EFFETS DES ESPÈCES FACILITATRICES SUR LES COMMUNAUTÉS BENTHIQUES CÔTIÈRES DE L'ESTUAIRE DU SAINT-LAURENT LE LONG D'UN GRADIENT DE STRESS ENVIRONNEMENTAL

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RÉSUMÉ

Les habitats côtiers sont sous l'influence de plusieurs perturbateurs, qui modulent les communautés benthiques locales. Ces habitats abritent des espèces facilitatrices, qui, en formant des microhabitats, réduisent les effets des stresseurs environnementaux. Le rôle facilitateur d'espèces abondantes, comme les macroalgues, les moules ou les zostères, commence à être clarifié, pour autant nous n'avons que peu ou pas de comparaison proportionnelle de leurs effets entre elles. Notre objectif est d'identifier et de quantifier les effets des espèces facilitatrices sur les communautés macrobenthiques côtières associées en lien avec un gradient de stress environnemental. L'étude a été réalisée dans l'estuaire maritime du Saint-Laurent (Québec, Canada) dans six habitats : macrophytes sur roches (macroalgues) moules sur roches, roches nues, macrophytes sur sédiments (zostères), moules sur sédiments et sédiments nus. Ainsi, nous avons échantillonné de manière standardisée, dans plusieurs sites, chacun de ces habitats sous l'influence d'un gradient de stress environnemental (comme leur hauteur dans l'estran, exposition aux vagues, etc.) (trois sites par habitats et par niveau d'expositions aux vagues = 36 sites au total). Nos résultats montrent que la présence d'espèces facilitatrices influence positivement les valeurs biologiques des communautés associées comparativement aux habitats nus, par exemple, la biomasse augmente de plus de trois fois et la densité d'individus et les richesses taxonomique et fonctionnelle de plus de six fois. Ces effets sont les plus marqués chez les macroalgues avec plus de 37 fois pour la biomasse. Les résultats montrent aussi que plusieurs organismes sont dépendants de la présence des espèces facilitatrices. De plus, nos résultats indiquent que la structure des communautés varie davantage entre les habitats qu'entre les niveaux de stress environnementaux, qui pour les niveaux considérés, ont eu des effets marginaux. Les données récoltées permettent de préciser la façon dont pourraient réagir les communautés intertidales de l'estuaire maritime du Saint-Laurent dans l'éventualité d'une augmentation du niveau de stress ou de l'introduction d'un nouveau facteur de stress. Dans ce contexte, il est possible de penser que les communautés dans des habitats qui hébergent des espèces facilitatrices seraient impactées négativement dans une moindre mesure que les habitats qui n'en ont pas.

Mots clés : écologie intertidal, macroinvertébrés, espèces facilitatrices, bioingénieurs, stress environnemental, communautés benthiques, facilitation.

ABSTRACT

Coastal habitats are influenced by several stressors that modulate local benthic communities. They harbour facilitator species that, by forming microhabitats, reduce the effects of environmental stressors. The facilitating role of abundant species, such as macroalgae, mussels or eelgrass, begin to be understood, yet we have little or no proportional comparison of their relative effects. Our objective was to identify and quantify the effects of habitat facilitator species on associated coastal macrobenthic communities in relation to an environmental stress gradient. The study was carried out in the St. Lawrence marine estuary (Québec, Canada) in six habitats: macrophytes on rocks (macroalgae), mussels on rocks, bare rocks, macrophytes on sediments (eelgrass), mussels on sediments and bare sediments. We sampled with a standardized method in several sites within each habitat that was under the influence of an environmental stress gradient (e. g.: height of the intertidal area and wave exposure). In total we sampled three sites per habitat and per level of stress = 36 sites in total. Our results show that the presence of habitat facilitator species positively influenced the biological value of associated communities compared to bare habitats. For example, the biomass increased by more than three times and the abundance of individuals and the taxa and functional richness by more than six times. These effects were most pronounced in macroalgae with more than 37 times higher biomass in the presence of facilitator species. The results also show that several organisms were dependent on the presence of facilitator species. Furthermore, our results indicate that community structure varied more among habitats than among levels of environmental stress, which for the levels considered, had marginal effects. The data collected allow to predict how intertidal communities in the St. Lawrence Estuary might react to increased stress levels or when facing a new stressor. In this context, it is possible to assume that communities in habitats that host facilitator species would be impacted to a lesser extent than habitats that do not have facilitator species.

Key words: intertidal ecology, macroinvertebrates, habitats forming species, facilitating species, bioengineer, environmental stress, benthic communities, facilitation.

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INTRODUCTION GÉNÉRALE

Importance du benthos

Les espèces benthiques sont omniprésentes et sont une partie intégrante des milieux marins, une proportion importante de ces espèces sont suspensivore et/ou détritivore et jouent un rôle majeur dans le renouvellement des nutriments (Welsh, 2003). Cependant, ce mode d'alimentation les rend tributaires des conditions du milieu pour leurs apports en nutriments (Shanks et Trent, 1980; Alldredge et Silver, 1988) et donc sensibles aux modifications de ce dernier (Minshall *et al.*, 2014). Avec leurs activités, les humains ont fortement eutrophisé les cours d'eau et indirectement les milieux marins. L'enrichissement graduel en éléments nutritifs a favorisé la prolifération incontrôlée de microorganismes (Smith *et al.*, 1999; Rosenberg & Loo, 2012), ce qui a eu pour effet d'accroître la taille et d'augmenter le nombre de zones hypoxiques dans les mers et les océans, passant de 146 en 2004 à 405 en 2008 (Diaz & Rosenberg, 2008). Comme les communautés benthiques régulent en partie l'énergie des écosystèmes, via le renouvellement des nutriments, des modifications du milieu peuvent avoir des répercussions conséquentes sur les écosystèmes. Avec leur mobilité réduite, leurs types d'alimentation et leurs cycles de vie, il est facile de suivre l'évolution dans le temps des communautés benthiques faisant des habitats benthiques de très bons bioindicateurs environnementaux et des modèles d'études favorables dans la détermination de la qualité environnementale d'une zone (Neumann *et al.*, 2003; Azrina *et al.*, 2006; Bennion *et al.*, 2014). En plus d'offrir une grande diversité d'habitats (Raffaelli & Hawkins, 1996), côtes rocheuses, plages, marais, zones anthropisées et autres, les milieux intertidaux, avec leur facilité d'accès, sont de parfaits candidats pour réaliser des études sur l'environnement benthique.

Milieu intertidal

En milieu intertidal les conditions environnementales sont changeantes, mais les espèces qui s'y trouvent sont particulièrement bien adaptées à cette spécificité (Leigh *et al.*, 1987; Somero, 2002) et elles supportent des passages du milieu aqueux au milieu aérien. Les cycles de marées induisent des variations majeures des paramètres physico-chimiques, la salinité (Stickle & Denoux, 1976) et la température (Sanford, 2002) fluctuent avec les phases d'immersion et d'émersions, avec les saisons et la latitude (Helmuth *et al.*, 2002), le niveau d'hydrodynamisme y est aussi très variable (Harley & Helmuth, 2003; McQuaid & Lindsay, 2007). Le milieu intertidal, ou zone médiolittorale, se subdivise en trois sections (Figure 1), dépendamment de leur période d'immersion, la partie supérieure immergée uniquement lors des marées hautes de vives-eaux, la partie moyenne immergée lors de chaque marée et la partie inférieure émergée uniquement lors des marées basses de vives-eaux. Chacune de ces sections possède des caractéristiques propres qui font du milieu intertidal un milieu hétérogène permettant la présence d'une grande diversité d'organismes et qui façonnent les communautés et leurs dynamiques.
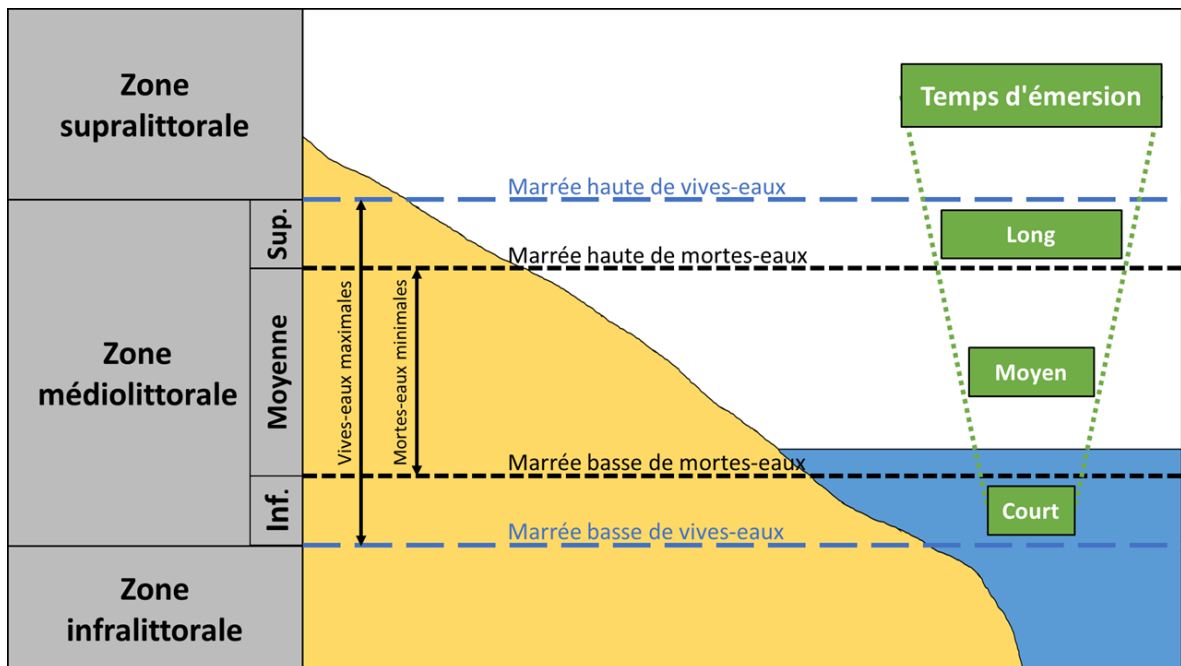
Figure 1: Schéma représentant les différentes zones littorales délimitées par leurs temps d'émersion et d'immersion lors des différents cycles de marées

Perturbateurs et stress en milieu intertidal

Les variations des conditions environnementales produisent des perturbations et du stress pour les organismes. Une perturbation est un événement d'origine biotique ou abiotique qui entraîne une perte, totale ou partielle, de la biomasse et de la biodiversité ainsi que des changements dans la configuration spatiale des écosystèmes (Grime, 1977; Paine, 2019). Les stress, bien que de mêmes origines engendrent des modifications des niveaux de production de biomasse (Menge, 2000; Menge *et al.*, 2002). Les perturbations et les stress peuvent être cycliques, comme les marées, réguliers ou ponctuels et de différentes ampleurs. Il n'est pas rare pour un écosystème d'être sous l'influence de plusieurs perturbations et/ou stress à la fois. En milieu intertidal, les principaux stress d'origines naturelles et abiotiques, appelés stress environnementaux, sont liés aux marées. Durant les phases émergées, l'exposition à l'air libre va provoquer une dessiccation des organismes (Boese *et al.*, 2003) et engendrer des variations importantes de température (Bertocci *et al.*, 2007). Plus le temps d'émersion est grand, plus un organisme sera stressé. Ainsi les individus situés dans la partie supérieure du milieu intertidal subissent un niveau de stress environnemental supérieur à ceux situés dans la partie inférieure (Raffaelli & Hawkins, 1996; Watt & Scrosati, 2013). Les vagues, en venant s'abattre contre les côtes, sont considérées comme un autre facteur de stress environnemental important dans le milieu intertidal (Bustamante & Branch, 1996; McQuaid & Lindsay, 2007). L'impact des effets des vagues dépend du niveau d'exposition, comme pour l'exposition à l'air libre, il est plus important dans la partie supérieure du milieu intertidal et lors des phases de marée montantes (Denny, 1985). Ces trois stress environnementaux, dessiccation, variation de température et exposition aux vagues forment un gradient de stress environnemental de la partie supérieure, où il est le plus élevé, vers la partie inférieure, où il est le plus faible (Figure 2) (Crain & Bertness, 2006; Scrosati *et al.*, 2011; He & Bertness, 2014).

Avec ce constat, différents études scientifiques ont émis deux grandes théories pouvant expliquer les variations dans la distribution de la biodiversité et de la biomasse dans l'intertidal. La première, "l'hypothèse de perturbation intermédiaire" (Intermediate

Disturbance Hypothesis - IDH) (Grime, 1973a, b; Levin & Paine, 1974; Connell, 1978; Jara *et al.*, 2006; Svensson *et al.*, 2007) suppose que la biodiversité est plus importante dans les milieux avec une intensité ou une fréquence de stress intermédiaire. En contrepartie, les milieux avec des intensités ou des fréquences faibles ou fortes ont une biodiversité moins importante. La seconde, "l'hypothèse du gradient de stress" (Stress-Gradient Hypothesis - SGH) (Bertness & Callaway, 1994; He *et al.*, 2013; He & Bertness, 2014), prédit que les interactions négatives diminuent avec le niveau de stress, mais qu'à contrario, les interactions positives inter- et intraspécifiques augmentent avec le niveau de stress.
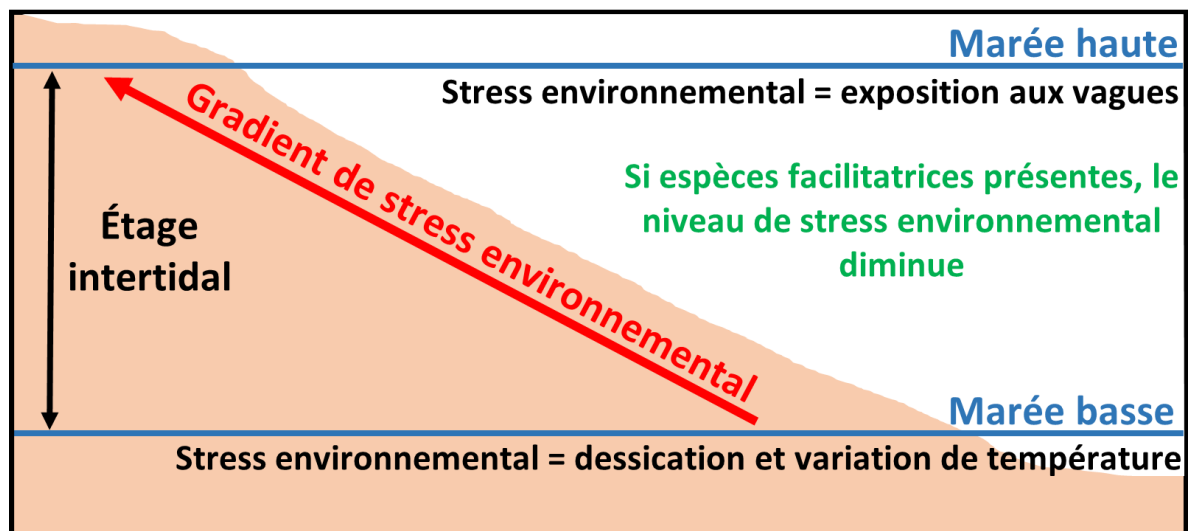
Figure 2: Schéma présentant brièvement les principaux types de stress environnemental rencontrés en milieu intertidal à l'origine du gradient de stress environnemental en fonction de la position dans l'étage intertidal, ainsi que l'effet de la présence dans le milieu d'espèces facilitatrices

En reprenant ces deux théories et les éléments évoqués précédemment, il devient possible d'affirmer que dans la partie supérieure du milieu intertidal, les facteurs de stress environnementaux sont les principaux facteurs limitant le développement des organismes et des populations (Connell, 1961). À l'inverse, dans la partie inférieure, ce sont les interactions biotiques inter- et intraspécifiques qui seront les principaux éléments limitants (Connell, 1961; Paine, 1974; Menge & Sutherland, 1987). Ces interactions peuvent prendre plusieurs formes, elles peuvent être négatives comme la prédation et la compétition pour l'espace et les ressources (Menge, 1995; Jenkins *et al.*, 1999; Trussell *et al.*, 2002) ou positives comme la facilitation (Bertness & Callaway, 1994; Bertness & Hacker, 1994; Bruno *et al.*, 2003). Grâce

à leurs interactions facilitantes dans le milieu sur les autres organismes, certaines espèces vont être nommées espèces facilitatrices (Jones *et al.*, 1994).

Espèces facilitatrices

Les espèces dites facilitatrices, parfois appelé bioingénieurs dans la littérature (Jones *et al.*, 1994; Lawton & Jones, 1995; Bruno, 2000; Watt & Scrosati, 2013), vont générer, grâce à leurs caractéristiques particulières, des conditions environnementales favorables au développement d'autres organismes (Jones *et al.*, 1994; Lawton & Jones, 1995; Watt & Scrosati, 2013). Avec leurs formes, leurs apports au milieu et/ou d'autres facteurs, les espèces facilitatrices forment des microhabitats créant une hétérogénéité dans le milieu et favorisant l'installation et le développement de diverses communautés d'espèces. Leur présence accroît la production primaire et secondaire locale ce qui augmente l'accès et la disponibilité en ressources (Witman, 1987; Miller & Hay, 1996; Bruno, 2000). La présence des espèces facilitatrices diminue localement les effets des stress environnementaux (Bruno *et al.*, 2003). En milieu intertidal, les principales espèces facilitatrices sont des macrophytes, telles que les macroalgues, et des bivalves, comme les colonies de moules. Les macrophytes forment un couvert végétal qui protège les autres organismes de la dessiccation et des variations de température lors des marées basses, et de l'action des vagues lors des marées hautes. Les bancs de bivalves vont réduire l'action des vagues lors de l'impact en augmentant la surface de contact. De plus, la structure tridimensionnelle produite par leur présence permet de retenir l'eau ou de ralentir son écoulement lors des marées descendantes. En milieu intertidal, les espèces facilitatrices jouent un rôle primordial dans le développement des communautés en réduisant les effets liés à l'activité des marées.

Problématique

L'introduction d'un nouveau facteur de stress dans des milieux intertidaux qui subissent déjà de multiples stress pourrait avoir des impacts négatifs significatifs sur les communautés benthiques côtières associées (Jenkins *et al.*, 1999; Underwood, 2000; Jara *et al.*, 2006; Bulleri *et al.*, 2012; Joseph & Cusson, 2015; Carrier-Belleau *et al.*, 2021). L'intensité des facteurs de stress risque d'augmenter avec l'intensification des activités anthropiques, en effet, plusieurs études montrent que plus de la moitié de la population mondiale vit à moins de 100 km du trait de côte, et que cette valeur est en constante augmentation (Creel, 2003; Martínez *et al.*, 2007). Les régions côtières sont des zones fortement urbanisées et/ou exploitées qui exercent une pression croissante sur les communautés benthiques des milieux intertidaux (Harris, 2012; Lowe & Peterson, 2014). Ces augmentations pourraient affecter la structure d'abondance, en faisant varier la répartition de la biomasse et de la densité d'individus au sein des communautés ainsi que la composition en espèces des assemblages benthiques, pouvant se traduire par des pertes locales de biodiversité, de biomasse et d'abondance (Arevalo *et al.*, 2007; Hillebrand *et al.*, 2008; Kraufvelin, 2007). De nombreuses études ont cherché à identifier, qualifier et quantifier les effets des activités anthropiques sur l'environnement (Cohen & Carlton, 1998; Azrina *et al.*, 2006; Harley *et al.*, 2006; Lin & Mendelssohn, 2012; Séguin *et al.*, 2014; Kenny *et al.*, 2018; Momota & Hosokawa, 2021). De manière générale, ces études tendent à montrer que les activités humaines induisent une réduction de la biodiversité et une perte de la biomasse. Ces phénomènes sont principalement causés par la destruction d'habitats essentiels et fragiles, la perte d'espèces facilitatrices, ainsi que des niveaux de perturbation et de stress élevés. De plus, les activités humaines semblent favoriser l'implantation et le développement d'espèces invasives. Cependant, afin de pouvoir évaluer convenablement les effets précis des activités anthropiques, il est nécessaire d'avoir une base de comparaison et il est donc primordial de bien comprendre les effets des stress actuels. Or, dans le cas des milieux intertidaux qui subissent de multiples stress, les effets combinés des stress ne correspondent pas à l'addition des effets de chaque stress pris indépendamment (Côté *et al.*, 2016; Galic *et al.*, 2018). Les effets liés à ce phénomène ne permettent pas d'utiliser les résultats d'études antérieures

portant sur des facteurs de stress isolés pour déterminer les effets causés par des combinaisons de facteurs de stress. Pour les milieux intertidaux, il existe des lacunes de connaissances sur les structures des communautés, leurs dynamiques, les stress environnementaux et les espèces facilitatrices. De ce fait, il est difficile de déterminer les effets des espèces facilitatrices sur les communautés associées le long d'un gradient sans réaliser de nouvelles études qui prennent en considération tous ces éléments au sein d'un même projet.

Objectifs et hypothèses

L'objectif de mon étude est d'identifier et quantifier les effets spécifiques des espèces facilitatrices sur les communautés macrobenthiques côtières associées face aux effets individuels et combinés des facteurs de stress environnemental. L'un des aspects novateurs de cette étude est l'emploi d'une méthodologie standardisée dans des habitats variés afin d'être en mesure d'établir des comparaisons valables.

En reprenant les éléments énoncés par l'IDH et la SGH, les effets généraux déjà connus des stress environnementaux et des espèces facilitatrices, nous supposons que i) parmi et au sein de chaque habitat, la présence des espèces facilitatrices améliore sensiblement les valeurs de biomasse, de densité d'individus et de diversité comparativement aux habitats ou elles sont absentes, et que ii) parmi les différentes espèces facilitatrices, les macroalgues, sont celles avec l'impact le plus marqué, car elles offrent la plus grande densité de couverture. Aussi, nous faisons l'hypothèse que iii) les habitats ont un impact plus important que les facteurs de stress sur la structure des communautés.

Estuaire maritime du Saint-Laurent

Pour cette étude, nous avons choisi de réaliser notre échantillonnage sur les côtes de l'estuaire maritime du Saint-Laurent (EMSL, Québec, Canada). L'EMSL est une voie

navigable très importante pour le commerce, au trafic en constante augmentation (Readman *et al.*, 1996; Transport-Canada, 2007), cette activité accroît implicitement les risques d'accident tels des déversements d'hydrocarbures dans le système (Transport-Canada, 2007; Allard & De Ladurantaye, 2015). L'EMSL se situe dans une région au climat subarctique avec des cycles de marées semi-diurnes et contient une multitude d'habitats benthiques côtiers. Au sein de ces habitats, nous avons décidé de cibler trois types d'espèces facilitatrices, deux macrophytes, les macroalgues (*Fucus* spp.) et les zostères marines (*Zostera marina*), et un bivalve (*Mytilus* spp.) qui subissent un gradient de stress environnemental afin de caractériser leurs effets sur les communautés benthiques qui leur sont associées. Mon étude permettra de mieux comprendre quels pourraient être les impacts liés à l'intensification des stress environnementaux sur les communautés benthiques côtières ou le cas advenant de changements dans l'abondance des espèces facilitatrices sur la structure, et possiblement le fonctionnement, des communautés littorales de plusieurs habitats du Saint-Laurent marin.

EFFECTS OF HABITAT FORMING SPECIES ON COASTAL BENTHIC ASSOCIATED SPECIES OF THE ST. LAWRENCE MARINE ESTUARY ALONG AN ENVIRONMENTAL STRESS GRADIENT

INTRODUCTION

Coastal regions host a wide variety of habitats such as rocky shores, beaches, marshes, mudflats which provide various functions and services important to the ecosystem. The communities shaped by environmental conditions (Raffaelli & Hawkins, 1996) inhabiting these habitats are highly diverse and are significantly involved in the nutrient cycle (Welsh, 2003). The increased pressure induced by human activities put the fragile equilibrium of communities within coastal habitats at risk. Today, more than half of the human population, value which continues to grow, lives at less than 100 km from the sea (Creel, 2003; Martínez *et al.*, 2007) increasing, by the way, the pressure of human activities upon the ecosystems by adding disturbances and stresses to the natural already existing.

Variations of the environmental conditions induce disturbances and stresses on habitats and communities. Disturbances are events that lead to partial or total loss of biomass (Grime, 1977), while stresses induce a change in the biomass production (Menge *et al.*, 2002), and both can have a biotic or an abiotic origin. In the intertidal region, the main natural abiotic stresses, called environmental stressors, are induced by tidal activity and shape the coastal community structure as well as the interactions within them. These environmental stressors are the desiccation (Foster, 1971; Bell, 1993; Boese *et al.*, 2003; Bertocci *et al.*, 2007) and the temperature variations (Helmuth, 2002; Helmuth *et al.*, 2002; Somero, 2002) induce by air exposure during low tides, and the wave actions, slashing the coast, during high tides (Denny *et al.*, 1985; McQuaid & Lindsay, 2007). Effects of these stressors are more

important in the upper part of the intertidal region than the lower part (Denny, 1985; Raffaelli & Hawkins, 1996; Bertocci *et al.*, 2007; Watt & Scrosati, 2013) creating an environmental stress gradient (Crain & Bertness, 2006; Scrosati *et al.*, 2011; He & Bertness, 2014). Introduction of new stressors with negative effect in environments already under the influence of multiple stressors can produce significant negative impacts on communities (Jenkins *et al.*, 1999; Underwood, 2000; Jara *et al.*, 2006; Bulleri *et al.*, 2012; Joseph & Cusson, 2015; Carrier-Belleau *et al.*, 2021). However, facing the stressors, biological interactions such as facilitation reduce their effects and increase the habitat quality (Bertness & Callaway, 1994; Bertness & Hacker, 1994; Bruno *et al.*, 2003).

Habitats forming species (HFS), also called bioengineers or foundation species (Jones *et al.*, 1994; Lawton & Jones, 1995; Bruno, 2000; Watt & Scrosati, 2013) reduce, with their morphological structure, the environmental stresses effects for associated organisms (Jones *et al.*, 1994; Lawton & Jones, 1995). The heterogeneity formed in the environment creates microhabitats (Burnaford, 2004) and offer refugees to other species (Menge & Lubchenco, 1981), hence, increase local biodiversity and community biomass (Jones *et al.*, 1994; Lawton & Jones, 1995). Benthic habitats with HFS support higher productivity and provide more nutrients and resources to associated species compared to habitats without HFS (Witman, 1987; Miller & Hay, 1996; Bruno, 2000; Duffy & Hay, 2000; Rodil *et al.*, 2020). Many studies have characterized HFS effects on associated communities in intertidal habitats with, among others, macroalgae (Seed, 1981; Jenkins *et al.*, 1999), eelgrass (Frost *et al.*, 1999; Reed & Hovel, 2006; Moore & Hovel, 2010; Duffy *et al.*, 2015) or mussel bed (Brinkman *et al.*, 2002; Arribas *et al.*, 2014). A given HFS effect is assessed with the comparison of associated community without their presence and/or along a gradient of presence. Generally, the HFS presence increases the diversity and biomass values of associated communities. Reed and Hovel (2010) showed that a reduction in the eelgrass cover reduces the species richness and the epibiont density in a disturbed environment. However, the comparative effects of several HFS from various habitats remains rare (e.g., Hosack and al., 2006, compared the effects of intertidal mudflats, eelgrass and oyster on the associated communities) and may suffer from a lack of comparability among studies that use different

sampling methods. To forecast changes in the drivers that shape coastal communities, high comparability of the HFS effects on associated communities in an ecosystem would be desirable.

The main objective of our study is to identify, quantify and compare individual effects of HFS on their associated communities along an environmental stress gradient. We hypothesized that i) among and within habitats the presence of HFS increases values of biomass, the density of individuals and diversity compared to bare habitats and ii) among HFS, macroalgae, as they offer the highest density of cover, are the HFS with the highest effects on associated communities. Also, we predicted that iii) the habitats have higher effects than the environmental stress gradient and stressors in structuring the communities.

The St-Lawrence marine estuary (Qc, Canada) supports various coastal habitats influenced by broad environmental stressors and the choice to proceed with our study on these habitats was manifest. We focus on rocky and sedimentary intertidal shores. In both, we can find abundant HFS known to support diverse associated species: macroalgae (Fucus spp.) forming a dense mat on rocks (Joseph & Cusson, 2015; Scrosati, 2017; Cimon & Cusson, 2018), eelgrass (Zostera marina) present in large sediment areas (Duffy *et al.*, 2015; Cimon *et al.*, 2021) and mussels (Mytilus spp.) forming a bed on both rocks and sediment (Largaespada *et al.*, 2012; Lemieux & Cusson, 2014). Bare rocks and bare sediments were sampled as control. All habitats were investigated under an environmental gradient composed of two stressors, the local stress (high or low, see methodology) and the wave exposition (sheltered or exposed).

As seen previously, the cumulative effects of stressors do not correspond to the addition of their individual and separated effect. Therefore, we cannot use previous studies on the HFS effects facing one stressor to estimate their effects along an environmental stress gradient involving multiple stressors. The use of a standardized methodology across the focused habitat is an innovative aspect of this study. It will allow better comparability and lower bias on the estimated effects of HFS on associated communities and environmental stressors. Moreover, such methodology would also document how HFS influence their

associated community within corresponding benthic compartments (epibionts / epibenthos / infauna).

MATERIALS AND METHODS

Study site

The sampling took place in locations on the North and South of the St. Lawrence marine estuary (Québec, Canada) (Figure 3) between late June and early September 2016 (see Annex II for geographical position and for the sampling date). In the St. Lawrence marine estuary, the summer surface temperature and salinity range from 6 to 15°C and from 20 to 25 PSU (OGSL.ca) respectively. Tides are dominated by a semidiurnal system and the average tide amplitude is 3.5 m (tides.gc.ca). The sampling was done in the intertidal zone during low tides.
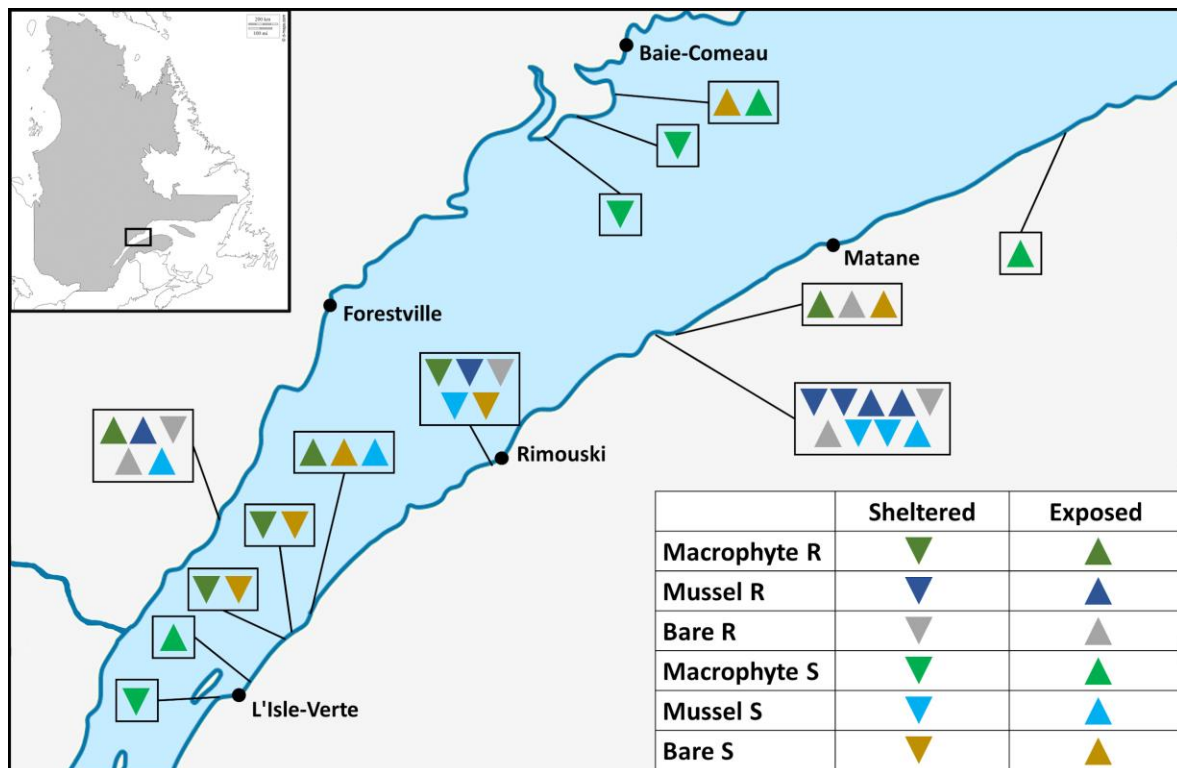
Figure 3: Locations of the sampling sites for each habitat in the St. Lawrence Marine Estuary, QC, Canada. Habitat on emerged rocks (R) or sedimentary shores (S) and Macrophyte R stand for macroalgae while Macrophyte S stand for eelgrass

Sampling design

The benthic communities from rocky and sedimentary shores were sampled in the presence or absence of macrophytes (macroalgae/eelgrass) and mussel bed along an environmental stress gradient defined by shore height and wave exposure (or density for eelgrass habitat only). The sampling design included four factors to compare the HFS effects on benthic communities across various habitats and stress levels (Figure 4). The use of two substrate types (rock or sediment) and two HFS identity (macrophytes or mussels) with controlled plots (no HFS) provided six different habitats: macrophytes on rocks (macroalgae), mussels on rocks, bare rocks, macrophytes on sediment (eelgrass), mussels on sediment and bare sediment. To ease the reading, macrophytes on rocks, mussels on rocks, bare rocks, macrophytes on sediment, mussels on sediment and bare sediment will be respectively called macroalgae, mussels R, bare R, eelgrass, mussels S and bare S. Moreover, for the rest of the study, it will be essential to distinguish the six habitats from the three HFS, effects of both will be investigated separately with different statistical analyses.
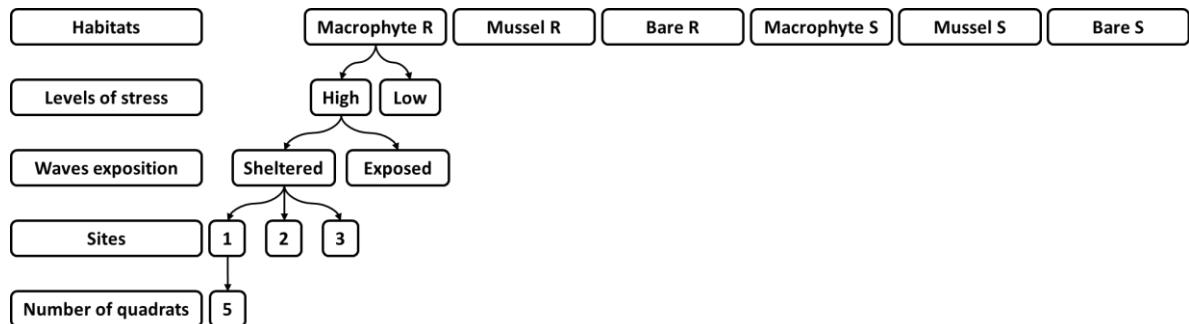
Figure 4: Sampling design used for this study (for simplicity, only part of the design is shown). Habitat on emerged rocks (R) or sedimentary shores (S) and Macrophyte R stands for macroalgae while Macrophyte S stands for eelgrass

Benthic communities were sampled across two stressors in each habitat: shore height (except for eelgrass see below) and wave exposition. The sampling was divided in shore height on the intertidal: 2-2.5 m and 0.5-1 m above the 0 m sea level, for the high and low stress, respectively. Since the range in the intertidal height for the eelgrass was limited, high stress levels were associated with low plant density (30-40% of cover) and proximity (< 0.5 m) to the eelgrass beds edge, while low stress level was associated with high plant density

(above 80% of cover) and away (> 2 m) to the eelgrass beds edge. Reduced shoot density and presence of habitat fragmentation can be the result of stressed eelgrass beds, thus showing altered community structure and function of associated organisms (Connolly, 1995; Pihl *et al.*, 2006; Reed & Hovel, 2006; Herkül & Kotta, 2009). Sampled sites were also distributed between two levels of wave exposition (sheltered or moderately exposed), determined by the coast morphology and the direction of the North-East winds causing high waves and storms in the estuary. Sheltered habitats were located in a bay or behind structure (islands, emerged rocks, rocky headlands, docks) while exposed habitats were directly facing the open water and dominant winds. Considering the habitats and levels of stressors, a total of 24 different environments (6 habitats, 2 levels of stress and 2 levels of waves exposition) were sampled with 5 replicates at three 3 sites each for a total of 360 samples (Figure 4).

Sampling procedure

In each site, 5 replicated quadrats (30 x 30 cm), haphazardly positioned at each height level (when applied, see above; height was measured with a graduated level staff and an optical level at low tide, serving as height reference), were sampled. Percentage cover of each HFS within quadrats was determined using 25 separated units each accounting for 4% of the surface of the quadrat. Quadrats with more than 80% cover of a given HFS, bare rocks or bare sediment were categorized as one of our habitat types (except for the eelgrass, see the above-mentioned criteria). Therefore, all visible macrobenthic (>1 mm) organisms within the sample were collected (except encrusting or very fragile species).

For sediment habitats, a smaller quadrat (15 x 15 cm) was used to collect epibenthos and infauna (up to 10 cm deep) while for eelgrass, we used a mesh bag to collect the epibiont organisms, with a size corresponding to a quadrat of 15 x 15 cm. All samples were filtered through a 1 mm sieve and afterwards, biomass and density data from habitats on sediments were multiplied to match data from habitats on rocks.

In each sample, organisms positions among following compartments were recorded: Epibiont on the HFS; Epibenthos on the substrate surface or within the sediments first 5 mm; or Infauna in the sediments (see representation in Annex I). Conserved in a 4% formaldehyde solution, organisms were identified under a stereomicroscope to the lowest taxonomic level possible, usually species, then all organisms were counted (density data) and weighed (biomass data) by taxon to the nearest 0.0001 g (1 g for large HFS individuals). The biomass of the encrusting and fragile species was obtained by giving an arbitrary value of 0.5 g per % cover units for *Gomontia polyrhiza*, *Hildenbrandia rubra*, *Petalonia fascia*, *Ralfsia verrucosa*, *Stragularia clavata* and Ulvaceae while a value of 1 g per % cover unit was given to *Clathromorphum circumscriptum*, *Raflsia fungiformis* and *Ulothrix flacca*.

Community variables considered

The values of biomass (total biomass of all species - g/sample) and density (number of individuals - individual/sample) were counted in each sample. *β*-diversity at the scale of habitat was estimated by the average community Bray-Curtis dissimilarity (on presence/absence data) among samples within habitat (Anderson *et al.*, 2006).

The taxa (or species) richness, the most common metric used to determine biodiversity, was calculated but as this value is lacking information, we complete it with the use of functional richness. Functional groups, used to calculate the functional richness, were determined by the use of four functional/biological traits combinations (body size, growth form, trophic type and motility type forming a functional code) (Wahl, 2009; Nock *et al.*, 2016) (Annex III and IV). The number of traits considered in the estimation of functional richness values is important since a small number of traits will increase the probability of functional redundancy (Petchey & Gaston, 2002). On the other hand, when a large number (>8) of traits are considered, estimates of the functional richness tend to the observed species/taxa richness (Laughlin, 2014). Furthermore, we calculated the Simpson diversity index and the Pielou evenness based on both biomass and density data which offer a

complementarity and allow us to have a more precise comparison and identification of the biodiversity among our associated benthic communities.

The interaction between taxa and functional richness regarding the communities exposed to environmental stress can help understand some of the results and past research (Wahl *et al.*, 2011). Following this idea, we used the ratio of taxa to functional richness which offers a good way to express the redundancy of individual functions within the different taxa observed. Note that high values indicate that some organisms bring no new function to the community and therefore could be replaced by any other organisms with the same function already present in the community or not without drastically changing the effect on the community interaction. On the contrary, a ratio of 1 means that every taxon has its function in the community. Their disappearance would lead to a loss of interaction within the habitat and the community.

We estimated the effect of each HFS by a comparison to their bare habitat with decomposed values of biomass, density, taxa richness and functional richness within each compartment for. Unless stated, HFS individuals were systematically removed from all estimates and analyses were done on corresponding HFS associated species (i.e., individuals found on epibiont, epibenthos and infauna). Mussels that were not part of mussel bed habitat were counted as an epibiont (e.g., mussels attached on macroalgae) or epibenthos (e.g., understory mussels) in other habitats.

Data analyses

We tested the effect of HFS and the stress-related factors among habitats on diversity variables (taxa richness, functional richness, Simpson diversity index and Pielou evenness) using biomass and density data by species (all compartments summed). A permutational analysis of variance (PER-ANOVA) was used (Anderson *et al.*, 2008) on the Euclidian distance resemblance matrix of each of the variables with four factors: habitat (6 levels,

fixed), level of stress (2 levels, fixed), wave exposition (2 levels, fixed) and site (3 levels, random nested within habitats and wave exposition).

Similarly, the community assemblage (all compartments summed) structure and composition were analyzed with the same above-mentioned factors using permutational multivariate analysis of variance (PERMANOVA) (Anderson *et al.*, 2008) on a Bray Curtis similarity matrix. Data were pretreated using a dispersion weighting (Clarke & Gorley, 2006) within replicates into each treatment combination (habitats x stress level x waves exposition x site) and transformed by the fourth root following a shade plot method (Clarke *et al.*, 2014). A dummy variable (with a low value of 0.00005 for the biomass data and 1 for the density data) was added to include samples with no associated species (Clarke *et al.*, 2014). To provide information about community dispersion, a PERMDISP routine following the PERMANOVA was used (Anderson *et al.*, 2008). The differences between the treatments were visualized using a non-metric multidimensional scaling (nMDS).

Additional permutational analyses were done using an array of 12 contrasts that allowed to detect the effect between specific pairs of (or combined) habitats. For example, Macroalgae effect was obtained by contrasting Macroalgae VS Bare R while the general substrate effect (sedimentary vs rocky shores) was obtained by contrasting pooled data from Macroalgae + Mussels R+ Bare R versus pooled data from Eelgrass + Mussels S + Bare S (see the complete list in Annex V).

Univariate analyses and multivariate analyses were conducted using PRIMER+PERMANOVA v.7 (Clarke & Gorley, 2015). A significance level of $\alpha = 0.05$ was used for all statistical tests, however, *p*-values close to significance were carefully considered.

RESULTS

A total of 83 different taxa distributed in 73 genera and 60 families were observed in this study (Annex IV). Six different HFS were found, including four species of macroalgae (*Fucus distichus edentatus, F. vesiculosus, Ascophyllum nodosum* and *F. evanescens* with their respective mean % cover, 57%, 40.9%, 1.6% and 0.5%), the eelgrass (*Zostera marina*) and the mussels (*Mytilus* spp.). All associate taxa to those HSF species were divided in 14 autotrophs and 68 invertebrate species with unidentified fish larvae considered as one taxa. These taxa represent a total of 40 different functional groups obtained with our biological/functional traits used (Table 1).

Table 1: Summary of total taxa and total ecological function richness for different groups: the habitats forming species (HFS), the autotroph (including macrophytes HFSs), the heterotrophs (including the HFS mussels) and the total numbers for all samples ($N_{tot} = 360$)

	HFS	Autotroph	Heterotroph	Total
Total taxa	6	14	69	83
Total functional group	3	4	36	40

We observed large differences in total taxa (taxa richness at the scale of the St. Lawrence marine estuary) and the total number of functional groups within associated communities among habitats, macroalgae support the highest values while the lowest values were observed for bare rocks (Table 2). The presence of HFS in a habitat dramatically increases values when compared to their bare habitats. For example, the total number of taxa and functional group increased by a factor of 5.2 and 3.9 respectively, in presence of macroalgae (Table 2)

Table 2: Summary of total taxa richness and total functional group richness of associated communities for each habitat ($N_{per\ habitat} = 60$). In parentheses, the magnitude factor of increase in comparison to corresponding bare substrates is shown

Habitats	Total taxa richness	Total functional richness
Macroalgae	62 (5.2)	35 (3.9)
Mussels R	39 (3.3)	22 (2.4)
Bare R	12	9
Eelgrass	40 (1.9)	24 (1.4)
Mussels S	32 (1.5)	19 (1.1)
Bare S	21	17

Habitats and stress effects on associated community structure

The results reported above show slight differences among habitats upon both taxa and functional richness. Factors habitat, stress level and site had a significant effect on community assemblage on both biomass and density ($p < 0.05$; Table 3; Figure 5). The community structure was affected differently by stress level across habitat (Habitat * Stress level: $p = 0.0017$ and 0.0004, in biomass and density respectively; Table 3). Mussels on rocks supported different communities between low and high stress levels ($p = 0.0518$ and 0.0315, Table 3 and Figure 5 for biomass data). Habitats mostly explained total variation of community structure on both biomass and density (Annex VI). The environmental stresses, stress level and wave actions, explained less than 1% of the variation, even within each habitat, they explained a small portion of the variation. The sites and the residuals are the other factors that explained most of the remaining part of the variation (Annex VI).

Table 3: Summary of PERMANOVAs showing the effect of factors on community structure based on biomass data (left) and density data (right). Degree of freedom (df), mean square (MS), the Pseudo-F and P(perm) are provided. Significant results ($p < 0.05$) are in bold ($N_{tot} = 360$; Permutations = 9999)

Source	df	Biomass MS	F-ratio	p	Density MS	F-ratio	p
Habitat	5	87892	11.72	**0.0001**	76196	13.66	**0.0001**
Stress level	1	4382	2.19	**0.0179**	3684	2.94	**0.0031**
Exposition	1	5864	0.78	0.6086	6177	1.11	0.3424
Habitat * Stress level	5	3750	1.87	**0.0017**	2621	2.09	**0.0004**
Habitat * Exposition	5	5513	0.74	0.8853	5023	0.90	0.6465
Stress level * Exposition	1	2023	1.01	0.4336	1299	1.04	0.4120
Site (Expo * Hab)	24	7499	9.96	**0.0001**	5579	13.22	**0.0001**
Habitat * Stress level * Exposition	5	2520	1.26	0.1172	1936	1.54	**0.0229**
Stress level * Site (Expo * Hab)	24	2001	2.66	**0.0001**	1255	2.97	**0.0001**
Residuals	288	753			422		
Total	359						
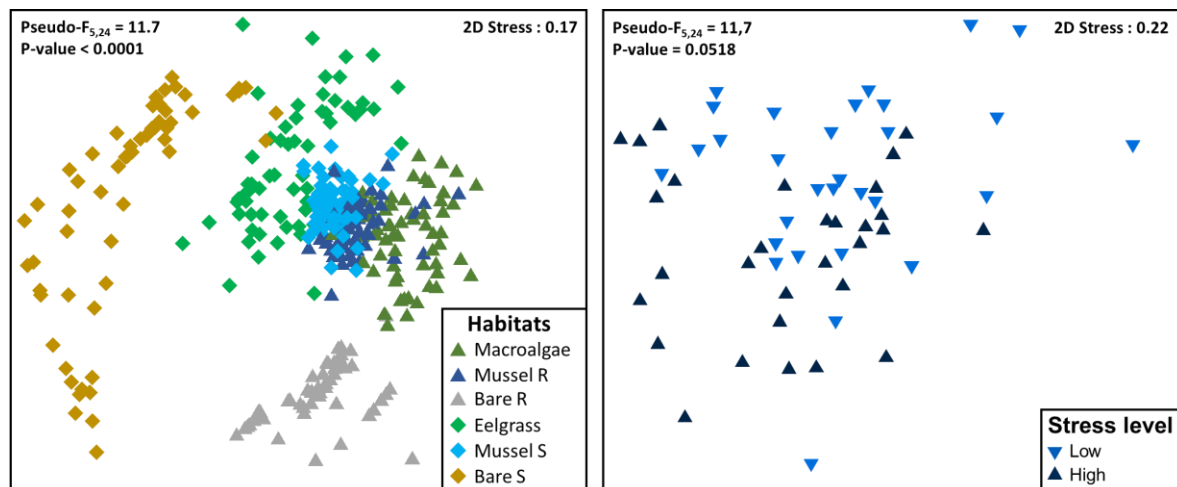
Figure 5: Non-metric multidimensional (nMDS) scaling plots illustrating the effect of habitats on community structure based on biomass data (left) and the zoom non-metric multidimensional (nMDS) scaling plots illustrating the effect the stress level on the habitat mussels on rocks on community structure base on biomass data (right). Values were calculated based on Bray-Curtis dissimilarities of the dispersion-weighted and fourth-root transformed standardized biomass of sum of species (+ Dummy variable)

The β-diversity, estimated with the Bray-Curtis community dissimilarity among samples within habitats, represents the dispersion within habitats of the community composition. The mean β-diversity is generally higher in sediment habitat than on rocks habitat and the β-diversity is highest on bare sediment and lowest in mussels on rocks (Figure 6). The β-div represents, as it has been estimated by dissimilarity, the dispersion within habitats of the community composition (see also the sizes of dispersion in each habitat in Figure 5).

Planned contrasts among types of habitats, such as macrophyte (macroalgae and eelgrass) effect and sedimentary versus rocky substrates (see details in Annex V and VII), reveals that they are all different in terms of community structures.
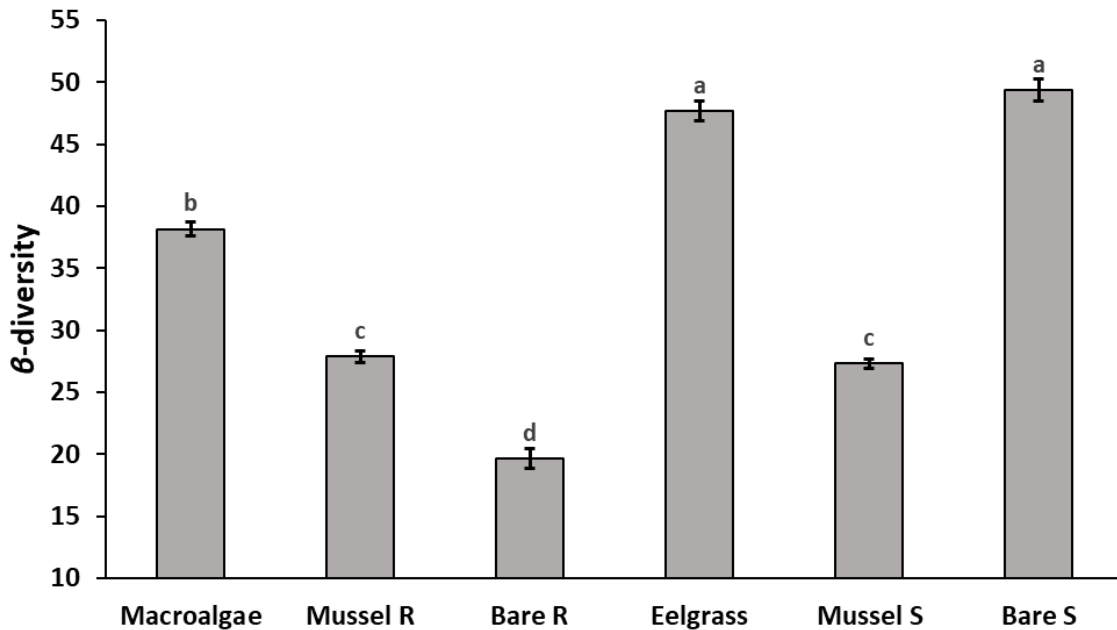
Figure 6: Mean (±95%CI) β-diversity for each habitat. β-diversity was estimated by communities Bray-Curtis dissimilarity (presence-absence data; $N_{per\ habitat} = 60$, see Methods) among samples within habitats

Habitats and stress effects on community variables

As shown previously, habitats and stress level and both coupled together have a significant effect on the community structure. However, for both biomass and diversity, most of the variations are explained by the habitats and in general, macroalgae, eelgrass and both mussels habitat show higher values for biomass and density while for both bare substrate lower values are expected (Figure 7, see Annex VIII for values per compartments within each habitat). The results well illustrate the level of variation explained by the habitats and the low difference between both stress levels within habitats. The very large biomass values in macroalgae habitats are an exception due to understory mussels counted as an associated species in this situation.
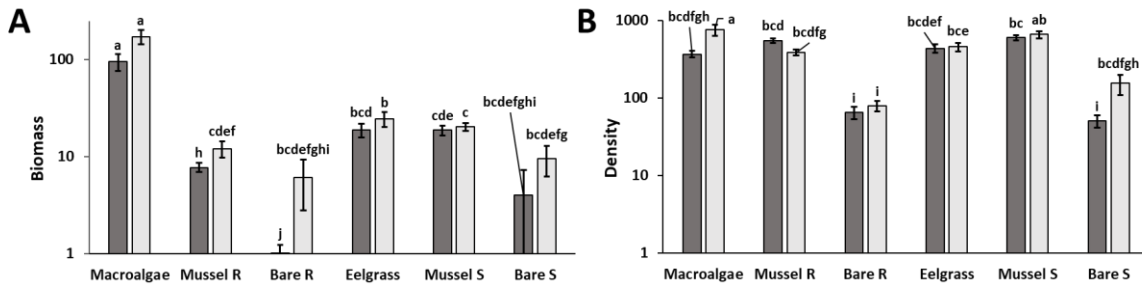
Figure 7: Mean (±SE) values of A) biomass (g/sample of 30 x 30 cm quadrat), B) density (count/sample) each habitat for both stress levels (dark gray = high stress level, light gray = low stress level). Different letters above bars indicate differences ($p < 0.05$, Pair-wise test; $N_{\text{per habitat * stress level}} = 30$). Note that in A) and B) the scale is log

The same type of analyses made on the other variables revealed that both factors habitat and stress level had a significant effect ($p < 0.05$) on diversity related variables (taxa and functional richness), while for the diversity index variables only the factors habitat was found significant ($p < 0.05$) (Table 4 and Annex IX). Unexpectedly, the factor wave exposition was never significant for our analyses (both multivariate and univariate).

Macroalgae, eelgrass and both mussels habitat significantly increase the values of both taxa and functional richness, on the other hand, high stress level decrease these values (Figure 8).

Similar patterns were observed with the Simpson diversity index on biomass and density data (Figure 9). Evenness values presented another situation where bare rock has the highest value and macroalgae the lowest based on biomass data, and on density data the highest value was on eelgrass and the lowest on bare rock (Figure 9).

Table 4: Summary of the PER-ANOVA on the species richness (top left), functional richness (top right), Simpson diversity index (bottom left) and Pielou evenness (bottom right) of the associated communities based on biomass data. Degree of freedom (df), mean square (MS), the Pseudo-F and P(perm) are provided. Significant results (p < 0.05) are in bold (N_{tot} = 360; Permutations = 9999)

Source	Taxa richness				Functional richness			
	df	MS	F-ratio	p	df	MS	F-ratio	p
Habitat	5	1517.7	68.787	**0.0001**	5	891.1	50.914	**0.0001**
Stress level	1	98.2	10.200	**0.0035**	1	32.4	6.535	**0.0187**
Exposition	1	0.9	0.041	0.8420	1	4.9	0.280	0.6016
Habitat * Stress level	5	15.9	1.653	0.1821	5	5.7	1.150	0.3677
Habitat * Exposition	5	18.7	0.849	0.5401	5	7.3	0.418	0.8401
Stress level * Exposition	1	16.9	1.756	0.1962	1	3.6	0.726	0.4057
Site (Expo * Hab)	24	22.1	5.639	**0.0001**	24	17.5	7.310	**0.0001**
Hab * Stress level * Exposition	5	13.0	1.346	0.2823	5	7.8	1.577	0.2021
Stress level * Site (Expo * Hab)	24	9.6	2.460	**0.0007**	24	5.0	2.071	**0.0037**
Residuals	288	3.9			288	2.4		
Total	359				359			

Source	Simpson diversity index				Pielou evenness			
	df	MS	F-ratio	p	df	MS	F-ratio	p
Habitat	5	2.541	18.878	**0.0001**	5	0.549	3.214	**0.0272**
Stress level	1	0.009	0.147	0.7117	1	0.090	1.960	0.1783
Exposition	1	0.056	0.418	0.5268	1	0.006	0.038	0.8546
Habitat * Stress level	5	0.087	1.489	0.2295	5	0.040	0.861	0.5200
Habitat * Exposition	5	0.080	0.598	0.7037	5	0.138	0.806	0.5626
Stress level * Exposition	1	0.098	1.680	0.2085	1	0.048	1.039	0.3273
Site (Expo * Hab)	24	0.135	5.179	**0.0001**	24	0.180	6.179	**0.0001**
Hab * Stress level * Exposition	5	0.066	1.124	0.3667	5	0.039	0.836	0.5401
Stress level * Site (Expo * Hab)	24	0.059	2.256	**0.0005**	23	0.047	1.627	**0.0361**
Residuals	286	0.026			252	0.029		
Total	357				322			
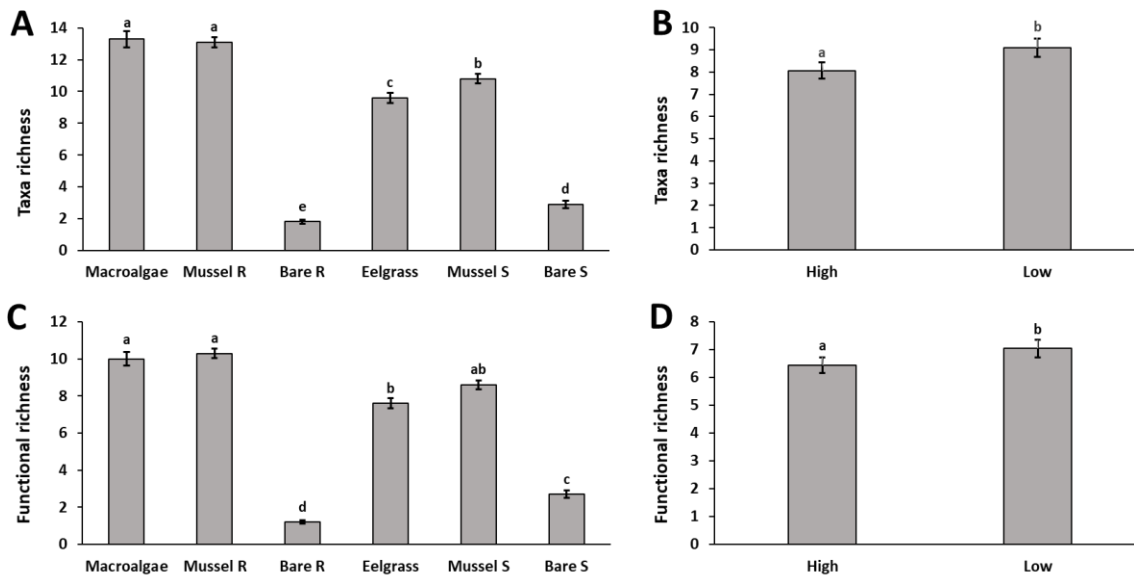
Figure 8: Mean (±SE) values of A) taxa richness by habitats, B) taxa richness by stress level, C) functional richness by habitats and D) functional richness by stress level. Different letters above bars indicate differences ($p < 0.05$, Pair-wise test; $N_{per\ habitat} = 60$; $N_{per\ stress\ level} = 180$)
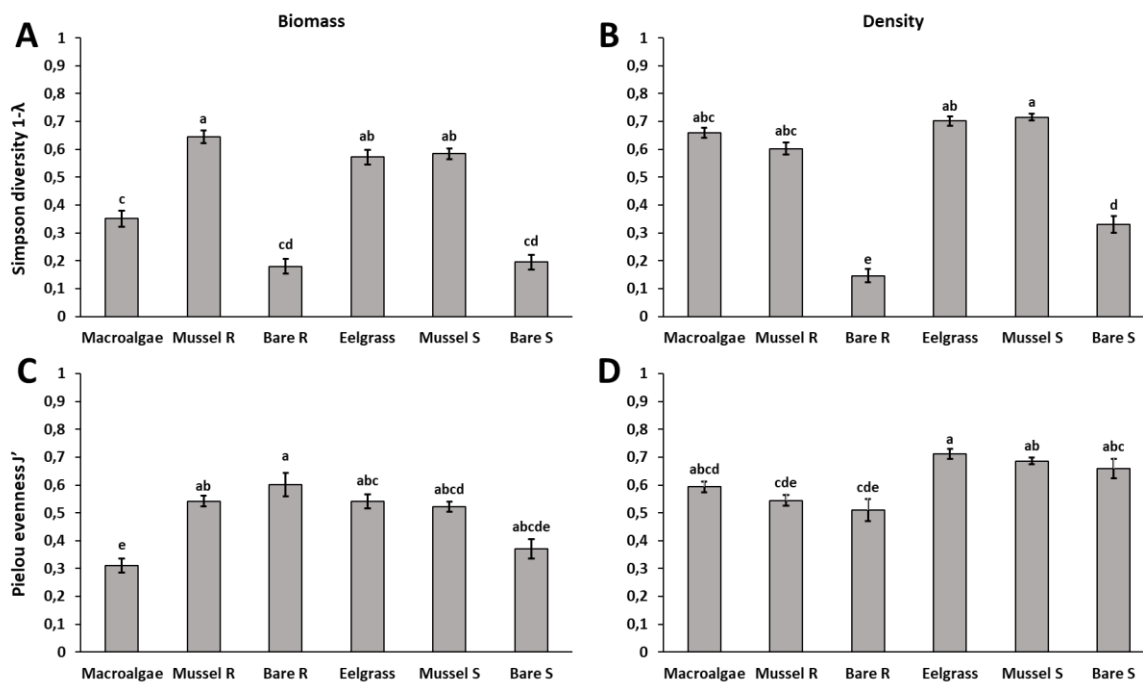
Figure 9: Mean (±SE) values of A) Simpson diversity index (1-λ) on biomass data B) Simpson diversity index (1-λ) on density data, C) Pielou evenness (J') on biomass data and D) Pielou evenness (J') on density data for each habitat. Different letters above bars indicate differences ($p < 0.05$, Pair-wise test; $N_{per\ habitat} = 60$)

HFS effects on community variables

Presence of HFS increases the biomass, density, taxa and functional richness compared to bare substrate, the magnitude varies among HFS and variables with macroalgae who had generally the highest effect of increase and eelgrass the lowest (Table 5).

Table 5: Magnitude of increase in biomass (also represented graphically below), density, taxa and functional richness values due to HFS presence in each habitat compared to their bare substrate. Bare rocks were used as reference for the macroalgae and the mussels on rocks while bare sediment was used for the eelgrass and the mussels on sediment ($N_{per\ habitat} = 60$)

Habitats	Biomass	Density	Taxa richness	Functional richness
Macroalgae	37.7	7.8	7.4	8.4
Mussels R	2.8	6.5	7.3	8.6
Eelgrass	3.2	4.4	3.3	2.8
Mussels S	2.9	6.1	3.7	3.2
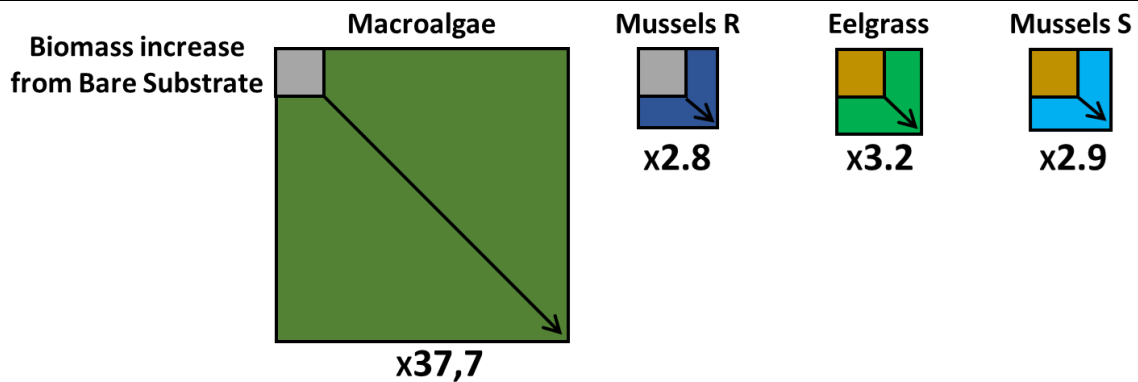
The repartition of biomass and density among compartments for each habitat varies highly (Table 6, see Annex VIII for graphic representation). For the mussels habitats, the situation is particular, due to the condition of the HFS it is impossible to distinguish associated species considered as epibiont and epibenthic, except for the encrusting species. Thereby, associated species were considered as epibiont for both biomass and density. For other habitats, the separation among compartments is strictly respected and allows to visualize the associated community distribution.

Table 6: Repartition (%) of biomass and density among compartments for each habitat ($N_{per\ habitat}$ = 60)

	Biomass			Density		
Habitats	Epibiont	Epibenthos	Infauna	Epibiont	Epibenthos	Infauna
Macroalgae	5.7	94.3	-	45.7	54.3	-
Mussels R	94.7	5.3	-	99.8	0.2	-
Bare R	-	100.0	-	-	100.0	-
Eelgrass	21.3	24.4	54.3	53.6	11.1	35.2
Mussels S	54.0	0.2	45.8	73.6	0.0	26.4
Bare S	-	0.4	99.6	-	8.6	91.4

Among the habitats, we observed an important variation in the species and functions found only in the epibiont compartment. Both values are similar for both mussels habitats and far superior to both macrophyte habitats, which happened for them to be also similar together (Table 7).

Table 7: Proportion (%) of taxa and functions found only in the epibiont compartment ($N_{per\ habitat}$ = 60)

Habitats	Epibiont taxa only	Epibiont function only
Macroalgae	13	11
Mussels R	87	91
Eelgrass	18	13
Mussels S	50	53

Bare rocks had the highest value for the ratio of species richness to functional richness while lowest was on bare sediment close to 1 and the four HFS habitats had values of the same order (Table 8). Values closer to 1 indicate a low redundancy among organisms functions while high values indicate a redundancy among organisms functions within a community in which there are several to operate the same function in the habitat.

Table 8: Ratio of taxa richness on functional richness for each habitat ($N_{per\ habitat}$ = 60)

Habitats	Ratio taxa/functional richness
Macroalgae Rocks	1.32
Mussels Rocks	1.27
Bare Rocks	1.49
Eelgrass Sediment	1.27
Mussels Sediment	1.26
Bare Sediment	1.07

DISCUSSION

The main objective of our study was to identify, quantify and compare the effects of HFS on benthic coastal communities from various habitats of the St. Lawrence marine estuary along an environmental stress gradient. Results showed that habitats had a significant effect on the structure of their associated community, but against our expectation results revealed no strong effects from the local stress. While wave exposition is known to affect benthic communities (Denny *et al.*, 1985; McQuaid & Lindsay, 2007) and often used to characterize differences in communities between sedimentary and rocky intertidal habitat, and within them (Brinkman *et al.*, 2002; Arribas *et al.*, 2014), we found no significant effect to this exposure. These non-significant or low effects results may not well represent such stressors as our sampling schemes might not have use of enough magnitude for both wave exposition and local stress to get higher signals in our study. However, with the sites we used in the St. Lawrence, our results support the idea that habitats are of significant importance in structuring the communities. Among our observations, the most interesting are that the HFS presence increases dramatically the values on most biological variables from communities compared to bare habitats, and among the HFS, macroalgae have the highest effects upon associated communities.

Habitat effects on associated community

The habitats significantly affected the distribution of associated benthic communities, and they explain almost half (> 40%) of the variation among samples and community structure. Also, although environmental stresses (local stress level and wave exposure) accounted for a tiny fraction (< 1%) of the variation explanation, the habitats coupled with the stress had a significant effect on community distribution and structure but were visible only in the Mussels on rocks habitat. Previous works showed that the habitats (e.g., macroalgae bed, mussels bed, bare sediment, eelgrass beds and oyster beds) have a significant effect on community structure and variables (Archambault & Bourget, 1996;

Hosack *et al.*, 2006), as well as the local stress linked to the shore height (Raffaelli & Hawkins, 1996; Watt & Scrosati, 2013), or for the eelgrass, the position inside the eelgrass bed (Connolly, 1995; Pihl *et al.*, 2006; Reed & Hovel, 2006; Herkül & Kotta, 2009). Results from contrasts, used to compare individually and among them the effect of the substrates, type of HFS and the HFS, were significant. Therefore, all habitats, HFS types, HFS and substrates supported different communities. By conducting a comparative study between different habitats including bare sediments, eelgrass and oyster beds, Hosack *et al.* (2006) found that each habitat supported different communities and, as well as us, presence of HFS increases community density.

Interestingly, the biomass originated differently among the three compartments (epibiont, epibenthos and infauna) depending on the habitats considered. For habitats on rocks, the distribution was quite extreme as, on macroalgae, most of the biomass was from the epibenthos, once again explained by the presence of understory mussels while for mussel beds, as the epibiont and the epibenthos are mingled, most of the biomass was originated into the epibiont compartment. These differences found in biomass are linked with the higher taxa richness found in HFS habitats than in bare habitats. As well as us, Norling and Kautsky (2007) found that mussels habitats increased the local specific richness and suggested that their three-dimensional structure was the main factor explaining it. But for them, without significant effect within sedimentary habitats, we observed major effects on both substrates in our study.

Among the sample and within the communities, we found generalist taxa, like *Gammarus* sp., present in all habitats (except bare rocks). On the other hand, some species like *Testudinalia testudinalis* were found only on hard substrates (rocks and mussels) and other taxa were HFS specific. For example, in our samples, *Idotea balthica* and *I. phosphorea* were observed only on eelgrass while *Skeneopsis planorbis* was just observed on macroalgae. This characteristic strengthened the differentiation among habitat communities. Indeed, our results showed that all studied habitats supported different community composition in both taxa and function. Therefore, that habitats had a significant effect on evenness and diversity

index. Furthermore, in our habitat, a gap between the mean and total taxa and function richness was present (Annex X), suggesting numerous uncommon species, like *Cancer irroratus* or *Edotia montosa*.

Among the specific effects of HFS, one of them is to reduce the effect of environmental stress and thereby the community variability and dispersion within the habitats (Crowe *et al.*, 2013). We observed this effect with our *β*-diversity results. Usually, habitats with the presence of HFS had a lower *β*-diversity except for bare rocks. In this peculiar case, such a low value was explained because most samples contained only one taxa, *Littorina* sp.

Effect of local stress level effect (height position or edge proximity)

A model introduced by Menge and Sutherland (1987) and refined later (e.g., Bruno *et al.*, 2003, among others) predicted that the community richness and diversity decrease with increased environmental stress. Several studies confirmed such trends in numerous systems (Davenport & Davenport, 2005; Reed & Hovel, 2006; Barnes & Ellwood, 2011) as well as in habitat related to ours (macroalgae: Scrosati & Heaven, 2007; Scrosati *et al.*, 2011; Cimon & Cusson, 2018 / mussels: Arribas *et al.*, 2014 / eelgrass: Cimon *et al.*, 2021). In our study, no significant effects from the wave exposition were found on the data. Nevertheless, as specified, the level of local stress depends on the height in the shore, except for eelgrass where it depends on the plant density and the proximity to the edge of eelgrass bed as theorized by Menge and Sutherland (1987). Results showed that a high level of the local stress negatively affects the community structure by reducing the biomass and the density, the same results were found concerning both taxa and functional richness but did not affect the evenness or the diversity index except for mussels on rocks. The HFS presence reduced the effect of the environmental stresses on associated communities, allowing a higher biomass and density, and for mussels on rocks also a higher diversity.

However, both stresses factors considered in our study (local stress and wave exposure) showed no strong effect on the distribution of associated communities among samples. They

explained less than 1% of the total variation, even within each habitat where they explained no more than 12% of the total variation. Even without detecting systematic effects of the environmental stress gradient in our study, we could consider that our sampling sites may well reflect the complexity of the St. Lawrence marine estuary habitats. Indeed, we observed strong effects from our random site factor in most of our analyses (21,6% of the variation on both biomass and density data) and they suggest that communities, and their diversity profiles, are strongly site-dependent. Interestingly, the residual counted for about 24% and 18% of the variation of associated community distribution and suggests that strong local variation within communities occurs. The extended sampling period during summer (end of June to early September) may also have added undesired temporal variation we cannot account for.

Role of habitats forming species across coastal habitats

We were unable to determine if the understory mussel was a consequence of the presence of the canopy in the macroalgae habitat. These mussels were collected and counted as epibenthic, in several samples their presence had a strong impact on the biomass and density value, surpassing by far the values of the other associated organisms. McCook and Chapman (1991) claim with previous work that in the absence of disturbance or predation, mussels (*Mytilus edulis*) will outcompete macroalgae (*Fucus vesiculosus* in their study). But in their study, the presence of mussels did not seem to affect either macroalgae cover or density. On the other hand, Albrecht and Reise (1994) found that the mussels density was lower in presence of macroalgae, and suggested that macroalgae increase the sediment deposit burying mussels under it and lowering the process of their recruitment and growth due to a reduced hydrodynamics. Bertness *et al.* (1999) suggested, that the macroalgae canopy had a positive effect upon the growth and recruitment of mussels with more facilitation interaction in mid than in low intertidal areas.

Nevertheless, our standardized sampling allowed us to comparatively quantify the effect of HFS presence on associated communities. Indeed, their presence increased the values of the biological variables (biomass, density, richness and diversity) from associated communities, compared to their equivalent bare substrate. Since evenness is less sensitive to uncommon species (Heip & Engels, 1974; Smith & Wilson, 1996), for this index, we did not see a similar pattern.

The magnitude of increase induced by the presence of an HFS was significantly higher in rocky habitats than in sedimentary habitats. Still, overall, in both substrates, they increase values of biomass, density and both taxa and functional richness by at least 2.8 times. These differences, and the lower values encountered in sedimentary habitats may be explained by the fact that bare sediments offer better protection against environmental stress than bare rocks allowing higher biomass and density of organisms, reducing the gap between biological values from bare sediments and habitats with HFS.

Macroalgae, among all HFS, had the highest magnitudes of increase in associated communities. For the biomass, the significantly high value was explained by the presence of abundant understory mussels, other biological variables were not as much affected by the presence of understory mussels as the biomass. However, for these variables (density, both taxa and functional richness, and diversity), in samples where both macroalgae and understory mussels were present we may have a combined effect from the presence on the associated communities. Joseph and Cusson (2015) observed increases in biomass and species richness by respectively 2.5 and 1.5 times with an experimental design comparing macroalgae and bare rocks effect on the associated benthic communities. Cimon and Cusson (2018) found identical patterns in associated communities with increases in biomass and species richness of 3 and 2 times between macroalgae and bare rocks with a similar experimental design. The effects encountered for the eelgrass in our results on biomass and density were similar to those observed in the literature. The previous comparison between eelgrass and bare sediment found increases in associated communities biomass and density ranging, for both, from 3 to 6 times (Connolly, 1995; Herkül & Kotta, 2009). For mussels on

sediment, Norling and Kautsky (2007) obtained increased values of 4.8, 4.3 and 6.2 times compared to bare sediments for the associated macrofauna biomass, density and species richness, respectively.

The distribution of the biomass and density among our three compartments (epibiont, epibenthos and infauna) offer interesting information about specific mechanisms of how HFS support their associated communities. In sedimentary habitats, the biomass and density are more evenly distributed among compartments than in rocky habitats. While the epibenthic compartments can be limited in mussel beds as available space on rocks or sediments is often nonexistent, epibionts on mussel beds are very important. Mussels significantly increase the heterogeneity and complexity of substrates and create refuges for numerous species (Commito & Rusignolo, 2000; Lawrie & McQuaid, 2011).

Some taxa and functions were only found in the epibiont compartment, meaning they depend on the HFS to live. For some of them, they are specific to one HFS in particular (e.g., *Idotea balthica* and *Skeneopsis planorbis* found respectively only on eelgrass and macroalgae). For macroalgae and eelgrass, values for both taxa and function richness located only the epibiont accounted for less than 20% of the total, suggesting that even if the macrophytes presence increases both richness, most of the organisms did not depend on their presence to live but took advantage of it. For example, *Littorina* spp. were observed in habitats with or without HFS, and in HFS habitat they were observed in both epibiont and epibenthos compartments. However, their biomass and density significantly increased with the presence of macroalgae. Most of the time, macroalgae, mussels and eelgrass with their body structure and shape offer microhabitats (Burnaford, 2004) for other species using it as refuges (Menge & Lubchenco, 1981). For mussels, the positive effect induced by their presence was mainly due to their physical structure and shape, Norling and Kautsky (2007) have shown that after a few months the effect from empty mussels shells on associated communities biomass, density and richness were substantially similar to that of alive mussels. Nonetheless, in their study, alive mussels always supported higher biomass and density of associated communities explained by the higher biodeposition and nutrient concentration,

often considered as limiting resources in coastal habitats, induced by the mussels activities. Norling and Kautsky (2007) results from alive mussels were similar to ours since infauna biomass and density from habitats with or without mussels were relatively close.

As well as the mussels, the macroalgae canopy improves, with their erected structure, the environmental conditions for the associated communities particularly in the mid and upper part of the intertidal areas (Scrosati *et al.*, 2011). Macroalgae also offer shades (Jenkins *et al.*, 1999) and are a source of food and nutrients for several organisms (Underwood, 1980; Rishworth *et al.*, 2018). These improvements were observed in the recruitment, growth and survival rate of associated organisms (Bertness *et al.*, 1999), and the presence of macroalgae also promotes the presence of grazing species and therefore increasing the local diversity (Albrecht & Reise, 1994; Joseph & Cusson, 2015; Cimon & Cusson, 2018). Eelgrass will affect the associated community in a similar way as macroalgae. In their survey, Reed and Hovel (2010) have shown that a decrease in the eelgrass cover reduces the associated community species richness as well as the epibiont density, results observed in other studies (Cimon *et al.*, 2021).

Concluding remarks

Our main objective was to identify, quantify and compare individual effects of HFS on their associated communities from various habitats along an environmental stress gradient. Positive effects of HFS on ecosystems have been well described in the scientific literature and our results supported such trends. Against expectation, we could not disentangle the potential effect of wave exposures and desiccation stress (mussels and macroalgae) or lower density and fragmentation (eelgrass), known to affect benthic communities and often used to describe community differences between habitats, and within them. However, we succeeded in assessing differences in diversity profiles and community structure among studied habitats. The relative importance of habitats versus stressors within habitats in terms of explanation of total variance (50 % versus less than 1%, respectively) mainly revealed stringing

differences in species composition among communities. Specific effects of HFS were seen in each habitat but their overall presence increased many values linked to diversity by three times their corresponding bare substrate values. Among mussel and eelgrass beds and macroalgae, the latter induced the largest effects within its associated communities.

If each studied habitat supported different communities, their multivariate dispersion within habitat was reduced in presence of HFS. Their presence promoted uncommon taxa and taxa dependent and specific to peculiar HFS. Mussels on both substrates had a similar and the lowest values of samples dispersion among all habitats, bare rocks match their level due to its low compositional richness. Moreover, generally low or non-significant results from our stressors may not represent them well as our sampling scheme might not have used enough stressors magnitude to get enough signals in our results.

However, and overall, in the context of the sites used in the St. Lawrence marine estuary, our results support the idea that the use of a standardized method allows illustrating the striking importance of habitats in structuring communities and allows compare respective HFS effects among them. Among the most interesting of our observations is that the HFS presence dramatically influenced the values of most community variables linked to diversity compared to bare habitats. Among HFS, macroalgae has the highest effects on associated communities.

For further research, increasing the environmental stress gradient by using sites with extreme wave expositions and/or extending the height of stress levels in terms of desiccation could be interesting to assert effects of stressors. On sedimentary shore, we may introduce variation in the granulometry to observe its effect on community structure and diversity in presence of HFS. Ultimately, we could do a natural experiment with varying density of HSF or even test the effect of interaction among HFS like mussels and macroalgae to pinpoint their specific effects.

Nonetheless, the data provided by our study allow a better understanding of intertidal habitats from the St. Lawrence marine estuary, and their associated community, and our

results can help to predict possible effects of increasing stresses or in a context of multiple stressors on benthic communities. In such a situation, bare habitats communities will suffer significantly higher consequences. Therefore, our results may also help to understand the role of HFS, and the importance and priorities that foundation species should have within conservation plans. We hope that the understanding of a better relative effect of HFS would give a new light to the management and conservation of the various ecosystems from the St. Lawrence marine estuary.

CONCLUSION GÉNÉRALE

Le rôle facilitateur d'espèces comme les macroalgues, les zostères ou les moules sur les habitats et sur les communautés est un fait bien établi par la science. De nombreuses études se sont employées à identifier, qualifier et quantifier leurs effets dans de multiples environnements. Pour autant, nous n'avons que peu ou pas de comparaison proportionnelle de leur fonction entre elles.

En employant un échantillonnage et des analyses standardisés, nous avons été capables d'offrir un point de vue comparatif supplémentaire entre les différentes espèces facilitatrices présent dans l'estuaire maritime du Saint-Laurent, le tout, le long d'un gradient de stress environnemental. En effet, les critères de sélection pour chacun des sites et des échantillons suivent un protocole normalisé en fonction des facteurs considérés, quel que soit l'habitat. De ce fait, nous arrivons avec des échantillons prélevés qui ont tous les mêmes dimensions et les mêmes caractéristiques permettant par la suite d'établir des analyses communes et similaires. Ces analyses, standardisées, nous ont permis, au travers de nos résultats, de montrer que les six habitats étudiés : macroalgues sur roches, moules sur roches et sur sédiments, zostères sur sédiments et roches et sédiments nus abritent des communautés d'espèces benthiques significativement différentes, aussi bien en biomasse, en densité d'individus qu'en richesses taxonomique et fonctionnelle et que le niveau de dispersion des échantillons varie avec les habitats. Les habitats expliquent près de la moitié de la dispersion des communautés, et contrairement à nos attentes, les facteurs de stress environnemental ne seraient responsables que d'une infime partie d'une infime partie de la variation, moins de 1%, et ce même au sein de chaque habitat, où ils n'expliquent pas plus de 12% de la variation totale.

Dans l'estuaire maritime du Saint-Laurent, la présence des espèces facilitatrices dans un habitat augmente les valeurs de biomasse, de densité d'individus, de richesse taxonomique et fonctionnelle d'au moins trois fois comparativement aux habitats dépourvus de ces espèces. Le facteur d'augmentation des variables biologiques précédentes varie entre les

espèces facilitatrices et selon la variable biologique considérée. De façon globale, ces effets sont plus importants dans les milieux rocheux que dans les milieux sédimentaires, et parmi tous les habitats, c'est dans celui des macroalgues que les effets étaient les plus marqués. Nos résultats montrent aussi que la répartition de la biomasse et de la densité d'individus entre les trois compartiments des échantillons, épibionte, epibenthos et endofaune, varient avec l'habitat. Certains taxons et certaines fonctions sont observables seulement dans le compartiment épibionte permettant d'affirmer l'existence et la présence d'organismes dépendants des espèces facilitatrices avec certains de ces organismes spécifiques à une espèce facilitatrice. De plus, les écarts importants entre les valeurs moyennes et les valeurs totales des richesses taxonomique et fonctionnelle attestent la présence d'espèces rares ou peu communes dans les habitats, comme *Calliopius laeviusculus*, *Cancer irroratus* ou *Naineris quadricuspida*.

Néanmoins, la structure des communautés benthiques côtières ne peut être entièrement expliquée par les paramètres et les facteurs considérés dans notre étude. Il est indéniable que d'autres paramètres et facteurs non considérés ont des effets sur les communautés benthiques côtières que nous avons étudiées. Entre autres, la température, la salinité (Stickle & Denoux, 1976), la granulométrie des sédiments (McLachan, 1996), les contaminants (Venturini *et al.*, 2004) ainsi que les interactions inter- et intraspécifiques jouent un rôle dans la structure des communautés. L'inclusion de ces variables, ou du moins une partie, pourrait améliorer grandement la qualité d'interprétation des résultats obtenus, notamment en ce qui concerne la variation entre les sites de même habitat. Nous n'avons pas été en mesure d'affirmer que le niveau d'exposition aux vagues avait un effet sur les communautés et pour la position dans l'estran son effet apparaît comme léger. Ces résultats vont un peu à contresens avec la littérature, c'est pourquoi nous conseillons d'utiliser des méthodes plus précises pour déterminer les niveaux de ces deux facteurs afin de préciser leurs effets et d'observer le réel impact d'un gradient de stress. Pour l'exposition aux vagues, il est envisageable de réaliser une campagne de terrain préalable à la campagne d'échantillonnage afin de mesurer les niveaux d'expositions aux vagues à l'aide de matériel spécifique (par ex. dynamomètres) et ainsi affiner le choix des sites. Dans la mesure où des données sur les vents, les courants et

la morphologie des côtes seraient disponibles, il serait possible de produire localement des simulations sur les niveaux d'hydrodynamisme. Pour la position dans l'estran, des positions plus extrêmes pourraient être choisies afin d'accroître l'effet du stress lié à la dessiccation ou à la densité et la fragmentation de l'habitat dans le cas des zostères.

Bien que notre étude puisse être améliorée et perfectionnée à différents niveaux, l'emploi d'un échantillonnage et d'analyses standardisés reste l'un des meilleurs moyens de combler des lacunes sur les effets des espèces facilitatrices de l'estuaire maritime du Saint-Laurent. Du fait de méthodologies employées différentes, en plus des variations temporelles, l'analyse comparative d'études antérieures n'aurait pas permis d'arriver aux mêmes conclusions.

Ainsi, lors d'études ultérieures, il serait intéressant, et nous suggérons, de choisir des sites qui permettent d'avoir un gradient de stress accru et plus marqué à l'aide des méthodes mentionnées précédemment. Nous conseillons aussi d'ajouter diverses variables environnementales afin d'affiner et de préciser les effets réels des espèces facilitatrices. Dans notre étude, nous n'avons fait que survoler la richesse fonctionnelle et les traits fonctionnels des communautés benthiques côtières. En outre l'utilisation de mesures de traits biologiques plus raffinée (par ex. : l'analyse des traits fonctionnels des espèces, « Community-Weighted Mean trait value » ou CWM, etc.), Pour autant, il pourrait être très enrichissant de se concentrer et d'analyser plus en détail les particularités des communautés benthiques côtières de l'estuaire maritime du Saint-Laurent ainsi que les effets des espèces facilitatrices sur ce sujet. Est-ce que les espèces facilitatrices apportent dans l'habitat plus d'espèces de prédateur, de suspensivores, de détritivores, de brouteurs? Est-ce que ce sont des espèces mobiles ou sessiles? Des questions auxquelles il serait intéressant de répondre. Ultimement, réaliser des expériences qui font varier la densité des espèces facilitatrices, qui testent les interactions entre espèces facilitatrices, comme les moules avec les macroalgues, ou bien de faire des suivis temporels afin d'étudier les variations saisonnières et/ou annuelles des communautés permettrait d'améliorer nos connaissances sur les effets des espèces facilitatrices. Une telle suite d'étude favoriserait la réalisation de modèles d'évolution des

habitats et des communautés et de prédiction dans un contexte où le niveau et/ou le nombre de facteurs de stress changeraient. En effet, afin d'être le plus complet possible, ce type de modèle nécessite des bases de données cohérentes et de bien connaître les conditions initiales. De plus, dans le cas hypothétique ou des bases de données précisant l'état des habitats et de leurs communautés avant et après variations des niveaux de stress seraient disponibles en assez grand nombre, il serait théoriquement possible d'employer des algorithmes d'apprentissage automatique (en anglais : machine learning). L'application de cette technologie émergente et innovante, mais gourmande en ressources et en informations permettrait néanmoins de simuler et de suivre de manière très précise et d'un niveau supérieur l'évolution des habitats et de leurs communautés à la suite de variations dans les paramètres environnementaux, tels que les stress et les perturbations.

Néanmoins, les données que nous avons récoltées permettent de préciser la façon dont pourraient réagir les communautés intertidales de l'estuaire maritime du Saint-Laurent dans l'éventualité de l'introduction d'un nouveau facteur de stress ou de l'augmentation d'un facteur de stress déjà présent, notamment dans un contexte où la pression anthropique sur les écosystèmes ne cesse de croître. En effet, dans cette éventualité les communautés présentes dans les habitats hébergeant des espèces facilitatrices seront impactées de manière importante que les habitats dépourvus d'espèces facilitatrices. Ainsi, nos résultats montrent l'importance de la prise en considération des espèces facilitatrices dans le cadre de programmes de gestion et de conservation de l'environnement ou de développement durable. Ces mêmes résultats pourraient servir d'appui dans la détermination de zones d'intervention prioritaire en cas d'accidents majeurs, comme des déversements d'hydrocarbures. Toutefois, notre étude identifie et quantifie les effets positifs des espèces facilitatrices présentes dans le milieu intertidal de l'estuaire maritime du Saint-Laurent sur les communautés de macroinvertébrés qui leurs sont associées le long d'un gradient de stress environnemental. Notre étude souligne leurs rôles indéniables pour la diversité du Saint-Laurent.

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ANNEXES

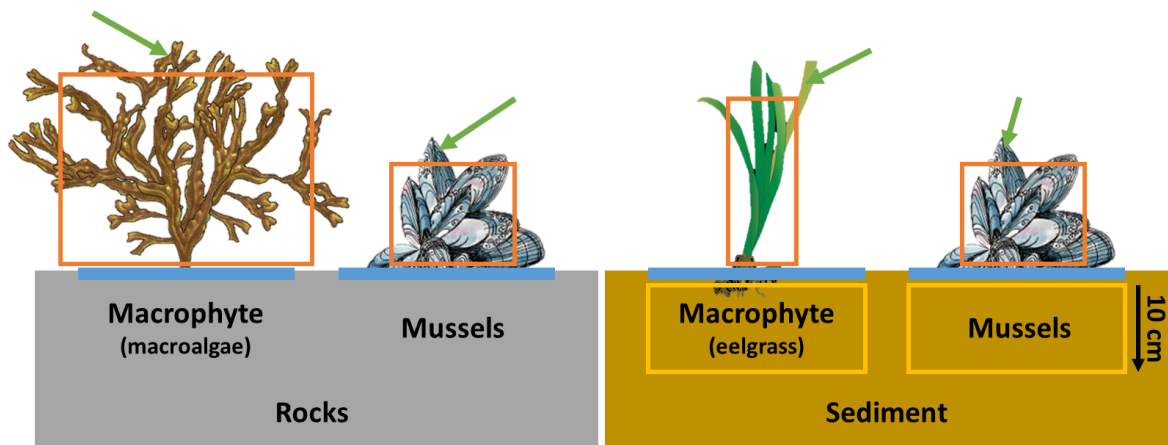**Annex I**: Representation of compartments origins and their respective signification

Compartments :

← HFS

☐ Epibiont

☐ Epibenthos

☐ Infauna

Macrophyte (macroalgae)   Mussels   Macrophyte (eelgrass)   Mussels

Rocks   Sediment

10 cm

Annex II: Position and date of sampling for each site

Site	Latitude	Longitude	Date of sampling
Exposed bare rocks 1	48.684482°	-67.964247°	02/07/16
Exposed bare rocks 2	48.371153°	-69.367253°	26/07/16
Exposed bare rocks 3	48.681400°	-68.030694°	05/08/16
Exposed macroalgae on rocks 1	48.684482°	-67.964247°	03/07/16
Exposed macroalgae on rocks 2	48.168056°	-69.133664°	20/07/16
Exposed macroalgae on rocks 3	48.373329°	-69.366798°	23/07/16
Exposed mussels on rocks 1	48.374737°	-69.364062°	24/07/16
Exposed mussels on rocks 2	48.682284°	-68.030481°	19/08/16
Exposed mussels on rocks 3	48.680407°	-68.038218°	03/09/16
Exposed bare sediments 1	48.684419°	-67.964535°	09/07/16
Exposed bare sediments 2	48.168056°	-69.133664°	22/07/16
Exposed bare sediments 3	49.113369°	-68.181749°	06/07/16
Exposed eelgrass on sediments 1	49.112910°	-68.179611°	06/07/16
Exposed eelgrass on sediments 2	48.041946°	-69.344386°	22/08/16
Exposed eelgrass on sediments 3	49.067376°	-66.787778°	05/09/16
Exposed mussels on sediments 1	48.168056°	-69.133664°	21/07/16
Exposed mussels on sediments 2	48.372098°	-69.367864°	25/07/16
Exposed mussels on sediments 3	48.681381°	-68.036945°	24/08/16
Sheltered bare rocks 1	48.437617°	-68.591944°	22/06/16
Sheltered bare rocks 2	48.373086°	-69.368408°	26/07/16
Sheltered bare rocks 3	48.680244°	-68.030077°	05/08/16
Sheltered macroalgae on rocks 1	48.437617°	-68.591944°	23/06/16
Sheltered macroalgae on rocks 2	48.133633°	-69.183089°	01/08/16
Sheltered macroalgae on rocks 3	48.141745°	-69.165513°	03/08/16
Sheltered mussels on rocks 1	48.437617°	-68.591944°	24/06/16
Sheltered mussels on rocks 2	48.681411°	-68.026620°	18/08/16
Sheltered mussels on rocks 3	48.683132°	-68.028233°	02/09/16
Sheltered bare sediments 1	48.435550°	-68.593402°	20/06/16
Sheltered bare sediments 2	48.133633°	-69.183089°	02/08/16
Sheltered bare sediments 3	48.141745°	-69.165513°	04/08/16
Sheltered eelgrass on sediments 1	49.087983°	-68.317758°	05/07/16
Sheltered eelgrass on sediments 2	49.054430°	-68.378688°	07/07/16
Sheltered eelgrass on sediments 3	48.034331°	-69.363474°	04/09/16
Sheltered mussels on sediments 1	48.435550°	-68.593402°	21/06/16
Sheltered mussels on sediments 2	48.680227°	-68.032123°	17/08/16
Sheltered mussels on sediments 3	48.683177°	-68.026475°	01/09/16

Annex III: Functional traits used to determine the functional richness

Size	Growth form	Trophic type	Motility
S (1 ≤ 2 mm)	E (encrusting)	A (autotroph)	A (attached)
M (2 ≤ 10 mm)	M (massive)	P (predators)	C (crawling)
L (10 ≤ 100 mm)	B (bushy)	S (suspension feeder)	S (swimming)
X (< 100 mm)	F (filamentous)	D (deposit feeder)	D (drifting)
		G (grazers)	B (burrowing)
		O (omnivore)	

Annex IV: List of taxa and compartment they were found on with their respective functional code derived from their functional traits

Taxa	HFS	Epibiont	Epibenthos	Endofauna	Functional code
Actiniaria		x	x		LMOA
Aeolidia papillosa		x	x		LMGC
Apohyale prevostii		x	x		MEOS
Arenicola marina			x	x	MFDB
Ascophyllum nodosum	x				XBAA
Autolytinae			x	x	MFPB
Balanus sp.		x	x		MMSA
Buccinidae		x	x		LMGC
Calliopius laeviusculus		x	x		MEOS
Cancer irroratus		x	x		LMPC
Capitella sp.				x	MFDB
Chiridotea coeca		x	x		MFSC
Clathromorphum circumscriptum			x		MEAA
Corophium volutator			x		MMOC
Crangon septemspinosa		x	x		LMPS
Ecrobia truncata		x	x		SMGC
Edotia montosa		x	x		SMSC
Eteone longa				x	MFPB
Eulalia bilineata		x	x	x	MFPB
Euspira heros		x	x		MMGC
Fucus d. edentatus	x				XBAA
Fucus evanescens	x				XBAA
Fucus vesiculosus	x				XBAA
Gammarus sp.		x	x		LMOS
Gemma gemma				x	MMSB
Gomontia polyrhiza			x		MEAA
Harpacticoida		x	x		SMOS
Hediste diversicolor				x	LFPB
Hildenbrandia rubra			x		MEAA
Hydrozoa		x			LBSA
Idotea balthica		x			MMGS
Idotea phosphorea		x			MMGS
Jaera albifrons		x	x		SMGC
Lacuna pallidula		x	x		MMGC
Lacuna vincta		x	x		MMGC
Larvae fish			x		SFSD
Lepidonotus squamatus		x	x		MFOC
Limecola balthica				x	MMSB
Littorina littorea		x	x		MMGC
Littorina obtusata		x	x		MMGC
Littorina saxatilis		x	x		MMGC
Macoma calcarea				x	MMSB
Manayunkia aestuarina				x	SFSB
Marenzelleria viridis				x	LFDB
Margarites helicinus		x	x		MMGC

Taxa	HFS	Epibiont	Epibenthos	Endofauna	Functional code
Micronereis sp.				x	MFPB
Monoculodes latimanus		x	x		MMGS
Mya arenaria				x	LMSB
Mysis stenolepis		x	x		LMGS
Mytilus spp.	x	x	x		LMSA
Naineris quadricuspida		x	x		LFDB
Nematoda		x	x	x	SFPB
Nephtys caeca				x	LFPB
Nucella lapillus		x	x		LMPC
Oligochatea 1		x	x	x	SFDB
Oligochatea 2		x	x	x	MFDC
Oligochatea 3		x	x	x	MFDC
Oligochatea 4		x	x	x	MFDC
Pectinariidae				x	MFDB
Petalonia fascia			x		LBAA
Pholoe sp.		x	x		MFPC
Phoxocephalus holbolli		x	x		MMGS
Phyllodoce groenlandica				x	LFPB
Pista maculata				x	LFSB
Platybdella sp.		x	x		LFPC
Polydora sp.				x	MFSB
Psammonyx nobilis				x	MMOS
Pseudoleptocuma minus				x	MMOS
Pygospio elegans				x	SFDB
Ralfsia fungiformis			x		MEAA
Ralfsia verrucosa			x		MEAA
Rhachotropis sp.		x	x		LMOS
Skeneopsis planorbis		x	x		SMGC
Spio sp.				x	SFDB
Spirorbis spirorbis		x	x		MFSA
Stragularia clavata			x		MEAA
Strongylocentrotus droebachiensis		x	x		MMGB
Terebellidae sp.				x	MFSB
Testudinalia testudinalis		x	x		MMGC
Ulothrix flacca			x		MEAA
Ulvaceae			x		XBAA
Westwoodilla sp.		x	x		MMOS
Zostera marina	x				XFAA

Annex V: List of contrasts used to compare individually (compared to the bare habitat) and among them the effects of the substrates, category of HFS (macrophyte and mussels) and each HFS. Habitat on emerged rocks (R) or sedimentary shores (S) and Macrophyte R stand for macroalgae while Macrophyte S stand for eelgrass

Contrasts name	Contrasts
Substrate (sediment vs rocks)	Macroalgae + MusselsR+ BareR VS Eelgrass + MusselsS + BareS
Macrophyte	Macroalgae + Eelgrass VS BareR + BareS
Global Mussels	MusselsR + MusselsS VS BareR + BareS
Macroalgae	Macroalgae VS BareR
Eelgrass	Eelgrass VS BareS
Mussels Rocks	MusselsR VS BareR
Mussels Sediment	MusselsS VS BareS
Macrophyte/Global Mussels	Macroalgae + Eelgrass VS MusselsR + MusselsS
Macroalgae/Mussels Rocks	Macroalgae VS MusselsR
Eelgrass/Mussels Sediment	Eelgrass VS MusselsS
Macroalgae/Eelgrass	Macroalgae VS Eelgrass
Mussels Rocks/Mussels Sediment	MusselsR VS MusselsS

Annex VI: Proportion (%) of the variation explained by different factors based on biomass and density abundance structure results from the PERMANOVA from the table 3

Source	Biomass	Density
Habitats	42.9	49.3
Stressors (Stress level + Exposition)	0.4	0.7
Site	21.6	21.6
Residuals	24.1	17.7
Max stressors within habitat	11.3	12.5

Annex VII: Summary of the extended version of the PERMANOVA based on biomass data from table 3 with contrasts added with the degree of freedom (df), the mean square (MS), the Pseudo-F and the P(perm). (E=effect). Significant results (p < 0.05) are in bold (N_{tot} = 360; Permutations = 9999)

Source	df	MS	F-ratio	p
Habitat	5	87892	11.721	**0.0001**
Substrate	1	110210	16.208	**0.0028**
Macrophyte	1	119910	12.571	**0.0026**
Global Mussels	1	161070	24.626	**0.0022**
Macroalgae	1	125630	20.325	**0.0017**
Eelgrass	1	74249	5.827	**0.0030**
Mussels Rocks	1	117410	20.129	**0.0027**
Mussels Sediment	1	107070	15.174	**0.0024**
Macrophyte/Global Mussels	1	41822	6.008	**0.0010**
Macroalgae/Mussels Rocks	1	34493	8.689	**0.0024**
Eelgrass/Mussels Sediment	1	35015	3.802	**0.0022**
Macroalgae/Eelgrass	1	69725	7.258	**0.0035**
Mussels Rocks/Mussels Sediment	1	12302	3.444	**0.0139**
Stress level	1	4382	2.190	**0.0178**
Exposition	1	5864	0.782	0.6058
Habitat * Stress level	5	3750	1.874	**0.0015**
Substrate * Stress level	1	3180	1.533	0.1788
Macrophyte * Stress level	1	5676	2.279	**0.0417**
Global Mussels * Stress level	1	7293	3.339	**0.0118**
Macroalgae * Stress level	1	3384	2.373	0.0508
Eelgrass * Stress level	1	7072	1.971	0.0988
Mussels Rocks * Stress level	1	2768	2.504	**0.0533**
Mussels Sediment * Stress level	1	6580	2.000	0.0998
Macrophyte/Global Mussels * Stress level	1	1138	0.936	**0.4855**
Macroalgae/Mussels Rocks * Stress level	1	2373	1.622	**0.1586**
Eelgrass/Mussels Sediment * Stress level	1	1180	1.043	0.4043
Macroalgae/Eelgrass * Stress level	1	2996	1.864	0.0983
Mussels Rocks/Mussels Sediment * Stress level	1	1003	1.015	0.4380
Habitat * Exposition	5	5513	0.735	0.8903
Substrate * Exposition	1	6185	0.910	0.4906
Macrophyte * Exposition	1	6543	0.686	0.6694
Global Mussels * Exposition	1	3705	0.566	0.7697
Macroalgae * Exposition	1	4795	0.776	0.4650
Eelgrass * Exposition	1	8093	0.635	0.7068
Mussels Rocks * Exposition	1	2330	0.400	0.7679
Mussels Sediment * Exposition	1	4498	0.637	0.6853
Macrophyte/Global Mussels * Exposition	1	8038	1.155	0.3244
Macroalgae/Mussels Rocks * Exposition	1	3757	0.946	0.4939
Eelgrass/Mussels Sediment * Exposition	1	8600	0.934	0.4140
Macroalgae/Eelgrass * Exposition	1	9033	0.940	0.4116
Mussels Rocks/Mussels Sediment * Exposition	1	1755	0.491	0.8797
Stress level * Exposition	1	2023	1.011	0.4349

Source	df	MS	F-ratio	p
Site (Expo * Hab)	24	7499	9.963	**0.0001**
Site (Expo * Substrate)	8	6800	3.046	**0.0001**
Site (Expo * Macrophyte)	8	9539	4.004	**0.0001**
Site (Expo * Global Mussels)	8	6541	3.633	**0.0001**
Site (Expo * Macroalgae)	8	6181	10.015	**0.0001**
Site (Expo * Eelgrass)	8	12742	10.258	**0.0001**
Site (Expo * Mussels Rocks)	8	5833	12.134	**0.0001**
Site (Expo * Mussels Sediment)	8	7056	6.738	**0.0001**
Site (Expo * Macrophyte/Global Mussels)	8	6961	5.627	**0.0001**
Site (Expo * Macroalgae/Mussels Rocks)	8	3970	7.101	**0.0001**
Site (Expo * Eelgrass/Mussels Sediment)	8	9209	16.170	**0.0001**
Site (Expo * Macroalgae/Eelgrass)	8	9607	13.160	**0.0001**
Site (Expo * Mussels Rocks/Mussels Sediment)	8	3572	8.963	**0.0001**
Habitat * Stress level * Exposition	5	2520	1.259	0.1178
Substrate * Stress level * Exposition	1	2491	1.201	0.3251
Macrophyte * Stress level * Exposition	1	2711	1.089	0.3800
Global Mussels * Stress level * Exposition	1	3118	1.428	0.2188
Macroalgae * Stress level * Exposition	1	1761	1.235	0.3151
Eelgrass * Stress level * Exposition	1	4302	1.199	0.3263
Mussels Rocks * Stress level * Exposition	1	1548	1.401	0.2459
Mussels Sediment * Stress level * Exposition	1	4738	1.440	0.2259
Macrophyte/Global Mussels * Stress level * Exposition	1	2125	1.749	0.1180
Macroalgae/Mussels Rocks * Stress level * Exposition	1	1984	1.356	0.2477
Eelgrass/Mussels Sediment * Stress level * Exposition	1	827	0.731	0.6047
Macroalgae/Eelgrass * Stress level * Exposition	1	836	0.520	0.7967
Mussels Rocks/Mussels Sediment * Stress level * Exposition	1	449	0.454	0.8944
Stress level * Site (Expo * Hab)	24	2001	2.658	**0.0001**
Stress level * Site (Expo * Substrate)	8	2075	0.929	0.6299
Stress level * Site (Expo * Macrophyte)	8	2491	1.046	0.3711
Stress level * Site (Expo * Global Mussels)	8	2184	1.213	0.1613
Stress level * Site (Expo * Macroalgae)	8	1426	2.310	**0.0001**
Stress level * Site (Expo * Eelgrass)	8	3588	2.889	**0.0001**
Stress level * Site (Expo * Mussels Rocks)	8	1105	2.300	**0.0003**
Stress level * Site (Expo * Mussels Sediment)	8	3290	3.141	**0.0001**
Stress level * Site (Expo * Macrophyte/Global Mussels)	8	1215	0.982	0.5090
Stress level * Site (Expo * Macroalgae/Mussels Rocks)	8	1463	2.618	**0.0001**
Stress level * Site (Expo * Eelgrass/Mussels Sediment)	8	1132	1.987	**0.0001**
Stress level * Site (Expo * Macroalgae/Eelgrass)	8	1607	2.202	**0.0001**
Stress level * Site (Expo * Mussels Rocks/Mussels Sediment)	8	988	2.479	**0.0001**
Residuals	288	753		
Total	359			

Annex VIII: Mean (±SE) values of A) biomass (g/sample 30 x 30 cm quadrat), B) density (count/sample), C) taxa richness and D) functional richness for each compartment in each habitat ($N_{per\ habitat}$ = 60). Note that in A) and B) the scale is log
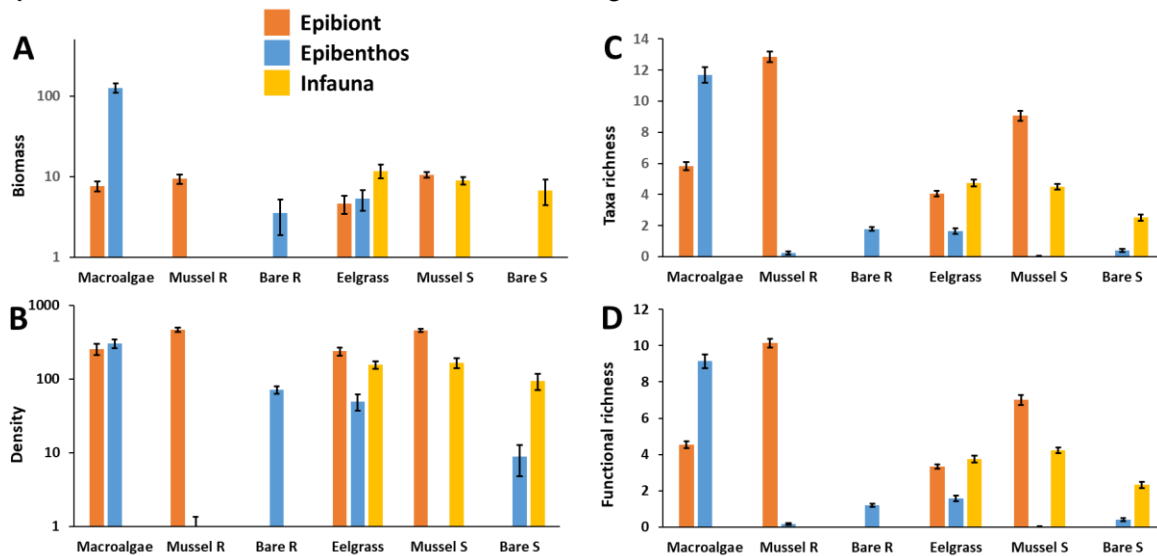
Annex IX: Summary of the PER-ANOVAs on the Simpson diversity index and the Pielou evenness from density data of the associated communities. Degree of freedom (df), mean square (MS), the Pseudo-F and P(perm) are provided. Significant results ($p < 0.05$) are in bold ($N_{tot\ Simpson}$ = 358; $N_{tot\ Evenness}$ = 323; Permutations = 9999)

Source	Simpson diversity index				Pielou evenness			
	df	MS	F-ratio	p	df	MS	F-ratio	p
Habitat	5	3.254	27.102	**0.0001**	5	0.388	2.566	0.0583
Stress level	1	0.063	2.393	0.1402	1	0.059	1.736	0.2010
Exposition	1	0.203	1.694	0.2103	1	0.199	1.518	0.2303
Habitat * Stress level	5	0.080	3.029	0.0289	5	0.136	3.920	**0.0082**
Habitat * Exposition	5	0.045	0.375	0.8595	5	0.149	0.985	0.4479
Stress level * Exposition	1	0.003	0.109	0.7479	1	0.012	0.368	0.5565
Site (Expo * Hab)	24	0.120	7.025	**0.0001**	24	0.160	9.231	**0.0001**
Hab * Stress level * Exposition	5	0.042	1.601	0.1993	5	0.039	1.117	0.3827
Stress level * Site (Expo * Hab)	24	0.026	1.543	0.0516	23	0.035	2.044	**0.0053**
Residuals	286	0.017			252	0.017		
Total	357				322			

Annex X: Summary of the total taxa richness, mean taxa richness, total function richness and mean function richness for each habitat

Habitats	Total taxa richness	Mean taxa richness	Total functional richness	Mean functional richness
Macroalgae	62	13.3	35	10.0
Mussel R	39	13.1	22	10.3
Bare R	12	1.8	9	1.2
Eelgrass	40	9.6	24	7.6
Mussel S	32	10.8	19	8.6
Bare S	21	2.9	17	2.7