, sediment stabilization, and/or other habitat-buffering processes) and its negative effects (e.g., ice scouring, erosion, and/or other physical disturbances) on intertidal benthic communities remain poorly understood, and no study has explicitly evaluated how these contrasting regimes shape associated community structure and biodiversity. This study aims to evaluate changes in the presence of foundation species between two contrasting ice regimes (Protected and Exposed) and to assess how shifts in icefoot protection influences the biodiversity and structure of macroalgal and mussel bed-associated communities. We hypothesized that the

presence of a seasonally persistent icefoot mitigates winter disturbance, thereby helping to maintain the cover of foundation species within intertidal communities. In contrast, under ice-free winter conditions, we expect that increased exposure to mechanical disturbance and thermal stress will reduce foundation species dominance. We further predict that disturbance-mediated substrate abrasion result in lower biodiversity (i.e., reduced taxonomic richness, biomass and diversity) and, thus, promote a shift toward a simplified community structure.

1.2.Materials and Methods

1.2.1. Study sites

The study was conducted from August 2024 to July 2025 on intertidal benthic communities along the north shore of the St. Lawrence Marine Estuary (SLME), Quebec, Canada. The coastline of the region is heterogeneous, with alternating rocky and sedimentary habitats distributed across enclosed bays, within a subarctic area of the SLME characterized by water masses ranging in temperature from -2 to 15 °C and 24 to 28 in salinity (Fradette and Bourget 1980). The tidal regime is mixed and predominantly semidiurnal, with an average tidal range of approximately 3.5 metres (see www.tides.gc.ca).

Based on Sentinel-2 L1C satellite imagery available between 2015 and 2024, two intertidal areas experiencing distinct ice conditions were identified. At Pointe-Mistassini (PM; 49.281507° N, 67.942232° W; **Fig. A.I.1a**), the intertidal zone forms a rocky terrace of approximately 0.2 km², where abundant boulder deposits provide substantial protection from drifting ice and favor the accumulation of ice. In addition, PM is partially sheltered from prevailing northerly winds by a narrow headland located immediately north of the site. This topographic protection may reduce wave exposure and promote the formation and persistence

of a protective icefoot. The Quai Franquelin (QF; 49.286995° N, 67.893605° W; **Fig. A.I.1b**) site is located 3.5 km east of Pointe-Mistassini. QF features an intertidal area of approximately 0.33 km², characterized by a sandy substrate with glacial boulders, although these boulders are less abundant and generally smaller at QF than at PM. Unlike PM, QF is more directly exposed to the estuary and to the more open sea to the northeast, which limits the accumulation and persistence of a protective icefoot. Consequently, QF is more vulnerable to wave action, storms, and drifting ice than PM, consistent with observations made since 2015. For example, during the winter 2025, PM experienced 55 days of icefoot persistence compared with only six days of ice cover at QF (Unpublished satellite imagery data). Based on these contrasting winter ice conditions, PM and QF were considered to represent two distinct ice regimes, hereafter referred to as Protected and Exposed, respectively, rather than geographic sites.

1.2.2. Experimental design

At both sites, macroalgal canopies on boulders and mussel beds on sediments were surveyed.

a) Macroalgal cover survey

Macroalgal communities were monitored on the rocky surfaces of boulders at each site. At both PM and QF, four boulder rocks were randomly selected (n = 4 per site) according to predefined criteria : each boulder had a minimum diameter of 2 m with its side covered of at least 50% of macroalgae, its base elevation relative to sea level was within 30 cm of the others, and it was isolated from nearby large boulders (at least 1 m from any other rock larger than 40 cm). To monitor the macroalgae and detect abrasion, we took photographs of the lateral side around each boulder from a distance of 1 metre using a 16,05-megapixel camera

(**Fig. A.I.4**). A total of six images of the rock walls were captured at 60° intervals around each boulder in August 2024 and again in May 2025. Using Photoquad (Schneider *et al.* 2012), we documented the benthic assemblages (see methods in **Annexe III**) in each ice regime condition for both periods (n = 24 photographs per ice regime, total = 48).

b) Mussel beds cover survey

Mussel beds surveys were monitored with areal pictures taken with the DJI Matrice 350 RTK drone equipped with a multispectral camera (pixel resolution of 1 cm on the ground), flights were conducted at an altitude of 84 m over the PM and QF sites (**Fig. A.I.2**; **Fig. A.I.3**). The surveyed area was 0.54 km² at PM and 1.05 km² at QF, with surveys conducted in October 2024 and early spring (May) 2025. Based on the orthomosaics obtained at PM and QF, ten 10 × 10 m subzones (100 m^2) were randomly selected across areas with at least 40% mussel cover (based on October 2024 data), with five subzones located in the center of the mussel bed and five along its edge. The size and positioning of the subzones were chosen as a compromise between capturing habitat heterogeneity and maintaining suitable resolution for fine-scale analysis of mussel bed cover and associated features. The mussel bed cover in each subzone was digitized using *Create Features* tool (ArcGIS pro), generating polygons that accurately represented the extent of mussel beds pre- and post-winter.

c) Identification of sampling states

Images collected in macroalgal and mussel beds communities pre- and post-winter were compared to assess changes in community cover. As winter impacts were unpredictable, impacted areas could not be identified *a priori*; therefore, macroalgal and mussel beds surveys were analyzed retrospectively to select our sampling plots. Based on these analyses,

three substratum states were identified according to changes observed in May 2025 relative to August 2024 : Stable, Abraded and Reference (**Fig. 2**). The Stable state corresponded to areas where foundation species (macroalgae and mussel beds) cover was maintained (i.e., no surface loss) whereas the Abraded state was characterized by a near-complete loss of foundation species cover. Finally, the Reference state corresponded to areas of bare sand/rocky and lacking foundation species cover (nearly 0%), both in August 2024 and May 2025. To minimize potential variability associated with compass direction of boulder surfaces, trios of substratum states (Stable, Abraded, and Reference) surrounding each boulders rocks were systematically selected from the same photographic image. Preliminary analyses (not shown) indicated that compass direction had no significant effect on community structure, and this factor was therefore excluded from subsequent analyses. For each state, ten sampling plots were randomly selected (n = 10 per state and foundation species, total n = 60 per ice regime).

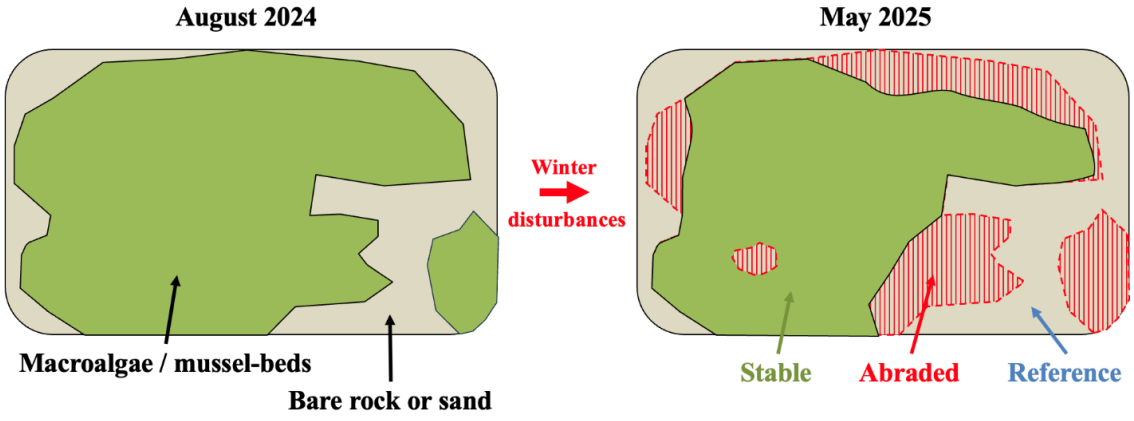


Figure 2. Schematic of the experimental design illustrating the three sampling conditions (Stable, Abraded, and Reference) based on foundation species cover pre- and post-winter season.

d) Intertidal benthic community sampling

Macroalgae and mussel communities were characterized in all plots across each predefined substratum states. First, a non-destructive technique was used in each state to visually estimate the percentage cover of macroalgae and mussels using 20 × 20 cm quadrats subdivided into 25 units, with each unit scored from 0 to 4 and representing 4% of the total surface area. This method was applied to both vertical surfaces (macroalgae on the lateral sides of boulders) and horizontal surfaces (mussel bed communities on the ground). In all plots, we first removed all macroalgae (or mussel) individuals and their associated epibionts and placed them in separate plastic bags and assigned them to the "foundation compartment". Within the same 20 x 20 cm quadrat, we then collected all other organisms, which were considered part of the "benthic compartment". Specifically, on vertical rocky surfaces, all sessile organisms were gently removed using a scraper. On horizontal surfaces, within mussel beds (mostly sedimentary surfaces), the benthic compartment was collected with a hand trowel from the surface together with the upper 1 cm of the sediment when present. This method ensured consistent sampling across all plots and allowed the benthic compartment to be sampled even when macroalgae or mussels were absent (3 states x 10 plots x 2 ice regimes = 60 samples).

After collection, epibiont organisms were gently removed by hand from macroalgae and mussels, rinsed through a 1 mm mesh sieve to retain macrobenthic species, and stored at -20C° until sorting and identification to the lowest possible taxonomic level (typically species level) under a stereomicroscope. Individuals were counted and wet (or towel-dried) biomass (g WW) was measured by taxa to the nearest 0.0001 g (or 0.5 g for very large individuals). Biomass of the turf and encrusting species was obtained by giving an arbitrary value of 0.5 g per % cover units (~ 4 cm^2) for *Hildenbrandia rubra* while a value of 1 g per % cover unit

was given to *Ulothrix flacca*. Only living organisms were included in biomass measurements. Living mussels were weighed with their shells, whereas empty shells and detrital material were excluded. Taxa richness and total biomass (g WW) of the associated community were subsequently calculated for each sample. Living macroalgae and mussels (for mussel community) were processed separately and were not included in the associated community biomass analyses. This procedure allowed us to estimate taxonomic richness, total biomass and Simpson's diversity for each sample.

1.2.3. Data analysis

Seasonal changes for both macroalgal and mussel beds, covering anomalies between autumn 2024 and spring 2025 were compared between ice regimes (two levels: Protected and Exposed, fixed factors) using a permutational analysis of variance (PER-ANOVA, 9999 runs; Anderson 2005). For mussel beds, a two-way permutational analysis of variance (PER-ANOVA, 9999 runs) with both factors treated as fixed, was used to assess the combined effects of ice regime (Protected or Exposed as described above) and placement within the mussel bed (Center or Edge), and their interaction on cover anomalies.

Taxa richness, total biomass and Simpson's diversity were compared among substratum states (Stable, Abraded and Reference), ice regimes (Protected and Exposed), and their interaction, using a two-ways permutational analysis of variance (PER-ANOVA, 9999 runs) based on a Euclidean distance matrix.

With the same design as mentioned above, the community abundance (g WW) structure was analyzed between ice regimes with a permutational multivariate analysis of variance (PERMANOVA, 9999 runs) using a Bray–Curtis similarity matrix from biomass transformed data (dispersion-weighted and square root transformed; Clarke *et al.* 2006;

Clarke *et al.* 2014). We added a dummy variable (0.1) to circumvent the joint zero problem (Clarke and Gorley 2015). Variance heterogeneity/dispersion was assessed with the PERMDISP routine (Clarke and Gorley 2015) : no strong effect of dispersion was observed in all tests. Post-hoc pairwise comparisons by PER-ANOVA or PERMANOVA were done if significance is detected. Community patterns were visualized using non-metric multidimensional scaling (nMDS) or by bootstrap averages and simulated 95% confidence region of the factors centroids in an mMDS. We evaluated the contribution of each taxon to the observed dissimilarities between states using a similarity percentage analysis (SIMPER). All analyses were performed using PRIMER-e v7 with the PERMANOVA+ add-on. An $\alpha = 0.05$ was used for all statistical tests, and marginally significant results were carefully considered.

1.3. Results

1.3.1. Surface cover changes between ice regimes

We observed no significant decline in macroalgal cover (average and ± SE : 1.39 ± 1.46 %; n = 24; min-max: +8.63 to -11.25 %) at the site Protected by a stable icefoot during winter 2024-2025, as the 95% confidence interval overlapped zero (**Fig. 3**). In contrast, the Exposed site exhibited a greater decline of 4.44 ± 2.41 % (n = 24; min-max: +3.34 to - 15.40%), which was marginally higher than in Protected site (Pseudo-$F_{1,46}$ = 3.74; p = 0.0528; **Fig. 3**; **Table A.I.3**).

Mussel bed cover anomalies (difference in foundation species cover between 2024 and 2025) did not differ significantly between ice regimes when all plots (i.e. from both Center and Edge) were analyzed together (Pseudo-$F_{1,18}$ = 2.94; p = 0.1019; **Fig. 4a**; **Table A.I.2**).

However, contrasting responses emerged when the factor of Placement (Centre and Edge) was included: mussel cover anomalies differed between the Center and the Edge of the mussel bed (Pseudo-$F_{1,16}$ = 8.10; p = 0.0082; **Fig. 4b**; **Table A.I.3**). The Center of the mussel bed remained stable between 2024 and 2025, irrespective of ice regimes (**Fig. 4b**; **Table A.I.4**), as the 95% confidence intervals overlapped zero. By contrast, significant variation occurred along the Edges of the mussel bed between ice regimes : in area Protected by a stable icefoot, mussel bed Edges exhibited a reduction in cover of 20.81 ± 2.92 %. In contrast, the Exposed site showed greatest decline in mussel cover, with an average loss of 46.58 ± 6.23 %, representing roughly twice the loss recorded at the Protected site.

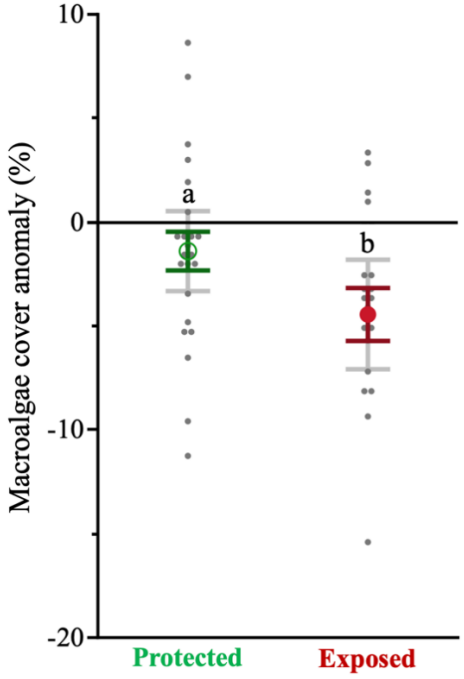


Figure 3. Average values (± SE; n = 24, total = 48) of the percentage cover anomaly of macroalgae between ice regimes. Colored bars represent standard errors (SE), whereas grey bars represent 95% confidence intervals (CI 95%). Grey points represent individual data samples. Averages with different letters indicate significant differences among groups (p ~ 0.05 or marginally).

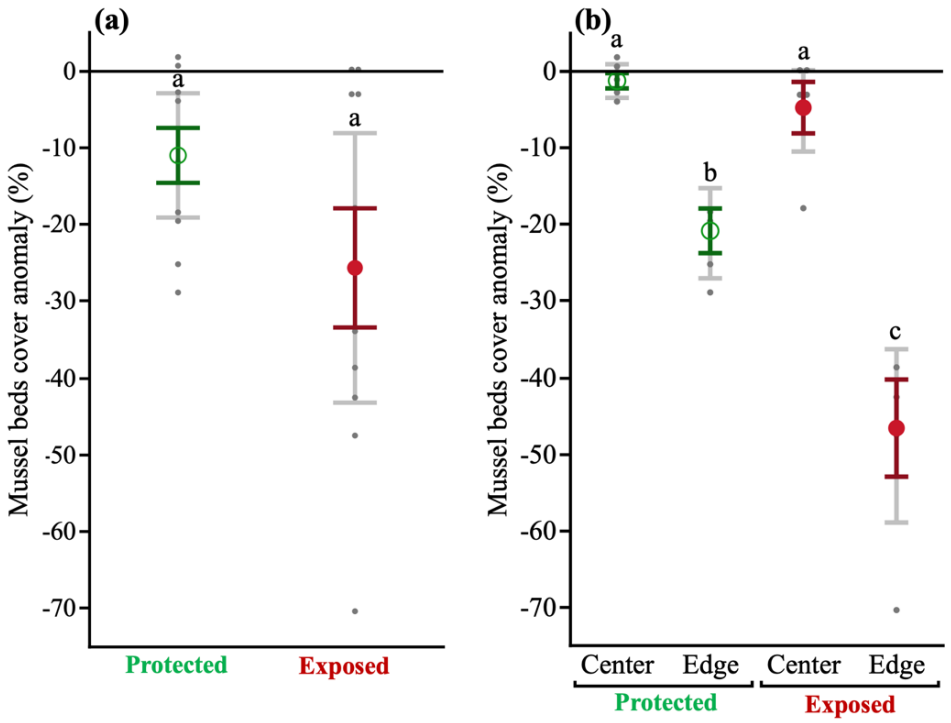


Figure 4. Average values (± SE) of the cover anomaly of mussel beds **(a)** between ice regimes (n = 10; total n = 20) and **(b)** as a function of ice regimes and placement within the mussel bed (n = 5; total n = 20). Colored bars represent standard errors (SE), whereas grey bars represent 95% confidence intervals (CI 95%). Grey points represent individual data samples. Averages with different letters indicate significant differences among groups ($p < 0.05$).

1.3.2. Biodiversity indices associated with macroalgae and mussel beds

Except for macroalgal-associated biomass (Pseudo-$F_{2,49}$ = 3.4; p = 0.0742), we generally observed decreasing values in macroalgae and mussel-associated communities for taxa richness, biomass, and Simpson's diversity from Stable to Abraded to Reference substratum states, respectively (cf. **Table I.1**; **Fig. 5**). In contrast, neither ice regimes or its interaction with substratum states had a significant effect on any of the biodiversity indices in either macroalgae or mussel communities (**Table 1.**). In macroalgae, taxa richness values were the highest in Stable substratum while the lowest in Reference one (**Fig. 5a; Table A.I.5**) while Simpson's diversity values were higher in both Stable and Abraded states than

in Reference states (**Fig. 5c**; **Table A.I.5**). In mussel beds, taxa richness and biomass of sampled associated community were significantly higher in Stable than in Abraded and Reference states, which exhibited similarly low values (**Fig. 5d,e**; **Table A.I.5**). Simpson's diversity also decreased from Stable to Abraded to Reference states (**Fig 5f**; **Table A.I.5**).

Table 1. Summary of PER-ANOVA results testing the effect of Ice regime, State and interacting factors on (**1**) macroalgae, and (**2**) mussel bed-associated species on (**a**) taxa richness, (**b**) associated biomass and (**c**) Simpson's diversity (1-λ). Significant factors are shown in **bold**. V% stands for estimate of variance components.

Source of variation	df	MS	Pseudo-F	*p*-value	%V
1a Macroalgal-associated richness					
Ice regime	1	0.003	0.002	0.9684	0
State	2	45.36	27.32	**<0.0001**	54.6
Ice regime x State	2	0.023	0.01	0.9879	0
Error	49	1.66			45.4
Corrected total	54				100
1b Macroalgal-associated biomass					
Ice regime	1	6917.7	3.40	0.0742	18.6
State	2	2724.6	1.34	0.2654	8.6
Ice regime x State	2	2498.0	1.23	0.3070	10.0
Error	49	2031.1			62.8
Corrected total	54				100
1a Macroalgal-associated Simpson diversity					
Ice regime	1	0.090	3.32	0.0749	11.9
State	2	0.356	13.20	**<0.0001**	33.3
Ice regime x State	2	0.056	2.09	0.1279	14.1
Error	49	0.027			40.7
Corrected total	54				100
2a Mussel bed-associated richness					
Ice regime	1	0.066	0.03	0.8667	0
State	2	87.20	37.67	**<0.0001**	57.5
Ice regime x State	2	1.26	0.54	0.5900	0
Error	54	2.31			42.5
Corrected total	59				100
2b Mussel bed-associated biomass					
Ice regime	1	20.84	0.18	0.7399	0
State	2	2424.40	21.22	**<0.0001**	50.1
Ice regime x State	2	92.44	0.81	0.5185	0
Error	54	114.23			49.9
Corrected total	59				100
2c Mussel bed-associated Simpson diversity					
Ice regime	1	0.00072	0.02	0.8829	0
State	2	0.48	14.62	**<0.0001**	45.2
Ice regime x State	2	0.018	0.54	0.5789	0
Error	54	0.033			54.8
Corrected total	59				100

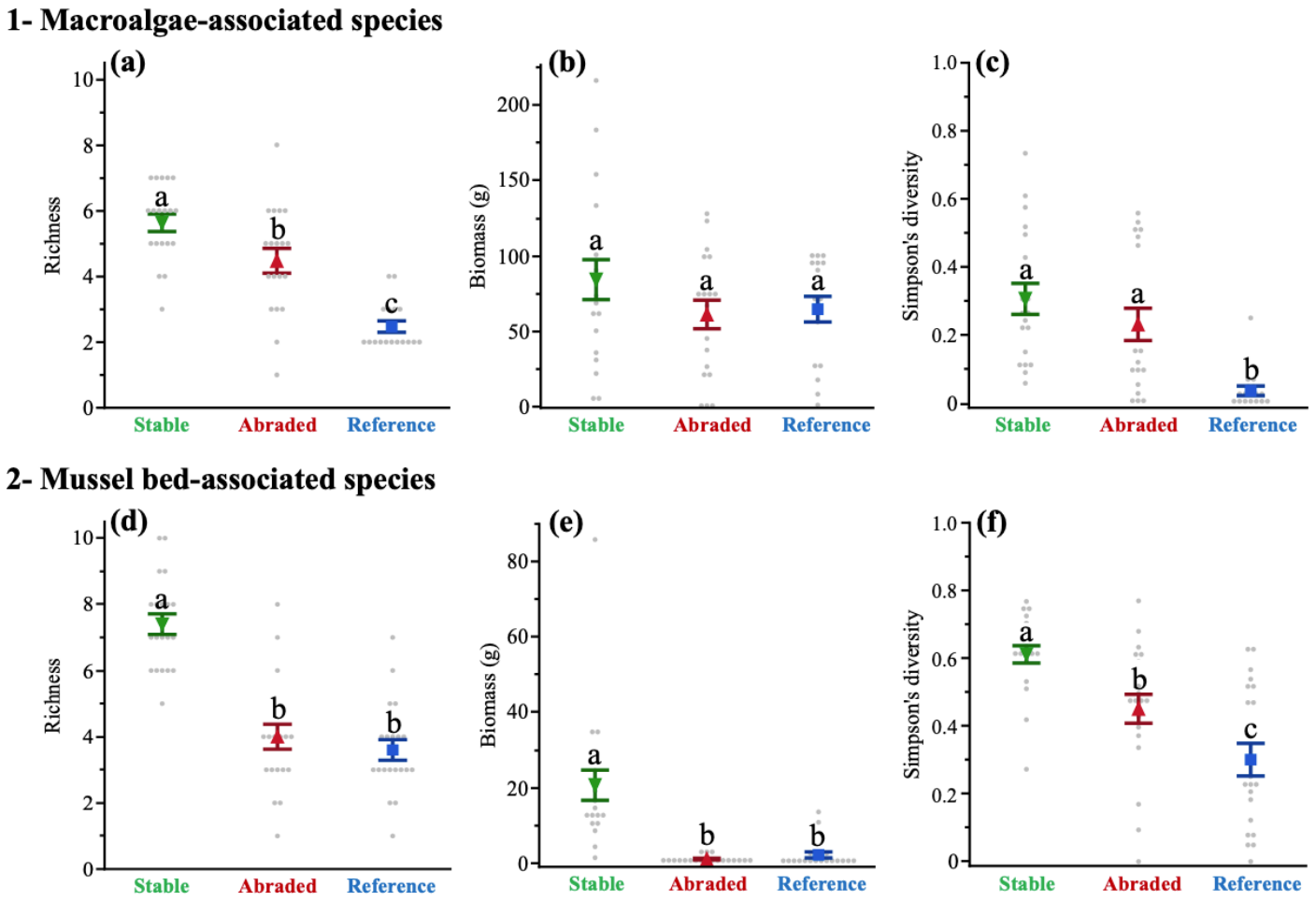


Figure 5. Average (± SE) values of **(a, d)** taxa richness, **(b, e)** associated biomass (WW; in g), and **(c, f)** Simpson diversity index (1-λ). Results from **a-c** represent macroalgae-associated species communities and from **d-f** mussel bed-associated species across substratum states (see **Fig. 2.** for details of the different conditions). Grey points represent individual data samples. Averages with different letters indicate significant differences among groups ($p < 0.05$).

1.3.3. Effects of changes on community structure

A significant interaction between substratum state and ice regimes was observed for both macroalgal and mussel bed-associated species (Pseudo-$F_{2,49} = 2.01$, $p = 0.0492$; Pseudo-$F_{2,54} = 2.44$, $p = 0.0007$, respectively; **Table 2**; **Fig. 6**), indicating that differences among states depended on the ice regime considered. Variance partitioning analyses further showed that substratum state explained a substantially greater proportion of variation in community structure than ice regime, particularly in macroalgal assemblages where explained variation was nearly threefold higher (**Table 2a**). Similar patterns were observed in mussel beds, emphasizing the strong influence of local disturbance and post-winter habitat conditions on associated community.

a) Macroalgal community structure

Pairwise comparisons (**Table A.I.6**) showed that, for macroalgal-associated species, all substratum states differed significantly under Protected ice regime (**Fig. 6a,c**), whereas under Exposed ice regime, Stable and Abraded states did not differ significantly (**Fig. 6a,c**; **Table A.I.6**). The undisturbed Stable states differed significantly between the two contrasting ice regimes (Protected and Exposed). We observed higher abundances of *Littorina saxatilis*, *Ulothrix flacca, Littorina obtusata* in Protected site, whereas *Mytilus* spp. and *Jaera (Jaera) albifrons* were less abundant there. Together, these species contributed most strongly to the dissimilarity observed between ice regimes, explained up to 75,7% of the differences (SIMPER results, **Table A.I.7**). Across all significant pairwise contrasts, *U. flacca* often contributed the most to the differences among ice regimes and states (**Table A.I.7**). References state also differed between ice regimes, mainly because *U. flacca*

was more abundant at Exposed site than at Protected ones (**Table A.I.7**). At both sites, shifts from Stable to Abraded states were mainly explained by declines in *L. obtusata* and *L. saxatilis*.

b) Mussels bed community structure

Community structure in mussel beds strongly responded to both ice regimes and states of substratum (**Table 2, Fig 6b,d**). Community structure in Stable states differed significantly from Abraded states under both ice regimes (both $p < 0.0001$; see **Table A.I.6**), as well as from Reference state (both $p < 0.0001$; see **Table A.I.6**). Conversely, communities from Abraded and Reference did not differ significantly under either Protected or Exposed ice regimes ($p = 0.3652$; $p = 0.1331$, respectively). The community structure in Stable states from Protected and Exposed sites differed with Exposed site characterized by lower abundances of *Macoma balthica*, *Littorina saxatilis*, *Balanus crenatus*, *Nereis diversicolor* and *Jaera (Jaera) albifrons* (**Table A.I.8**). Winter disturbances induced a marked shift from Stable to Abraded states at both Protected and Exposed sites, mainly driven by declines in *Littorina saxatilis*, *Gammarus* spp., *Balanus crenatus* and *Nereis diversicolor*. By contrast, Abraded and Reference states exhibited relatively similar community compositions, resulting in lower dissimilarity values compared with the other pairwise comparisons for both ice regimes (**Table A.I.8**).

Table 2. Summary of PERMANOVA results testing the effect of Ice regime, State and interacting factors on **(a)** Macroalgae, and **(b)** Mussel bed-associated species community structure. Significant values are shown in **bold**. V% stands for estimate of variance components.

Source of variation	df	MS	Pseudo-F	*p*-value	%V
(a) Macroalgae					
Ice regime	1	2840	3.23	**0.0138**	11.9
State	2	1092	12.41	**<0.0001**	32.8
Ice regime x State	2	1769	2.01	**0.0492**	13.8
Error	49	879			41.5
Corrected total	54				100
(b) Mussel beds					
Ice regime	1	17031	11.31	**<0.0001**	21.7
State	2	18039	11.98	**<0.0001**	27.4
Ice regime x State	2	3679	2.44	**0.0007**	14.0
Error	54	1505			36.9
Corrected total	59				100

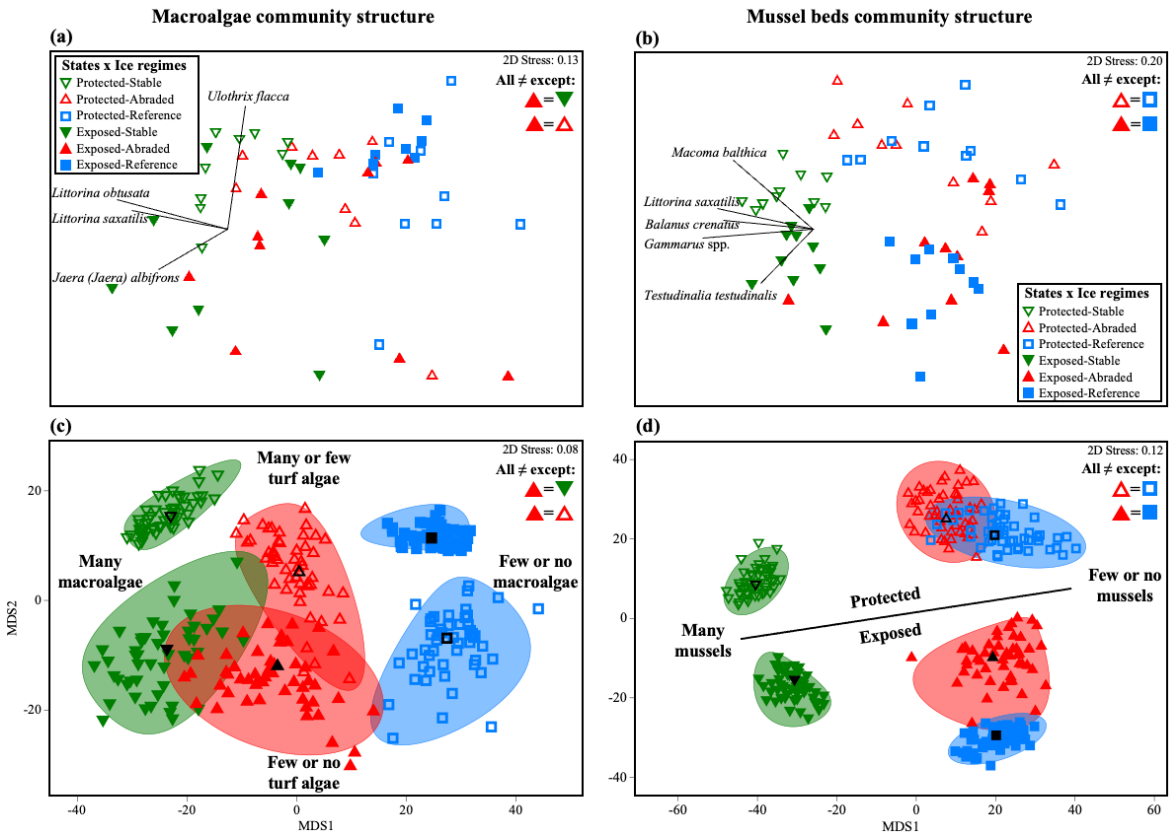


Figure 6. Non-metric multidimensional scaling (nMDS) plot based on a Bray–Curtis similarity matrix (DW + square root transformed) showing differences in benthic community composition among states conditions and ice regimes. **(a)** Macroalgae-associated species ($F_{2,49} = 2.01$; $p = 0.0492$, $n = 60$), and **(b)** Mussel bed-associated species ($F_{2,54} = 2.68$; $p = 0.0007$; $n = 60$). Symbols represent sampled quadrats according to substratum states and ice regimes (see legend for color and shape codes), while vectors indicate the taxa contributing most to the ordination pattern (based on SIMPER; see main text). For greater clarity of the patterns shown in **(a)** and **(b)**, we also present the same data in **(c)** for macroalgae and **(d)** mussel beds as bootstrap-averaged MDS plots, showing simulated factor centroids ($n = 50$ per group, total = 300) and their 95% confidence regions.

1.4. Discussion

Our study shows that winter-related disturbances may profoundly alter benthic intertidal biodiversity and community structure, highlighting the key role of contrasting winter ice regimes in shaping these responses. To our knowledge, this is the first study that demonstrates the protective function of stable ice cover against winter disturbance in an

intertidal environment. During our study, the Protected area was characterized by approximately 55 days of stable ice-foot cover during winter 2024-2025 (measured by satellite imagery; data unpublished), whereas the Exposed area experienced only about six days of ice cover. This contrast created a natural difference in exposure to winter disturbance, allowing us to assess how different ice regimes influence habitat changes. Our sampling design, which explicitly compared and measured several states of habitat change, also highlighted the importance of macroalgal and mussel bed-associated communities in maintaining local biodiversity.

1.4.1. Icefoot as a protection for benthic communities

Winter disturbances induced contrasting responses between macroalgal assemblages and mussel beds. Overall, macroalgal habitats remained relatively stable throughout winter, whereas mussel beds experienced stronger declines in cover and greater spatial variability, particularly at Exposed site lacking stable icefoot protection. These findings emphasize the important role of stable icefoot formation in buffering intertidal ecosystems against winter disturbances. The protective function of the icefoot has long been recognized in cold coastal environments, where it can act as a physical barrier reducing shoreline exposure to waves, currents, and especially drifting ice (Forbes and Taylor 1994). In contrast, site lacking such protection, such as our Exposed areas, remain directly exposed during winter to hydrodynamic stress and ice abrasion generated by mobile sea ice (Scrosati and Eckersley 2007; Petzold *et al.* 2014). In addition to reducing mechanical stress, the thermal buffering effect of the icefoot likely alleviates winter stress during low tides by limiting exposure to extreme freezing, thereby promoting the persistence of foundation species and contributing

to the maintenance of community structure under protected conditions (Scrosati and Eckersley 2007; Scrosati and Heaven 2007). In the absence of an icefoot, intertidal organisms remain exposed to severe thermal stress during low tides, particularly during extreme cold events, which can increase mortality rates and ultimately reduce species cover, as documented by Helmuth *et al.* (2006) and Scrosati and Eckersley (2007).

1.4.2. Foundation species covers monitoring

Macroalgal assemblages remained comparatively stable across both ice regimes, although a marginally significant difference in cover was detected between Protected and Exposed sites. The modest decline observed at the Exposed site (approx. -5%) remained lower than values reported following severe ice disturbance events, which can remove substantial portions of intertidal macroalgal cover (Scrosati and Heaven 2007; Heaven and Scrosati 2008; Petzold *et al.* 2014). These observations suggest that although drifting ice likely contributed to some abrasion at Exposed site, the resulting losses in macroalgal cover remained relatively limited during winter 2024–2025. This limited loss may partly be related to the position of macroalgal assemblages on the vertical surfaces of boulders, where ice abrasion is likely restricted to a narrow vertical band corresponding to the maximum height reached by drifting ice, rather than affecting the entire rock face. On rocky shores, ice abrasion mainly removes organisms by severing algal fronds or attachment structures such as holdfasts and byssal threads (Archambault and Bourget 1983; Bergeron and Bourget 1986). However, some individuals may persist within crevices and other microtopographic refuges that reduce direct mechanical stress (Dayton 1971; Bergeron and Bourget 1986; Denny and Wethey 2001).

In contrast, mussel beds experienced substantially greater losses than macroalgal assemblages, suggesting that communities established on unconsolidated substrates such as coarse sand and pebbles are more vulnerable to winter disturbances than those attached to rocky substrates. On soft-sediment shores, ice disturbance can extend beyond simple surface abrasion, as drifting ice may excavate and remove several centimetres of sediment through ice scouring (Dionne 1985). Such disturbances remove not only organisms but also the sediment matrix forming the habitat itself (Archambault and Bourget 1983; Cusson and Bourget 2005). Hummocking within mussel beds may further increase their vulnerability to drifting ice by weakening attachment to the substratum and increasing exposure to hydrodynamic forces (Seed and Suchanek 1992; Carrington *et al.* 2009; Gutiérrez *et al.* 2015), thereby contributing to greater temporal dynamics at Exposed site. Similar patterns have been reported in other benthic systems, where communities inhabiting unconsolidated sediments tend to be more susceptible to physical disturbances than those associated with rocky substrates (Hall 1994; Dernie *et al.* 2003). This effect, combined with the absence of a protective icefoot at Quai Franquelin, likely explains why cover anomalies were greater at this Exposed site than at the Protected site of Pointe-Mistassini, where a more persistent icefoot provided greater protection for intertidal habitats. Strong spatial differences were also observed within mussel beds, as plots located in bed centers remained relatively stable between autumn 2024 and spring 2025, whereas substantial losses occurred along bed edges. This pattern is consistent with previous studies showing that mussel bed margins are generally more exposed to hydrodynamic forces and mechanical disturbances than central portions, which benefit from the structural stability created by dense mussel aggregations (Paine and Levin 1981; Bertness and Grosholz 1985; Seed and Suchanek 1992; Commito *et*

al. 2006; Commito *et al.* 2008). Consequently, edges may constitute relatively dynamic zones within mussel beds and could therefore be more susceptible to disturbances.

1.4.3. Winter disturbance on macroalgae-associated community and biodiversity

Winter disturbances effects on foundation species cover induced measurable shifts in the biodiversity and community structure of macroalgae-associated community. Our results showed a progressive decline in taxa richness from Stable to Abraded and, finally, to Reference states, whereas total biomass and Simpson's diversity of associated species remained relatively similar between Stable and Abraded conditions under both ice regimes. Likewise, community assemblages from Abraded states occupied an intermediate position between Stable and Reference states in ordinations, suggesting a transitional response of associated species following a single winter, rather than a complete community reorganization. These patterns suggest that winter disturbances only partially altered the structure of macroalgal habitats, allowing part of the associated assemblages to persist following canopy loss while also reflecting the strong contribution of the turf *Ulothrix flacca* to community dissimilarities and its increasing dominance within disturbed assemblages. *U. flacca* was particularly abundant in Stable and Abraded states from Protected site, as well as in Reference state from Exposed site, where it was generally associated with higher abundances of *Littorina saxatilis* and *Littorina obtusata*. This association suggests that filamentous turf algae may provide favorable conditions and feeding surfaces for grazing gastropods (Lubchenco 1983; Watson and Norton 1985). In contrast, the absence of significant differences between Stable and Abraded assemblages under the Exposed ice regime may be explained by the persistence of *Mytilus* spp. and *Jaera (Jaera) albifrons* in

both states. The continued occurrence of mussels within these assemblages likely maintained associated fauna through increased habitat complexity and refuge availability (Seed and Suchanek 1992; Gutiérrez *et al.* 2003; Norling and Kautsky 2007; Commito *et al.* 2008). Together, these patterns likely contributed to maintaining biomass values relatively similar between Stable and Abraded assemblages despite reductions in canopy-forming macroalgae.

Opportunistic filamentous taxa such as *U. flacca* were frequently observed in our samples and exhibited marked seasonal increases during winter, indicative of a rapid opportunistic response to disturbances (Pers. Obs.;(Wikström and Kautsky 2007; Pessarrodona *et al.* 2023). Such taxa may rapidly colonize disturbed habitats and partially compensate for canopy loss by maintaining habitat complexity and food availability for associated species (Archambault and Bourget 1983; Susini 2022). Stable states, where macroalgal canopies remained largely intact after winter, tended to be associated with more similar community assemblages across samples. Similar patterns have previously been associated with the persistence of foundation species, which stabilize environmental conditions and promote more predictable community composition (Seed and Suchanek 1992; Bertness *et al.* 1999; Bruno *et al.* 2003). Conversely, associated community from Abraded states shifted toward Reference states, indicating that reductions in macroalgal canopy cover reduced the physical structure and refuge available to associated organisms, while only partially reorganizing the community. Such responses are consistent with the well-established role of foundation species in structuring benthic assemblages through habitat complexity and environmental buffering (Bruno *et al.* 2003; Cimon and Cusson 2018).

1.4.4. Winter disturbance on mussel bed-associated community and biodiversity

In contrast to macroalgal habitats, post-winter disturbances induced stronger changes in biodiversity and community structure within mussel bed assemblages. Community structure differed significantly between Stable and Abraded states under both ice regimes, whereas Abraded and Reference assemblages remained relatively similar under both Protected and Exposed conditions. Winter disturbances induced marked shifts from Stable to Abraded states, mainly driven by declines in *Littorina saxatilis*, *Gammarus* spp., *Balanus crenatus*, and *Nereis diversicolor*, which are commonly associated with mussel beds because they use interstitial spaces as a refuge from hydrodynamic stress, predation, desiccation, and thermal variability (Tsuchiya and Nishihira 1985; Seed and Suchanek 1992; Borthagaray and Carranza 2007; Commito *et al.* 2008). Stable assemblages also differed between the Protected and the Exposed site, with Exposed area characterized by lower abundances of several associated taxa, including *Macoma balthica*, *L. saxatilis*, *Balanus crenatus*, *N. diversicolor*, and *Jaera (Jaera) albifrons*. Such results suggest that mussel-associated assemblages strongly depended on the persistence of mussel bed structure and responded rapidly to winter disturbance (e.g. autumn/winter storms, ice scour, and/or wave action). The strong similarity observed between Abraded and Reference states indicates that reductions in mussel cover occurring over a single winter season were sufficient to shift associated assemblages toward communities resembling those found in areas without mussel beds. Mussel beds also promote sediment retention and increase organic matter accumulation, thereby supporting diverse associated assemblages (Kautsky and Evans 1987; Gutiérrez *et al.* 2003; Cusson and Bourget 2005; Commito *et al.* 2008; Lafferty and Suchanek 2016). Consequently, reductions in mussel bed structure likely decreased habitat availability and

weakened the environmental buffering normally provided by dense mussel matrices (Bertness *et al.* 1999; Bruno *et al.* 2003).

Lower abundances of several associated taxa at the Exposed site may reflect greater environmental stress and disturbance intensity under reduced icefoot protection. Similar reductions in associated biodiversity following disturbances affecting habitat-forming species have been documented in several benthic systems, where losses of structural complexity rapidly alter species composition and favor more disturbance-tolerant assemblages (Gutiérrez *et al.* 2003; Commito *et al.* 2008; Lafferty and Suchanek 2016; Scrosati 2023). Stable mussel beds also tended to support more similar community assemblages when mussel structure remained intact. Conversely, Abraded assemblages showed greater variability in species composition following disturbance, likely reflecting increasing habitat heterogeneity after winter ice impacts (Carrington *et al.* 2009; Donker *et al.* 2015). Consequently, winter disturbances affecting mussel bed structure may rapidly propagate through associated community and progressively shift communities toward simplified and disturbance-dominated states.

Overall, these results emphasize the central role of foundation species in maintaining the structure and stability of intertidal communities. They further suggest that future changes in ice regimes, particularly a reduction in protective icefoot formation, could lead to substantial alterations in assemblages associated with macroalgae and mussel beds. By modifying the cover and spatial distribution of foundation species, winter ice dynamics may indirectly reshape associated assemblages through changes in habitat complexity and availability, refuge space, and local environmental conditions. Ongoing reductions in coastal ice cover and stable ice-foot formation are expected to contribute to the broader borealization

of northern marine ecosystems (Kortsch *et al.* 2012; Krause-Jensen *et al.* 2020). Recent studies have shown that declining sea-ice conditions can promote major shifts in benthic ecosystem structure, including the expansion of boreal foundation species and the reorganization of associated communities (Kortsch *et al.* 2012; Assis *et al.* 2022). In this context, reductions in stable ice-foot formation may progressively shift intertidal ecosystems toward more dynamic and structurally simplified community states increasingly dominated by disturbance-tolerant or expanding boreal species (Krause-Jensen *et al.* 2020; Lebrun *et al.* 2022).

1.5. Concluding remarks

Winter sea-ice dynamics play a fundamental role in shaping intertidal ecosystems in subarctic coastal environments. In this study, contrasting ice regimes revealed both Protective and Exposed effects on foundation species and their associated species. The presence of a stable icefoot appeared to buffer intertidal habitats from mechanical and/or thermal stress, allowing macroalgal assemblages and mussel beds to persist through winter with relatively limited losses in cover. In contrast, site lacking this protection may be more exposed to winter disturbances, resulting in greater abrasion and localized reductions in foundation species cover, particularly along the edges of mussel beds. Although these disturbances modified the cover of macroalgae assemblages, the biodiversity indices of associated assemblages remained relatively stable. This apparent resistance likely reflects the persistence of macroalgal habitat following disturbances, the presence of disturbance-tolerant taxa such as turf algae, and the high adaptation of intertidal organisms to naturally variable physical conditions. Our results also revealed shifts in community structure associated with habitat

conditions, indicating that changes in foundation species cover can propagate through associated assemblages and alter patterns of species dominance and composition. Taken together, these results highlight the key role of macroalgal canopies and mussel beds in maintaining habitat complexity and structuring intertidal biodiversity in disturbance-prone intertidal systems. As climate warming continues to alter sea-ice dynamics across northern coastlines, reductions in stable ice-foot formation may increase the exposure of intertidal habitats to drifting ice disturbances as well as waves and extreme air conditions. Over time, such changes could gradually shift community structures away from ice-protected states, with potential consequences for biodiversity patterns and ecosystem functioning in subarctic coastal systems.

1.6. References

Anderson FE. 1983. The Northern Muddy Intertidal: Seasonal Factors Controlling Erosion and Deposition - A Review. Canadian Journal of Fisheries and Aquatic Sciences, 40 : 143-159.

Anderson MJ. 2005. PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Auckland, Department of Statistics, University of Auckland, New Zealand.

Archambault D and Bourget E. 1983. Importance du régime de dénudation sur la structure et la succession des communautés intertidales de substrat rocheux en milieu subarctique. Canadian Journal of Fisheries and Aquatic Sciences, 40 : 1278-1292.

Assis J, Serrão EA, Duarte CM, Fragkopoulou E et Krause-Jensen D. 2022. Major Expansion of Marine Forests in a Warmer Arctic. Frontiers in Marine Science, 9 : 850368.

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC et Silliman BR. 2011. The value of estuarine and coastal ecosystem services. Ecological Monographs, 81 : 169-193.

Barnes DKA. 1999. The influence of ice on polar nearshore benthos. Journal of the Marine Biological Association of the United Kingdom, 79 : 401-407.

Barnhart KR, Overeem I et Anderson RS. 2014. The effect of changing sea ice on the physical vulnerability of Arctic coasts. The Cryosphere, 8 : 1777-1799.

Bergeron P and Bourget E. 1984. Effet du froid et des glaces sur les peuplements intertidaux des régions nordiques, particulièrement dans l'estuaire du Saint-Laurent. Oceanis, 10 : 279-304.

Bergeron P and 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 MD and Grosholz E. 1985. Population dynamics of the ribbed mussel, *Geukensia demissa*: The costs and benefits of an aggregated distribution. Oecologia, 67 : 192-204.

Bertness MD, Leonard GH, Levine JM, Schmidt PR et Ingraham AO. 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. Ecology, 80 : 2711-2726.

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 : 2061-2067.

Boroda AV, Kipryushina YO et Odintsova NA. 2020. The effects of cold stress on Mytilus species in the natural environment. Cell Stress Chaperones, 25 : 821-832.

Borthagaray AI and Carranza A. 2007. Mussels as ecosystem engineers: Their contribution to species richness in a rocky littoral community. Acta Oecologica, 31 : 243-250.

Braby CE. 2007. Cold stress. Dans : Denny MW et Gaines SD éds. Encyclopedia of Tidepools and Rocky Shores. University of California Press, Berkeley, p. 148-150.

Bruno JF, Stachowicz JJ et Bertness MD. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution, 18 : 119-125.

Carrington E, Moeser GM, Dimond J, Mello JJ et Boller ML. 2009. Seasonal disturbance to mussel beds: Field test of a mechanistic model predicting wave dislodgment. Limnology and Oceanography, 54 : 978-986.

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

Clarke KR and Gorley RN. 2015. PRIMER v7: User Manual/Tutorial. Plymouth, UK, PRIMER-E.

Clarke KR, Tweedley JR et Valesini FJ. 2014. 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 : 1-16.

Clarke KR, Chapman MG, Somerfield PJ et Needham HR. 2006. Dispersion-based weighting of species counts in assemblage analyses. Marine Ecology Progress Series, 320 : 11-27.

Commito JA, Dow WE et Grupe BM. 2006. Hierarchical spatial structure in soft-bottom mussel beds. Journal of Experimental Marine Biology and Ecology, 330 : 27-37.

Commito JA, Como S, Grupe BM et Dow WE. 2008. Species diversity in the soft-bottom intertidal zone: Biogenic structure, sediment, and macrofauna across mussel bed spatial scales. Journal of Experimental Marine Biology and Ecology, 366 : 70-81.

Cusson M and Bourget E. 2005. Small-scale variations in mussel (*Mytilus* spp.) dynamics and local production. Journal of Sea Research, 53 : 255-268.

Dayton PK. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs, 41: 351-389.

Denny MW. 1995. Predicting Physical Disturbance: Mechanistic Approaches to the Study of Survivorship on Wave-Swept Shores. Ecological Monographs, 65 : 371-418.

Denny MW and Wethey DS. 2001. Physical processes that generate patterns in marine communities. Dans: Bertness MD, Hay ME, Gaines SD, éds. Marine Community Ecology. New York: Sinauer Associates. p. 3–37.

Dernie KM, Kaiser MJ et Warwick RM. 2003. Recovery rates of benthic communities following physical disturbance. Journal of Animal Ecology, 72 : 1043-1056.

Dionne J-C. 1973. La notion de pied de glace (Icefoot), en particulier dans l'estuaire du Saint-Laurent. Cahiers de géographie du Québec, 17 : 221-250.

Dionne J-C. 1985. Formes, figures et faciès sédimentaires glaciels des estrans vaseux des régions froides. Palaeogeography, Palaeoclimatology, Palaeoecology, 51 : 415-451.

Donker JJA, van der Vegt M et Hoekstra P. 2015. Erosion of an intertidal mussel bed by ice- and wave-action. Continental Shelf Research, 106 : 60-69.

Everett RA. 1994. Macroalgae in marine soft-sediment communities: effects on benthic faunal assemblages. Journal of Experimental Marine Biology and Ecology, 175 : 253-274.

Forbes DL and Taylor RB. 1994. Ice in the shore zone and the geomorphology of cold coasts. Progress in Physical Geography: Earth and Environment, 18 : 59-89.

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.

Galbraith PS, Chassé J, Shaw J-L, Lefaivre D et Bourassa M-N. 2025. Physical oceanographic conditions in the Gulf of St. Lawrence during 2024. Can. Tech. Rep. Hydrogr. and Ocean Sci. 397: v + 95 p.

Galbraith PS, Caverhill C, Chassé J, Nicot P, Gilbert D, Lefaivre D et Lafleur C. 2018. Physical Oceanographic Conditions in the Gulf of St. Lawrence during 2017. DFO Can. Sci. Advis. Sec. Doc. 2018/050. 80 p.

Gattuso JP, Frankignoulle M et Wollast R. 1998. Carbon and carbonate metabolism in coastal aquatic ecosystems. Annual Review of Ecology and Systematics, 29 : 405-434.

Gill LT, Kennedy JR, Box ICH et Marshall KE. 2024. Ice in the intertidal: patterns and processes of freeze tolerance in intertidal invertebrates. Journal of Experimental Biology, 227.

Gutiérrez JL, Jones CG, Strayer DL et Iribarne OO. 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos, 101 : 79-90.

Gutiérrez JL, Palomo MG, Bagur M, Arribas LP et Soria SA. 2015. Wave action limits crowding in an intertidal mussel. Marine Ecology Progress Series, 518 : 153-163.

Gutt J. 2001. On the direct impact of ice on marine benthic communities, a review. Polar Biology, 24 : 553-564.

Hall JS. 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. Oceanography and Marine Biology: An Annual Review, 32 : 178-239.

Hardwick-Witman MN and Mathieson AC. 1983. Intertidal macroalgae and macroinvertebrates: Seasonal and spatial abundance patterns along an estuarine gradient. Estuarine, Coastal and Shelf Science, 16 : 113-129.

Heaven CS and Scrosati RA. 2008. Benthic community composition across gradients of intertidal elevation, wave exposure, and ice scour in Atlantic Canada. Marine Ecology Progress Series, 369 : 13-23.

Helmuth B, Mieszkowska N, Moore P et Hawkins SJ. 2006. Living on the Edge of Two Changing Worlds: Forecasting the Responses of Rocky Intertidal Ecosystems to Climate Change. Annual Review of Ecology, Evolution, and Systematics, 37 : 373-404.

Johnson LE. 2007. Ice scour. Dans : Denny MW et Gaines SD éds. Encyclopedia of Tidepools and Rocky Shores. University of California Press, Berkeley, p. 289-291.

Jones CG, Lawton JH et Shachak M. 1994. Organisms as Ecosystem Engineers. Oikos, 69 : 373-386.

Kautsky N and Evans S. 1987. Role of biodeposition by Mytilus edulis in the circulation of matter and nutrients in a Baltic coastal ecosystem. Marine Ecology Progress Series, 38 : 201-212.

Kortsch S, Primicerio R, Beuchel F, Renaud PE, Rodrigues J, Lønne OJ et Gulliksen B. 2012. Climate-driven regime shifts in Arctic marine benthos. Proceedings of the National Academy of Sciences, 109 : 14052-14057.

Krause-Jensen D, Archambault P, Assis J, Bartsch I, Bischof K, Filbee-Dexter K, Dunton KH, Maximova O, Ragnarsdóttir SB, Sejr MK, Simakova U, Spiridonov V, Wegeberg S, Winding MHS et Duarte CM. 2020. Imprint of Climate Change on Pan-Arctic Marine Vegetation. Frontiers in Marine Science, 7 : 617324.

Lafferty KD and Suchanek TH. 2016. Revisiting Paine's 1966 Sea Star Removal Experiment, the Most-Cited Empirical Article in the American Naturalist. Am Nat, 188 : 365-378.

Largaespada C, Guichard F et Archambault P. 2012. Meta-ecosystem engineering: Nutrient fluxes reveal intraspecific and interspecific feedbacks in fragmented mussel beds. Ecology, 93 : 324-333.

Lebrun A, Comeau S, Gazeau F et Gattuso J-P. 2022. Impact of climate change on Arctic macroalgal communities. Global and Planetary Change, 219 : 103980.

Lemieux J and Cusson M. 2014. Effects of Habitat-Forming Species Richness, Evenness, Identity, and Abundance on Benthic Intertidal Community Establishment and Productivity. PLoS ONE, 9 : e109261.

Lubchenco J. 1983. Littornia and Fucus: Effects of Herbivores, Substratum Heterogeneity, and Plant Escapes During Succession. Ecology, 64 : 1116-1123.

Murphy DJ and Johnson LC. 1980. Physical and temporal factors influencing the freezing tolerance of the marine snail *Littorina littorea* (L.). The Biological Bulletin, 158 : 220-232.

Nicholls RJ. 2004. Coastal flooding and wetland loss in the 21st century: Changes under the SRES climate and socio-economic scenarios. Global Environmental Change, 14 : 69-86.

Norling P and Kautsky N. 2007. Structural and functional effects of *Mytilus edulis* on diversity of associated species and ecosystem functioning. Marine Ecology Progress Series, 351 : 163-175.

Paine RT and Levin SA. 1981. Intertidal Landscapes: Disturbance and the Dynamics of Pattern. Ecological Monographs, 51 : 145-178.

Pearson GA et Davison IR. 1993. Freezing rate and duration determine the physiological response of intertidal fucoids to freezing. Marine Biology : International Journal on Life in Oceans and Coastal Waters, 115 : 353-362.

Peck LS, Brockington S, Vanhove S et Beghyn M. 1999. Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica. Marine Ecology Progress Series, 186 : 1-8.

Pessarrodona A, Filbee-Dexter K et Wernberg T. 2023. Recovery of algal turfs following removal. Marine Environmental Research, 192 : 106185.

Petzold W, Willers M et Scrosati R. 2014. Visual record of intertidal disturbance caused by drift ice in the spring on the Atlantic coast of Nova Scotia. F1000Research, 3 : 112.

Saucier FoJ, Roy Fo, Gilbert D, Pellerin P et Ritchie H. 2003. Modeling the formation and circulation processes of water masses and sea ice in the Gulf of St. Lawrence, Canada. Journal of Geophysical Research: Oceans, 108 : 3269.

Schneider CA, Rasband WS et Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods, 9 : 671-675.

Scrosati R. 2022. Low Winter Extremes in Intertidal Temperature in Nova Scotia in the Absence of an Ice Foot. Frontiers in Marine Science, 8 : 811545.

Scrosati R and Heaven C. 2006. Field technique to quantify intensity of scouring by sea ice in rocky intertidal habitats. Marine Ecology Progress Series, 320 : 293-295.

Scrosati R and Heaven C. 2007. Spatial trends in community richness, diversity, and evenness across rocky intertidal environmental stress gradients in eastern Canada. Marine Ecology Progress Series, 342 : 1-14.

Scrosati R and Eckersley LK. 2007. Thermal insulation of the intertidal zone by the ice foot. Journal of Sea Research, 58 : 331-334.

Scrosati RA. 2023. Further Loss of Intertidal Mussel Stands on the Nova Scotia Coast (Canada) after the Passage of Cyclone Lee. Diversity, 15 : 1150.

Seed R and Suchanek TH. 1992. Population and community ecology of Mytilus. Dans : Gosling E éd. The mussel *Mytilus*: ecology, physiology, genetics and culture. Elsevier, London, p. 87-169.

Senneville S, St-Onge Drouin S, Dumont D, Bihan-Poudec AC, Belemaalem Z, Corriveau M, Bernatchez P, Bélanger S, Tolszczuk-Leclerc S et Villeneuve R. 2014. Modélisation des glaces dans l'estuaire et le golfe du Saint-Laurent dans la perspective des changements climatiques (Rapport final). Rimouski: Québec. Institut de sciences de la mer de Rimouski., http://www.bv.transports.gouv.qc.ca/mono/1147874.pdf

Stachowicz JJ. 2001. Mutualism, Facilitation, and the Structure of Ecological Communities: Positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend. BioScience, 51 : 235-246.

Suchanek T. 1985. Mussels and their role in structuring rocky shore communities. Dans : Moore PG et Seed R éds. The ecology of rocky coasts. London: Hodder and Stoughton, p. 70-96.

Susini C. 2022. Effets de l'abrasion par la glace sur la dynamique temporelle de la productivité macroalgale intertidale du Saint-Laurent. Mémoire de Maîtrise. Université du Québec à Chicoutimi, Chicoutimi, 59 p.

Tsuchiya M and Nishihira M. 1985. Islands of *Mytilus* as a habitat for small intertidal animals: effect of island size on community structure. Marine Ecology Progress Series, 25 : 71-81.

Watson DC and Norton TA. 1985. Dietary preferences of the common periwinkle, *Littorina littorea* (L.). Journal of Experimental Marine Biology and Ecology, 88 : 193-211.

Wikström SA and Kautsky L. 2007. Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. Estuarine, Coastal and Shelf Science, 72 : 168-176.

Witman JD and Suchanek TH. 1984. Mussels in flow: drag and dislodgement by epizoans. Marine Ecology Progress Series, 16 : 259-268.

CHAPITRE II
WINTER DISTURBANCES DRIVE COMMUNITY CHANGE IN SUBARCTIC EELGRASS MEADOW

2.1. Introduction

In subarctic environments, winter is a dominant structuring season for coastal ecosystems and their communities (Bergeron and Bourget 1984; Bergeron and Bourget 1986). During this period, air temperatures can drop below −40 °C, and a coastal ice formation known as the icefoot develops along much of the shoreline (Dionne 1973). This semi-stable band of shore-attached ice plays a crucial role in regulating environmental conditions in the intertidal zone (Forbes and Taylor 1994). More specifically, the icefoot acts as a mechanical barrier against drifting pack ice and storm-generated waves, thereby limiting free-floating sea ice disturbance and sediment erosion (Ellis and Wilce 1961; Gutt 2001). It also provides thermal insulation, protecting organisms from extreme air exposure during low tide (McKindsey and Bourget 2001; Scrosati and Eckersley 2007). Under these conditions, benthic communities remain relatively protected despite otherwise harsh winter climates, allowing foundation species such as eelgrasses and mussel beds to persist.

However, ongoing climate change is increasingly disrupting this protective winter regime by altering winter conditions across cold-temperate and subarctic regions, resulting in decreased ice-cover duration, reduced ice thickness, and increased instability of coastal ice formations (Galbraith *et al.* 2025). As the icefoot forms later in the season, breaks up earlier, and becomes more mobile, or does not form, its protective capacity decreases. Consequently, intertidal habitats are increasingly exposed to mechanical abrasion from drifting ice, storm disturbance, and extreme temperature fluctuations (Conlan *et al.* 1998; Scrosati and Heaven

2006). Such disturbances can lead to vegetation removal (Susini 2022), sediment destabilization, and generate bare sediment patches (Pascal *et al.* 2020), potentially shifting habitats toward degraded states resembling naturally unvegetated areas (Orth *et al.* 2006; Waycott *et al.* 2009).

Among the coastal habitats particularly vulnerable to such disturbances are eelgrass meadows. These marine angiosperms create structurally complex and highly productive coastal habitats (Hemminga and Duarte 2000; Duffy 2006). They have been extensively studied worldwide, particularly in tropical and temperate regions, where they are recognized as major foundation species (Duarte 2002; Röhr *et al.* 2018). By providing refuge, nursery grounds, and attachment surfaces, eelgrass supports diverse biological assemblages and sustains important ecological processes (Orth *et al.* 1984; Heck *et al.* 2003). Eelgrass plants stabilize sediments, attenuate hydrodynamic energy, improve water clarity, and contribute substantially to blue carbon storage (Smith 1981; Fonseca and Fisher 1986; Röhr *et al.* 2018). Eelgrass meadows rank among the most threatened coastal habitats due to their sensitivity to anthropogenic and physical disturbance (Orth *et al.* 2006).

As a foundation species, eelgrass plays a key role in structuring coastal communities, and its loss may strongly affect associated assemblages. Changes in habitat complexity can influence species richness, diversity, and assemblage composition, particularly for organisms closely associated with vegetation structure (Attrill *et al.* 2000; Boström *et al.* 2006). Understanding how altered ice regimes affect both the persistence of foundation species and their associated communities is therefore critical for predicting ecosystem responses to climate change in northern coastal environments.

This study aims to quantify the potential winter changes in eelgrass cover and to determine how the lack of a protective icefoot influences the biodiversity and the structure

of associated species assemblages in a subarctic intertidal ecosystem. This study represents the first attempt to characterize eelgrass-associated communities under winter conditions lacking icefoot protection in subarctic environments, thereby providing novel insights into how these ecosystems respond to increasing ice-free disturbance regimes. We hypothesize that the absence of a protective icefoot during winter increases disturbance intensity, leading to significant losses of eelgrass cover and canopy biomass in intertidal zones. We expect that this reduction in eelgrass habitat will negatively affect both univariate and multivariate assemblage characteristics, resulting in decreased species richness, lower abundance of associated taxa, and a simplified community structure. We further expect that eelgrass meadows functioning as stable habitats will support higher biodiversity and more complex assemblages than abraded areas. Finally, we predict that winter disturbance will act as a primary driver of community structuring, favoring opportunistic and stress-tolerant species over habitat-dependent taxa.

2.2.Materials and Methods

2.2.1. Study site

The study was conducted from August 2024 to August 2025 in an intertidal eelgrass meadow at Anse à la Peinture (AP) located in the St. Lawrence Marine Estuary (SLME), Québec, Canada (49.092027° N, 68.210877° W). This region is considered subarctic, as the average temperature remains below 0°C for five months of the year (see www.climat.meteo.gc.ca) and the strong effect of ice scouring drives coastal benthic community dynamics (Bergeron and Bourget 1986). Water temperatures range from −2 to 15 °C and salinity from 24 to 28 (see www.slgo.ca). The tidal regime is mixed and

predominantly semi-diurnal, with a mean tidal range of approximately 3.5 m (see www.tides.gc.ca). The AP site was selected because it exhibited a relatively stable coastal icefoot (unpublished data from the authors and observations from local residents). However, since 2015, Sentinel-2 Level-1C satellite imagery has shown the persistence absence of a stable coastal icefoot. Although temporary accumulations of drifting ice occasionally occurred, they are short-lived (typically <1 week) and do not provide sustained protection to the intertidal habitat. In addition to these changes in ice conditions, this region is undergoing significant transformations eelgrass meadow structure, including an estimated loss of 3.5 km^2 between 2014 and 2023 (Araújo *et al.* 2025), alongside an increased frequency of reported storm events (Bandet *et al.* 2020). These combined environmental shifts make the AP site a particularly relevant and representative natural laboratory for investigating the ecological consequences of changing ice regimes on seagrass meadows.

2.2.2. Experimental design

a) Drone survey and studied conditions

To monitor and detect changes in the eelgrass meadow, we surveyed the Anse à la Peinture (AP) site using two types of drones. We used a DJI Matrice 350 RTK equipped with a multispectral camera. Flights were conducted at an altitude of 84 m over the AP site, covering an area of 0.808 km^2 (pixel resolution of 1 cm; **Fig. 1a**, **b**) in August 2024 and 2025. We also used a DJI Mini 3 drone to conduct high-resolution flights in August 2024 and May 2025 at an altitude of 10 m over three targeted survey areas (~ 41 × 41 m) randomly distributed within the AP site (pixel resolution: 0.67 cm; mean area: 1664.55 m^2).

The high-altitude (84 m) survey allowed us to quantify eelgrass cover at its peak seasonal development, at the end of summer (Cimon *et al.* 2021). The difference in eelgrass cover between the August 2024 and 2025 survey dates is defined hereafter referred to as the "post-winter annual cover change". The acquired images were processed using geomatics software to generate orthomosaics for both years. To estimate post-winter annual cover change across the AP eelgrass meadow, we randomly selected eight 60 × 60 m subzones (**Fig. A.1**) with a minimum eelgrass cover of 40% in 2024. Eelgrass cover was quantified within each subzone before and after winter, and the mean change across the eight subzones was used to estimate the overall post-winter annual cover change for the eelgrass meadow. We determined the subzone size as a compromise between capturing habitat heterogeneity and maintaining sufficient spatial resolution for fine-scale analysis, such as changes in eelgrass cover and other features (e.g., mussel beds or sediment patchiness). Subzones of eelgrass cover were delimited and digitized using the *Create Features* tool (ArcGIS Pro), generating polygons that accurately represented the spatial extent of eelgrass meadows pre- and post-winter (cf. **Fig. 7c, d**).

The lower-altitude (10 m) drone survey images were used to identify three substratum conditions and to precisely position the plots that would be sampled for biological communities (see below) within the eelgrass bed and its immediate surroundings. Based on the habitat configuration observed after the 2024–2025 winter season, plots were assigned to one of three post-winter substratum conditions (Stable, Abraded, and Reference), defined according to changes observed in spring 2025 relative to summer 2024. These conditions were used to compare benthic communities assemblages rather than to infer temporal changes within individual plots. The Stable substratum condition corresponded to areas where eelgrass cover was maintained (i.e., no surface loss), whereas the Abraded condition

was characterized by a near-complete loss of eelgrass cover, as determined from visual interpretation of drone imagery acquired in May and corroborated by field observations in August 2025. Finally, Reference substratum condition corresponded to stable bare-sand patches located within the eelgrass meadow matrix or along its margins that lacked eelgrass cover (approximately 0%) in August 2024, May 2025, and August 2025. These areas were selected to represent persistently unvegetated habitat throughout the study period. However, we cannot exclude the possibility that they supported eelgrass before the study period. Based on these three substratum conditions and the high-resolution survey (10 m altitude), we positioned 10 plots per condition for biological sampling (**Fig. 7d**; total n = 30).

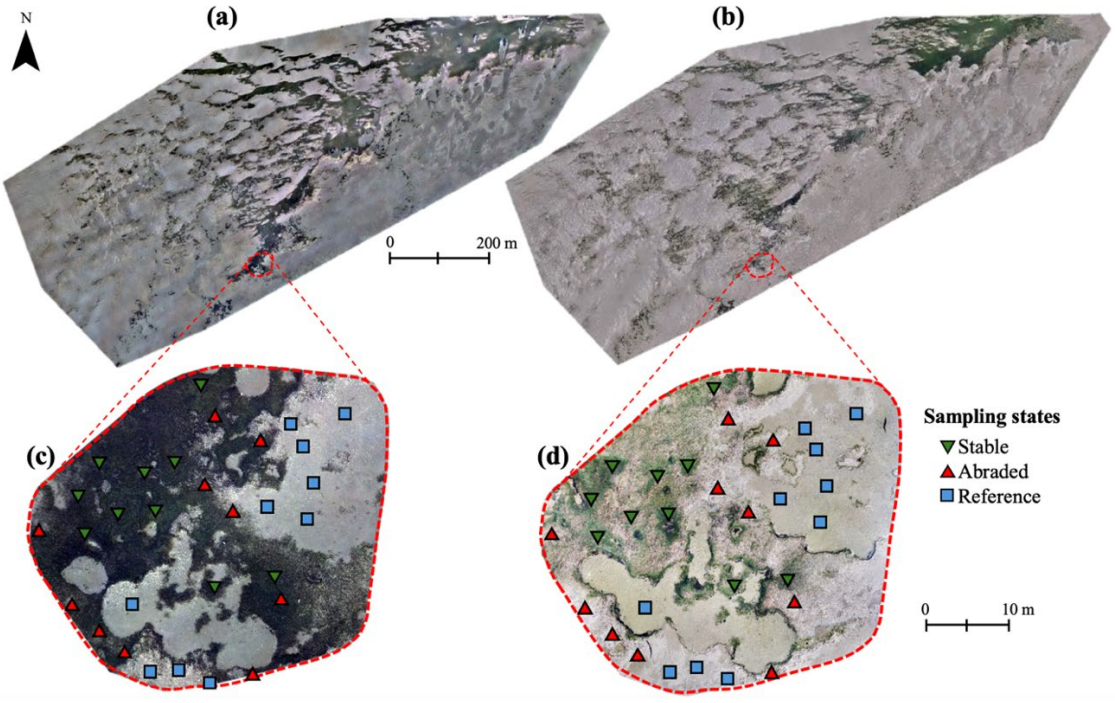


Figure 7. Orthomosaics of Anse à la Peinture (AP) acquired in **(a)** August 2024 and **(b)** August 2025, both from surveys conducted at an altitude of 84 m. High-resolution survey conducted in **(c)** August 2024 and **(d)** May 2025 at an altitude of 10 m, from which sampling plots were selected for each state (Stable, Abraded and Reference; see **Fig. 2.** for details).

a) Intertidal benthic community sampling

Eelgrass-associated macrofaunal communities were characterised in all plots across predefined substratum states using a three-step sampling protocol conducted in July 2025. First, eelgrass percent cover was visually estimated in the immediate vicinity of each plot (to avoid disturbing the Aboveground organisms) using 1 × 1 m quadrats subdivided into 25 units, with each unit representing 4% of the total surface area. Second, in each plot, the Aboveground compartment (including organisms within eelgrass leaves and/or in the 40 cm water mass above the substrate; to ensure standardized sampling efforts) was collected using a 500 μm-mesh bag (18 cm diameter; see (Reynolds *et al.* 2014). Third, the Benthic compartment (including organisms at the sediment surface and within the top 1 cm), located directly beneath the Aboveground samples, was collected into a 20 x 20 cm quadrat. Mussel percentage cover, as a secondary foundation species, was estimated beforehand, after which all organisms were collected using a hand trowel and placed in a plastic bag. All samples were sieved through a 1 mm-mesh to retain the macrofaunal component of the community and were then frozen until processing. In the lab, organisms were sorted and identified to the lowest possible taxonomic level (typically the species level) under a stereomicroscope. Individuals were counted, and the total wet biomass (WW; in g) of each taxon was measured to the nearest 0.0001 g (or 0.5 g for very large individuals). Only living organisms were included in biomass measurements. Living mussels were weighed with their shells, whereas empty shells and detrital material were excluded. Taxa richness and total biomass (g WW) of the associated community were subsequently calculated for each sample. Living eelgrass leaves were processed separately and were not included in the associated community biomass analyses.

2.2.3. Data analysis

In a pre-analysis, we found out that mussels percentage cover and biomass was similar between Stable and Abraded conditions (18% and 21% cover; 122.68 g and 143.06 g biomass; respectively), but much lower in the Reference condition (0.8% and 6.48 g; Pseudo-$F_{2,27} = 5.59$; $p = 0.0039$; **Table A.II.4**; **Fig. A.II.3**), a pattern that led us to include compartment as an additional factor in the analyses to disentangle its interaction with the main factor, substratum condition. As such, taxa richness and total biomass of all organisms in each samples were each compared among the fixed factors of substratum conditions (Stable, Abraded, and Reference), compartments (Aboveground, Benthic, and Whole as composite of the latter two), and their interaction using two-ways permutational analysis of variance (PER-ANOVA, 9999 runs; Anderson 2005) with Euclidian distances matrix. With the same design mentioned above, the community abundance structure was analysed with a permutational multivariate analysis of variance (PERMANOVA, 9999 runs) using a Bray–Curtis similarity matrix from biomass transformed data (Dispersion-Weighted and square-root transformed; Clarke *et al.* 2006; Clarke *et al.* 2014). We added a dummy variable (0.1) to address the joint-zero problem when analysing aboveground community data alone, thereby minimizing the influence of joint absences while having a negligible effect on observed community dissimilarities (Clarke and Gorley 2015). Variance heterogeneity/dispersion was assessed with the PERMDISP routine (Clarke and Gorley 2015) and no strong effect of dispersion was observed in all tests. Post-hoc pairwise comparisons by PER-ANOVA or PERMANOVA were performed when significant effects were detected. Community patterns were visualized using non-metric multidimensional scaling (nMDS) or bootstrap averages and simulated 95% confidence regions of the factor centroids in an MDS. We evaluated the contribution of each taxon to the observed

similarities/dissimilarities between substratum conditions using a similarity percentage analysis (SIMPER). All analyses were performed using PRIMER-e v7 with the PERMANOVA+ add-on. An $\alpha = 0.05$ was used for all statistical tests.

2.3. Results

During the winter 2024-2025, we measured at least 15 days of ice presence (based on satellite imageries during the winter season; see www.browser.dataspace.copernicus.eu) at AP. Between the two 2024 and 2025 surveys, we observed an overall eelgrass meadow cover decline of 19.7 ± 3.6 % (subzones n = 8; min-max: 2.6 - 30.7%; **Table 3**) at AP. This represents an average loss of 710 m² by 3600 m² subzones.

Table 3. Changes in eelgrass (*Zostera marina*) percentage cover (%) among subzones between initial (August 2024) and final (August 2025) cover based on drone surveys. Absolute change corresponds to the difference in percent cover between surveys, while relative loss represents the proportional decline in eelgrass cover relative to initial conditions. Surface loss indicates the estimate ed area of eelgrass lost within each subzone during the study period.

Subzones	Initial cover (August 2024; %)	Final cover (August 2025; %)	Absolute change (%)	Relative loss (%)	Surface loss (m^2)
#1	46.6	19.4	-27.2	58.4	-990.6
#2	44.3	15.2	-29.1	65.7	-1046.1
#3	52.2	38.5	-13.7	26.2	-490.0
#4	68.6	41.1	-27.5	40.1	-988.3
#5	86.0	70.2	-15.8	18.4	-569.6
#6	92.0	80.5	-11.5	12.5	-412.9
#7	90.7	88.1	-2.6	2.9	-93.2
#8	71.2	40.5	-30.7	43.1	-1102.3
Mean	68.9	49.2	-19.7	33.4	-710.3

A total of 10 taxa was recorded across all samples; however, taxa richness varied significantly among substratum states (Pseudo-$F_{2,81}$ = 19.04; $p < 0.0001$; **Table A.II.1a; Fig. 8a**). Taxa richness was higher in Stable plots compared to both Abraded and Reference states, while no significant difference was detected between Abraded and Reference states (cf. **Table A.II.2**). Taxa richness also varied across habitat compartments (Pseudo-$F_{2,81}$ = 35.11; $p < 0.0001$; **Table A.II.1a; Fig. 8b**) with lower values in the Aboveground compartment compared to both Benthic and Whole compartments, which displayed similar values (cf. **Table A.II.2**). Total biomass (g WW) of sampled community varied among substratum states (Pseudo-$F_{2,81}$ = 7.53; $p = 0.0011$; **Table A.II.1b; Fig. 8c**) with higher values in Stable and Abraded states and lower values in the Reference state (cf. **Table A.II.2**). Among compartments, for both taxa richness and biomass (Pseudo-$F_{2,81}$ = 35.11; $p < 0.0001$; Pseudo-$F_{2,81}$ = 7.81; $p = 0.0006$, respectively; **Fig. II.1b,d**), values varied similarly with lower values in the Aboveground compared to both Benthic and Whole compartments (cf. **Table A.II.2**).

We observed an interacting effect of substratum state and compartment on the whole community structure (Pseudo-$F_{2,54}$ = 3.51, $p = 0.0005$; **Table 4**; **Fig. 9**), indicating that the differences among states depended on the compartment considered. Pairwise comparisons showed (cf. **Table A.II.3**) that all State X Compartment combination groups significantly differed except between the Aboveground compartment of both Abraded and Reference states ($p = 0.5741$) as well as in the Benthic compartment of both Abraded and Stable states ($p = 0.3884$; see **Fig. 9a,b).** SIMPER analyses (**Table A.II.5**) revealed that differences in the Aboveground compartments were mainly driven by *Littorina saxatilis* and *Gammarus* spp., both more abundant among eelgrass leaves, together explaining most (50.3% and 71.3% respectively) of the differences associated with eelgrass loss (see **Fig. 9a,b**). In the benthic

compartment, differences between Reference and the two vegetated or post vegetated states were mainly due to taxa associated with mussel aggregations (e.g. *Mytilus* spp.; *Testudinalia testudinalis*, *Balanus crenatus*) and other sediment-related species (*Macoma balthica* and *Mya arenaria*), which explained between respectively 40.3% and 58.6% of differences with Benthic Stable and Abraded together with Reference samples.

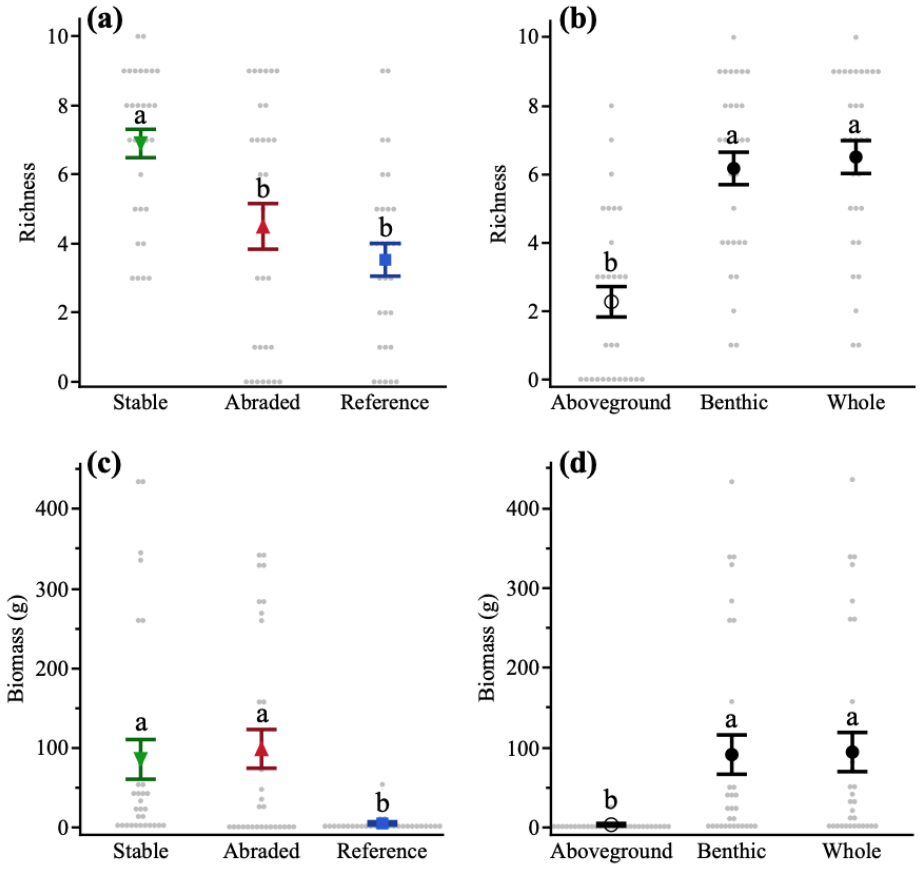


Figure 8. Mean (± SE) values of **(a-b)** taxa richness and **(c–d)** total wet biomass (WW; in g) of eelgrass-associated communities in each sample plot (n = 20). Panels **(a)** and **(c)** show variations among sampling states (Stable; Abraded; and Reference), while panels **(b)** and **(d)** present differences among compartments (Aboveground, Benthic, and Whole; see Methods). Grey points represent individual data samples. Different letters above bars denote significant differences among groups ($p < 0.05$).

Table 4. Summary of PERMANOVA results testing the effect of substratum State and the studied compartments on Whole community structure (both Aboveground and Benthic compartments combined). Significant values are shown in bold. V% stands for estimate of variance components.

Source of variation	df	Mean square	Pseudo-F	*p*-value	V%
Whole community structure					
State	2	12422	7.48	**<0.0001**	19.3
Compartment	1	39508	23.80	**<0.0001**	29.6
State x Compartment	2	5836	3.51	**0.0005**	17.1
Residuals	54	1660			34.0
Total	59				100

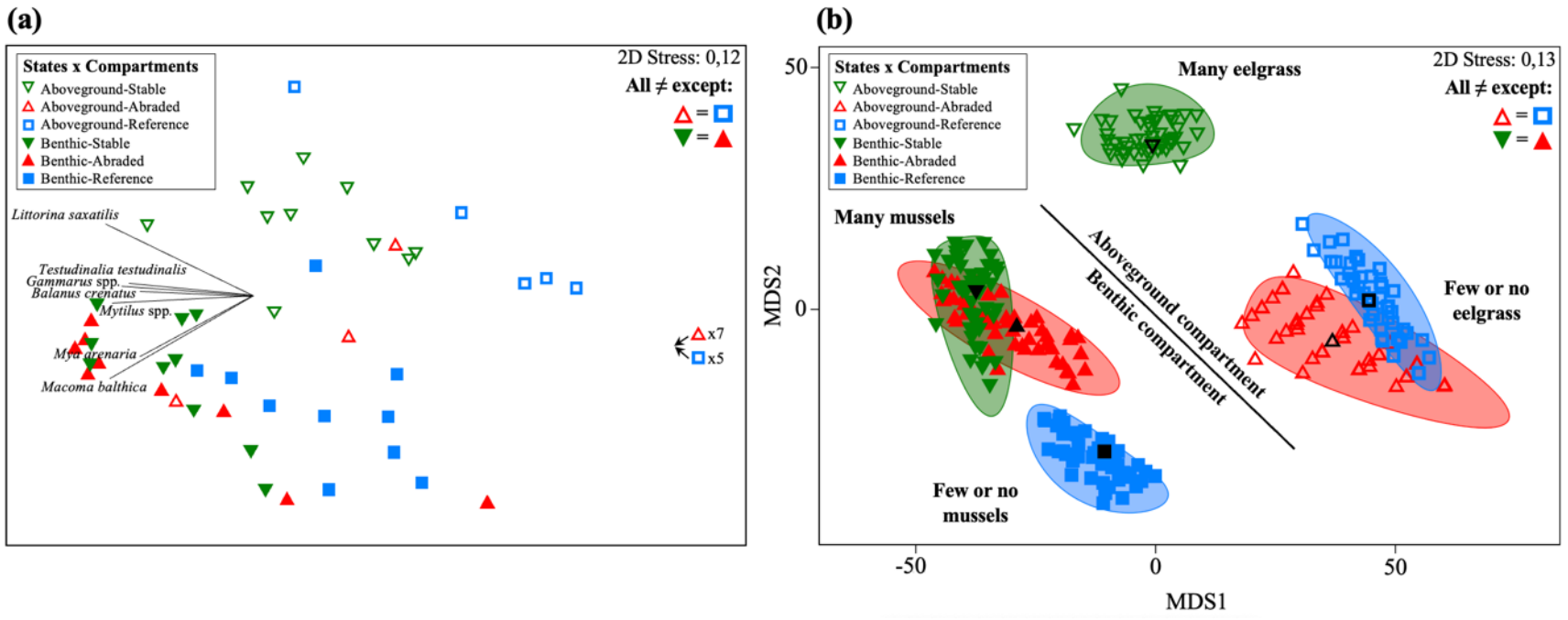


Figure 9. (a) Non-metric multidimensional scaling (nMDS) plot based on a Bray–Curtis similarity matrix (DW + square root transformed) showing differences in benthic community composition among states conditions for Whole eelgrass habitat communities (i.e., both Aboveground and Benthic associated species; Pseudo-$F_{2,54}$ = 3.51; p = 0.0005; n = 60). Symbols in **(a)** represent sampled quadrats according to treatments (see legend for colour and shape codes), while vectors indicate the taxa that generally contributing most to the ordination pattern. For greater clarity of the pattern shown in **(a)**, we also present the same data in **(b)** as bootstrap-averaged MDS plots, showing simulated factor centroids (n = 50 per group, total = 300) and their 95% regions.

2.4. Discussion

In a context of climate change and the progressive decline of ice cover in subarctic environments, this study provides empirical evidence of post winter eelgrass cover loss and associated community differences under reduced icefoot protection. Our study has shown that changes can be large within an eelgrass seascape over a single year. Under conditions characterized by the absence of a protective icefoot, increased exposure to winter disturbances led to marked shifts in taxa richness and community structure. By comparing contrasting substratum conditions (Stable, Abraded and Reference) and integrating both Aboveground and Benthic compartments, this study provides new insights into how the dynamics of eelgrass-associated communities may change under changing ice regimes.

Based on drone survey conducted in August 2025, we observed a significant loss of eelgrass cover at our study site (Anse à la Peinture; AP). Despite reaching peak growth in the same late summer, the extent of eelgrass meadows remained reduced, with an average loss of 20% and no evidence of recovery. We consider that the observed loss at AP was due to the absence of a protective icefoot which left the shore exposed to numerous physical disturbances from late autumn to spring, including large temperature variations and abrasion from sea ice rafts (ice scouring). Such ice-driven disturbance has been shown to cause physical damage and loss of eelgrass cover by promoting sediment mobilization, erosion, and rhizome destabilization, thereby reducing eelgrass resistance and recovery potential (Robertson et Mann 1984).

Reductions in three-dimensional structures (i.e., loss of eelgrass leaves) are expected to decrease habitat complexity, leading to fewer refuges and feeding opportunities for associated fauna (Duffy 2006). Accordingly, this reduction is also expected to decrease taxa

richness, consistent with the lower values observed in Abraded plots compared with Stable substratum conditions. Thus, the disappearance of canopy habitat in Abraded areas largely accounts for the overall reduction in taxa richness. In contrast, high taxa richness values occurred in the Benthic compartment, were mostly due to the presence of mussels and their associated hard-substratum taxa (e.g., *Testudinalia testudinalis*, *Balanus crenatus*, *Littorina saxatilis*). The lack of significant differences in taxa biomass between Stable and Abraded substratum conditions, and between Benthic and Whole compartments, suggests that the total biomass of the associated community was maintained despite the removal of eelgrass leaves. This pattern may be explained by the high abundance of mussels observed in many Abraded plots, where mussels remained attached to persistent eelgrass rhizomes.

While eelgrass loss reduces canopy-derived complexity, the persistence of living *Mytilus* spp. in Abraded areas may have partially buffered the effects of eelgrass loss on Benthic community structure by maintaining biogenic habitat and structural complexity. However, this apparent buffering did not extend to the Aboveground community, where Abraded areas more closely resembled the unvegetated Reference substratum conditions, highlighting the unique ecological role of the eelgrass canopy. Mussels, like eelgrass, are key foundation species known to provide colonization surfaces for many organisms, creating micro-refuges among mussel individuals (Largaespada *et al.* 2012; Lafferty and Suchanek 2016) and offering feeding opportunities (Norling and Kautsky 2007). More broadly, the co-occurrence of foundation species can enhance biodiversity and ecosystem stability (Thomsen *et al.* 2018). At AP, the eelgrass and mussels provide complementary habitats, and this functional complementarity may have contributed to the observed differences from the Reference assemblages by increasing community resistance to winter disturbance. Beyond these effects on richness and associated community biomass, the lack of a protective icefoot was

associated with changes in overall assemblage structure. The strong differentiation between compartments suggests that Aboveground communities are more directly affected by eelgrass loss, whereas the Benthic assemblages remain comparatively stable, likely due to mussel presence. Together, the lack (or loss) of mussels in the Benthic compartment and the lack (or loss) of eelgrass leaves in the Aboveground compartment, led to simplified, low-richness and low-biomass community structure. Overall, the results show persistence in abundance structure, associated community biomass, and taxa richness, suggesting that eelgrass habitat exhibited a degree of resistance (or inertia; *sensu* Sousa 1984) to winter disturbances during the study period. Such resistance and the ability to recover of eelgrass meadows were also demonstrated when exposed to multiple disturbances, including hydrodynamic stress, sediment burial, and grazing (Cimon *et al.* 2021). The effects of the co-occurrence of two relatively complementary foundation species in sedimentary habitats on biodiversity and associated communities, and in their functioning, warrant further research attention. This was also documented in numerous studies when eelgrass is lost (Bruno *et al.* 2003; Hughes *et al.* 2009).

Overall, our results indicate that the ecological impact of icefoot loss may depend less on abrasion intensity alone than on the ecosystem's capacity to retain habitat-forming ecosystem engineers (Jones *et al.* 1994). Thus, benthic community responses rely on facilitation by foundation species rather than on the persistence of a single dominant species (Angelini *et al.* 2011). These results suggest that biotic interactions may contribute to the resistance of coastal habitats to increasing winter disturbances. Further studies across multiple sites and years will be necessary to determine whether the observed patterns are consistent under different winter conditions and disturbance regimes.

In a context of more unstable winters and reduced icefoot formation, the persistence of secondary foundation species (*sensu* Altieri *et al.* 2007) may buffer the local effects of physical disturbance. However, such compensation remains partial, since key ecosystem functions linked to the vegetative canopy cannot be fully replaced (Duarte 2002), particularly carbon sequestration (Röhr *et al.* 2018) and the provision of nursery habitats supporting early life stages of numerous species (Heck *et al.* 2003; Orth *et al.* 2006). Over the long term, the increasing frequency of disturbances by drifting ice rafts on shores no longer protected by icefoot may drive a more dynamic intertidal habitat, where benthic engineers such as mussels, when locally maintained, may play an unexpected role in resistance.

2.5. Concluding remarks

The observed disturbances, most likely associated with winter processes, substantially altered eelgrass cover, biodiversity, and associated community structure. Reduced coastal protection by icefoot would increase intertidal habitat exposure to mechanical (e.g., ice scouring, erosion, and waves) and physical (thermal variation and desiccation) stressors, thereby progressively influencing benthic assemblages and their ecological functions. Secondary foundation species, such as mussels, may partly offset localized habitat loss by maintain some ecological complexity. However, they do not prevent major physical disturbances associated with reduced icefoot protection, although they may help maintain local habitat complexity and support associated communities. Our findings highlight the importance of further investigating how ongoing abovementioned changes may influence subarctic eelgrass meadows, particularly with respect to ecosystem functioning and the services these ecosystems provide.

2.6. References

Altieri AH, Silliman BR et Bertness MD. 2007. Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. Am Nat, 169 : 195-206.

Anderson MJ. 2005. PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Auckland, Department of Statistics, University of Auckland, New Zealand.

Angelini C, Altieri AH, Silliman BR et Bertness MD. 2011. Interactions among Foundation Species and Their Consequences for Community Organization, Biodiversity, and Conservation. BioScience, 61 : 782-789.

Araújo CAS, Bélanger S, Bernatchez P et Cusson M. 2025. Massive increase of intertidal seagrass coverage in a large estuarine system revealed by four decades of Landsat imagery. Remote Sensing Applications: Society and Environment, 39 : 101623.

Attrill MJ, Strong JA et Rowden AA. 2000. Are Macroinvertebrate Communities Influenced by Seagrass Structural Complexity? Ecography, 23 : 114-121.

Bandet M, Caulet C, Baudry J, Didier D, Dubuc D, Marion N, McKinnon R, Paul-Hus C, Caveen J, Sévigny C, Senneville S, Dumont D et et Bernatchez P. 2020. Programme de mesure et de modélisation de la morphodynamique de l'érosion et de la submersion côtière dans l'estuaire et le golfe du Saint-Laurent (MoDESCo), Phase III : rapport final. Chaire de recherche en géoscience côtière, Laboratoire de dynamique et de gestion intégrée des zones côtières, Université du Québec à Rimouski. Rapport remis au ministère de la Sécurité publique du Québec, novembre 2020, 259 p.

Bergeron P and Bourget E. 1984. Effet du froid et des glaces sur les peuplements intertidaux des régions nordiques, particulièrement dans l'estuaire du Saint-Laurent. Oceanis, 10 : 279-304.

Bergeron P and 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.

Boström C, Jackson EL et Simenstad CA. 2006. Seagrass landscapes and their effects on associated fauna: A review. Estuarine, Coastal and Shelf Science, 68 : 383-403.

Bruno JF, Stachowicz JJ et Bertness MD. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution, 18 : 119-125.

Cimon S, Deslauriers A et Cusson M. 2021. Multiple stressors and disturbance effects on eelgrass and epifaunal macroinvertebrate assemblage structure. Marine Ecology Progress Series, 657 : 93-108.

Clarke KR and Gorley RN. 2015. PRIMER v7: User Manual/Tutorial. Plymouth, UK, PRIMER-E.

Clarke KR, Tweedley JR et Valesini FJ. 2014. 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 : 1-16.

Clarke KR, Chapman MG, Somerfield PJ et Needham HR. 2006. Dispersion-based weighting of species counts in assemblage analyses. Marine Ecology Progress Series, 320 : 11-27.

Conlan KE, Lenihan HS, Kvitek RG et Oliver JS. 1998. Ice scour disturbance to benthic communities in the Canadian High Arctic. Marine Ecology Progress Series, 166 : 1-16.

Dionne J-C. 1973. La notion de pied de glace (Icefoot), en particulier dans l'estuaire du Saint-Laurent. Cahiers de géographie du Québec, 17 : 221-250.

Duarte CM. 2002. The future of seagrass meadows. Environmental Conservation, 29 : 192-206.

Duffy JE. 2006. Biodiversity and the functioning of seagrass ecosystems. Marine Ecology Progress Series, 311 : 233-250.

Ellis DV and Wilce RT. 1961. Arctic and Subarctic Examples of Intertidal Zonation. ARCTIC, 14 : 224-235.

Fonseca MS and Fisher JS. 1986. A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. Marine Ecology Progress Series, 29 : 15-22.

Forbes DL and Taylor RB. 1994. Ice in the shore zone and the geomorphology of cold coasts. Progress in Physical Geography: Earth and Environment, 18 : 59-89.

Galbraith PS, Chassé J, Shaw J-L, Lefaivre D et Bourassa M-N. 2025. Physical oceanographic conditions in the Gulf of St. Lawrence during 2024. Can. Tech. Rep. Hydrogr. and Ocean Sci. 397: v + 95 p.

Gutt J. 2001. On the direct impact of ice on marine benthic communities, a review. Polar Biology, 24 : 553-564.

Heck KL, Hays G et Orth RJ. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Marine Ecology Progress Series, 253 : 123-136.

Hemminga MA and Duarte CM. 2000. Seagrass Ecology. Cambridge University Press. 298 p.

Hughes AR, Williams SL, Duarte CM, Heck Jr KL et Waycott M. 2009. Associations of concern: declining seagrasses and threatened dependent species. Frontiers in Ecology and the Environment, 7 : 242-246.

Jones CG, Lawton JH et Shachak M. 1994. Organisms as Ecosystem Engineers. Oikos, 69 : 373-386.

Lafferty KD and Suchanek TH. 2016. Revisiting Paine's 1966 Sea Star Removal Experiment, the Most-Cited Empirical Article in the American Naturalist. Am Nat, 188 : 365-378.

Largaespada C, Guichard F et Archambault P. 2012. Meta-ecosystem engineering: Nutrient fluxes reveal intraspecific and interspecific feedbacks in fragmented mussel beds. Ecology, 93 : 324-333.

McKindsey CW and Bourget E. 2001. Diveristy of a northern rocky intertidal community: the influence of body size and succession. Ecology, 82 : 3462-3478.

Norling P and Kautsky N. 2007. Structural and functional effects of *Mytilus edulis* on diversity of associated species and ecosystem functioning. Marine Ecology Progress Series, 351 : 163-175.

Orth RJ, Heck KL et Van Montfrans J. 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries, 7 : 339-350.

Orth RJ, Carruthers TJ, Dennison WC et & Duarte CM. 2006. A global crisis for seagrass ecosystems. BioScience, 56 : 987-996.

Pascal L, Bernatchez P, Chaillou G, Nozais C, Lapointe Saint-Pierre M et Archambault P. 2020. Sea ice increases benthic community heterogeneity in a seagrass landscape. Estuarine, Coastal and Shelf Science, 243 : 106898.

Reynolds PL, Richardson JP et Duffy JE. 2014. Field experimental evidence that grazers mediate transition between microalgal and seagrass dominance. Limnology and Oceanography, 59 : 1053-1064.

Robertson AI and Mann KH. 1984. Disturbance by ice and life-history adaptations of the seagrass *Zostera marina*. Marine Biology, 80 : 131-141.

Röhr ME, Holmer M, Baum JK, Björk M, Boyer K, Chin D, Chalifour L, Cimon S, Cusson M, Dahl M, Deyanova D, Duffy JE, Eklöf JS, Geyer JK, Griffin JN, Gullström M, Hereu CM, Hori M, Hovel KA, Hughes AR, Jorgensen P, Kiriakopolos S, Moksnes P-O, Nakaoka M, O'Connor MI, Peterson B, Reiss K, Reynolds PL, Rossi F, Ruesink J, Santos R, Stachowicz JJ, Tomas F, Lee K-S, Unsworth RKF et Boström C. 2018. Blue Carbon Storage Capacity of Temperate Eelgrass (*Zostera marina*) Meadows. Global Biogeochemical Cycles, 32 : 1457-1475.

Scrosati R and Heaven C. 2006. Field technique to quantify intensity of scouring by sea ice in rocky intertidal habitats. Marine Ecology Progress Series, 320 : 293-295.

Scrosati R and Eckersley LK. 2007. Thermal insulation of the intertidal zone by the ice foot. Journal of Sea Research, 58 : 331-334.

Smith SV. 1981. Marine Macrophytes as a Global Carbon Sink. Science, 211 : 838-840.

Sousa WP. 1984. The role of disturbance in natural communities. Annual Review of Ecology, Evolution, and Systematics, 15 : 353-391.

Susini C. 2022. Effets de l'abrasion par la glace sur la dynamique temporelle de la productivité macroalgale intertidale du Saint-Laurent. Mémoire de Maîtrise. Université du Québec à Chicoutimi, Chicoutimi, 59 p.

Thomsen MS, Altieri AH, Angelini C, Bishop MJ, Gribben PE, Lear G, He Q, Schiel DR, Silliman BR, South PM, Watson DM, Wernberg T et Zotz G. 2018. Secondary foundation species enhance biodiversity. Nature Ecology & Evolution, 2 : 634-639.

Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL, Hughes AR, Kendrick GA, Kenworthy WJ, Short FT, Williams SL et Paine RT. 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 : 12377-12381.

CONCLUSION GÉNÉRALE

Mon travail de maîtrise a permis d'acquérir de nouvelles connaissances sur les effets des perturbations hivernales et des modifications des régimes de glaces côtières sur les communautés benthiques médiolittorales de l'Estuaire maritime du Saint-Laurent. En étudiant trois espèces fondatrices d'une grande importance écologique, soit les macroalgues, les moules et les zostères, leur recouvrement a été comparé avant et après une saison hivernale. Cette approche a permis de définir trois états de substrat et d'évaluer l'influence des régimes de glace entre l'automne et le printemps suivant sur la biodiversité associée ainsi que sur la structure des communautés benthiques à la suite des perturbations hivernales.

Les résultats obtenus démontrent que les habitats protégés par un pied de glace ont conservé un recouvrement stable en espèces fondatrices ainsi qu'une grande complexité structurelle des communautés associées. À l'inverse, les habitats exposés à une réduction de cette protection hivernale ont présenté davantage de perturbations physiques, entraînant des pertes localisées de recouvrement, particulièrement importantes en marge des bancs de moules et au sein des herbiers de zostères. Les analyses multivariées se sont révélées particulièrement pertinentes pour détecter les variations dans la structure des communautés benthiques, même lorsque certaines métriques univariées ne montraient pas de différences significatives. La présence d'un pied de glace stable semble ainsi agir comme un facteur de protection contre les stress mécaniques et physiques hivernaux, notamment l'abrasion par les glaces dérivantes, l'érosion, l'action des vagues et les variations thermiques. Cette étude met également en évidence l'importance écologique des espèces fondatrices dans le maintien de la biodiversité médiolittorale. Les assemblages macroalgaux, les bancs de moules et les

herbiers de zostère soutiennent une richesse spécifique élevée et structurent fortement les communautés associées en fournissant refuge, substrat et complexité d'habitat. Les zones abrasées à la suite des perturbations hivernales présentaient généralement des communautés moins riches et moins diversifiées, particulièrement au sein des habitats de moules. Toutefois, certains habitats, comme les herbiers de zostère et les assemblages de macroalgues, ont démontré une certaine capacité à limiter les effets des perturbations grâce à la persistance d'espèces fondatrices secondaires, comme les moules ou par le développement d'algues opportunistes telle que *Ulothrix flacca*, contribuant ainsi au maintien local d'une certaine complexité écologique après perturbation. Malgré cela, ces espèces ne permettent pas de compenser entièrement les effets des perturbations physiques majeures. Dans l'ensemble, plusieurs communautés ont démontré une certaine résistance, favorisée par la persistance de structures d'habitat résiduelles, la présence d'espèces tolérantes aux perturbations et l'adaptation naturelle des organismes médiolittoraux aux conditions environnementales variables. Toutefois, les résultats suggèrent que les changements dans les régimes de glace pourraient progressivement mener les communautés autrefois protégées par un pied de glace vers des états davantage exposés et perturbés, ce qui pourrait entraîner des répercussions à long terme sur le fonctionnement des écosystèmes côtiers.

Dans le but de quantifier l'impact des régimes de glace sur les communautés benthiques médiolittorales, des tiges en acier ont été installées autour et sur les blocs rocheux épars de nos sites protégés et exposés. Malgré les efforts méthodologiques déployés afin d'obtenir des résultats probants, ceux-ci se sont révélés peu concluants. La perte de certaines tiges, ainsi que l'absence de relation constante entre leur pliage, générée par la force des glaces et les pertes de macroalgues observées par nos suivis photographiques, illustrent le caractère

complexe et imprévisible des régimes de glace et de leurs effets sur les communautés benthiques. En effet, certaines roches présentaient des tiges fortement pliées sans qu'aucune modification du recouvrement macroalgal ne soit observée, alors qu'à l'inverse, d'importantes pertes de macroalgues ont parfois été associées à des tiges demeurées intactes. Par ailleurs, la mise en place de senseurs de température sur les différents sites permettant d'évaluer l'effet de protection thermique du pied de glace s'est révélée peu concluante. Le dispositif ayant été installé trop bas sur les blocs rocheux, les senseurs sont demeurés immergés la majeure partie du temps, ce qui n'a pas permis de caractériser adéquatement les températures sous le pied de glace et à l'extérieur de celui-ci, lors de sa présence comme de son absence. Quelques enregistrements suggèrent néanmoins que les températures mesurées sous le pied de glace étaient légèrement plus élevées que celles observées à l'extérieur. Toutefois, l'ensemble des observations n'a pas permis de dégager de conclusions solides. Malgré ces limites, ces résultats mettent en évidence le potentiel de protection thermique associé au pied de glace, un aspect qui fera l'objet d'analyses plus approfondies dans une étude ultérieure. Le protocole d'échantillonnage utilisé constitue également une limite dans l'interprétation des résultats. Les observations photographiques ayant été réalisées uniquement avant l'hiver et à la fin de la saison de croissance suivante (juillet/août 2025), il n'est pas possible de distinguer les effets immédiats des perturbations hivernales des processus de récupération ou de l'influence d'autres facteurs environnementaux ayant pu agir entre le printemps et la fin de l'été sur la structure des communautés (même si ces derniers sont limités). De plus, le suivi limité à une seule année ne permet pas de déterminer si les différences observées entre les sites reflètent uniquement les conditions de l'hiver étudié ou si elles s'inscrivent dans des trajectoires de récupération/détérioration distinctes liées à des

historiques de perturbation différentes. Ces limites doivent donc être prises en considération dans l'interprétation des résultats.

Dans un contexte de changements climatiques et de "boréalisation" croissante des environnements subarctiques (associée à une réorganisation des communautés, notamment observée en milieu pélagique), une augmentation des tempêtes hivernales ainsi qu'une diminution de la formation de glace côtière sont anticipées d'ici 2100 (Bandet *et al.* 2020). Ces changements pourraient accroître la fréquence et l'intensité des perturbations hivernales subies par les communautés médiolittorales. À long terme, ces changements risquent de modifier la distribution, la résistance et le fonctionnement des habitats structurés par les espèces fondatrices du Saint-Laurent, avec des répercussions possibles sur les services écologiques qu'ils procurent aux communautés humaines. Dans des environnements où les changements peuvent survenir rapidement et où les événements naturels demeurent difficiles à prévoir, il est essentiel de mieux comprendre les conséquences futures sur ces habitats. La poursuite des recherches dans ce domaine demeure donc nécessaire afin de mieux anticiper la réponse des écosystèmes côtiers nordiques aux changements climatiques rapides. Des suivis à long terme intégrant des approches de télédétection, notamment à l'aide de drones et d'imageries satellitaires, permettraient d'évaluer l'évolution des régimes de glace côtière, de déterminer les zones les plus exposées à l'abrasion, d'estimer la capacité de récupération des habitats médiolittoraux ainsi que d'évaluer les conséquences écologiques associées à des perturbations hivernales futures potentiellement plus fréquentes et imprévisibles.

LISTE DE RÉFÉRENCES

Anderson FE. 1983. The Northern Muddy Intertidal: Seasonal Factors Controlling Erosion and Deposition - A Review. Canadian Journal of Fisheries and Aquatic Sciences, 40 : 143-159.

Angelini C, Altieri AH, Silliman BR et Bertness MD. 2011. Interactions among Foundation Species and Their Consequences for Community Organization, Biodiversity, and Conservation. BioScience, 61 : 782-789.

Archambault D et Bourget E. 1983. Importance du régime de dénudation sur la structure et la succession des communautés intertidales de substrat rocheux en milieu subarctique. Canadian Journal of Fisheries and Aquatic Sciences, 40 : 1278-1292.

Arribas LP, Donnarumma L, Palomo MG et Scrosati RA. 2014. Intertidal mussels as ecosystem engineers: their associated invertebrate biodiversity under contrasting wave exposures. Marine Biodiversity, 44 : 203-211.

Attrill MJ, Strong JA et Rowden AA. 2000. Are Macroinvertebrate Communities Influenced by Seagrass Structural Complexity? Ecography, 23 : 114-121.

Bandet M, Caulet C, Baudry J, Didier D, Dubuc D, Marion N, McKinnon R, Paul-Hus C, Caveen J, Sévigny C, Senneville S, Dumont D et et Bernatchez P. 2020. Programme de mesure et de modélisation de la morphodynamique de l'érosion et de la submersion côtière dans l'estuaire et le golfe du Saint-Laurent (MoDESCo), Phase III : rapport final. Chaire de recherche en géoscience côtière, Laboratoire de dynamique et de gestion intégrée des zones côtières, Université du Québec à Rimouski. Rapport remis au ministère de la Sécurité publique du Québec, novembre 2020, 259 p.

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC et Silliman BR. 2011. The value of estuarine and coastal ecosystem services. Ecological Monographs, 81 : 169-193.

Barnes DKA. 1999. The influence of ice on polar nearshore benthos. Journal of the Marine Biological Association of the United Kingdom, 79 : 401-407.

Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF et Weinstein MP. 2001. The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates: A better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. BioScience, 51 : 633-641.

Bertness MD, Leonard GH, Levine JM et Bruno JF. 1999. Climate-Driven Interactions among Rocky Intertidal Organisms Caught between a Rock and a Hot Place. Oecologia, 120 : 446-450.

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 : 2061-2067.

Boller ML et Carrington E. 2006. The hydrodynamic effects of shape and size change during reconfiguration of a flexible macroalga. Journal of Experimental Biology, 209 : 1894-1903.

Boroda AV, Kipryushina YO et Odintsova NA. 2020. The effects of cold stress on *Mytilus* species in the natural environment. Cell Stress Chaperones, 25 : 821-832.

Borthagaray AI et Carranza A. 2007. Mussels as ecosystem engineers: Their contribution to species richness in a rocky littoral community. Acta Oecologica, 31 : 243-250.

Braby CE. 2007. Cold stress. Dans : Denny MW et Gaines SD éds. Encyclopedia of Tidepools and Rocky Shores. University of California Press, Berkeley, p. 148-150.

Bruno JF, Stachowicz JJ et Bertness MD. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution, 18 : 119-125.

Burke L, Kura Y, Kassem K, Revenga C, Spalding M, McAllister D et Caddy J. 2001. Pilot Analysis of Global Ecosystems: Coastal ecosystems. World Resources Institute, Washington D.C, 77 p.

Cazenave A et Cozannet GL. 2014. Sea level rise and its coastal impacts. Earth's Future, 2 : 15-34.

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

Colman J. 1933. The Nature of the Intertidal Zonation of Plants and Animals. Journal of the Marine Biological Association of the United Kingdom, 18 : 435-476.

Connell JH. 1972. Community Interactions on Marine Rocky Intertidal Shores. Annual Review of Ecology and Systematics, 3 : 169-192.

Connolly RM. 1995. Effects of removal of seagrass canopy on assemblages of small, motile invertebrates. Marine Ecology Progress Series, 118 : 129-137.

Cosby AG, Lebakula V, Smith CN, Wanik DW, Bergene K, Rose AN, Swanson D et Bloom DE. 2024. Accelerating growth of human coastal populations at the global and continent levels: 2000-2018. Sci Rep, 14 : 22489.

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

Cusson M et Bourget E. 2005. Small-scale variations in mussel (*Mytilus* spp.) dynamics and local production. Journal of Sea Research, 53 : 255-268.

Davison IR et Pearson GA. 1996. Stress tolerance in intertidal seaweeds. Journal of Phycology, 32 : 197-211.

Denny MW et Wethey DS. 2001. Physical processes that generate patterns in marine communities. Dans: Bertness MD, Hay ME, Gaines SD, éds. Marine Community Ecology. New York: Sinauer Associates. p. 3–37.

Duarte CM et Cebrian J. 1996. The Fate of Marine Autotrophic Production. Limnology and Oceanography, 41 : 1758-1766.

Duarte CM, Middelburg JJ et Caraco N. 2005. Major role of marine vegetation on the oceanic carbon cycle. Biogeosciences, 1 : 1-8.

Duffy JE. 2006. Biodiversity and the functioning of seagrass ecosystems. Marine Ecology Progress Series, 311 : 233-250.

Ellis DV et Wilce RT. 1961. Arctic and Subarctic Examples of Intertidal Zonation. ARCTIC, 14 : 224-235.

Forbes DL et Taylor RB. 1994. Ice in the shore zone and the geomorphology of cold coasts. Progress in Physical Geography: Earth and Environment, 18 : 59-89.

Galbraith PS, Chassé J, Shaw J-L, Lefaivre D et Bourassa M-N. 2025. Physical oceanographic conditions in the Gulf of St. Lawrence during 2024. Can. Tech. Rep. Hydrogr. and Ocean Sci. 397: v + 95 p.

Galbraith PS, Caverhill C, Chassé J, Nicot P, Gilbert D, Lefaivre D et Lafleur C. 2018. Physical Oceanographic Conditions in the Gulf of St. Lawrence during 2017. DFO Can. Sci. Advis. Sec. Doc. 2018/050. 80 p.

Gollety C, Thiebaut E et Davoult D. 2011. Characteristics of the *Ascophyllum nodosum* stands and their associated diversity along the coast of Brittany, France. Journal of the Marine Biological Association of the United Kingdom, 91 : 569-577.

Gutiérrez JL, Jones CG, Strayer DL et Iribarne OO. 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos, 101 : 79-90.

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R et Watson R. 2008. A Global Map of Human Impact on Marine Ecosystems. Science, 319 : 948-952.

Harley CDG, Randall Hughes A, Hultgren KM, Miner BG, Sorte CJB, Thornber CS, Rodriguez LF, Tomanek L et Williams SL. 2006. The impacts of climate change in coastal marine systems. Ecology Letters, 9 : 228-241.

Heck KL, Hays G et Orth RJ. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Marine Ecology Progress Series, 253 : 123-136.

Helmuth B, Mieszkowska N, Moore P et Hawkins SJ. 2006. Living on the Edge of Two Changing Worlds: Forecasting the Responses of Rocky Intertidal Ecosystems to Climate Change. Annual Review of Ecology, Evolution, and Systematics, 37 : 373-404.

Helmuth B, Harley CD, Halpin PM, O'Donnell M, Hofmann GE et Blanchette CA. 2002. Climate change and latitudinal patterns of intertidal thermal stress. Science, 298 : 1015-1017.

Hemminga MA et Duarte CM. 2000. Seagrass Ecology. Cambridge University Press. 298 p.

Jones CG, Lawton JH et Shachak M. 1994. Organisms as Ecosystem Engineers. Oikos, 69 : 373-386.

Joseph L et Cusson M. 2015. Resistance of benthic intertidal communities to multiple disturbances and stresses. Mar Ecol Prog Ser, 534 : 49-64

Kautsky N et Evans S. 1987. Role of biodeposition by *Mytilus edulis* in the circulation of matter and nutrients in a Baltic coastal ecosystem. Marine Ecology Progress Series, 38 : 201-212.

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 : e109261.

McCook LJ et Chapman ARO. 1991. Community succession following massive ice-scour on an exposed rocky shore: effects of Fucus canopy algae and of mussels during late succession. Journal of Experimental Marine Biology and Ecology, 154 : 137-169.

Menge BA et Sutherland JP. 1987. Community Regulation: Variation in Disturbance, Competition, and Predation in Relation to Environmental Stress and Recruitment. The American Naturalist, 130 : 730-757.

Möller I, Kudella M, Rupprecht F, Spencer T, Paul M, van Wesenbeeck BK, Wolters G, Jensen K, Bouma TJ, Miranda-Lange M et Schimmels S. 2014. Wave attenuation over coastal salt marshes under storm surge conditions. Nature Geoscience, 7 : 727-731.

Murphy DJ et Johnson LC. 1980. Physical and temporal factors influencing the freezing tolerance of the marine snail *Littorina littorea* (L.). The Biological Bulletin, 158 : 220-232.

Nicholls RJ. 2004. Coastal flooding and wetland loss in the 21st century: Changes under the SRES climate and socio-economic scenarios. Global Environmental Change, 14 : 69-86.

Norling P et Kautsky N. 2007. Structural and functional effects of *Mytilus edulis* on diversity of associated species and ecosystem functioning. Marine Ecology Progress Series, 351 : 163-175.

Ørberg SB, Krause-Jensen D, Mouritsen KN, Olesen B, Marbà N, Larsen MH, Blicher ME et Sejr MK. 2018. Canopy-Forming Macroalgae Facilitate Recolonization of Sub-Arctic Intertidal Fauna and Reduce Temperature Extremes. Frontiers in Marine Science, 5 : 332.

Orth RJ, Heck KL et Van Montfrans J. 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries, 7 : 339-350.

Orth RJ, Carruthers TJ, Dennison WC et & Duarte CM. 2006. A global crisis for seagrass ecosystems. BioScience, 56 : 987-996.

Pearson GA et Davison IR. 1993. Freezing rate and duration determine the physiological response of intertidal fucoids to freezing. Marine Biology : International Journal on Life in Oceans and Coastal Waters, 115 : 353-362.

Peck LS, Brockington S, Vanhove S et Beghyn M. 1999. Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica. Marine Ecology Progress Series, 186 : 1-8.

Petzold W, Willers M et Scrosati R. 2014. Visual record of intertidal disturbance caused by drift ice in the spring on the Atlantic coast of Nova Scotia. F1000Research, 3 : 112.

Pugh PJA et Davenport J. 1997. Colonisation vs. disturbance: the effects of sustained ice-scouring on intertidal communities. Journal of Experimental Marine Biology and Ecology, 210 : 1-21.

Raffaelli D et Hawkins S. 1999. The shore environment: major gradients. Dans : Raffaelli D et Hawkins S éds. Intertidal Ecology. Springer Netherlands, Dordrecht, p. 1-35.

Robertson AI et Mann KH. 1984. Disturbance by ice and life-history adaptations of the seagrass *Zostera marina*. Marine Biology : International Journal on Life in Oceans and Coastal Waters, 80 : 131-141.

Röhr ME, Holmer M, Baum JK, Björk M, Boyer K, Chin D, Chalifour L, Cimon S, Cusson M, Dahl M, Deyanova D, Duffy JE, Eklöf JS, Geyer JK, Griffin JN, Gullström M, Hereu CM, Hori M, Hovel KA, Hughes AR, Jorgensen P, Kiriakopolos S, Moksnes P-O, Nakaoka M, O'Connor MI, Peterson B, Reiss K, Reynolds PL, Rossi F, Ruesink J, Santos R, Stachowicz JJ, Tomas F, Lee K-S, Unsworth RKF et Boström C. 2018. Blue Carbon Storage Capacity of Temperate Eelgrass (*Zostera marina*) Meadows. Global Biogeochemical Cycles, 32 : 1457-1475.

Saucier FoJ, Roy Fo, Gilbert D, Pellerin P et Ritchie H. 2003. Modeling the formation and circulation processes of water masses and sea ice in the Gulf of St. Lawrence, Canada. Journal of Geophysical Research: Oceans, 108 : 3269.

Schiel DR, Steinbeck JR et Foster MS. 2004. Ten Years Of Induced Ocean Warming Causes Comprehensive Changes In Marine Benthic Communities. Ecology, 85 : 1833-1839.

Scrosati R. 2022. Low Winter Extremes in Intertidal Temperature in Nova Scotia in the Absence of an Ice Foot. Frontiers in Marine Science, 8 : 811545.

Scrosati R et Eckersley LK. 2007. Thermal insulation of the intertidal zone by the ice foot. Journal of Sea Research, 58 : 331-334.

Senneville S, St-Onge Drouin S, Dumont D, Bihan-Poudec AC, Belemaalem Z, Corriveau M, Bernatchez P, Bélanger S, Tolszczuk-Leclerc S et Villeneuve R. 2014. Modélisation des glaces dans l'estuaire et le golfe du Saint-Laurent dans la perspective des changements climatiques (Rapport final). Rimouski: Québec. Institut de sciences de la mer de Rimouski., http://www.bv.transports.gouv.qc.ca/mono/1147874.pdf

Spalding MD, Ruffo S, Lacambra C, Meliane I, Hale LZ, Shepard CC et Beck MW. 2014. The role of ecosystems in coastal protection: Adapting to climate change and coastal hazards. Ocean & Coastal Management, 90 : 50-57.

Stachowicz JJ. 2001. Mutualism, Facilitation, and the Structure of Ecological Communities: Positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend. BioScience, 51 : 235-246.

Stephenson TA et Stephenson A. 1949. The Universal Features of Zonation Between Tide-Marks on Rocky Coasts. Journal of Ecology, 37 : 289-305.

Telesh I, Schubert H et Skarlato S. 2013. Life in the salinity gradient: Discovering mechanisms behind a new biodiversity pattern. Estuarine, Coastal and Shelf Science, 135 : 317-327.

Vitousek PM, Mooney HA, Lubchenco J et Melillo JM. 1997. Human Domination of Earth's Ecosystems. Science, 277 : 494-499.

Watt CA et Scrosati RA. 2013. Regional consistency of intertidal elevation as a mediator of seaweed canopy effects on benthic species richness, diversity, and composition. Marine Ecology Progress Series, 491 : 91-99.

Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL, Hughes AR, Kendrick GA, Kenworthy WJ, Short FT, Williams SL et Paine RT. 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 : 12377-12381.

Wikström SA et Kautsky L. 2007. Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. Estuarine, Coastal and Shelf Science, 72 : 168-176.

World Meteorological Organization. 1970. Sea-Ice Nomenclature. WMO/OMM/BMO No. 259, Supplement No. 5. World Meteorological Organization, Geneva.

ANNEXE I

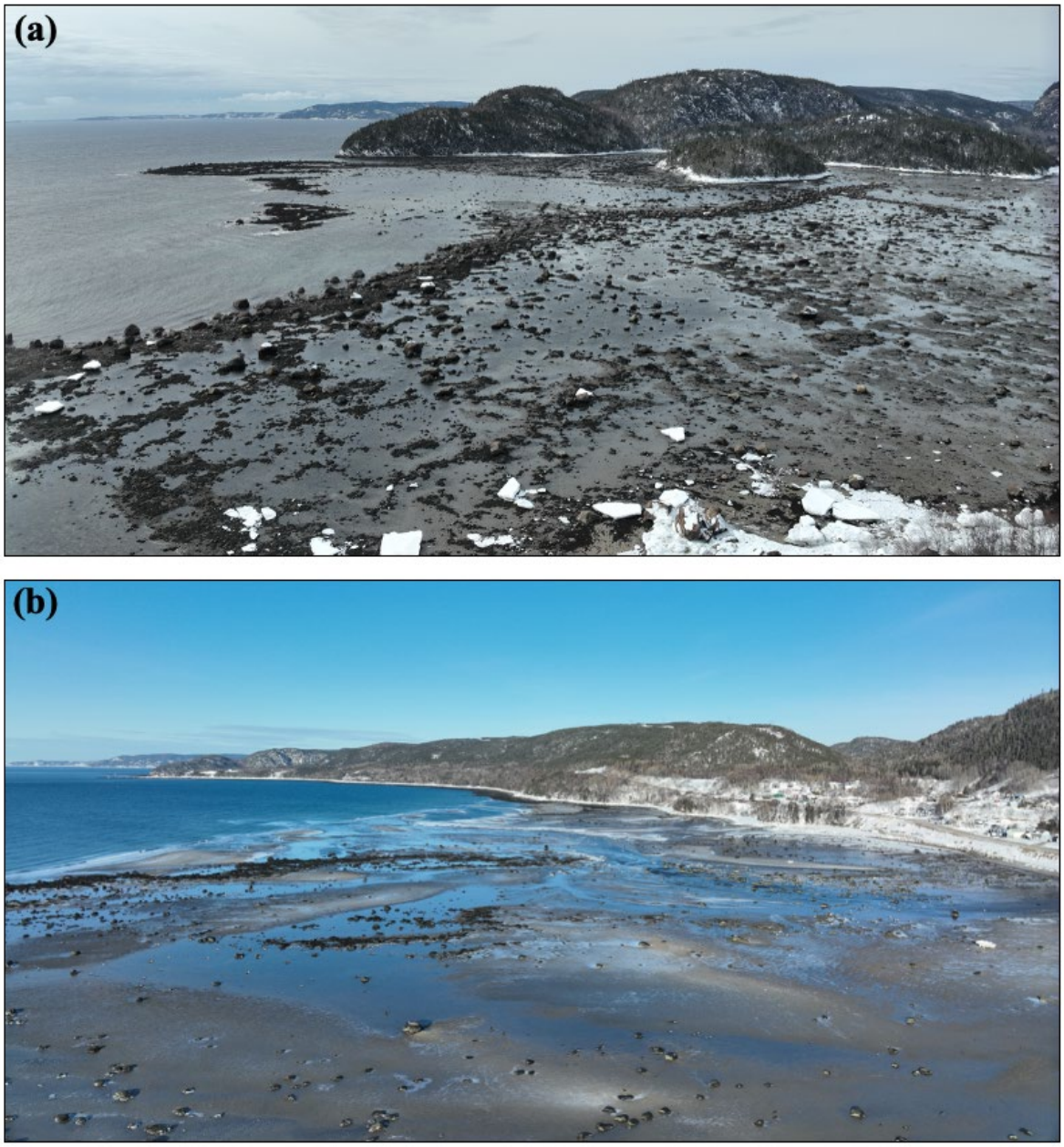


Figure A.I.1. Overall views of the study sites, (**a**) Pointe-Mistassini (Protected) and (**b**) Quai Franquelin (Exposed), after most of the protected icefoot had disappeared in March 2025

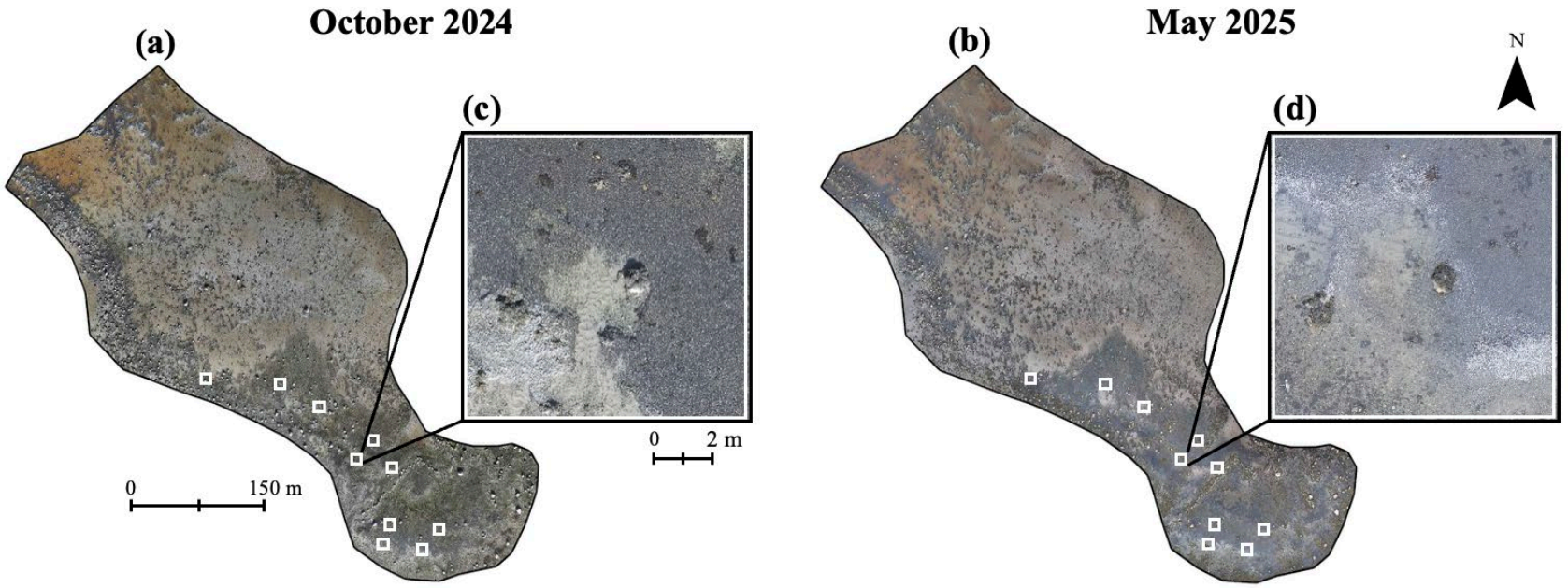


Figure A.I.2. Orthomosaics of Pointe-Mistassini (Protected) acquired in (**a;c**) October 2024 and (**b;d**) Mai 2025, from surveys conducted at an altitude of 84 m. The position of the ten sampled subzones (10 × 10 m) is indicated with white squares, with example subzone (**c;d**).

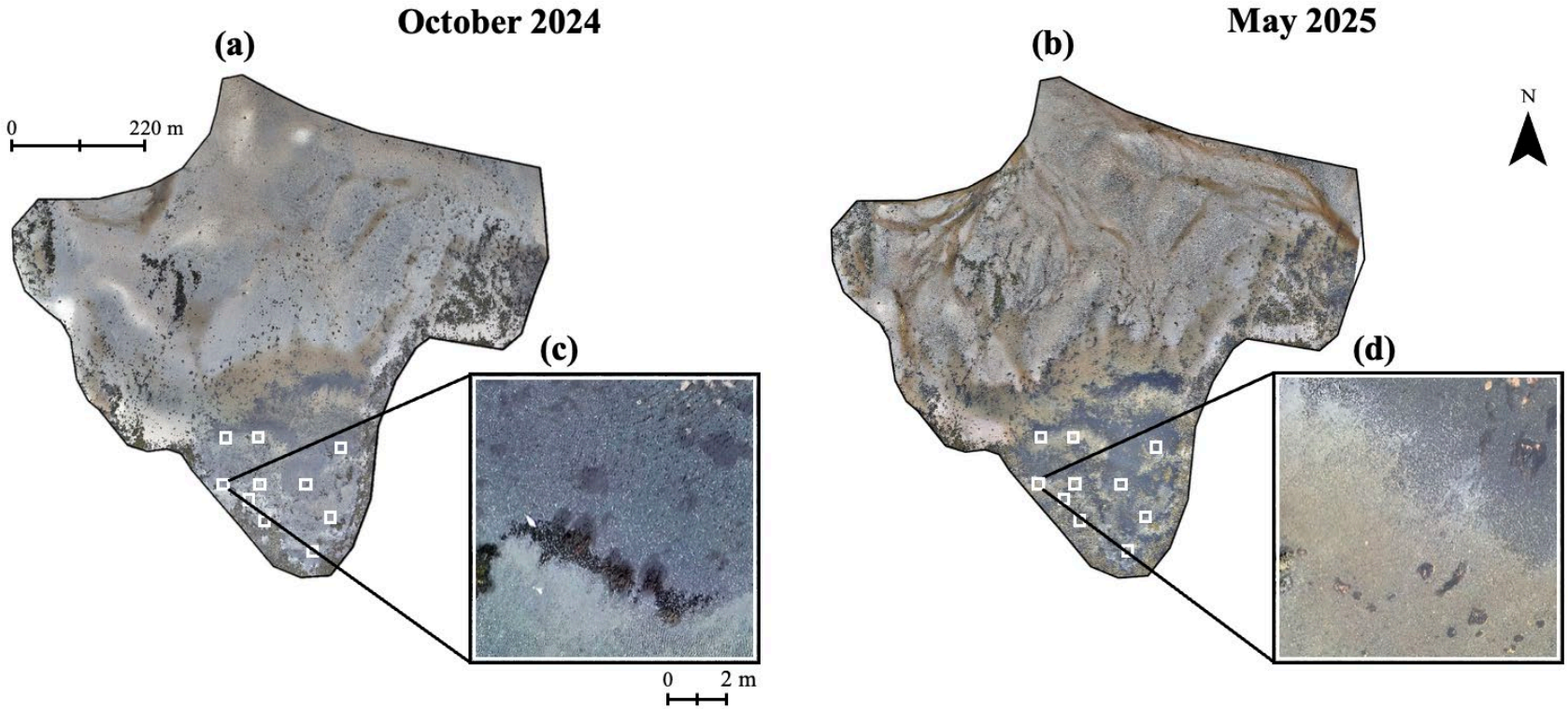


Figure A.I.3. Orthomosaics of Quai Franquelin (Exposed) acquired in (**a;c**) October 2024 and (**b;d**) Mai 2025, from surveys conducted at an altitude of 84 m. The position of the ten sampled subzones (10 × 10 m) is indicated with white squares, with example subzone (**c;d**).

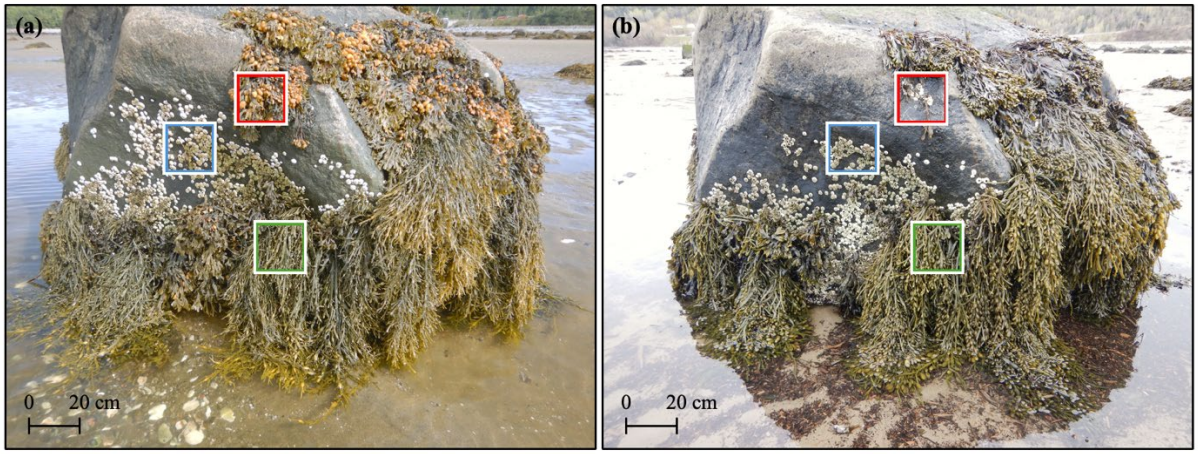


Figure A.I.4. Example of the same monitored boulder rock at Quai Franquelin (Exposed site), shown in (**a**) August 2024 and (**b**) May 2025. Trio of the three substratum states are illustrated: Stable (green), Abraded (red), and Reference (blue).

Table A.I.1. Summary of PER-ANOVA results testing the effect of substratum states ("States") on macroalgae cover anomalies. Significant values are shown in **bold**. V% stands for estimate of variance components.

Source of variation	df	Mean Square	Pseudo-F	*p*-value	V%
States	1	111.7	3.74	**0.0528**	25.2
Residuals	46	29.9			74.8
Total	47				100

Table A.I.2. Summary of PER-ANOVA results testing the effects of substratum state ("State") on mussel beds cover anomalies. Significant values are shown in **bold**. V% stands for estimate of variance components.

Source of variation	df	Mean Square	Pseudo-F	*p*-value	V%
States	1	1072	2.94	0.1019	30.6
Residuals	18	365			69.4
Total	19				100

Table A.I.3. Summary of PER-ANOVA results testing the effects of substratum state ("States"), Placement on mussels in beds ("Placement"), and their interaction on mussel bed cover anomalies. Significant values are shown in **bold**. V% stands for estimate of variance components.

Source of variation	df	Mean Square	Pseudo-F	*p*-value	V%
States	1	1072	14.03	**0.0005**	19.7
Placement	1	4722	61.83	**0.0002**	42.5
State x Placement	1	619	8.11	**0.0082**	20.5
Residuals	16	76			17.3
Total	19				100

Table A.4. Results of p-values from pairwise tests comparing substratum states on macroalgae cover anomalies. Significant values (< 0.05) are shown in **bold**.

Source of variation	*p*-value
Protected-Center X Protected-Edge	**0,0091**
Exposed-Center X Exposed-Edge	**0,0083**
Protected-Center X Exposed-Center	0,4429
Exposed-Edge x Protected-Edge	**0,0082**

Table A.5. Results of pairwise tests comparing taxa richness and biomass across states and habitat compartments. Significant values (< 0.05) are shown in **bold**.

Source of variation	***P-value***	***P-value***	***P-value***
	For richness	**For biomass**	**For diveristy**
(a) Macroalgae			
Stable x Abraded	**0.0209**	0.1806	0.2123
Abraded x Reference	**0.0004**	0.6664	**0.0008**
Stable x Reference	**0.0001**	0.2593	**0.0001**
(b) Mussel beds			
Stable x Abraded	**0.0001**	**0.0001**	**0.0028**
Abraded x Reference	0.4257	0.1952	**0.0311**
Stable x Reference	**0.0001**	**0.0001**	**0.0001**

Table A.I.6. Results of pairwise tests comparing macroalgal associated community structure between ice regimes and states. Significant values are shown in **bold**.

Source of variation	*p-value*
(a) Macroalgae	
Protected-Reference vs. Protected-Stable	**0,0001**
Protected-Reference vs. Protected-Abraded	**0.0037**
Protected-Reference vs. Exposed-Stable	**0.0002**
Protected-Reference vs. Exposed-Abraded	**0.0112**
Protected-Reference vs. Exposed-Reference	**0.0336**
Protected-Stable vs. Protected-Abraded	**0.0019**
Protected-Stable vs. Exposed-Stable	**0.0051**
Protected-Stable vs. Exposed-Abraded	**0.0002**
Protected-Stable vs. Exposed-Reference	**0.0002**
Protected-Abraded vs. Exposed-Stable	**0.0023**
Protected-Abraded vs. Exposed-Abraded	0.2402
Protected-Abraded vs. Exposed-Reference	**0.0012**
Exposed-Stable vs. Exposed-Abraded	0.1767
Exposed-Stable vs. Exposed-Reference	**0.0003**
Exposed-Abraded vs. Exposed-Reference	**0.0036**
(b) Mussel beds	
Protected-Reference vs. Protected-Stable	**0,0001**
Protected-Reference vs. Protected-Abraded	0.3652
Protected-Reference vs. Exposed-Stable	**0.0001**
Protected-Reference vs. Exposed-Abraded	**0.0047**
Protected-Reference vs. Exposed-Reference	**0.0001**
Protected-Stable vs. Protected-Abraded	**0.0001**
Protected-Stable vs. Exposed-Stable	**0.0001**
Protected-Stable vs. Exposed-Abraded	**0.0001**
Protected-Stable vs. Exposed-Reference	**0.0001**
Protected-Abraded vs. Exposed-Stable	**0.0001**
Protected-Abraded vs. Exposed-Abraded	**0.0034**
Protected-Abraded vs. Exposed-Reference	**0.0001**
Exposed-Stable vs. Exposed-Abraded	**0.0001**
Exposed-Stable vs. Exposed-Reference	**0.0001**
Exposed-Abraded vs. Exposed-Reference	0.1331

Table A.I.7. Macroalgae community: Similarity percentage (SIMPER) analysis results of dissimilarity between the interaction of ice regimes and substratum states (**bold**, in parentheses) along with mean transformed biomass values (DW-SqRt) for each comparison group named (X1 vs. X2). Taxa are ordered by decreasing percentage contributions to dissimilarity (%C), with cumulative contributions reached at least 70%.

Taxa	Av Ab X1	Av Ab X2	%C
Protected-Reference vs. Protected-Stable (**61.73 %**)			
Littorina obtusata	0.08	2.16	41.38
Littorina saxatilis	0.72	1.83	22.54
Ulothrix flacca	1.04	1.21	14.20
Protected-Reference vs. Protected-Abraded (**45.76 %**)			
Littorina saxatilis	0.72	1.40	29.97
Littorina obtusata	0.08	0.93	29.77
Ulothrix flacca	1.04	1.21	29.18
Protected-Stable vs. Protected-Abraded (**39.09 %**)			
Littorina obtusata	2.16	0.93	29.97
Ulothrix flacca	1.21	1.21	29.77
Littorina saxatilis	1.83	1.40	29.18
Protected-Reference vs. Exposed-Stable (**63.48 %)**			
Littorina obtusata	0.08	1.03	19.92
Ulothrix flacca	1.04	0.89	18.17
Littorina saxatilis	0.72	1.38	17.19
Jaera (Jaera) albifrons	0.00	0.70	14.19
Mytilus spp.	0.00	0.70	13.47
Protected-Reference vs. Exposed-Abraded (**52.44 %**)			
Ulothrix flacca	1.04	0.96	33.02
Littorina saxatilis	0.72	1.21	21.98
Littorina obtusata	0.08	0.55	15.50
Protected-Reference vs. Exposed-Reference (**31.63 %**)			
Ulothrix flacca	1.04	1.74	54.40
Littorina saxatilis	0.72	0.79	27.91
Protected-Stable vs. Exposed-Abraded (**50.90 %**)			
Littorina obtusata	2.16	0.55	34.03
Ulothrix flacca	1.21	0.96	17.23
Littorina saxatilis	1.83	1.21	16.98
Mytilus spp.	0.32	0.44	8.58
Protected-Stable vs. Exposed-Stable (**43.89 %**)			

Littorina obtusata	2.16	1.03	23.46
Ulothrix flacca	1.21	0.89	16.56
Littorina saxatilis	1.83	1.38	12.71
Mytilus spp.	0.32	0.70	12.12
Jaera (Jaera) albifrons	0.18	0.70	10.84
Protected-Stable vs. Exposed-Reference (**52.77 %**)			
Littorina obtusata	2.16	0.22	40.85
Littorina saxatilis	1.83	0.79	22.18
Ulothrix flacca	1.21	1.74	13.76
Protected-Abraded vs. Exposed-Stable (**49.51 %**)			
Ulothrix flacca	1.21	0.89	19.11
Littorina obtusata	0.93	1.03	15.98
Littorina saxatilis	1.40	1.38	15.15
Jaera (Jaera) albifrons	0.00	0.70	14.55
Mytilus spp.	0.05	0.70	13.67
Protected-Abraded vs. Exposed-Abraded (**46.98 %**)			
Ulothrix flacca	1.21	0.96	26.58
Littorina saxatilis	1.40	1.21	21.00
Littorina obtusata	0.93	0.55	19.83
Mytilus spp.	0.05	0.44	10.52
Protected-Abraded vs. Exposed-Reference (**38.31%**)			
Littorina obtusata	0.93	0.22	29.88
Ulothrix flacca	1.21	1.74	29.31
Littorina saxatilis	1.40	0.79	28.92
Exposed-Stable vs. Exposed-Abraded (**50.78 %**)			
Ulothrix flacca	0.89	0.96	20.00
Littorina obtusata	1.03	0.55	16.24
Littorina saxatilis	1.38	1.21	15.24
Mytilus spp.	0.70	0.44	14.56
Jaera (Jaera) albifrons	0.70	0.34	12.57
Exposed-Stable vs. Exposed-Reference (**57.29 %**)			
Ulothrix flacca	0.89	1.74	21.98
Littorina obtusata	1.03	0.22	18.44
Littorina saxatilis	1.38	0.79	15.84
Jaera (Jaera) albifrons	0.70	0.00	13.89
Exposed-Abraded vs. Exposed-Reference (**46.56 %**)			
Ulothrix flacca	0.96	1.74	35.57

Littorina saxatilis	1.21	0.79	19.92
Littorina obtusata	0.55	0.22	15.78

Table A.I.8. Mussel bed community: Similarity percentage (SIMPER) analysis results of dissimilarity between the interaction of ice regimes and substratum states (**bold**, in parentheses) along with mean transformed biomass values (DW-SqRt) for each comparison group (X1 vs. X2). Taxa are ordered by decreasing percentage contributions to dissimilarity (%C), with cumulative contributions reached at least 70%.

Taxa	**Av X1**	**Av X2**	**%C**
Protected-Reference vs. Protected-Stable (**75.33 %**)			
Macoma balthica	0.55	1.87	18.01
Gammarus spp.	0.37	1.84	17.27
Littorina saxatilis	0.36	1.67	15.09
Balanus crenatus	0.00	1.19	13.62
Nereis diversicolor	0.12	1.17	12.02
Protected-Reference vs. Protected-Abraded (**62.97 %**)			
Macoma balthica	0.55	0.82	34.93
Gammarus spp.	0.37	0.36	17.40
Littorina saxatilis	0.36	0.24	14.91
Mya arenaria	0.09	0.29	11.19
Protected-Stable vs. Protected-Abraded (**72.66 %**)			
Gammarus spp.	1.84	0.36	16.81
Littorina saxatilis	1.67	0.24	16.33
Macoma balthica	1.87	0.82	15.12
Balanus crenatus	1.19	0.05	13.09
Nereis diversicolor	1.17	0.03	12.28
Protected-Reference vs. Exposed-Stable (**79.31 %)**			
Gammarus spp.	0.37	1.87	21.50
Testudinalia testudinalis	0.01	1.04	13.35
Nereis diversicolor	0.12	0.76	12.01
Balanus crenatus	0.00	0.88	11.53
Macoma balthica	0.55	0.38	7.66
Eteone longa	0.00	0.46	7.35
Protected-Reference vs. Exposed-Abraded (**72.62 %**)			
Macoma balthica	0.09	0.55	20.82
Testudinalia testudinalis	0.39	0.01	19.98

Gammarus spp.	0.39	0.37	15.51
Littorina saxatilis	0.22	0.36	13.33
Eteone longa	0.21	0.00	5.68
Protected-Reference vs. Exposed-Reference (**77.30 %**)			
Testudinalia testudinalis	0.01	0.86	35.28
Macoma balthica	0.55	0.09	17.12
Gammarus spp.	0.37	0.29	11.22
Littorina saxatilis	0.36	0.23	11.08
Protected-Stable vs. Exposed-Abraded (**79.90 %**)			
Macoma balthica	1.87	0.09	20.91
Gammarus spp.	1.84	0.39	15.76
Littorina saxatilis	1.67	0.22	15.40
Balanus crenatus	1.19	0.04	12.12
Nereis diversicolor	1.17	0.07	11.36
Protected-Stable vs. Exposed-Stable (**51.39 %**)			
Macoma balthica	1.87	0.38	17.96
Littorina saxatilis	1.67	0.71	10.57
Gammarus spp.	1.84	1.87	10.49
Balanus crenatus	1.19	0.88	10.06
Nereis diversicolor	1.17	0.76	9.75
Testudinalia testudinalis	0.76	1.04	9.64
Jaera (Jaera) albifrons	0.57	0.15	5.82
Protected-Stable vs. Exposed-Reference (**78.26 %**)			
Macoma balthica	1.87	0.09	20.75
Gammarus spp.	1.84	0.29	16.20
Littorina saxatilis	1.67	0.23	15.07
Balanus crenatus	1.19	0.03	12.12
Nereis diversicolor	1.17	0.00	11.52
Exposed-Stable vs. Protected-Abraded (**79.61 %**)			
Gammarus spp.	1.87	0.36	20.08
Testudinalia testudinalis	1.04	0.05	12.34
Nereis diversicolor	0.76	0.03	11.55
Balanus crenatus	0.88	0.05	10.77
Macoma balthica	0.38	0.82	9.24
Eteone longa	0.46	0.12	6.95
Protected-Abraded vs. Exposed-Abraded (**72.53 %**)			

Macoma balthica	0.82	0.09	27.13
Testudinalia testudinalis	0.05	0.36	16.64
Gammarus spp.	0.36	0.39	12.89
Eteone longa	0.12	0.21	8.82
Mya arenaria	0.29	0.04	8.63
Exposed-Reference vs. Protected-Abraded (**76.20 %**)			
Testudinalia testudinalis	0.86	0.05	29.61
Macoma balthica	0.09	0.82	23.73
Gammarus spp.	0.29	0.36	9.34
Mya arenaria	0.06	0.29	7.68
Exposed-Stable vs. Exposed-Abraded (**76.56 %**)			
Gammarus spp.	1.87	0.39	21.58
Nereis diversicolor	0.76	0.07	12.38
Testudinalia testudinalis	1.04	0.39	12.00
Balanus crenatus	0.88	0.04	11.51
Eteone longa	0.46	0.21	8.20
Littorina saxatilis	0.71	0.22	7.14
Exposed-Stable vs. Exposed-Reference (**74.62 %**)			
Gammarus spp.	1.87	0.29	21.86
Nereis diversicolor	0.76	0.00	12.38
Balanus crenatus	0.88	0.03	11.41
Testudinalia testudinalis	1.04	0.86	10.87
Eteone longa	0.46	0.06	7.25
Littorina saxatilis	0.71	0.23	7.01
Exposed-Abraded vs. Exposed-Reference (**57.94 %**)			
Testudinalia testudinalis	0.39	0.86	27.17
Gammarus spp.	0.39	0.29	12.86
Littorina littorea	0.05	0.30	11.71
Littorina saxatilis	0.22	0.23	9.71
Eteone longa	0.21	0.06	8.57

ANNEXE II

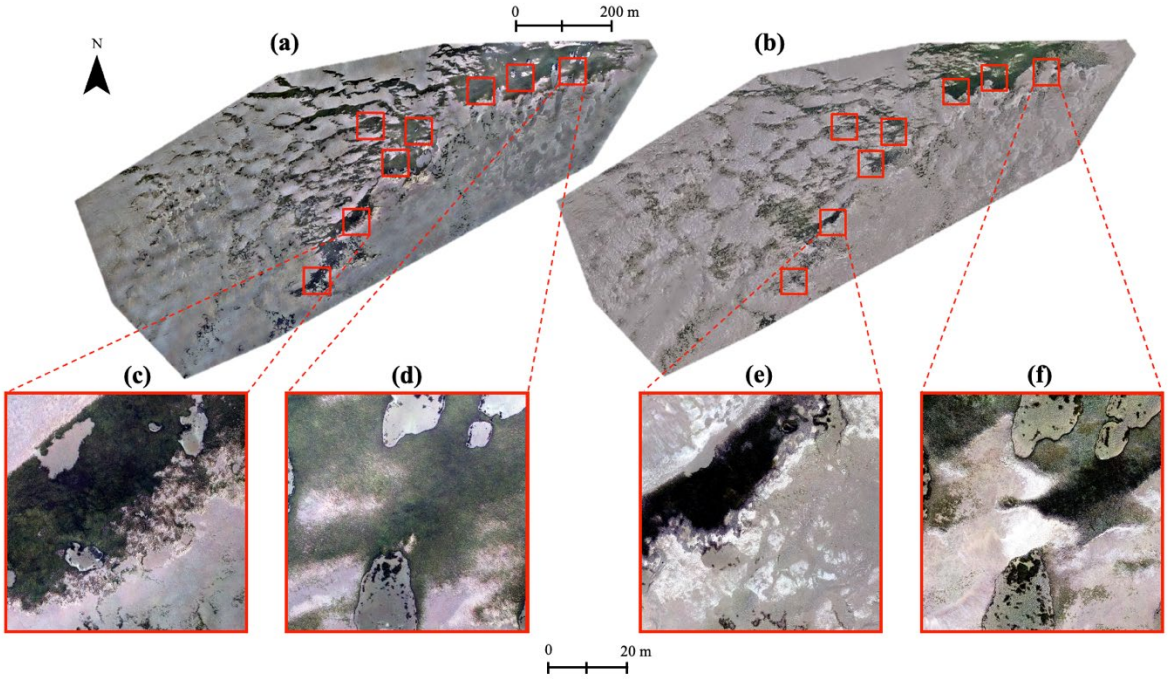


Figure. A.II.1. Orthomosaics of the study site (Anse à la Peinture) acquired at an altitude of 84 m with a ground resolution of 1 cm per pixel, showing (**a**) pre-winter (August 2024) and (**b**) post-winter (August 2025) conditions. The position of the eight sampled subzones (60 × 60 m) is indicated with red squares, with two example subzones #2 (**c, e**) and #8 (**d, f).**

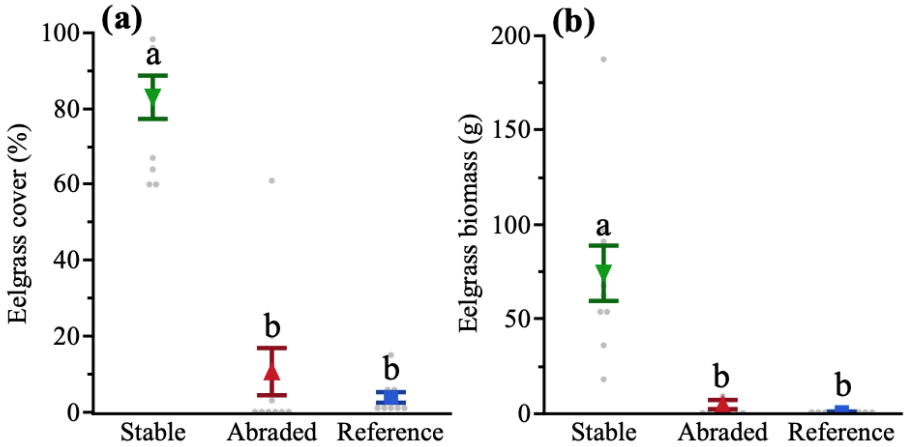


Figure. A.II.2. Mean (± SE) of (**a**) eelgrass cover (%) measured within 1 × 1 m quadrats (Pseudo-$F_{2,27}$ = 78.75; $p < 0.0001$) and (**b**) eelgrass leaves biomass (g WW) collected using mesh bags (18 cm diameter; Pseudo-$F_{2,27}$ = 23.29; $p < 0.0001$) across substratum states (Stable, Abraded, Reference). Grey dots represent individual data samples. Different letters above bars denote significant differences among substratum states ($p < 0.05$).

Table A.II.1. Summary of PER-ANOVA results testing the effects of state ("State"), compartment ("Compartment"), and their interaction on (a) species richness and (b) biomass of associated communities. Significant values are shown in **bold**. V% stands for estimate of variance components.

Source of variation	df	Mean square	Pseudo-F	*p*-value	V%
(a) Richness					
State	2	90.14	19.04	**<0.0001**	27.3
Compartment	2	166.21	35.11	**<0.0001**	37.5
State x Compartment	4	1.46	0.30	0.8705	0
Residuals	81	4.73			35.2
Total	89				100
(b) Biomass					
State	2	77298	7.53	**0.0011**	21.1
Compartment	2	80165	7.81	**0.0006**	21.6
State x Compartment	4	17661	1.72	0.1509	12.1
Residuals	81	10255			45.2
Total	89				100

Table A.II.2. Results of p-values from pairwise tests comparing taxa richness and biomass across states and habitat compartments. Significant values (< 0.05) are shown in **bold**.

Source of variation	*p*-value	*p*-value
	For richness	For biomass
(a) States		
Stable x Abraded	**<0.0001**	0.6739
Abraded x Reference	0.1326	**<0.0001**
Stable x Reference	**<0.0001**	**0.0004**
(b) Compartments		
Aboveground x Benthic	**<0.0001**	**0.0002**
Aboveground x Whole	**<0.0001**	**0.0002**
Benthic x Whole	0.5799	0.9248

Table A.II.3. Results of pairwise tests comparing the Whole associated community structure between states and compartment. Significant values are shown in **bold**.

Source of variation	*p*-value
Aboveground-Abraded x Benthic-Abraded	**0.0008**
Aboveground-Abraded x Aboveground-Stable	**0.0011**
Aboveground-Abraded x Benthic-Stable	**0.0002**
Aboveground-Abraded x Aboveground-Reference	0.5741
Aboveground-Abraded x Benthic-Reference	**0.0002**
Benthic-Abraded x Aboveground-Stable	**<0.0001**
Benthic-Abraded x Benthic-Stable	0.3884
Benthic-Abraded x Aboveground-Reference	**0.0002**
Benthic-Abraded x Benthic-Reference	**0.0082**
Aboveground-Stable x Benthic-Stable	**<0.0001**
Aboveground-Stable x Aboveground-Reference	**<0.0001**
Aboveground-Stable x Benthic-Reference	**<0.0001**
Benthic-Stable x Benthic-Reference	**<0.0001**
Benthic-Stable x Aboveground-Reference	**<0.0001**
Aboveground-Reference x Benthic-Reference	**<0.0001**

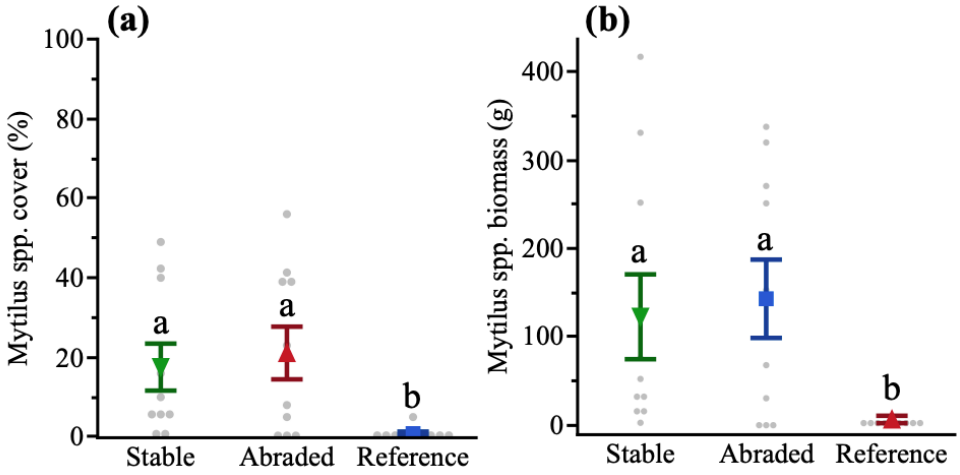


Figure. A.II.3. (**a**) *Mytilus* spp. cover (%; Pseudo-$F_{2,27}$ = 4.44; p = 0.0189), and (**b**) *Mytilus* spp. biomass (g; Pseudo-$F_{2,27}$ = 5.59; p = 0.0039) measured within 20 × 20 cm quadrats across habitat states (Stable, Abraded, Reference). Data are presented as mean ± SE, and grey points represent individual data samples. Different letters above bars denote significant differences among groups (p < 0.05).

Table A.II.4. Results of p-values from pairwise tests comparing *Mytilus* spp. percentage cover and biomass across states and habitat compartments. Significant values (< 0.05) are shown in **bold**.

Source of variation	*p*-value	*p*-value
	For percentage cover	**For biomass**
Stable x Abraded	0.6942	0.2868
Abraded x Reference	**0.0050**	**0.0191**
Stable x Reference	**0.0004**	**0.0006**

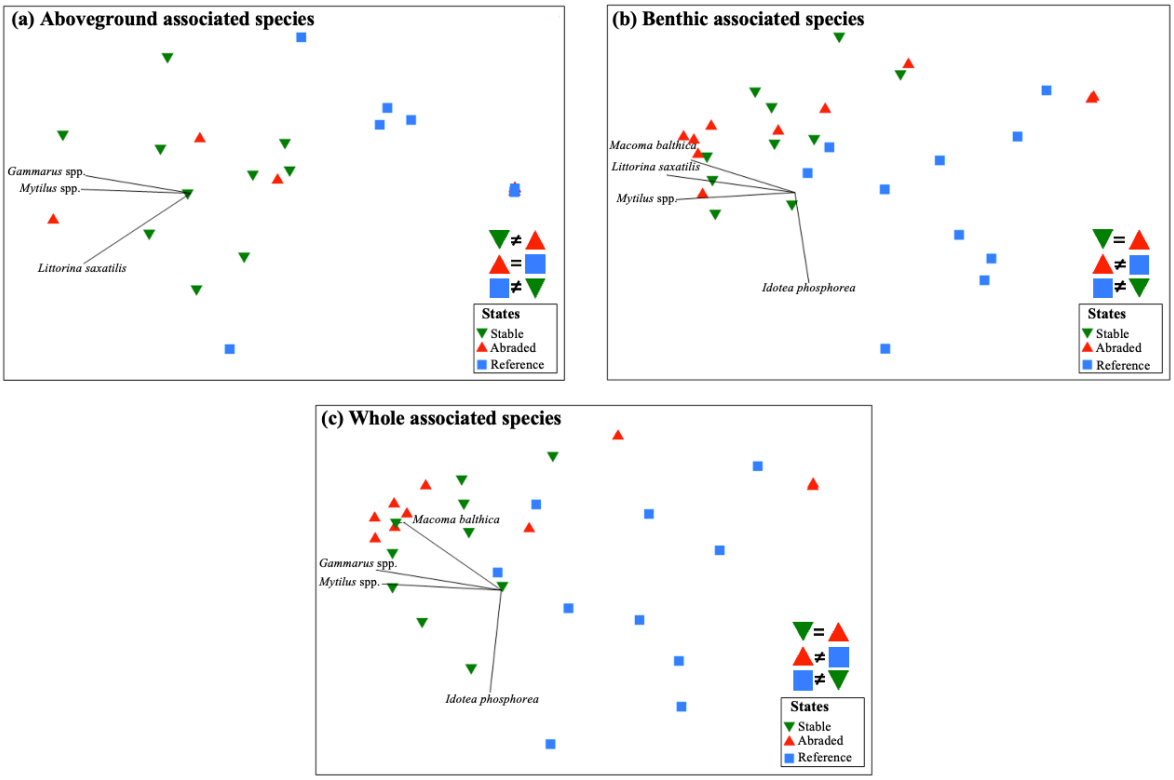


Figure. A.II.4. Non-metric multidimensional scaling (nMDS) plot based on a Bray–Curtis similarity matrix (DW + square root transformed) showing differences in benthic community composition among states conditions. (**a**) aboveground associated species (stress = 0.08; $F_{2,27}$ = 6.59; p < 0.001), (**b**) benthic associated species (stress = 0.13; $F_{2,27}$ = 3.98; p = 0.0014), and (**c**) Whole associated species (stress = 0.12; $F_{2,27}$ = 4.39; p = 0.0005). Symbols represent sampled quadrats according to treatments (colour and shape codes), while vectors indicate the taxa contributing most to the ordination pattern (e.g., *Macoma balthica*, *Mytilus* spp., *Gammarus* spp., *Idotea phosphorea* and *Littorina saxatilis*).

Table A.II.5. Similarity percentage (SIMPER) analysis results of dissimilarity between the interaction of substratum states and compartments (**bold**, in parentheses) as well as percentage contribution of each taxa (%C).

Taxa	%C
Aboveground-Abraded x Benthic-Abraded (**90.44%**)	
Macoma balthica	34.93
Mytilus spp.	10.98
Mya arenaria	10.22
Littorina saxatilis	9.79
Gammarus spp.	9.55
Aboveground-Abraded x Aboveground-Stable (**86.70%**)	
Littorina saxatilis	30.21
Gammarus spp.	20.06
Testudinalia testudinalis	10.83
Idotea phosphorea	10.06
Aboveground-Abraded x Benthic-Stable (**88.53%**)	
Macoma balthica	18.91
Mya arenaria	13.22
Mytilus spp.	12.38
Testudinalia testudinalis	11.29
Balanus crenatus	9.60
Littorina saxatilis	9.41
Aboveground-Abraded x Aboveground-Reference (**94.48%**)	
Gammarus spp.	41.01
Littorina saxatilis	30.32
Aboveground-Abraded x Benthic-Reference (**89.36%**)	
Macoma balthica	28.65
Idotea phosphorea	18.78
Gammarus spp.	11.99
Eteone longa	10.71
Benthic-Abraded x Aboveground-Stable (**80.86%**)	
Macoma balthica	21.37
Gammarus spp.	12.27
Littorina saxatilis	11.35
Mytilus spp.	11.29
Testudinalia testudinalis	10.20
Mya arenaria	8.65
Benthic-Abraded x Benthic-Stable (**52.61%**)	
Mytilus spp.	13.55
Testudinalia testudinalis	12.83
Macoma balthica	12.79
Gammarus spp.	12.53
Eteone longa	10.61
Balanus crenatus	10.38
Benthic-Abraded x Aboveground-Reference (**97.35%**)	
Macoma balthica	33.95
Littorina saxatilis	11.21
Gammarus spp.	10.36

Mytilus spp.	10.23
Mya arenaria	9.51
Benthic-Abraded x Benthic-Reference (**69.59%**)	
Macoma balthica	15.23
Mytilus spp.	12.82
Gammarus spp.	12.22
Eteone longa	10.56
Mya arenaria	10.34
Idotea phosphorea	10.06
Aboveground-Stable x Benthic-Stable (**71.01%**)	
Macoma balthica	18.80
Mya arenaria	12.52
Testudinalia testudinalis	11.31
Mytilus spp.	11.05
Balanus crenatus	9.65
Eteone longa	9.06
Aboveground-Stable x Aboveground-Reference (**88.01%**)	
Littorina saxatilis	35.84
Gammarus spp.	17.62
Idotea phosphorea	12.17
Testudinalia testudinalis	11.12
Aboveground-Stable x Benthic-Reference (**73.97%**)	
Macoma balthica	20.05
Littorina saxatilis	16.99
Idotea phosphorea	16.62
Eteone longa	8.18
Gammarus spp.	7.97
Testudinalia testudinalis	7.73
Benthic-Stable x Benthic-Reference (**66.03%**)	
Testudinalia testudinalis	12.33
Mya arenaria	12.08
Macoma balthica	11.97
Mytilus spp.	11.95
Balanus crenatus	10.27
Eteone longa	9.76
Littorina saxatilis	9.10
Benthic-Stable x Aboveground-Reference (**95.89%**)	
Macoma balthica	19.26
Mya arenaria	12.64
Mytilus spp.	12.63
Littorina saxatilis	11.15
Testudinalia testudinalis	10.76
Balanus crenatus	9.17
Aboveground-Reference x Benthic-Reference (**91.28%**)	
Macoma balthica	29.91
Idotea phosphorea	19.14
Eteone longa	10.54
Littorina saxatilis	10.49

ANNEXE III

Protocol for Estimating Macroalgal Cover Around Intertidal Boulders

1. **Image Acquisition (Small Spatial Scale)**

See Methods

2. **Image Pre-processing (ImageJ)**

Each image was processed using ImageJ as follows:

2.1. Open the image in ImageJ.

2.2. Using the *Rectangle* selection tool, delineate the entire boulder along with all associated macroalgae.

2.3. Navigate to **Analyze → Measure** and record the total area (in pixels) in the associated Excel dataset.

2.4. Apply **Edit → Clear Outside** to isolate the boulder and its associated algal assemblage from the background.

2.5. Save the processed image as a TIFF file (**File → Save As → TIFF**).

This step ensures that only the relevant substrate and biological cover are retained for subsequent analysis.

3. Macroalgal Cover Estimation (PhotoQuad)

3.1. Library Setup

- In PhotoQuad, load the species reference library via the **Library** panel. This library contains all macroalgal taxa expected in the images and ensures standardized classification.

3.2. Image Preparation

- Open the image via **File → Browse**.
- Apply image enhancement:
  - **Image → Decolorate → Linear Contrast Stretch**
  - Set tolerance to **0.040**
- This step improves contrast between macroalgae and substrate, facilitating segmentation.

3.3. Segmentation and Species Classification

1. Navigate to **Regions/Segment → Segment**.
2. Delineate regions corresponding to individual species by selecting all pixels associated with a given taxon.
3. Use the *Snapshot* and *Imported Image (ROOT)* options to toggle between processed and original images for improved visual identification.
4. Use the *Navigator* tool for zooming and precise selection.

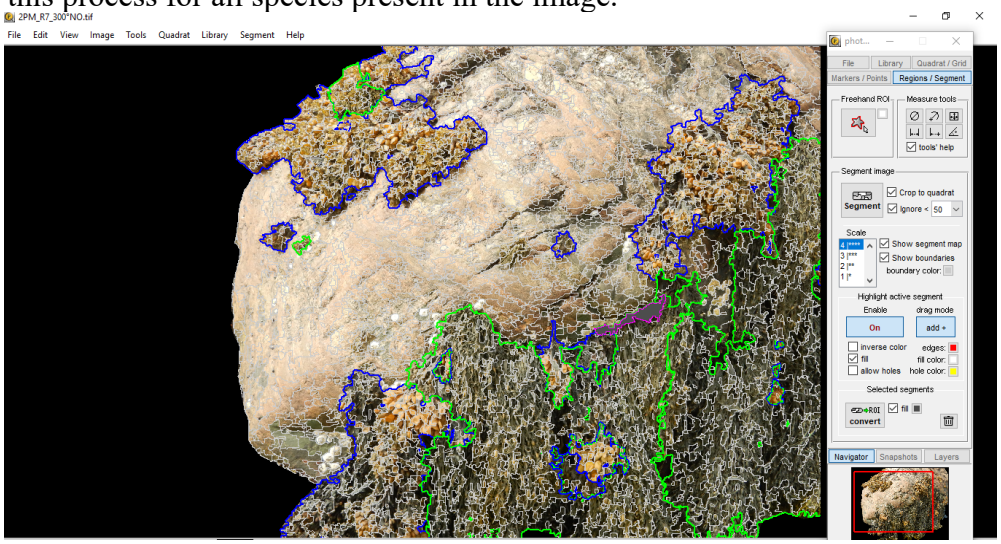
Once a species is fully selected:

- Click **ROI Convert**
- Right-click the resulting contour → **Convert to Species Region**
- Assign the correct species from the library (Group: *Algae*)

Color coding used:

- *Fucus vesiculosus* → dark blue
- *Fucus edentatus* → red
- *Ascophyllum nodosum* → light green

Repeat this process for all species present in the image.



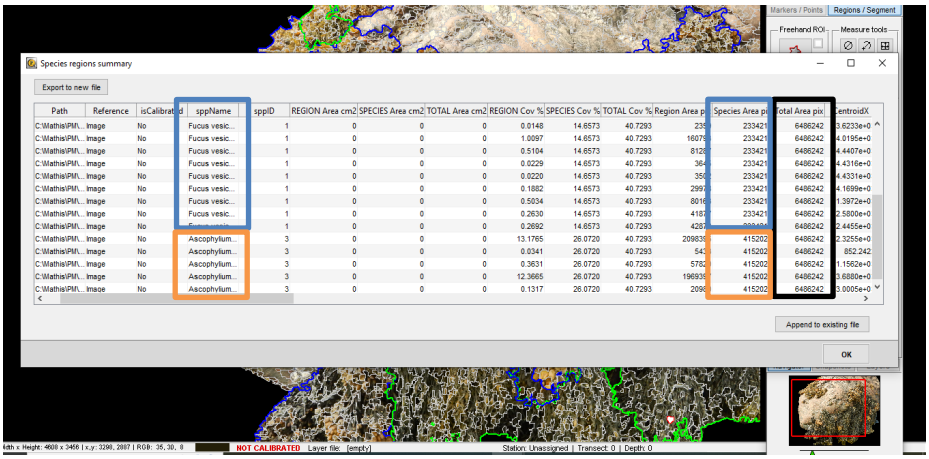
3.4 Data Extraction

After all regions have been classified:

- Right-click any species layer → **Show Summary**

The output provides:

- **Species area (pixels):** area covered by each species (species-specific cover)
- **Total area (pixels):** total area of all classified regions (total macroalgal cover)



These values are transferred into the Excel database, where automated calculations yield:

- Percent total macroalgal cover (species pixel area / total area from ImageJ)
- Percent cover per species (total pixel area / total area from ImageJ)

3.5 Saving Outputs

To preserve segmentation results:

- Go to **Layers** panel
- Select **Species Regions only** (ensure ROIs are not left unassigned)
- Save layers in the appropriate directory (organized by project, site, and boulder ID)