Université du Québec
à Rimouski

Étude de la diversité spécifique et fonctionnelle des communautés benthiques d'estuaires subarctiques le long de gradients de salinité et détermination des seuils de tolérance d'espèces clés aux stress hypoosmotique et associés aux inondations printanières

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Never be so kind, you forget to be clever

Never be so clever, you forget to be kind

T. Swift

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AVANT-PROPOS

Ce projet de doctorat en biologie intitulé « Étude de la diversité spécifique et fonctionnelle des communautés benthiques d'estuaires subarctiques le long de gradients de salinité et détermination des seuils de tolérance d'espèces clés aux stress hypoosmotique et associés aux inondations printanières » a été réalisé à l'Université du Québec à Rimouski (UQAR) et à l'Institut Maurice Lamontagne, Ministère des Pêches et Océans (IML-MPO). Il a été réalisé sous la co-supervision du professeur Piero Calosi (UQAR), du professeur Mathieu Cusson (UQAC) et du docteur Yanick Gendreau (IML-MPO), en collaboration avec le chercheur David Drolet (IML-MPO).

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Cette thèse commencera par une introduction générale écrite en français visant à décrire l'état des connaissances sur les écosystèmes estuariens et sur les modifications du cycle hydrologique associées aux changements globaux, puis à introduire la méthodologie des chapitres subséquents. Ces trois chapitres seront écrits en anglais, sous forme d'articles scientifiques. Le premier chapitre a été publié dans le journal *Estuarine, Coastal and Shelf Science*. Le deuxième chapitre est en cours de révision dans le *Journal of Experimental Marine Biology and Ecology*. Le troisième article va être soumis dans le journal *Limnology and oceanography*, lorsque les mesures de l'alcalinité de l'eau auront été prises.

Je tiens à souligner que l'Université du Québec à Rimouski et l'Institut Maurice-Lamontagne sont situés sur les territoires traditionnels et non cédés des Premières Nations

Wolastoqiyik Wahsipekuk et Mi'kmaq. Les inventaires et la récolte des organismes ont été faits sur les territoires de la Nation Innue. L’Université du Québec à Chicoutimi est située sur le territoire traditionnel non cédé de la Première Nation des Pekuakamiulnuatsh.

RÉSUMÉ

Les communautés estuariennes, qui soutiennent diverses fonctions écosystémiques, sont vulnérables aux modifications dans les cycles hydrologiques liées aux changements globaux. Les précipitations accrues et les inondations associées entraînent des variations brusques des paramètres physico-chimiques de l'eau dans les estuaires (p. ex. salinité, pH, turbidité), causant des stress pour les macroalgues et macroinvertébrés benthiques. Les modifications du climat se font particulièrement ressentir en hautes latitudes, pourtant les écosystèmes subarctiques restent peu étudiés. Cette thèse a donc comme objectif principal d'évaluer la vulnérabilité des communautés benthiques estuariennes subarctiques aux inondations. Elle sera composée d'une introduction écrite en français, suivie de trois chapitres rédigés en anglais sous forme d'articles scientifiques, et d'une conclusion générale rédigée en français.

Dans le **chapitre 1**, nous avons décrit la composition et diversité taxonomique et fonctionnelle des communautés benthiques de substrat dur retrouvées dans de petits estuaires de la Côte-Nord. Le long du gradient de salinité, l'apport en eau douce causait une perte de biomasse et de richesse taxonomique et fonctionnelle, en plus d'une diminution de la taille des macroalgues. Il façonnait aussi les structures taxonomiques et fonctionnelles des communautés, en diminuant la proportion de filtreurs et d'espèces aux larves se déplaçant sur de longues distances. Les indices de traits fonctionnels se sont avérés efficaces pour détecter les changements de communauté le long des gradients de salinité, et dévoilent une possible perte de services écosystémiques en cas d'inondations plus fréquentes.

Dans le **chapitre 2**, nous avons utilisé un gradient de stress hypoosmotique pour évaluer la vulnérabilité à des inondations intenses plus ou moins prolongées chez trois espèces de mollusques (c.-à-d. la littorine des rochers *Littorina saxatilis*, la macoma baltique *Macoma balthica* et la moule bleue *Mytilus* spp.). L'utilisation d'un gradient de 15 durées de pulses d'eau douce durant de 0 à 9 jours, entrecoupés de 1 jour en eau salée et répétés pendant 6 semaines, a permis de déterminer que les inondations de 2 jours ou moins ne posent pas de risque majeur pour notre assemblage de mollusques. *Littorina saxatilis* présentait la vulnérabilité la plus élevée, suivie par *M. balthica* et *Mytilus* spp. De plus, la croissance de la coquille et la masse corporelle chez *L. saxatilis* diminuaient avec l'augmentation de la durée des pulses d'eau douce, tandis que seule la masse corporelle était affectée négativement chez *M. balthica*. Ni la masse corporelle ni la croissance n'était affectée chez *Mytilus* spp., mais sa teneur énergétique était plus élevée dans les pulses d'eau douce les plus longs, suggérant des réponses physiologiques complexes au stress hypoosmotique.

Ces résultats contrastant avec la distribution des espèces dans les estuaires, nous avons exploré dans le **chapitre 3** si les conditions des inondations printanières pouvaient modifier la vulnérabilité de ces espèces au stress hypoosmotique, en ajoutant une diminution du pH et une augmentation de la turbidité aux pulses d'eau douce. Pendant cinq semaines, les organismes ont été exposés en laboratoire à des conditions d'eau douce « d'inondations printanières » ou à des conditions d'eau douce « sans conditions d'inondations printanières », avec un gradient de 12 durées de pulses d'eau douce d'une durée comprise entre 0 et 9 jours, entrecoupées d'une exposition de 1 jour à l'eau de mer. Comme pour le chapitre précédant, *L. saxatilis* présentait la mortalité la plus rapide et la plus élevée, tandis que *M. balthica* et *Mytilus* spp. ont montré une plus grande résistance, bien que la mortalité ait augmenté chez les deux espèces en conditions d'inondation printanière. La vulnérabilité prononcée de *L. saxatilis* en conditions d'inondation printanière est probablement due à la dissolution de sa coquille, qui n'a pas été observée chez les deux espèces plus résistantes.

Les résultats de cette thèse montrent que les communautés subarctiques semblent vulnérables aux modifications futures des régimes d'inondation, affectant potentiellement des services écosystémiques comme la filtration des matières en suspension. De plus, l'utilisation d'un gradient de niveau de stress (ici, la durée des pulses d'eau douce) s'avère efficace pour détecter des seuils de vulnérabilité, qui peuvent apparaitre ou être avancés vers des niveaux de stress plus faibles avec l'addition d'autres stresseurs ou avec le temps. La détermination de ces seuils permet d'émettre des recommandations précises pour la gestion des barrages et évacuateurs de crues. Enfin, nos résultats soulignent le besoin crucial d'étudier les facteurs de stress combinés représentant mieux les conditions naturelles et permettant de ne pas sous-estimer les risques (contrairement à l'étude de stresseur individuel) pour une gestion efficace des écosystèmes estuariens.

Mots clés : inondations, estuaires, changements globaux, salinité, traits fonctionnels, pH, turbidité, gradient, multi-facteurs, communautés

ABSTRACT

Estuarine communities, which support various ecosystem functions, are vulnerable to modifications in the hydrological cycle related to global changes. Increased precipitation and associated flooding lead to abrupt changes in the physicochemical parameters of the water in the estuaries (*e.g.*, salinity, pH, turbidity), causing stresses for benthic macroalgae and macroinvertebrates. Climate changes are particularly noticeable at high latitudes, yet subarctic ecosystems remain poorly studied. The main objective of this thesis is to assess the vulnerability of subarctic estuarine benthic communities to flooding. It will consist of an introduction written in French, followed by three chapters written in English in the form of scientific articles, and a general conclusion written in French.

Chapter 1 describes the composition and taxonomic and functional diversity of hard substrate benthic communities found in small estuaries on the northern shore of the St-Lawrence marine estuary. Along the salinity gradient, freshwater input causes a loss of biomass and taxonomic and functional richness, in addition to a decrease in the size of macroalgae. It also shapes taxonomic and functional community structures, decreasing the proportion of filter feeders and long-distance larval dispersers. Functional trait indices were shown to be effective in detecting community changes along salinity gradients and reveal a possible loss of ecosystem services in the event of more frequent flooding.

In **Chapter 2**, we used a hypoosmotic stress gradient to assess the sensibility to intense flooding of various durations in three mollusk species (*i.e.*, rough periwinkle *Littorina saxatilis*, Baltic clam *Macoma balthica*, and blue mussel *Mytilus* spp.). The use of a gradient of duration of freshwater pulses lasting 0 to 9 days, interspersed with 1 day in salt water and repeated for 6 weeks, determined that flooding of two days or less does not pose a major risk to our mollusk assemblage. *Littorina saxatilis* had the highest sensibility, followed by *M. balthica* and *Mytilus* spp. In addition, shell growth and body mass in *L. saxatilis* decreased with increasing duration of freshwater pulses, while only body mass was negatively affected in *M. balthica*. Neither body mass nor growth were affected in *Mytilus* spp., but its energy content was higher in the longest freshwater pulses, suggesting complex physiological responses to hypoosmotic stress.

As these results contrast with the distribution of species in estuaries, we explored in **Chapter 3** whether spring flood conditions could modify the sensibility of these species to hypoosmotic stress, by adding a decrease in pH and an increase in turbidity to freshwater pulses. For five weeks, organisms were exposed in the laboratory to "spring flood" or “no spring flood” freshwater, with a gradient of 12 levels of freshwater pulses lasting between 0 and 9 days, interspersed with 1-day exposure to seawater. As in the previous chapter, *L. saxatilis* had the fastest and highest mortality, while *M. balthica* and *Mytilus* spp. showed greater tolerance, although mortality increased in both species under flood conditions. The pronounced sensibility of *L. saxatilis* to spring flooding conditions is likely due to the dissolution of its shell, which was not observed in the two more tolerant species.

The results of this thesis show that subarctic communities appear vulnerable to future changes in flood regimes, potentially affecting ecosystem services such as the filtration of suspended matter. In addition, the use of a stress level gradient (in this case, the duration of freshwater pulses) is effective in detecting thresholds of sensibility, which can appear or be advanced to lower stress levels with the addition of other stressors or over time. The determination of these thresholds makes it possible to put forward precise recommendations for the management of dams and spillways. Finally, our results highlight the crucial need to study combined stressors that better represent natural conditions and allow not to underestimate the risks (unlike the study of individual stressors) for an effective management of estuarine ecosystems.

Keywords: floods, estuaries, global changes, salinity, functional traits, pH, turbidity, gradient, multi-factors, communities

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LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

Cette liste est présentée dans l'ordre de l'apparition des abréviations dans le texte.

SSC Quantité de sédiment en suspension (*Suspended sediment content*)

DOC Carbone organique dissous (*dissolved organic carbon*)

CID/DIC Carbone inorganique dissous (*dissolved inorganic carbon*)

TA Alcalinité totale (*total alkalinity*)

OA acidification des océans (*ocean acidification*)

FRic Richesse fonctionnelle (*functional richness*)

S Richesse taxonomique (*taxonomic richness*)

RaoQ Entropie Quadratique de Rao (*Rao Quadratic Entropy*)

D indice de Simpson (*Simpson index*)

CWM moyennes pondérées par la communauté (*community weighted mean*)

SLME Estuaire marin du Saint-Laurent (*St. Lawrence marine estuary*)

PERMANOVA Analyse de variance multivariée par permutations (*permutational multivariate analyses of variance*)

PER-ANOVA Analyse de variance par permutations (*permutational analyses of variance*)

HR rapport de risque (*hazard ratio*)

LISTE DES SYMBOLES

Ω_{arag}	saturation en aragonite
$\Omega_{calcite}$	saturation en calcite

INTRODUCTION GÉNÉRALE

Les estuaires, où l'eau douce des rivières se mêle aux eaux salées de la mer, sont étroitement liés à l'histoire humaine, car ils fournissent des fonctions écologiques et des services culturels et économiques uniques (Kainamu-Murchie *et al.,* 2018). Depuis des millénaires, de nombreux peuples autochtones à travers le monde ont tiré parti de ces écosystèmes exceptionnellement productifs pour subvenir à leurs besoins alimentaires, par exemple, par la récolte d'huîtres (Rick *et al.*, 2017) ou de racines comestibles (Maurice-Hammond *et al.*, 2023). Par la suite, l'expansion du commerce maritime mondial ont encouragé l'établissement de populations humaines dans ces zones de transition entre la terre et la mer, y intensifiant ainsi la pression anthropique (Kennish, 2002). Ces écosystèmes deviennent alors particulièrement vulnérables à la pollution et aux changements globaux (Kennish, 2002; Statham, 2012) ce qui risque de réduire tant leurs fonctions écologiques que les services qu'ils procurent (Lotze *et al.,* 2006). Les changements climatiques se manifestent plus intensément aux hautes latitudes comparées au reste du globe (Constable *et al.*, 2023), mais leurs effets sur les communautés des estuaires subarctiques demeurent peu étudiés. En particulier, les répercussions de l'augmentation en fréquence et en intensité des phénomènes climatiques extrêmes, tels que les inondations, sur ces communautés restent largement inconnues.

1. LES ECOSYSTEMES ESTUARIENS

1.1 Caractéristiques des estuaires

Les *estuaires* sont des baies côtières recevant de l'eau douce provenant du continent (p. ex. rivière, fleuve), et un afflux d'eau salée provenant de l'océan ouvert *via* les marées (Davis et FitzGerald, 2020). Ce mélange d'eaux douce et salée représente leur caractéristique

principale, soit la présence d'eau saumâtre. Ainsi, les estuaires ne sont pas des entités isolées, et leurs processus écologiques doivent donc être considérés dans un gradient horizontal de la rivière à la mer (Kaiser *et al.*, 2020). Ils sont souvent divisés en trois zones : l'estuaire maritime (*lower*), directement connecté au milieu marin; l'estuaire moyen (*middle*), soumis à un fort mélange d'eau de mer et d'eau douce; et l'estuaire fluvial (*upper*), caractérisé par une eau douce sujette à l'action quotidienne des marées (Kaiser *et al.*, 2020) (**Figure 1**). Ces trois zones peuvent être difficiles à établir, et ne peuvent pas se rapporter à des valeurs fixes de salinité, puisque l'apport en eau douce, bien que constant, fluctue fortement en fonction des saisons et des conditions météorologiques (Davis et FitzGerald, 2020).

De nombreux gradients abiotiques se retrouvent le long des estuaires. La salinité peut varier entre 0 à la tête de l'estuaire jusqu'à environ 34 au niveau de l'embouchure. Durant les marées, la zone de l'estuaire moyen voit sa salinité changer de façon plus drastique que les zones maritime et fluviale, qui restent plus stables dans leurs valeurs extrêmes. De la même façon, les sédiments vont être généralement de plus grandes tailles (p. ex. sable et gravier) dans les zones maritime et fluviale à cause des courants plus importants, tandis qu'ils seront plus fins (p. ex. argile et limon) dans la partie moyenne, où la turbidité sera aussi plus élevée (Uncles *et al.*, 2002). Ces sédiments contiennent une grande quantité de matière organique pouvant soutenir une forte activité bactérienne qui peut faire diminuer le niveau d'oxygène dissout dans la partie moyenne des estuaires (Goosen *et al.*, 1999; Lung et Nice, 2007). Dans les estrans vaseux, où les sédiments sont trop fins pour permettre une réoxygénation par diffusion, l'activité aérobie et anaérobie des bactéries peut même mener à la production de sous-produits potentiellement toxiques, comme le méthane (CH_4) ou le sulfure d'hydrogène (H_2S) (Kaiser *et al.*, 2020).

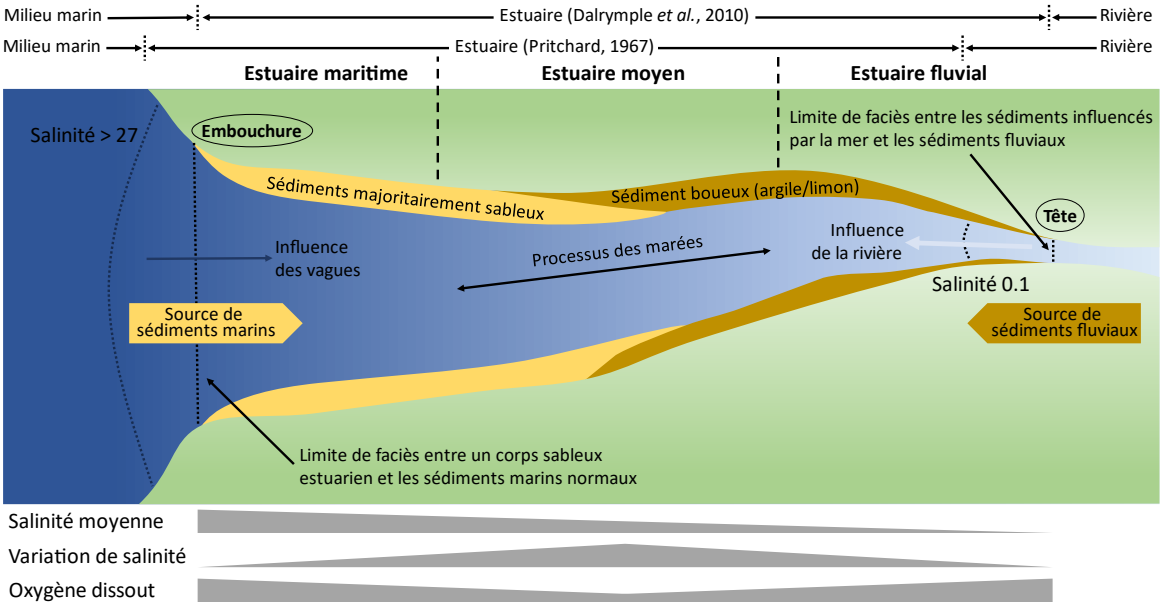


Figure 1. Représentation d'un estuaire (traduit et adapté de Davis et FitzGerald, 2020)

En plus des gradients horizontaux décrits plus hauts, les estuaires comprennent des gradients de stress verticaux créés par les marées qui varient selon la hauteur dans l'estran (**Figure 2**). L'estran est un laboratoire naturel idéal pour étudier le rôle combiné de facteurs physiques et biologiques sur l'abondance, la répartition (Tomanek et Helmuth, 2002), et l'adaptation physiologique ou la capacité d'adaptation (Bozinovic *et al.*, 2011) des organismes dans le milieu naturel. La zone intertidale représente un des environnements les plus rudes sur la planète, où des communautés spatialement condensées subissent l'assaut des vagues, des périodes d'exondation, des variations en salinité et en température pendant les périodes de marée basse, mais aussi de fortes pressions sélectives liées à la prédation et à la compétition pour l'espace (Connell, 1961; Denny et Wethey, 2011; Tomanek et Helmuth, 2002). Ces différents facteurs peuvent être décrits comme des *déterminants* (*driver*, c.-à-d. qu'ils entraînent une réponse biologique quantifiable, allant du stress à l'amélioration) mais sont plus fréquemment décrits comme des *stresseurs* (*stressor*, qui diminuent le *fitness* d'un organisme) (Boyd et Hutchins, 2012). Ces stresseurs peuvent suivre des cycles réguliers (c.-à-d. journaliers, saisonniers ou annuels) (Helmuth, 1999; Zhang *et al.*, 2010) ou être causés par des évènements stochastiques (Williams *et al.*, 2011). Ils s'intensifient avec l'élévation

dans l'estran, où la température et la dessiccation fluctuent davantage à cause des marées (Menge et Branch, 2001). Dans la partie haute de l'estran, la répartition des espèces est principalement dictée par différents paramètres physico-chimiques (p. ex. salinité, température et dessiccation) (Attrill *et al.*, 1999; Barnes, 1989; Kaiser *et al.*, 2005; Kinne, 1971), tandis que dans la partie basse, les facteurs biotiques (p. ex. compétition pour l'espace et prédation) ont plus d'influence (Connell, 1961).

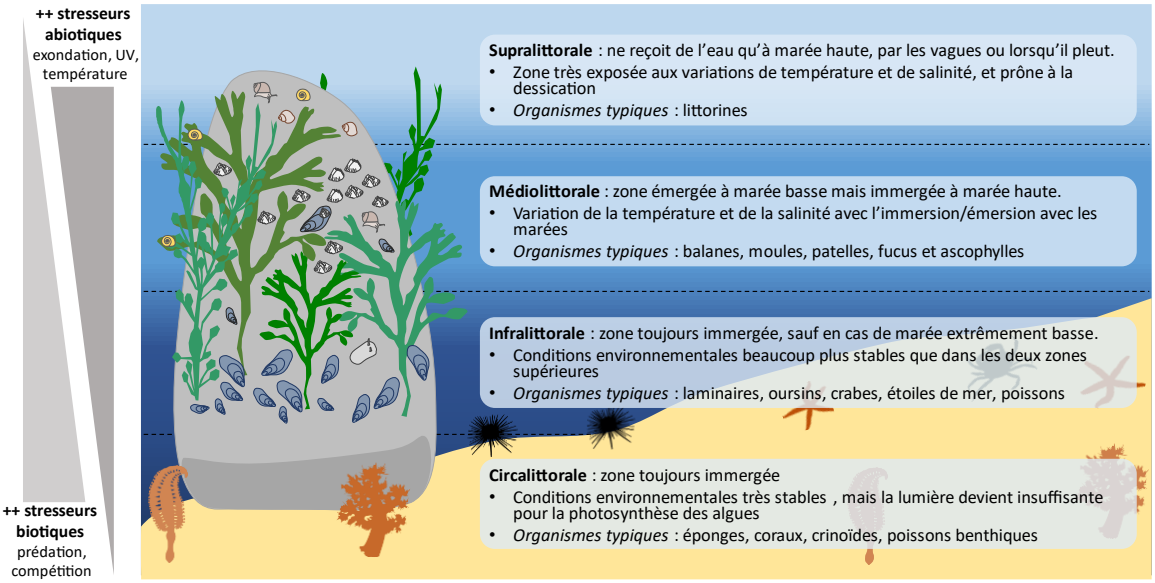


Figure 2. Représentation des différents niveaux de la zone médiolittorale, avec les espèces qui y sont fréquemment associées.

1.1.1 Processus, fonctions et services des écosystèmes estuariens

Un *écosystème* est défini comme une unité constituée d'une composante abiotique et biotique qui interagissent entre elles afin de former un système stable (Allaby, 2010). Les *fonctions* ou *processus écosystémiques* sont les caractéristiques physiques et chimiques et les activités biologiques qui influencent les flux, le stockage et la transformation des matériaux et de l'énergie au sein des écosystèmes et à travers eux (Bertness, 2014). Les *services écosystémiques* quant à eux décrivent les avantages que les personnes tirent des écosystèmes fonctionnels, c.-à-d. les caractéristiques écologiques, les fonctions ou les processus qui

contribuent directement ou indirectement au bien-être humain (Bertness, 2014; Granek *et al.*, 2010). Par exemple, les marais côtiers fournissent un habitat pour les poissons juvéniles (fonction), ce qui peut contribuer à la pêche commerciale ou récréative (service), et aide à l'atténuation des vagues (fonction), ce qui peut protéger les zones côtières des tempêtes et empêcher une forte érosion (service) (Granek *et al.*, 2010). Les services écosystémiques sont habituellement divisés en quatre catégories, soient les services d'approvisionnement (p. ex. production de nourriture ou autre produit), de régulation (p. ex. purification de l'eau ou protection des berges), culturels (p. ex. paysage esthétique ou pêche récréative) et de support (services qui ont un effet indirect sur d'autres services, p. ex. fixation du carbone, production primaire) (Costanza *et al.*, 2011) (**Figure 3**).

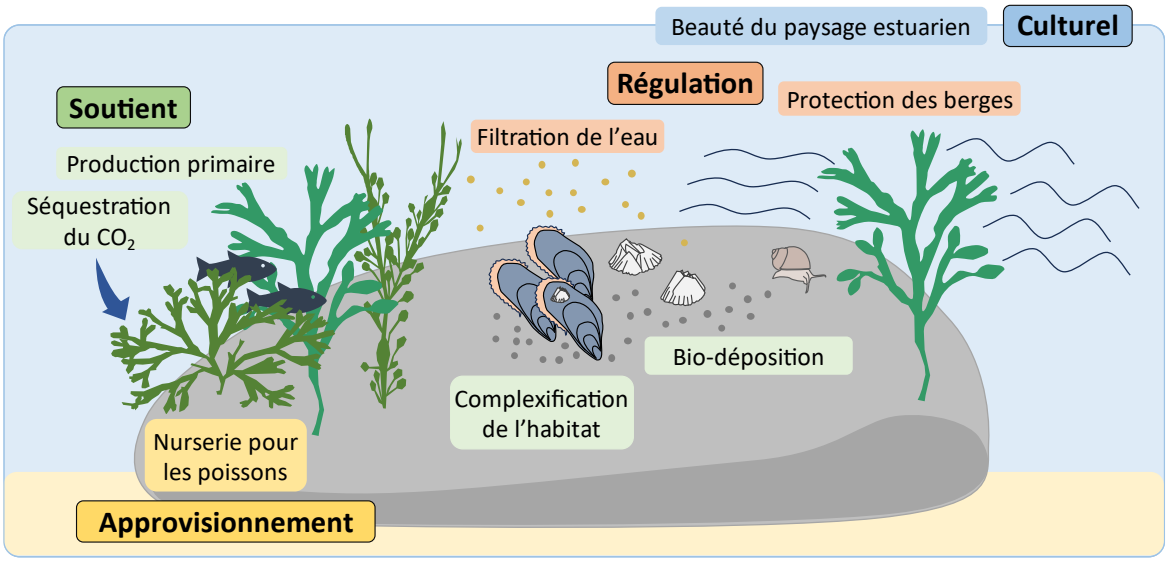


Figure 3. Exemples des fonctions écosystémiques fournies par les communautés benthiques estuariennes. La couleur représente le type de service auquel chaque fonction peut être associée, soit un service de soutient (vert), d'approvisionnement (jaune), de régulation (orange) ou culturel (bleu).

Les écosystèmes estuariens soutiennent de nombreuses fonctions écologiques à grande échelle, notamment en fournissant des nutriments à l'environnement marin avoisinant (Bauer *et al.*, 2013) qui sont redistribués aux niveaux trophiques supérieurs (Kemp et Boynton, 1984; Savage *et al.*, 2012). Leur végétation souvent abondante offre une grande quantité de

nourriture, tout en abritant moins de gros prédateurs que les milieux marins adjacents (Whitfield, 2020). Dans la zone médiolittorale rocheuse, les fucus et ascophylles sont considérées comme étant des espèces formant l'habitat car elles abritent une forte biodiversité en réduisant de nombreux stress, incluant ceux liés à la température et à la dessiccation (Ape *et al.*, 2018; Joseph et Cusson, 2015; Watt et Scrosati, 2013a, 2013b). Elles peuvent être considérées comme des espèces facilitatrices (Bruno *et al.*, 2003), car elles vont permettre à des organismes d'étendre leur niche à des hauteurs de la zone médiolittorale qu'ils seraient habituellement incapables d'occuper (Bertness *et al.*, 1999). Les macroalgues sont aussi considérées comme un puits de carbone (Krause-Jensen et Duarte, 2016), bien que cela fasse encore l'objet de débats (Bach *et al.*, 2021; Gallagher *et al.*, 2022).

Les estuaires abritent ainsi des habitats divers et interconnectés (p. ex. herbiers marins, marais salés, vasières), qui peuvent être utilisés de façon variée entre les espèces, mais aussi selon les stades de vie et les saisons (Day *et al.*, 2021; Litvin *et al.*, 2018). Les communautés estuariennes servent d'habitats d'alevinage ou de croissance pour les juvéniles de nombreuses espèces marines, de façon opportunistes (c.-à-d. facultative) ou dépendantes (c.-à-d. obligatoire pour compléter leur cycle de vie) (Able, 2005; Lewis *et al.*, 2021; Vasconcelos *et al.*, 2011). Ainsi, 72 % des espèces marines de poissons sauvages péchés commercialement auraient au moins un stade de vie associé aux estuaires, principalement parce qu'ils sont liés à une augmentation de la disponibilité des ressources trophiques pélagiques et benthiques, comme le phytoplancton, le zooplancton, les détritus ou les poissons fourrages (Broadley *et al.*, 2022).

Les écosystèmes estuariens agissent également comme systèmes naturels de filtration d'eau (Petersen *et al.*, 2014a; zu Ermgassen *et al.*, 2013). La filtration des matières en suspension par les espèces filtreuses des estuaires améliore la qualité de l'eau, en réduisant la turbidité et en laissant pénétrer la lumière, permettant la photosynthèse chez les photoautotrophes (Cloern, 1982; Dame, 2012). Les estuaires pourraient aussi servir de filtre pour les microplastiques venant des rivières, en les bloquant sur les plages avant qu'ils ne se

rendent jusqu'aux océans (López *et al.*, 2021). Les espèces de filtreurs participent également au relargage des nutriments et des éléments chimiques entre les sédiments et la colonne d'eau, car nombre d'entre eux sont à la base du réseau trophique (p. ex. détritivore, filtreurs) (Menge *et al.*, 1997). Les moules en particulier sont des proies importantes de nombreux prédateurs (des gastéropodes aux oiseaux; Dame, 2012) et peuvent servir d'espèces fondatrices en augmentant la complexité de l'habitat (Commito et Rusignuolo, 2000; Norling et Kautsky, 2007; Palomo *et al.*, 2007).

Ces services écosystémiques sont particulièrement à risque dû à la pollution, à l'utilisation des terres et aux changements globaux (Beck *et al.*, 2023; Lotze *et al.*, 2006).

1.2 Les communautés benthiques estuariennes

Les estuaires boréaux et tempérés modernes sont des formations très récentes, tant sur le plan de la géologie que de l'évolution : ils ne sont apparus qu'il y a environ 6 000 ans, lorsque le retrait des glaces durant l'Holocène a entraîné une élévation rapide du niveau de la mer et inondé les parties exposées du plateau continental et les rivières (Kaiser *et al.*, 2020). Les organismes qui peuplent aujourd'hui ces estuaires peuvent avoir trois origines : (1) ils sont issus de « zones refuges » leur ayant permis de survivre aux périodes de glaciation et de fonte, (2) ils ont colonisé les estuaires depuis des latitudes plus basses après la dernière glaciation, ou (3) ils ont évolué dans ces milieux après la fonte des glaces, à partir d'espèces marines ou d'eau douce (Kaiser *et al.*, 2020; Väinölä, 2003).

Les espèces retrouvées dans les estuaires sont majoritairement des espèces marines, celles d'eau douce disparaissant lorsque la salinité dépasse 5 et les espèces spécifiquement d'eau saumâtres étant rares (Whitfield *et al.*, 2012). Les macroinvertébrés sont principalement des annélides, nématodes, crustacés et mollusques (Kaiser *et al.*, 2020). Ils constituent un élément central du réseau trophique estuarien puisqu'ils sont des consommateurs primaires et une source de nourriture importante pour de nombreux organismes marins dont les pinnipèdes (Estes *et al.*, 2016), les poissons, et les oiseaux (Day *et al.*, 1989). Majoritairement sessiles et sédentaires, les macroinvertébrés benthiques doivent

faire preuve d'une bonne capacité de tolérance et/ou d'acclimatation aux stresseurs environnementaux durant chaque marée (Bilyard, 1987; Newell, 1979). Incapables d'éviter les conditions leurs étant défavorables en raison de leur faible locomotion, et possédant une durée de vie longue (notamment les bivalves), ils sont fréquemment utilisés comme des sentinelles lors de suivis environnementaux (Bilyard, 1987).

En raison des fortes fluctuations de salinité et de la turbidité élevée, seules quelques espèces de macroalgues résistantes, comme certaines algues vertes (*Ulva* spp.) ou brunes (*Fucus* spp., *Ascophyllum* spp.), parviennent à prospérer dans ces environnements (Middelboe *et al.*, 1998; Wilkinson *et al.*, 1995). Cependant, les macroalgues peuvent se faire rares dans les estuaires, car elles dépendent de la présence de substrat dur sur lequel se fixer.

1.2.1 Les communautés estuariennes et le gradient de salinité

La salinité est considérée comme le principal déterminant biogéographique dans les estuaires (Kinne, 1971; Lu *et al.*, 2008) et peut entraîner une diminution du nombre d'espèces présentes depuis les eaux marines vers les eaux fluviales (Whitfield *et al.*, 2012). L'apport en eau douce entraîne également une diminution de la biomasse et de la richesse globales des invertébrés et des macroalgues (McGovern *et al.*, 2020; Middelboe *et al.*, 1998; Montague et Ley, 1993). La capacité des organismes à répondre à un stress hypoosmotique, c.-à-d. à une diminution de la concentration en sels dans leur environnement, conditionne la survie des espèces marines dans les estuaires et influence leur distribution le long de ce gradient. Une réduction de la salinité représente un stress hypoosmotique pour les organismes marins, dont l'osmolarité interne est supérieure à celle de l'eau environnante. Pour éviter la dilution de leurs fluides internes, l'absorption d'eau par les tissus doit être limitée, par exemple à l'aide de pompes actives ou de mécanismes de déplacement des ions contenus dans les tissus. Deux stratégies sont alors mises en œuvre : les organismes *osmoconformes*, comme la plupart des mollusques et autres invertébrés marins, possèdent une capacité limitée d'osmorégulation et survivent dans les estuaires grâce à une tolérance accrue à la dilution de leurs fluides

internes (Moyes et Schulte, 2008). En revanche, les organismes *osmorégulateurs*, comme certains crustacés ou la majorité des vertébrés, maintiennent une osmolarité interne dans une gamme étroite, indépendamment des variations dans l'osmolarité de l'environnement externe (Moyes et Schulte, 2008). Une grande variété d'invertébrés estuariens se comportent aussi comme des hyper-/iso-régulateurs, ne recourant à l'osmorégulation que lorsque la salinité de l'environnement devient particulièrement faible (Bozza *et al.*, 2024; Lockwood, 1962). Les organismes peuvent également être classés en fonction de leur tolérance aux variations d'osmolarité interne : les espèces *euryhalines*, capables de supporter de larges variations de salinité, et les espèces *sténohalines*, limitées à des conditions de salinité restreintes (Moyes et Schulte, 2008). Cette tolérance peut influencer leur répartition dans les estuaires, les espèces euryhalines se trouvant plus près des sources d'eau douce, tandis que les espèces sténohalines se concentrent dans les zones infralittorales marines, où la salinité reste plus stable (Freire *et al.*, 2011). La tolérance des macroinvertébrés estuariens aux variations de salinité dépend de plusieurs facteurs, tels que leur patrimoine génétique et leur stade de développement (Eierman et Hare, 2013; Kinne, 1966; Pruett *et al.*, 2022). Les réponses physiologiques des individus d'une même espèce au stress de salinité peuvent aussi varier selon leur localisation dans l'estuaire et la salinité de leur milieu d'origine (Letendre *et al.*, 2008; Muraeva *et al.*, 2016).

Les macroalgues vont répondre aux variations de salinité par deux processus : le premier implique des changements rapides de pression de turgescence, causés par des flux massifs d'eau entrant ou sortant de l'organisme en suivant le gradient osmotique. Le second correspond à l'ajustement des concentrations intracellulaires des ions inorganiques actifs et des osmolites organiques jusqu'à l'atteinte d'un nouvel état d'équilibre (Kirst, 1990). De la même façon que chez les invertébrés, les macroalgues de la zone infralittorale sont plus sténohalines que leurs homologues de la zone médiolittorale, principalement euryhalines (Hurd *et al.*, 2014; Zaneveld, 1969).

Les études portant sur les communautés de substrat meuble dans des estuaires tropicaux sont nombreuses (Lam-Gordillo *et al.*, 2022; Medeiros *et al.*, 2021; Morais *et al.*, 2019)

mais celles portant sur les communautés de substrat dur ont été largement négligées (Lam-Gordillo *et al.*, 2020). Pourtant, ces habitats peuvent soutenir une importante biomasse de macroinvertébrés et de macroalgues et influencer grandement la composition des communautés adjacentes de substrats meubles (Ricciardi et Bourget, 1999; Wetzel *et al.*, 2014). De la même façon, les communautés estuariennes subarctiques sont rarement étudiées (p. ex. McGovern *et al.*, 2020) comparativement aux estuaires tropicaux.

2. INONDATIONS : CHANGEMENTS CLIMATIQUES, PREDICTIONS ET CONSEQUENCES

Depuis le début de la révolution industrielle au 18ème siècle, les activités humaines (p. ex. la combustion des combustibles fossiles, la production de ciment) ont conduit à une accumulation croissante de gaz à effet de serre (GES) naturellement présents dans l'atmosphère, comme le dioxyde de carbone (CO_2), le méthane (CH_4) et le protoxyde d'azote (N_2O). En piégeant la chaleur dans l'atmosphère, ces concentrations de plus en plus élevées de GES provoquent une élévation des températures mondiales, perturbant les systèmes climatiques. Ceux-ci impliquent notamment une augmentation des évènements climatiques extrêmes, telles que les fortes pluies, qui sont observés depuis plusieurs décennies et qui devraient continuer à s'intensifier (Tabari, 2020; IPCC, 2023b; Jong *et al.*, 2023).

2.1 Prédictions à l'échelle mondiale

Le cycle de l'eau décrit la circulation continue de l'eau à travers l'atmosphère, la surface et sous le sol de la Terre, depuis les vastes réserves des océans, des glaces et des eaux souterraines aux réservoirs plus petits et temporaires des rivières, lacs, et de la végétation (Allan *et al.*, 2020). Les changements dans le cycle de l'eau sont de plus en plus affectés par les activités humaines, à travers la réponse climatique aux émissions de GES et de particules d'aérosols, mais aussi par l'utilisation des sols et l'extraction d'eau des systèmes souterrains et fluviaux pour des usages agricoles, industriels et domestiques (Abbott *et al.*, 2019; Asoka *et al.*, 2017; Li *et al.*, 2019) (**Figure 4**). La *relation de Clausius-Clapeyron* joue un rôle clé dans l'intensification de certains évènements climatiques extrêmes, particulièrement en ce

qui concerne les précipitations. Pour chaque augmentation de 1 °C de la température de l'air, l'atmosphère peut contenir environ 7 % de plus de vapeur d'eau, ce qui se vérifie à basse altitude (Allan *et al.*, 2014). Or, une plus grande quantité de vapeur d'eau dans l'atmosphère conduit à des précipitations plus intenses lorsqu'elle se condense. Il est donc de plus en plus évident que le cycle de l'eau « s'intensifie » avec l'augmentation des flux d'humidité entraînant des précipitations plus abondantes (Allan *et al.*, 2020). L'amplification du transport d'eau douce et des échanges entre l'atmosphère et la surface intensifie les saisons humides et sèches et les évènements météorologiques (Allan *et al.*, 2020).

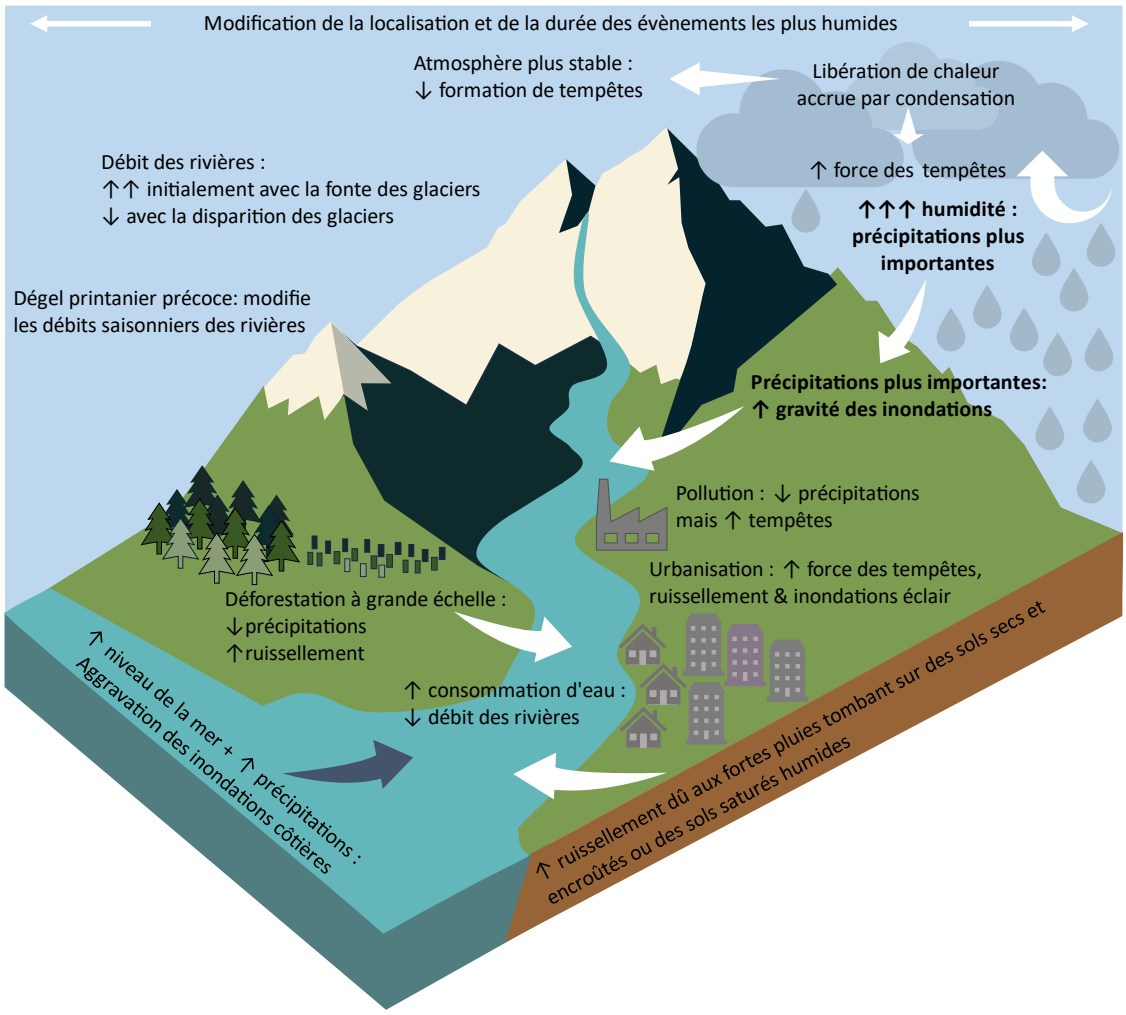


Figure 4. Illustration des facteurs influençant les changements dans les fortes précipitations et les inondations (traduit de Allan *et al.*, 2020).

2.2 Risques d'inondation et hydrologie au Canada

Dans l'est du Canada, la configuration du système fluvial et les conditions climatiques, avec des hivers froids et un manteau neigeux important, créent des conditions favorables aux inondations liées à la fonte des neiges et à la formation d'embâcles durant la période printanière (Rokaya *et al.*, 2018). Avec les changements globaux, il est attendu que le risque et la fréquence des inondations augmente dans cette région (Clavet-Gaumont *et al.*, 2017; Faghfouri *et al.*, 2023). Dans le système Saint-Laurent (fleuve-estuaire-golfe), le régime hydraulique devrait passer d'un régime neigeux à un régime pluvieux dans le siècle prochain (Boyer *et al.*, 2010). Une augmentation de la fréquence des inondations dans la région du Saint-Laurent a par ailleurs été observée ces 100 dernières années (Saint-Laurent *et al.*, 2010), et il est attendu que cette tendance se maintienne dans le siècle prochain (Turcotte *et al.*, 2020; Verhaar *et al.*, 2011;).

En plus des changements climatiques, l'anthropisation des cours d'eau et le harnachement des grandes rivières est un phénomène mondial (**Figure 5a**) qui constitue un changement global à part entière (Habersack *et al.*, 2014). De plus, la demande croissante en énergie verte nourrit un intérêt majeur en matière de développement de l'hydroélectricité : en 2015, c'est au-moins 3 700 grands barrages qui étaient prévus ou en cours de construction, principalement dans les pays à économie émergente (**Figure 5b**; Zarfl *et al.*, 2015). Ces infrastructures sont très présentes au Canada : on retrouve 1 157 « grands » barrages sur l'ensemble du pays, dont 651 dans la province du Québec (Canadian Dam Association, 2019). Les barrages hydroélectriques ont un impact sur la température, la salinité, et la turbidité du Saint-Laurent, bien que leur influence varie selon les saisons et la position des barrages (Lavoie *et al.*, 2017). Ces derniers influencent l'hydrologie de leurs cours d'eau, en causant notamment une homogénéisation des débits des rivières et une diminution des débits annuels maximaux au printemps (Assani *et al.*, 2006). Cependant, la multiplication des phénomènes extrêmes causée par les changements globaux montre l'importance de faire des études portant non seulement sur les tendances moyennes, mais aussi sur les évènements extrêmes ponctuels (Jentsch *et al.*, 2007; Ledger et Milner, 2015). Ainsi, dans le cas des

barrages, il est parfois nécessaire d'ouvrir ponctuellement les évacuateurs de crues lorsque le niveau d'eau dans les réservoirs est trop élevé, comme cela a été le cas à l'automne 2017 et en juin 2019 sur plusieurs barrages de la Côte-Nord du Québec (Paquet, 2017, 2019). Il est fort probable qu'en raison des changements dans le régime de précipitation, il soit nécessaire d'ouvrir leurs évacuateurs de crues plus longtemps et plus fréquemment qu'actuellement (Lin *et al.*, 2021). Il est aussi devenu nécessaire de prendre en compte les changements climatiques dans la révision des critères de conception des infrastructures hydrauliques (Huaringa Alvarez *et al.*, 2014), en particulier concernant les évacuateurs de crues, afin de réduire les risques d'accidents (Herbozo *et al.*, 2022; Lompi *et al.*, 2023).

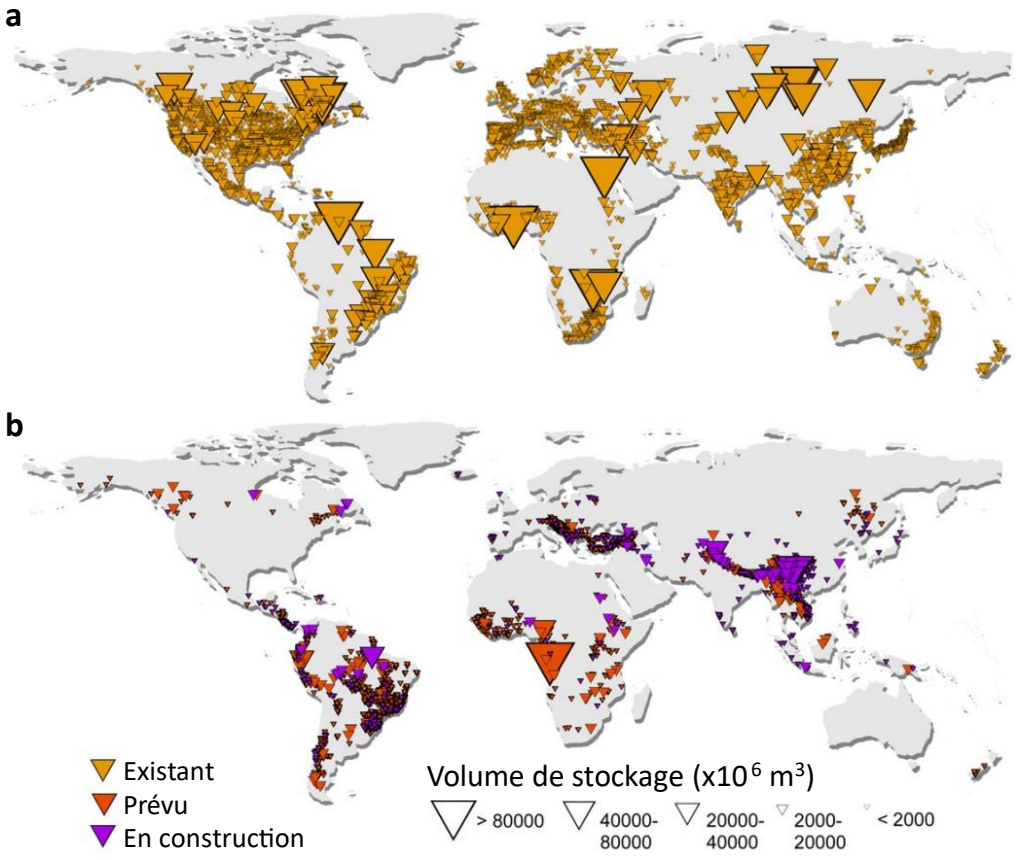


Figure 5. Vue d'ensemble (a) des barrages existants (Lehner *et al.*, 2011) et (b) des futurs barrages prévus et en construction (Zarfl *et al.*, 2015) en 2015, par classe de volume de stockage (volumes en millions de mètres cubes d'après Lehner *et al.*, 2011)(traduit de Grill *et al.*, 2015).

Bien que Najibi et Devineni (2018) aient montré que les inondations les plus fréquentes en Amérique du Nord durent moins de 7 jours (**Figure 6**), il y a un manque de recherche portant sur la durée moyenne et la fréquence des inondations, qu'elles soient passées, présentes ou futures. Cependant, les inondations causées par des évènements intenses et courts, tels que de fortes précipitations (Kendon *et al.*, 2014; Zeeb *et al.*, 2024) et les épisodes de pluie sur neige (Bonsal *et al.*, 2019) devraient augmenter à mesure que le changement climatique progresse. À l'inverse, on s'attend à ce que les évènements à plus long terme (c.-à-d. la fonte des neiges) deviennent plus courts en raison de la réduction de

l'accumulation de neige en hiver et de la fonte des neiges plus précoce (Burn et Whitfield, 2016).

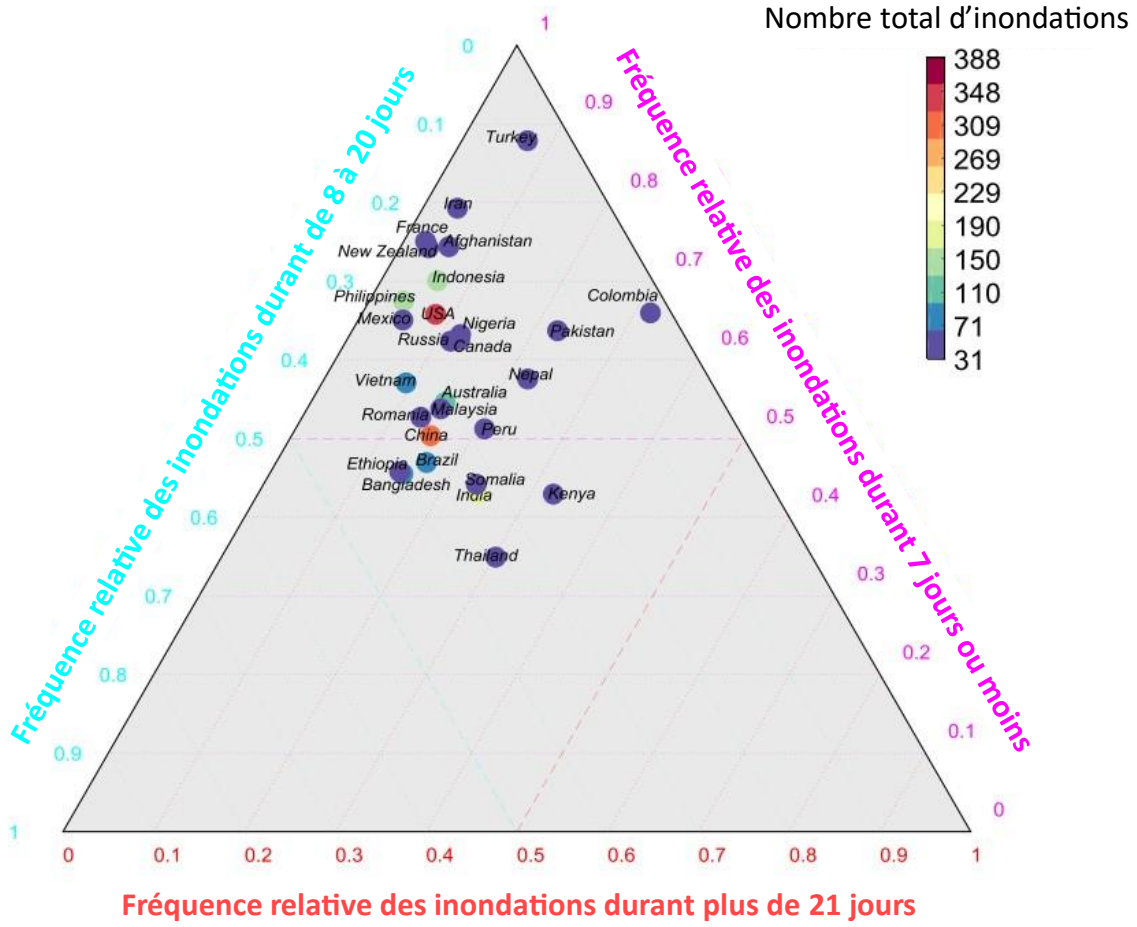


Figure 6. Fréquence relative des inondations de courte durée (moins de 7 jours), de durée modérée (8 à 20 jours) et de longue durée (21 jours et plus) pour les pays ayant enregistré au moins 31 événements entre 1985 et 2015 (traduit de Najibi et Devineni, 2018).

2.3 Changements abiotiques survenant suite aux inondations dans les estuaires

Les inondations provoquent des changements brusques dans les principaux paramètres environnementaux des eaux estuariennes. La salinité peut chuter considérablement et prendre jusqu'à deux mois pour revenir à la normale dans l'ensemble de l'estuaire (Nichols, 1977; Voynova *et al.*, 2016). Des concentrations très élevées de sédiments en suspension peuvent être observées pendant plus d'une semaine (Nichols, 1977). Les valeurs de turbidité atteintes varient considérablement d'une rivière et d'un estuaire à l'autre, influencées par l'utilisation des terres, les régimes de précipitations, l'humidité du sol et l'hydrologie du bassin versant (Vercruysse *et al.*, 2017). L'afflux massif de nutriments et de carbone organique dissous dans les eaux côtières de surface après une inondation peut engendrer une prolifération rapide de phytoplancton (Voynova *et al.*, 2016). Cette prolifération entraîne une sursaturation en oxygène dissous ainsi qu'une augmentation du pH, dépassant les niveaux habituels dans les mois qui suivent l'inondation (Voynova *et al.*, 2016). De la même façon, l'ouverture de barrages hydro-électriques peut provoquer dans les cours d'eau une augmentation de la concentration de matière en suspension et une diminution importante du pH et de l'oxygène dissous (Doretto *et al.*, 2019).

Comme la salinité, le pH dans les estuaires se modifie le long d'un gradient, passant d'un pH neutre ou légèrement acide dans les rivières à un pH légèrement basique dans l'eau salée. Contrairement aux eaux marines, les eaux douces des rivières sont sursaturées en CO_2 par rapport à l'atmosphère (Cai *et al.*, 2021; Meybeck, 1993; Salisbury *et al.*, 2008; Wallace *et al.*, 2014; Dinauer et Mucci, 2017). Cela est dû notamment à une forte activité respiratoire des organismes hétérotrophes soutenue par des apports en carbone organique terrestre ou fluvial d'origine naturelle ou anthropique provenant de leur bassin versant (Salisbury *et al.*, 2008; Wallace *et al.*, 2014). Lors des inondations printanières, une diminution du pH des eaux de surface peut se produire naturellement dans les cours d'eau boréaux en raison du rinçage des acides organiques et de la dissolution des cations basiques (Alexander *et al.*, 2017). Ce processus peut être exacerbé par des précipitations acides ou des dépôts acides préexistants, entraînant des épisodes acides plus graves qui durent de quelques jours à

quelques semaines (Marty *et al.*, 2021). L'exploitation forestière à blanc dans le bassin versant peut également contribuer à l'acidification des cours d'eau en causant une perte nette de cations basiques (Akselsson *et al.*, 2007).

Les processus liés à l'acidification côtière (*coastal acidification*) observés durant les inondations printanières diffèrent de ceux impliqués dans l'acidification océanique (*ocean acidification*) causée par l'augmentation du CO_2 dans l'atmosphère (**Figure 7**). L'acidification côtière implique non seulement une diminution du pH, mais aussi une réduction de l'alcalinité totale (TA) et de la saturation en aragonite (Ω_{arag}) et en calcite ($\Omega_{calcite}$). L'alcalinité totale, qui correspond à l'excès d'accepteurs de protons par rapport aux donneurs, joue un rôle crucial dans la chimie de l'eau en stabilisant le pH et en influençant la précipitation et la dissolution du carbonate de calcium ($CaCO_3$). Le carbone inorganique dissous (CID), qui inclut l'ensemble du CO_2 dissous, de l'acide carbonique (H_2CO_3), du bicarbonate (HCO_3^-) et du carbonate (CO_3^{2-}), est un paramètre clé dans cette dynamique. Dans les estuaires, les eaux douces des rivières ont habituellement une alcalinité inférieure à celle des eaux marines (Howland *et al.*, 2000; Lansard *et al.*, 2012). Ces eaux fluviales, souvent plus acidifiées, ont un rapport CID/TA plus élevé que celui de l'eau de mer, ce qui peut réduire la capacité tampon des estuaires (Cai *et al.*, 2021; Huang *et al.*, 2015; Salisbury *et al.*, 2008). Par ailleurs, l'apport massif d'eau douce pendant les inondations, notamment en milieu subarctique lors de la fonte des neiges, peut diluer l'alcalinité des eaux estuariennes, entraînant une baisse de Ω_{arag} et $\Omega_{calcite}$ en réduisant les concentrations en calcium (Ca^{2+}) et en carbonate (CO_3^{2-}) (Salisbury *et al.*, 2008).

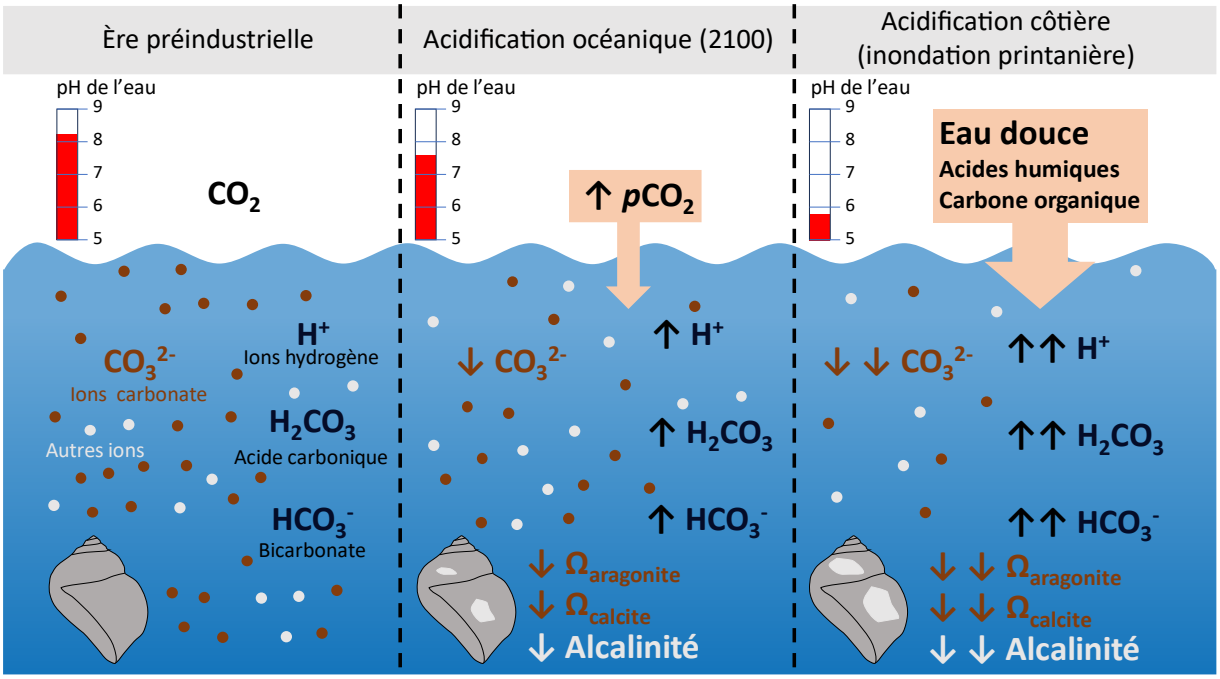


Figure 7. Représentation des changements dans les paramètres physico-chimiques de l'eau dans le cadre de l'acidification océanique ou côtière.

3. PROBLEMATIQUE

Bien que les communautés estuariennes soient particulièrement exposées aux changements climatiques liés à l'intensification du cycle hydrologiques (c.-à-d. intensification et multiplication des phénomènes extrêmes de fortes pluies), nos connaissances sur leurs vulnérabilités faces à des inondations fréquentes et intenses sont limitées, en particulier dans le climat subarctique pourtant particulièrement concerné. Ma thèse vise donc à approfondir nos connaissances sur la vulnérabilité des communautés benthique des estuaires subarctiques face aux changements climatiques liés à l'intensification du cycle hydrologique, en alliant des études sur le terrain et en laboratoire. Dans un premier temps, nous allons décrire ces communautés le long de gradients naturels de salinité en milieu subarctique, en utilisant des mesures et indices taxonomiques et fonctionnels. Ensuite, nous utiliserons un gradient de stress hypoosmotique imitant des inondations intenses et répétées

pour identifier les seuils de vulnérabilité d'un assemblage d'espèces clefs au sein de ces communautés. Enfin, nous évaluerons la vulnérabilité de ces mêmes espèces aux conditions d'inondations printanières en milieu subarctique, en combinant un gradient d'exposition au stress hypoosmotique à l'ajout de stresseurs multiples (c.-à-d. eau douce acide et turbide).

3.1 Décrire les communautés benthiques en utilisant des indices taxonomiques et fonctionnels

Une grande diversité est observée chez les invertébrés dans les écosystèmes marins en raison du nombre important d'espèces provenant de phyla différents (May, 1988; Ray et Grassle, 1991), contrairement aux milieux terrestres et d'eau douce où le nombre de phyla est plus limité (Gerino *et al.*, 2003). Cela amène une coexistence de nombreux modes de vie, créant des stratégies de survie variées pouvant être réparties à travers différents groupes fonctionnels par l'utilisation de traits (Gerino *et al.*, 2003). Les *traits* sont des caractéristiques morphologiques, physiologiques et biologiques qui décrivent une propriété bien définie d'un organisme (p. ex. taille, diète) (Bremner *et al.*, 2003, 2006a, 2006b; McGill *et al.*, 2006). Les traits peuvent être mesurés au niveau individuel et être utilisés comparativement entre toutes les espèces (McGill *et al.*, 2006). Ils reflètent les adaptations morphologiques et comportementales, les exigences physiologiques, et l'histoire de vie d'un organisme (Vieira *et al.*, 2006). Les *traits fonctionnels* permettent de décrire la contribution des espèces aux services et aux processus écosystémiques, ainsi que leur tolérance aux stress et aux perturbations environnementales (De Bello *et al.*, 2010). Comme les traits ne sont pas limités par la taxonomie, ils sont applicables à plusieurs échelles spatiales (locale, régionale, continentale) (Vieira *et al.*, 2006) et permettent d'avoir une vision plus globale et synthétique que les assemblages d'espèces (Fukami *et al.*, 2005; McGill *et al.*, 2006). L'étude des communautés à travers les traits fonctionnels est de plus en plus utilisée car elle permet d'évaluer à la fois les potentielles causes et les conséquences fonctionnelles des changements dans la biodiversité (Suding *et al.*, 2008). Les traits peuvent ainsi être utilisés pour détecter des changements dans l'état de l'écosystème (Engelhardt, 2006) et dans les tendances de répartition (Gaspar *et al.*, 2017). Ils permettent aussi d'évaluer les changements de diversité

fonctionnelle dans les scénarios de changements globaux (Strain *et al.*, 2014) ou les pertes au niveau des services écosystémiques (Díaz *et al.*, 2013).

3.1.1 Choix des traits fonctionnels

Chaque trait fonctionnel peut être décrit en plusieurs *modalités*, soit des catégories nominale ou ordinale, qui vont permettre de classifier les espèces. Par exemple, le type trophique (trait fonctionnel) peut être divisé en plusieurs modalités : photoautotrophe, brouteur, prédateur et filtreur. De même, la taille maximale (trait fonctionnel) peut être divisée en plusieurs modalités représentant des gammes de taille (petit, moyen, grand). Les *groupes fonctionnels* regroupent les espèces partageant la même combinaison de plusieurs modalités de traits fonctionnels (Hooper *et al.*, 2005). Dans les études utilisant une approche par traits fonctionnels, chaque trait sélectionné doit avoir au moins deux modalités différentes représentées chez plusieurs espèces afin de placer les espèces dans l'espace fonctionnel (voir plus bas) (de Bello *et al.*, 2021b). Les traits choisis ne doivent pas être corrélés entre eux; il n'est par exemple pas approprié d'utiliser simultanément la longueur maximale et la masse individuelle maximale, car ces traits peuvent refléter des variations similaires dans les caractéristiques des espèces (de Bello *et al.*, 2021b).

Dans notre étude, six traits fonctionnels (c.-à-d. la mobilité des adultes, la durée de vie, la taille potentielle maximale, le type trophique, le potentiel de dispersion des larves et les saisons de ponte) chacun contenant entre deux et cinq modalités, pour un total de 19 modalités, ont été sélectionnés pour décrire la communauté (**Figure 8**). Ces traits ont été choisis car ils peuvent être utilisés pour étudier les différences dans les stratégies de vie (p.ex. durée de vie, potentiel de dispersion des larves) ou pour exprimer la contribution d'une espèce aux fonctions de l'écosystème (p. ex. type trophique) (Bremner *et al.*, 2006; Wahl, 2009). Puisque nous les considérons dans la même étude, les traits sélectionnés devaient également permettre de décrire les macroalgues et les macroinvertébrés.

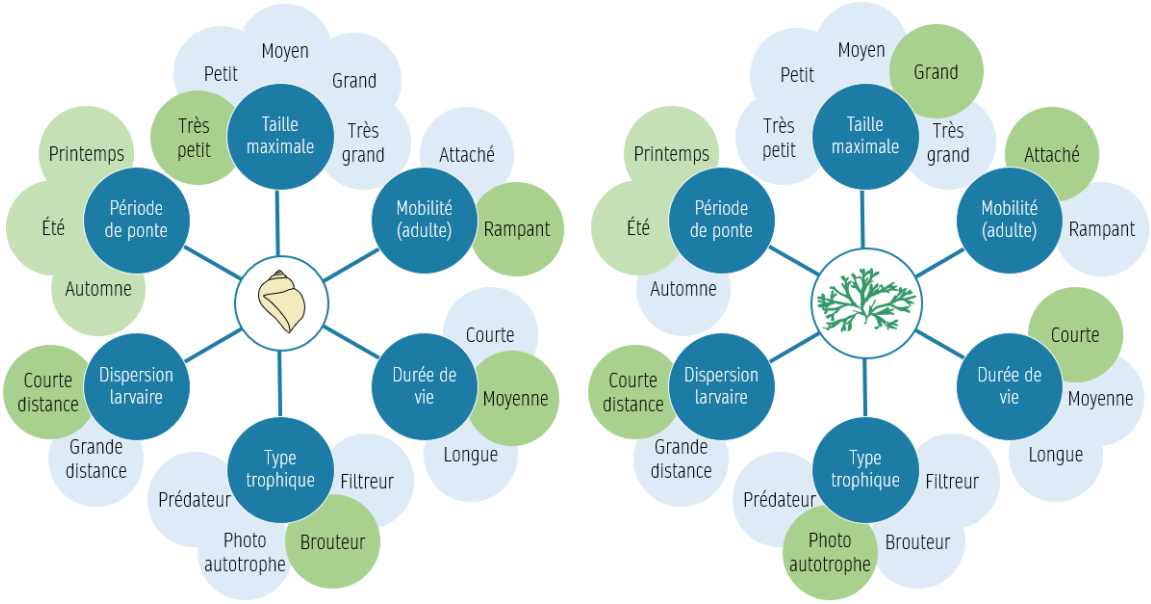


Figure 8. Représentation des traits fonctionnels (bleu foncé) et de leur modalité (bleu pâle). En vert sont représentés les modalités qui ont un score > 0 pour *Littorina saxatilis* à gauche et *Fucus distichus* subsp. *evanescens* à droite.

L'approche par « *fuzzy coding* » (Chevenet *et al.*, 1994), qui permettra de calculer les indices fonctionnels décrit plus bas, requière la création d'une matrice « Espèce X Trait » qui décrit l'affinité de chaque espèce avec les modalités des traits fonctionnels. Pour chaque trait, chaque espèce reçoit un score total de 1 qui peut être réparti entre les modalités, avec « 1 » montrant une affinité élevée et « 0 » une absence d'affinité. Pour chaque espèce, il faut donc recueillir les scores de chaque trait dans la littérature scientifique. Avec la popularité croissante des études fonctionnelles, les bases de données en ligne dédiées aux traits fonctionnelles se multiplient et facilite largement la recherche intégrative; pour les espèces marines, une des plus complètes est la base de données BIOTIC (MarLIN, 2006). À partir de cette matrice, il est alors possible de standardiser la dissimilarité entre les espèces en utilisant la *distance de Gower*, qui accorde la même importance à chaque trait, quel que soit le nombre de modalités, et qui est la technique la plus fréquemment utilisée pour les analyses fonctionnelles (de Bello *et al.*, 2021b; Laliberté et Legendre, 2010). Cette matrice de distance permet de créer un espace fonctionnel, dans lequel les espèces les plus similaires sont proches, et les espèces les plus différentes sont plus éloignées (**Figure 9**).

3.1.2 Indices fonctionnels et taxonomiques et leurs significations écologiques

Cet espace fonctionnel, qui regroupe toutes les espèces retrouvées dans l'ensemble de l'étude, va permettre de calculer les indices fonctionnels utilisés pour décrire les communautés (**Figure 9**). Ainsi, la *richesse fonctionnelle* (FRic) est calculée à partir du volume (ou *convex hull*) multidimensionnel de l'espace fonctionnel. Cet indice ne prend pas en compte l'abondance des espèces, mais plus le nombre de taxons différents est élevé, plus le volume (et donc FRic) est élevé. La perte d'une espèce « unique », située en périphérie de l'espace fonctionnel, entraîne une diminution plus importante de la richesse fonctionnelle qu'une espèce ayant des traits similaires à une autre espèce proche (**Figure 9**). Du point de vue taxonomique, la richesse (*S*) compte simplement le nombre d'espèce, sans prendre en compte leurs spécificités. Ainsi, proportionnellement, la perte d'une espèce « unique » peut influencer davantage FRic que *S*.

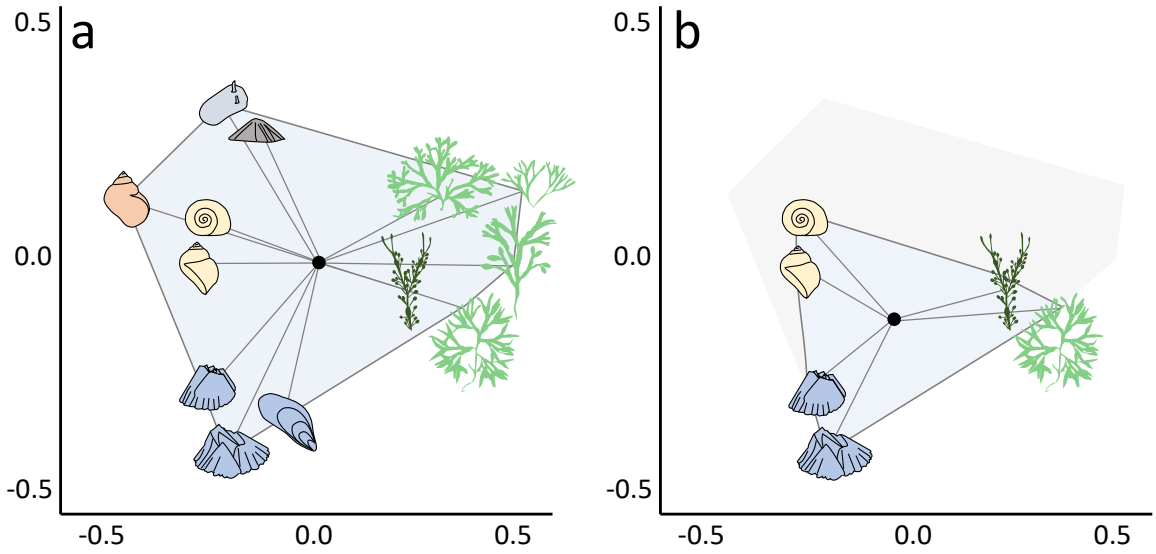


Figure 9. Visualisation des concepts d'espace fonctionnel, de richesse fonctionnelle (surface bleu clair) et de RaoQ (moyenne des distances entre les individus, simplifié ici par la distance au centroïde). La communauté (a) aura des valeurs de richesse fonctionnelle et taxonomique, RaoQ et Simpson plus élevées que la communauté (b).

Le second indice que nous avons utilisé est l'*Entropie Quadratique de Rao* (ou *Rao Quadratic Entropy*, nommée *RaoQ* par la suite) exprime la distance moyenne entre deux individus de la communauté dans l'espace fonctionnel (de Bello *et al.*, 2021). Cet indice permet d'évaluer la dissimilarité moyenne de la communauté, et tient compte de la richesse fonctionnelle et de la réparation de l'abondance. C'est une forme généralisée de l'*indice de Simpson* (*D*) (Botta-Dukát, 2005; Lepš *et al.*, 2006), son équivalent taxonomique, qui exprime la probabilité que deux individus tirés au hasard dans une communauté infiniment grande appartiennent à la même espèce.

Enfin, la *redondance fonctionnelle* est un concept plus récent mais de plus en plus populaire dans la littérature scientifique (Biggs *et al.*, 2020). Cet indice vise à refléter la stabilité de la structure fonctionnelle d'une communauté face à la perte d'espèces, et donc à évaluer sa résistance ou sa résilience (Biggs *et al.*, 2020). Un nombre élevé d'espèces remplissant les mêmes fonctions permettrait une meilleure résilience des communautés, car la perte d'espèces n'entrainerait pas une perte immédiate de fonction (**Figure 10**). Plusieurs façons de calculer cet indice ont été proposées, dont celle de Ricotta *et al.* (2016) (c.-à-d. FRed = 1 - (RaoQ/Simpson) et de De Bello *et al.* (2007) (c.-à-d. FRed = Simpson – RaoQ). La redondance fonctionnelle peut aussi être évaluée par le nombre moyen d'espèces à l'intérieur d'un groupe fonctionnel (Biggs *et al.*, 2020).

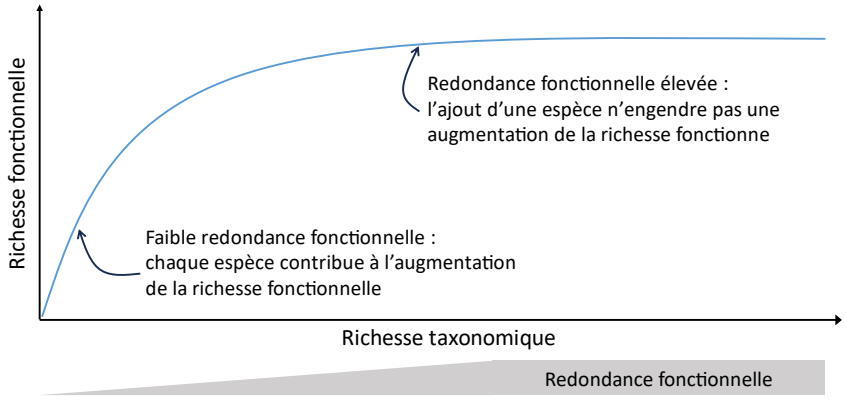


Figure 10. Représentation théorique du lien entre la diversité fonctionnelle et spécifique (adapté de Strong *et al.*, 2015).

3.1.3 Utilisation des moyennes pondérées par la communauté

Les moyennes pondérées par la communauté (CWM, *community weighted mean*) peuvent être utilisées pour décrire plus en détail la structure fonctionnelle des communautés. Elles sont calculées en utilisant à la fois l'abondance des espèces (c.-à-d. biomasse par espèce) et la matrice « Espèce X Trait » et représentent pour chaque trait les valeurs moyennes des caractères dans une communauté pondérées par l'abondance de l'espèce (de Bello *et al.*, 2021). Dans notre étude, les traits fonctionnels étant catégoriques, la CWM reflète la proportion de chaque modalité au sein de la communauté. Par exemple, si une communauté est constituée de trois espèces de filtreurs avec une biomasse totale de 0,8 kg, deux espèces prédatrices (0,1 kg au total) et cinq espèces de brouteurs (0,1 kg), la CWM pour les filtreurs sera de 80 %, de 10 % pour les prédateurs et 10 % pour les brouteurs. Ainsi, alors que les indices fonctionnels décrivent les changements globaux de la communauté, l'étude des CWM permet d'identifier les traits responsables de ces changements.

3.2 À la recherche des seuils : utilisation d'un gradient de niveau de stress en milieu contrôlé

En termes statistiques, la définition habituelle d'un *seuil* (en anglais : *threshold* ou *tipping-point*) est basée sur un *point de rupture* (en anglais : *break-point*), soit un changement de pente, de sorte qu'une régression est continue et linéaire par morceaux (Toms et Villard, 2015). Dans le cadre biologique, lors de l'intensification d'un ou plusieurs stresseurs, il est théoriquement possible de distinguer des réponses linéaires ou par seuil dans la physiologie et la vulnérabilité des espèces, ou encore dans l'état général d'un écosystème (Hiddink *et al.*, 2023; Suding et Hobbs, 2009; Toms et Villard, 2015). Les modèles linaires suggèrent qu'une variation des conditions environnementales entraîne un ajustement proportionnel au niveau des individus, des populations et éventuellement des communautés (**Figure 11a**) (Suding et Hobbs, 2009). À l'inverse, les modèles de seuils indiquent que des changements environnementaux ont peu d'effet jusqu'à ce qu'un seuil soit franchi, provoquant alors un changement abrupt. Dans le cas des modèles de seuils sans hystérésis (**Figure 11b**), la

réponse est identique quelle que soit la direction du changement, et un changement soudain pourrait être réversible, permettant une récupération rapide (Hare et Mantua, 2000; Suding et Hobbs, 2009). En revanche, les modèles de seuils avec hystérésis (**Figure 11c**), plusieurs états stables existent pour une même condition, rendant le chemin vers un système restauré complexe (Liu *et al.*, 2024; Petraitis et Dudgeon, 2004; Suding et Hobbs, 2009).

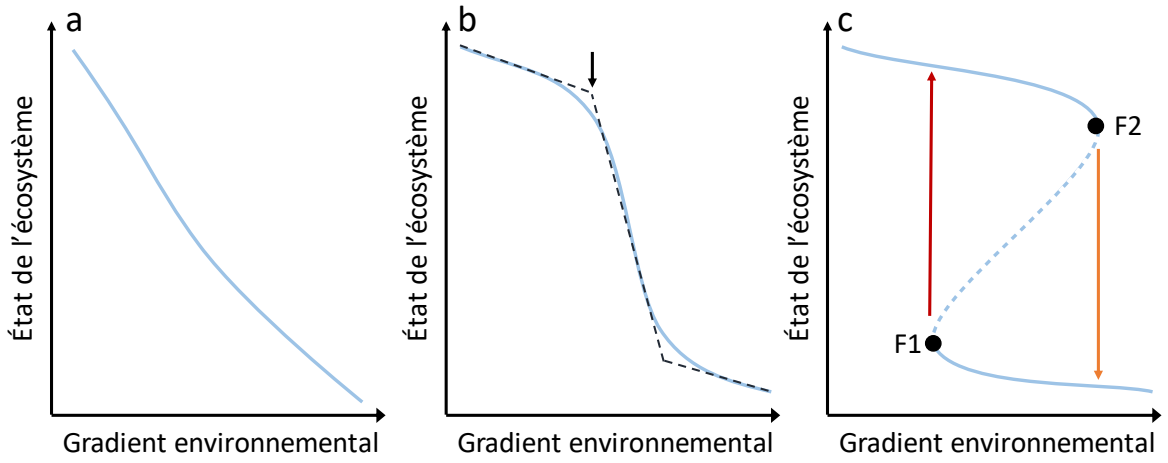


Figure 11. Modèles de dynamique des écosystèmes, avec (a) un changement linéaire, (b) un modèle à seuil sans hystérésis et (c) un modèle à seuil avec hystérésis. Pour le modèle (b), la ligne pointillée noire représente le modèle par morceau avec point de rupture, le seuil à partir duquel l'état de l'écosystème se dégrade fortement étant indiqué par la flèche noire. Pour le modèle (c), si le système se trouve sur la branche supérieure, près du point de bifurcation F2, un léger changement de conditions peut le faire basculer vers l'état stable inférieur alternatif (flèche orange); pour restaurer l'état initial sur la branche supérieure en inversant les conditions, un retour en arrière n'est possible que si les conditions atteignent l'autre point de bifurcation, F1 (flèche rouge) (traduit et adapté de Suding et Hobbs, 2009).

En amenant ce concept dans un milieu contrôlé en laboratoire, l'utilisation d'un gradient de stresseur peut permettre de produire des recommandations de gestion en identifiant des seuils dans les réponses des espèces (Carrier-Belleau *et al.*, 2022a). De plus, lorsqu'on utilise un gradient de niveaux de stress pour étudier la tolérance des espèces, l'ajout de plusieurs stresseurs le long du gradient peut augmenter la sensibilité des espèces et révéler de nouveaux seuils, ou avancer les seuils existants vers des niveaux de stress plus faibles (Carrier-Belleau *et al.*, 2023; Carrier-Belleau *et al.*, 2022b).

3.3 Analyse expérimentale des impacts des inondations sur les communautés benthiques : sélection de trois stresseurs clés et description des réponses attendues

Les inondations dans les estuaires causent des changements abrupts dans de nombreux paramètres environnementaux, en particulier la salinité, le pH, la turbidité et l'oxygène dissous (voir partie 2.3). Dans notre projet, nous avons d'abord ciblé l'effet d'une exposition répétée à l'eau douce, variant de quelques heures à plusieurs jours sur plusieurs semaines, puisque le stress hypoosmotique est inhérent aux inondations. Ensuite, pour mieux représenter les conditions des inondations printanières, nous avons ajouté deux stresseurs supplémentaires au stress hypoosmotique, soit une diminution du pH et une augmentation de la turbidité. Bien que ces facteurs aient déjà été étudiés individuellement, leur impact combiné en conditions contrôlées n'a pas encore été exploré, alors qu'ils se produisent simultanément lors des inondations.

3.3.1 Diminution de la salinité

Les mollusques marins montrent une faible capacité d'osmorégulation lors d'un stress hypoosmotique (Medeiros *et al.*, 2020). Pour éviter le gonflement excessif des cellules par une absorption trop importante d'eau, la régulation de l'osmolalité intracellulaire se fait par la libération ou le catabolisme de certains ions inorganiques et osmolites organiques (Podbielski *et al.*, 2022). Chez la moule bleue (*Mytilus edulis*), Barrett *et al.* (2022) ont observé la régulation à la hausse des gènes supposés impliqués dans le transport actif membranaire (c.-à-d. pompes ATPase, canaux membranaires pour les ions potassium et chlorure, échangeurs d'ions) ainsi que des gènes des transporteurs d'osmolites organiques. Similairement chez *L. saxatilis* et *L. obtusata*, Muraeva *et al.* (2017) ont identifié l'implication d'enzymes liées au métabolisme énergétique et à la réponse antioxydante, des chaperons, des protéines de la matrice extracellulaire et du cytosquelette, des canaux ioniques et des régulateurs de la croissance et de la prolifération cellulaires lors de l'acclimatation à un stress hypoosmotique.

Lorsque la salinité s'approche de zéro, les mollusques utilisent principalement une défense comportementale : les gastéropodes et les bivalves s'enferment dans leur coquille afin de limiter l'échange de sel et d'eau entre leur fluide interne et le milieu externe (Sokolova *et al.*, 2000a; Woodin *et al.*, 2020). Lorsque le stress perdure, l'isolement de l'environnement extérieur devient nocif, car les organismes perdent l'accès à l'oxygène externe, doivent recourir à un métabolisme anaérobie et ne peuvent pas excréter leurs déchets (Shick *et al.*, 1988). Cela peut entraîner l'hypercapnie (c.-à-d. l'accumulation de CO_2 dans les tissus), l'acidose (c.-à-d. augmentation l'acidité du plasma et des liquides interstitiels), l'accumulation de déchets toxiques (p. ex. lactate et succinate) et enfin la mort (Shick *et al.*, 1988; Sokolova *et al.*, 2000b, 2000c). Les réponses des communautés face à un stress hypoosmotique intense lié aux inondations pourraient donc différer de celles causées par les variations de salinité journalières rencontrées habituellement dans les estuaires. Des conditions d'hyposalinité extrêmes et prolongées ont ainsi entraîné la mortalité massive de nombreux bivalves marins, par exemple chez des huitres suite à des inondations naturelles (Pollack *et al.*, 2011) ou causées par l'ouverture d'un déversoir (Gledhill *et al.*, 2020).

3.3.2 Diminution du pH

Les réponses des invertébrés à une réduction modérée du pH sont globalement négatives (p. ex. diminution de la survie, de la calcification, de la croissance, du développement et de l'abondance) mais l'ampleur de ces réponses peut varier selon les groupes taxonomiques (Kroeker *et al.*, 2013). Comme pour le stress hypoosmotique, les réponses des organismes à ce stress dépendraient également de leur capacité d'osmorégulation (Melzner *et al.*, 2009; Whiteley, 2011). Lors d'une diminution abrupte du pH, les bivalves et les gastéropodes vont avoir la même stratégie que lors d'un stress hypoosmotique en s'enfermant dans leur coquille (Proum *et al.*, 2017). L'acidification, qu'elle soit côtière ou océanique, aurait tout de même un impact plus direct sur les espèces formant des squelettes et des coquilles de carbonate de calcium (Benoît *et al.*, 2012; Kroeker *et al.*, 2010) comme les mollusques bivalves (Beniash *et al.*, 2010; Stevens et Gobler, 2018), les crustacés (Whiteley, 2011) et les gastéropodes (Leung *et al.*, 2017). En particulier,

l'acidification côtière intense (pH < 7) rencontrée dans certains estuaires peut entraîner des lésions tissulaires et une réduction des taux de survie (Dove et Sammut, 2007a; Proum *et al.*, 2017), ainsi que la dissolution des coquilles due à la dissolution du carbonate de calcium (Marshall *et al.*, 2008).

La dissolution des coquilles est directement liée aux saturations en aragonite et en calcite calculées par l'équation suivante :

$$(1)\ \Omega_{\text{aragonite ou calcite}} = \frac{[Ca^{2+}][CO_3^{2-}]}{K'_{sp}}$$

Dans laquelle $[Ca^{2+}]$ et $[CO_3^{2-}]$ sont des concentrations d'ions calcium et carbonate, respectivement, et K'_{sp} est la constante de produit de solubilité de l'aragonite ou de la calcite. Bien que la dissolution des coquilles devrait théoriquement commencer lorsque $\Omega_{aragonite} < 1$, de la dissolution des coquilles de *Limacina helicina* a été observée à des valeurs de $\Omega_{aragonite}$ supérieures à 1,4 (Bednaršek and Ohman, 2015). Les coquilles formées d'aragonite et de calcite à haute teneur en magnésium (*high-Mg calcite*), plus solubles, sont plus affectées par l'acidification côtière et la diminution de la saturation en aragonite/calcite que celles formées de calcite à faible teneur en magnésium (*low-Mg calcite*). Les mollusques qui en dépendent pour leur coquille peuvent rencontrer un plus grand défi pour maintenir l'intégrité de la coquille (Findlay *et al.*, 2009; Morse *et al.*, 2007; Ries *et al.*, 2009).

3.3.3 Augmentation de la turbidité

L'augmentation de la turbidité (et par la suite de la sédimentation) a souvent un impact négatif sur les communautés d'invertébrés (Thrush *et al.*, 2003) et d'algues (Rubin *et al.*, 2017). La baisse de la luminosité causée par une forte quantité de sédiments en suspension va entrainer une diminution de la croissance, de la diversité et de l'abondance des communautés de macroalgues (Bach *et al.*, 1998; Magris et Ban, 2019). Une augmentation de la sédimentation peut également affecter la composition de ces communautés sur plusieurs années, en favorisant les espèces dont la période de reproduction est la plus étendue (Eriksson

et Johansson, 2005). Chez les invertébrés, la sédimentation va causer une plus forte mortalité chez les espèces sessiles, qui ne pourront pas éviter l'enfouissement, plutôt que chez les espèces mobiles, qui seront capables de remonter à la surface des sédiments (Hinchey *et al.*, 2006). En revanche, une espèce sessile capable de survivre en anaérobie lors de l'enfouissement sera plus à même de survivre qu'une pour laquelle l'aérobie est obligatoire (Hinchey *et al.*, 2006). Une hausse de la turbidité peut cependant être bénéfique pour les organismes filtreurs si elle est accompagnée d'une plus grande disponibilité de matière organique en suspension (Hawkins *et al.*, 1996; Rubin *et al.*, 2017). Enfin, un apport élevé de matière organique lié à la hausse de la turbidité peut favoriser la prolifération bactérienne, ce qui entraîne une diminution des niveaux d'oxygène dissous (Goosen *et al.*, 1999; Lung et Nice, 2007).

3.3.4 Réponses à plusieurs facteurs de stress combinés

L'amélioration des connaissances sur les effets combinés entre de multiples facteurs de stress permet de mieux cibler les mesures de gestion pouvant renforcer la résilience des écosystèmes face à l'intensification des régimes de stress, en se concentrant sur celui qui aurait le plus d'impact sur les réponses écosystémiques (Côté *et al.*, 2016; Stockbridge *et al.*, 2020). Les études qui s'intéressent aux impacts de plusieurs facteurs de stress combinés représentent mieux la réalité des milieux naturels et permettent de former de meilleurs modèles pour développer des méthodes de conservation plus appropriées (Côté *et al.*, 2016), par exemple pour le système Saint-Laurent où se superposent de nombreux facteurs de stress tel que l'hypoxie, l'apport en nutriments et la pêche intensive (Beauchesne *et al.*, 2020). En effet, les écosystèmes sont souvent soumis à plusieurs stress simultanés (p. ex. variation de salinité, du pH et de turbidité), et il est parfois supposé que leurs effets sont additifs, c.-à-d. que les réponses aux facteurs combinés sont égales à la somme des réponses de chacun des facteurs (Piggott *et al.*, 2015; Côté *et al.*, 2016). Pourtant, en raison de la complexité du fonctionnement des écosystèmes et des organismes, les effets combinés de plusieurs facteurs entrainent souvent des réponses interactives non additives, qui se manifestent par une interaction significative entre les deux facteurs individuels dans une analyse de variance

(ANOVA) (Piggott *et al.,* 2015). Lorsque la réponse des facteurs cumulés est inférieure à la somme des réponses de chacun des facteurs, on parle d'effet antagoniste (Folt *et al.*, 1999). Cependant, de plus en plus de preuves montrent que différentes combinaisons de facteurs de stress sont interactives et peuvent avoir des impacts synergiques (c.-à-d. les réponses aux facteurs combinés sont supérieures à la somme des réponses de chacun des facteurs) et imprévisibles (surprises écologiques) sur les communautés (Cimon *et al.*, 2021; Cimon et Cusson, 2018; Joseph et Cusson, 2015) et les écosystèmes (Stockbridge *et al.*, 2020). Par exemple, une baisse de la salinité, une hausse de la turbidité, et la combinaison de ces deux facteurs ont des effets différents et synergétiques sur le réseau trophique d'un récif d'huîtres, en favorisant différents types de prédateurs selon les facteurs de stress (Reustle et Smee, 2020).

3.4 Sites d'intérêt : les petits estuaires subarctiques

Les changements climatiques liés à l'intensification du cycle hydrologique et au réchauffement se produisent plus rapidement dans les environnements des hautes latitudes que dans d'autres régions du monde (Constable *et al.*, 2023) mais les communautés estuariennes subarctiques sont rarement étudiées (McGovern *et al.*, 2020). Les petits estuaires offrent un cadre idéal pour étudier ces changements, car les petits bassins fluviaux sont plus sensibles aux changements environnementaux que les grands bassins fluviaux (Rokaya *et al.*, 2018). Leur taille plus réduite permet de mieux délimiter les gradients environnementaux sur des distances courtes, facilitant ainsi les analyses écologiques (Callaway *et al.*, 2014). De plus, leur faible volume d'eau fait en sorte que l'ensemble de l'estuaire peut être affecté par des évènements tels que les inondations, contrairement aux grands systèmes comme celui du Saint-Laurent, où l'impact est souvent localisé. Ces caractéristiques offrent l'avantage de permettre une plus grande réplication des études, comme c'est le cas avec les cinq estuaires sélectionnés dans le premier chapitre.

Par conséquent, la Côte-Nord du Québec constitue un emplacement privilégié pour mener cette étude puisqu'elle abrite de nombreux petits estuaires. De plus, cette région, l'une

des plus vastes et des moins peuplées du Québec, présente une faible densité de population humaine, ce qui limite les pressions anthropiques et les sources de pollution, réduisant ainsi les interférences externes sur les écosystèmes naturels (MRNF, 2007). La présence de barrages hydroélectriques dans la région en fait également un lieu stratégique pour évaluer l'impact potentiel des aménagements humains sur ces milieux sensibles. Notre étude s'est concentrée sur les municipalités régionales de comté de la Haute-Côte-Nord et de Manicouagan.

3.5 Sélection des espèces utilisées dans les expériences en laboratoire

Les trois espèces de mollusques utilisées dans les expériences en laboratoire ont été sélectionnées à la suite des inventaires des communautés benthiques effectués dans de petits estuaires subarctiques dans le cadre du premier chapitre. Ces espèces, qui sont toutes d'importance dans les estuaires subarctiques, présentent des patrons de répartition distincts le long du gradient de salinité. Leur utilisation permet ainsi d'examiner si ces schémas de répartition, spécifiques à chaque espèce, peuvent s'expliquer, au moins en partie, par des vulnérabilités différentes face aux inondations. De plus, chacune des espèces choisies occupe un rôle distinct dans l'écosystème estuarien, notamment en raison de leur mode d'alimentation (brouteur, filtreur de matière en suspension et déposée). L'utilisation de cet assemblage d'espèce nous permettra, grâce aux résultats de nos expériences, d'obtenir une vision plus globale de la vulnérabilité des communautés estuariennes face aux inondations.

La littorine des rochers *Littorina saxatilis* (Olivi, 1792) est un gastéropode de petite taille (jusqu'à 18 mm de hauteur et 14 mm de largeur) que l'on trouve généralement à la surface des substrats rocheux, dans les crevasses et au sein des macroalgues, de la zone supralittorale jusqu'à la frange infralittorale. Elle broute des micro et macroalgues benthiques. *Littorina saxatilis* est une espèce numériquement dominante dans la zone intertidale haute des estuaires (Dexter, 1947) et une espèce modèle pour l'étude de la colonisation et de l'adaptation locale (Johannesson, 2016). Dans nos inventaires, cette espèce se retrouvait en plus grande abondance proche des rivières (chapitre 1).

La macoma baltique *Macoma balthica* (Linnaeus, 1758) est un petit bivalve (longueur maximale de 18 à 20 mm pour les individus adultes) qui, contrairement aux deux autres espèces, vit à quelques centimètres sous la surface des sédiments sablonneux et vaseux entre les zones supérieures et inférieure du médiolittorale jusque dans l'infralittoral (Budd et Rayment, 2001). Cette espèce peut filtrer les particules en suspension dans l'eau sus-jacente en maintenant son siphon dans une position verticale fixe, ou étendre et déplacer activement son siphon sur les sédiments pour consommer les particules de nourriture déposées (Skilleter et Peterson, 1994). Les macomas constituent un lien important entre l'eau et les sédiments grâce à une intense activité de bioturbation (Michaud *et al.*, 2005, 2006). Lors de nos inventaires, nous avons pu observer que cette espèce se retrouvait tout le long des estuaires (chapitre 1).

La moule bleue *Mytilus* spp. (composée de *Mytilus edulis* Linnaeus, 1758, de *M. trossolus* A. Gould, 1850 et leurs hybrides, ci-après appelés *Mytilus* spp.; voir Moreau *et al.*, 2005) est un bivalve de grande taille (de 5 à 10 cm de longueur à maturité) que l'on trouve de la zone médiolittorale haute à la zone infralittorale peu profonde, où il est fixé à un substrat dur et s'attache à l'aide des fils fibreux de byssus qu'il produit. C'est un filtreur actif de particules en suspension, se nourrissant de phytoplancton, mais aussi de bactéries, de détritus et de matière organique dissoute. Les moules sont des espèces formant un habitat (Arribas *et al.*, 2014) et des filtreurs très efficaces qui améliorent la qualité de l'eau (Timmermann *et al.*, 2019) et sont élevées pour la consommation humaine (Petersen *et al.*, 2014a). Dans nos inventaires, la moule bleue se retrouvait principalement en milieu marin et dans la zone de l'estuaire maritime et était pratiquement absente de la tête de l'estuaire (chapitre 1).

4. OBJECTIFS SPÉCIFIQUES ET ORGANISATION DE LA THÈSE

Cette thèse a pour objectif principal d'approfondir nos connaissances sur la vulnérabilité des communautés benthiques des estuaires subarctiques face à la multiplication des inondations dans le contexte des changements globaux. Pour ce faire, la thèse comprend un chapitre portant sur la diversité et structure taxonomiques et fonctionnelles des communautés estuariennes le long de gradients de salinité naturels (chapitre 1) et deux chapitres portant sur des expériences réalisées en laboratoire. Le chapitre 2 se concentre sur l'exposition à un stress hypoosmotique, et le chapitre 3 porte sur une exposition à des conditions d'inondations printanières (c.-à-d. eau douce acide et turbide).

Pour le **chapitre 1**, notre étude visait à décrire la diversité et la structure taxonomique et fonctionnelle des communautés de macroalgues et de macroinvertébrés benthiques le long de gradients de salinité. Nous avons utilisé des indices taxonomiques et fonctionnels, ainsi que des mesures de traits observés (taille) sur les macroalgues et macroinvertébrés retrouvés dans plusieurs petits estuaires subarctiques du Québec (Canada), dans quatre niveaux d'apport en eau douce. Ces nouvelles connaissances nous ont permis de générer des prédictions sur les réponses fonctionnelles potentielles de ces communautés aux futures conditions de faible salinité avec l'augmentation de la fréquence et de l'intensité des pluies intenses et des inondations, pour la première fois dans un environnement subarctique. Les hypothèses pour ce chapitre sont :

Hypothèse 1.1 : les communautés épibenthiques plus proches de l'apport fluvial seront moins diversifiées et abondantes sur le plan taxonomique que celles trouvées dans des conditions entièrement marines.

Hypothèse 1.2 : la perte d'espèces induira une perte de diversité fonctionnelle due au filtrage environnemental.

Hypothèse 1.3 : les individus de macroinvertébrés et de macroalgues seront plus petits dans des salinités plus faibles.

Pour le **chapitre 2**, l'objectif était de déterminer la sensibilité relative de trois mollusques benthiques marins subarctiques d'importance retrouvés dans les estuaires à l'exposition à l'eau douce. En laboratoire, nous les avons exposés à un gradient de 15 durées de pulses d'eau douce durant de 0 à 9 j, suivi de 1 j en eau salée, pendant cinq semaines. Nous avons mesuré la survie, la masse et les taux de croissance individuels, ainsi que le contenu énergétique (ce dernier seulement chez *Mytilus* spp.), en tant qu'indicateurs de la performance physiologique, et évalué à la fois l'effet de la durée du pulse de stress hypoosmotique sur ces paramètres et la présence de seuils de sensibilité le long du gradient (Suding et Hobbs, 2009). Les hypothèses pour ce chapitre sont :

Hypothèse 2.1 : les effets négatifs de l'exposition à des conditions hypoosmotiques entraîneront une diminution de la survie, de la croissance et de la masse individuels et du contenu énergétique (pour les moules uniquement) avec l'augmentation de la durée des pulses d'eau douce.

Hypothèse 2.2 : ces effets négatifs s'intensifieront avec le temps, en particulier pour les traitements avec des pulses d'eau douce prolongés.

Hypothèse 2.3 : des seuils spécifiques à l'espèce et aux traits (correspondant à la durée des pulses d'eau douce) seront observés.

Hypothèse 2.4 : sur la base de la littérature, nous nous attendons à ce que la tolérance au stress hypoosmotique augmente, pour tous les traits, dans l'ordre : *L. saxatilis* < *Mytilus* spp. < *M. balthica.*

Pour le **chapitre 3**, le but était de déterminer la sensibilité du même assemblage de macroinvertébrés intertidaux aux conditions d'inondation printanière (c.-à-d. exposition à une eau douce acide et turbide) le long d'un gradient de stress hypoosmotique. Nous avons utilisé les mêmes espèces que dans l'expérience précédente. Le design expérimental était similaire, avec un gradient de 12 durées de stress hypoosmotique (exposition à de l'eau douce allant de 0 à 9 j suivi de 1 j en eau salée) en conditions d'inondations printanières (pH 5.7, turbidité 325 mg L^{-1}) ou sans conditions d'inondations printanières (pH 8.1, turbidité 0 mg L^{-1}). Nous avons mesuré la survie, les taux de croissance et l'usure des coquilles individuels en tant

qu'indicateurs de la performance physiologique, et évalué à la fois l'effet du stress hypoosmotique et des conditions d'inondations sur ces paramètres et la présence de seuils le long du gradient. Les hypothèses sont :

Hypothèse 3.1 : les pulses d'eau douce de plus longue durée réduiront la survie et la croissance.

Hypothèse 3.2 : les conditions d'inondations printanières réduiront la survie et l'intégrité des coquilles.

Hypothèse 3.3 : des seuils spécifiques à l'espèce et au trait (correspondant à la durée des pulses d'eau douce) seront observés.

Hypothèse 3.4 : les conditions d'inondations printanières amplifieront l'effet de l'exposition à l'eau douce en créant de nouveaux seuils ou en avançant des seuils existants à des durées de pulse d'eau douce plus courts, et/ou en augmentant l'impact négatif de l'exposition à l'eau douce à toutes les durées de pulses d'eau douce.

Hypothèse 3.5.a : sur la base de la littérature et de l'expérience précédente, nous prévoyons que la tolérance au stress hypoosmotique augmentera dans l'ordre : *L. saxatilis* < *M. balthica* < *Mytilus* spp.

Hypothèse 3.5.b : d'après la composition et la structure de la coquille, nous nous attendons également à ce que la tolérance aux conditions d'inondation (c.-à-d. les eaux acides) augmente dans l'ordre : *M. balthica* (aragonite) < *L. saxatilis* (aragonite et calcite à faible teneur en Mg) < *Mytilus* spp. (aragonite, calcite à faible teneur en Mg et *periostracum*).

Hypothèse 3.5.c : dans les traitements combinés d'une longue exposition en eau douce et de conditions d'inondation, nous nous attendons donc à ce que *L. saxatilis* soit l'espèce la plus vulnérable, et que *M. balthica* et *Mytilus* spp. soient plus tolérants.

CHAPITRE 1
L'APPORT D'EAU DOUCE REDUIT LA DIVERSITE SPECIFIQUE ET FONCTIONNELLE DES PETITS ESTUAIRES SUBARCTIQUES

1.1 RESUME EN FRANÇAIS DU PREMIER ARTICLE

Les estuaires font face à des pressions anthropiques croissantes. Il est attendu que les changements climatiques augmentent les fortes précipitations, tandis que les activités agricoles et forestières réduisent la perméabilité des terres, ce qui entraîne des inondations plus fréquentes qui réduisent la salinité des estuaires. Ces conditions hyposalines posent des défis physiologiques aux espèces marines, réduisant potentiellement la diversité taxonomique et la biomasse et, en fin de compte, les fonctions et les services écosystémiques des estuaires. Les estuaires polaires et subpolaires, historiquement peu étudiés, subiront des changements importants dans le moment et la variabilité des débits d'eau douce en raison de la modification prévue du régime neigeux en régime de pluie dans ces hautes latitudes. L'étude de la structure des communautés biotiques à travers les traits fonctionnels est cruciale pour comprendre les changements de biodiversité, évaluer la tolérance des écosystèmes et lutter contre la perte de fonction dans des conditions stressantes. Par conséquent, notre étude vise à caractériser la diversité taxonomique et fonctionnelle des communautés benthiques à substrat dur le long d'un gradient de salinité dans les petits estuaires subarctiques. Nous émettons l'hypothèse que les communautés plus proches de l'apport fluvial seront moins diversifiées et abondantes sur le plan taxonomique et avec des individus plus petits, ce qui entraînera une perte de fonctions due au filtrage environnemental. Pour tester nos hypothèses, nous avons mesuré les indices traditionnels (biomasse, richesse taxonomique et diversité) et fonctionnels (richesse fonctionnelle et entropie quadratique de Rao), ainsi que les traits observés, des macroalgues et des macroinvertébrés épibenthiques de substrat dur le long d'un gradient de salinité à quatre niveaux trouvé dans cinq petits estuaires subarctiques au Québec

(Canada). Comme attendu, les apports d'eau douce ont induit une diminution de la biomasse, de la richesse taxonomique, de la richesse fonctionnelle et de l'entropie quadratique de Rao, avec une réduction de la biomasse totale de la communauté épibenthique par un facteur de cinq des zones marines aux zones à faible salinité. Les apports d'eau douce ont considérablement façonné les structures taxonomiques et fonctionnelles des communautés, car la proportion de filtreurs et d'espèces dont les propagules peuvent être transportés sur de grandes distances a diminué avec l'augmentation des apports d'eau douce. Bien qu'il n'y ait pas de tendance claire pour la structure par classe de taille des taxons d'invertébrés, les macroalgues étaient plus petites à de faibles salinités. Les communautés estuariennes des régions subarctiques pourraient donc être vulnérables aux modifications futures des régimes d'inondation causées par les changements planétaires, ce qui pourrait affecter des services écosystémiques clés tels que la filtration des matières en suspension. Les indices de traits fonctionnels se sont avérés efficaces et constituent un complément précieux aux mesures taxonomiques pour détecter les changements de communauté le long des gradients de salinité, soulignant leur utilité dans l'élaboration de stratégies de conservation et de gestion efficaces.

Cet article, intitulé « *Freshwater input significantly reduces specific and functional diversity of small subarctic estuaries* », a été publié en octobre 2024 dans la revue *Estuarine, Coastal and Shelf Science*. Tous les auteurs ont participé à la conceptualisation du projet et de sa méthodologie et à la révision et à l'édition de l'article. En tant que première auteure, j'ai pris en charge la collecte et l'analyse des données, ainsi que la rédaction de l'ébauche originale. Dr. Yanick Gendreau, Prof. Piero Calosi et Prof. Mathieu Cusson ont contribué à la supervision du projet, à la gestion des ressources, à l'administration du projet et à l'acquisition de financement. Une version abrégée de l'article a été présentée à la Réunion Scientifique Annuelle de Québec-Océan à Rivière-du-Loup (CA) en hiver 2023 et hiver 2024 sous forme d'affiche. Les résultats ont aussi été présenté à la Conférence Annuelle de la *Society for Experimental Biology* à Prague (République Tchèque) en été 2024 sous forme de présentation orale et d'affiche.

Loiseau, V., Gendreau, Y., Calosi, P. et Cusson, M. (2024). Freshwater input significantly reduces specific and functional diversity of small subarctic estuaries. *Estuarine, Coastal and Shelf Science*, *305*, 108856. https://doi.org/10.1016/j.ecss.2024.108856

1.2 FRESHWATER INPUT SIGNIFICANTLY REDUCES SPECIFIC AND FUNCTIONAL DIVERSITY OF SMALL SUBARCTIC ESTUARIES

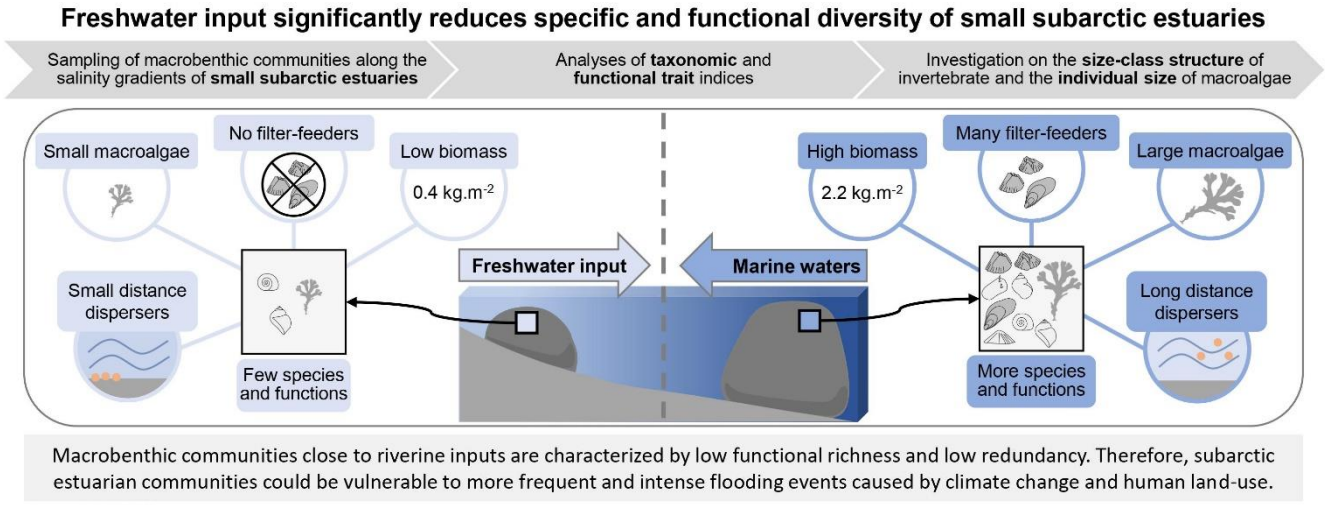
1.2.1 Abstract

Estuaries face mounting anthropic pressures. Climate change is projected to increase heavy precipitations, while agricultural and logging activities reduce land permeability, leading to more frequent flooding events that lower estuarine salinity. These hyposaline conditions pose physiological challenges for marine species, potentially reducing taxonomic diversity and biomass, and ultimately, ecosystem functions and services. Polar and subpolar estuaries, historically understudied, will undergo significant changes in freshwater discharge timing and variability due to predicted shifts from snow to rainfall regimes in these high latitudes. The investigation of biotic communities' structure through functional traits is crucial for understanding biodiversity changes, evaluating ecosystem tolerance, and addressing the loss of function under stressful conditions. Therefore, our study aims to characterize the taxonomic and functional diversity of hard-substrate benthic communities along a salinity gradient in small subarctic estuaries. We hypothesize that communities closer to the riverine input will be less taxonomically diverse and abundant and with smaller individuals, leading to a loss of functions due to environmental filtering. To test our hypotheses, we measured traditional (biomass, taxonomic richness and diversity) and functional (functional richness and Rao's quadratic entropy) indices, as well as observed traits, of epibenthic hard-substrate macroalgae and macroinvertebrates along a four-level salinity gradient found in five small subarctic estuaries in Quebec (Canada). As predicted, freshwater inputs induced a decrease in biomass, taxonomic richness, functional richness, and Rao's quadratic entropy, with a fivefold reduction in total biomass of the epibenthic community from marine to low salinity zones. Freshwater inputs significantly shaped both taxonomic and functional trait structures, as the proportion of suspension feeders and long-distance dispersers decreased with rising freshwater inputs. While there was no clear trend for the size-class structure of invertebrate taxa, macroalgae were smaller at low salinities. Estuarine communities in subarctic regions may be vulnerable to future alterations in

flooding patterns caused by global change, potentially affecting key ecosystem services such as suspended matter filtration. Functional trait indices were found to be efficient and serve as a valuable complement to taxonomic measures in detecting community shifts along salinity gradients, highlighting their usefulness in developing effective conservation and management strategies.

Keywords: Macrobenthos, rocky-shore, riverine inputs, biological trait analyses, hyposaline, ecological gradient

1.2.2 Visual abstract



1.2.3 Highlights

- Freshwater input affects hard-substrate subarctic estuarian community structure.
- Freshwater input decreases biomass and taxonomic and functional richness.
- Filter-feeders and long-distance dispersers are almost absent at low salinities.
- Low functional redundancy at low salinities suggest vulnerability to disturbances.
- Function-based indices are more sensitive to low salinities than taxonomic ones.

1.2.4 Introduction

Estuaries are highly anthropized ecosystems (Kennish *et al.*, 2014; Robb, 2014) that provide numerous services to humans: *e.g.*, fishing, harvesting shellfish, maritime traffic and leisure (Kainamu-Murchie *et al.*, 2018). They also support many ecological functions at a large scale, as they deliver nutrients to the marine environment (Bauer *et al.*, 2013) that are redistributed to upper trophic levels (Kemp and Boynton, 1984; Savage *et al.*, 2012). The filtration of suspended matter by estuarine filter feeder species provides an important function by improving water quality, reducing turbidity and ultimately allowing light to penetrate, enabling photosynthesis in autotrophs (Dame, 2012). These ecosystem services might be reduced due to the increasing vulnerability of estuaries to human pollution, habitat loss, invasive species and other global change drivers (Kennish, 2002; Williams and Grosholz, 2008; Cooley *et al.*, 2022). Since estuaries are dynamic ecosystems that naturally differ considerably in terms of geomorphology and tidal range (Robins *et al.*, 2016), conducting *in situ* monitoring and research is necessary to better assess their responses to environmental changes (Biguino *et al.*, 2023).

An expected consequence of climate change and anthropisation of estuary systems is the increase of high intensity precipitations and flooding events (Clavet-Gaumont *et al.*, 2017; Tabari, 2020). The projected shift from snow to rainfall regimes in the winter at high latitudes could change the timing and variability of freshwater discharges (Boyer *et al.*, 2010; IPCC, 2023a), with important implications for the phenology of ecosystems (Staudinger *et al.*, 2019). These changes are occurring much faster in high latitudes environments than in other world regions (Constable *et al.*, 2023), yet subarctic estuarian communities are rarely studied (McGovern *et al.*, 2020). In addition, the continuous increase in land use for agricultural and logging purposes is making a greater proportion of Earth surface less permeable to rain, ultimately promoting flooding (Mao and Cherkauer, 2009; Bathurst *et al.*, 2020). Consequently, heavy rainfalls and runoffs can significantly reduce locally the salinity levels in estuaries (Weise *et al.*, 2002). Small estuaries (< 50 km^2 *sensu* Callaway *et al.*, 2014) in particular can be valuable for detecting potential changes in processes and disturbances that

affect the entire ecosystem, as larger estuaries may only experience disturbances in specific areas (Callaway *et al.*, 2014). Changes in hydrology regimes can significantly impact estuary communities and functions, since salinity is considered the primary biogeographic determinant in estuaries (Kinne, 1971; Lu *et al.*, 2008) and can lead to a decrease in the number of species present from marine to riverine waters (Whitfield *et al.*, 2012). Indeed, an increasing freshwater input is known to cause decreases in both overall invertebrate and macroalgae biomass and richness (Montague and Ley, 1993; Middelboe *et al.*, 1998; McGovern *et al.*, 2020). Additionally, brown macroalgae and sessile invertebrates size were reported to be smaller in low salinity compared to marine conditions (Gunter, 1961), likely due to reduced photosynthetic activity or increasing costs in osmoregulation, respectively (Kirst, 1990; Podbielski *et al.*, 2022a).

While traditional taxonomic-based indices (*i.e.*, richness, taxonomic diversity and abundance) can describe temporal or spatial changes in community composition and structure, they provide less information regarding the relationship between biodiversity and ecosystem functioning (Verberk *et al.*, 2013) and can be less efficient to evaluate ecosystem services, tolerance and resilience (Cimon and Cusson, 2018; de Bello *et al.*, 2010b). Community analyses through the investigation of functional traits (here defined as an organism's phenotype that determines its potential to affect an ecosystem function) allows us to better evaluate the potential causes and functional consequences of changes in biodiversity (Lam-Gordillo *et al.*, 2020). Ecosystems tolerance and resilience from disturbance can be evaluated based on species richness within a functional group and by the spatio-temporal occupancy of that group (Stachowicz *et al.*, 2007; Gladstone-Gallagher *et al.*, 2019). In stressful environments in particular, the loss of species often induces a loss of function (van der Linden *et al.*, 2016). Indeed, studies focusing on tropical estuaries have shown that salinity can shape the functional diversity of soft-sediment communities (Morais *et al.*, 2019; Medeiros *et al.*, 2021; Lam-Gordillo *et al.*, 2022), but hard-substrate communities have been largely neglected (Lam-Gordillo *et al.*, 2020). Nonetheless, these important habitats can sustain large biomass of macroinvertebrates and macroalgae and greatly influence the

composition of adjacent soft-substrate communities (Ricciardi and Bourget, 1999; Wetzel *et al.*, 2014).

Field research that integrates salinity gradients in estuaries is necessary, not only to better describe and understand community functioning, but also to monitor them within the context of potential changes in salinity regimes. Therefore, our study aims to describe the taxonomic and functional diversity and structure of the macroalgae and macroinvertebrate fraction of hard-substate benthic communities of small estuaries. We aim to use theoretical and observed traits of macroalgae and macroinvertebrates along the salinity gradient found in five small subarctic estuaries in Quebec (Canada). In these habitats, we hypothesize that (a) hard-substrate epibenthic communities closer to the riverine input would be less taxonomically diverse and abundant that communities found in fully marine conditions, (b) the loss of species would induce a loss of functional diversity due to environmental filtering, and (c) both invertebrates and macroalgae individuals will be smaller in lower salinities. These novel insights will allow us to generate predictions, notably for the first time in a subarctic environment, about the potential functional responses of marine hard-substrate communities to future low salinity conditions with the ongoing increase in floodings and flash-foods frequency and intensity.

1.2.5 Material and Methods

1.2.5.1 Study area and selection of estuaries

We tested our hypotheses in small estuaries found along the northern shore of the St. Lawrence marine estuary (SLME) (Quebec, Canada). This region is an ideal study area as it has a limited anthropisation level, and there are at least 40 rivers ending in marine conditions. The estuaries used in this study (see coordinates in **Table A.1**) were selected ensuring they met the following conditions: (i) presence of hard substrate, (ii) riverbed width between 15 and 50 m, and (iii) easy access. Among those that met such conditions, we haphazardly selected five estuaries: St. Nicolas (northernmost), Franquelin, Mistassini, Barthelemy and Cap-Colombier (southernmost) (see **Figure 12**; **Table A.1**). The first three support boulder substrates, while the two lasts are characterised by bedrocks. These small estuaries end into the SLME, which surface waters have a mean annual salinity around 28 (annual range 20.9 – 29.1), and a weekly mean temperature ranging from -1 °C in February to 12 °C in July (Galbraith *et al.*, 2022). The semidiurnal tide in the study area ranges between 3 and 3.5 m (Government of Canada, 2023).

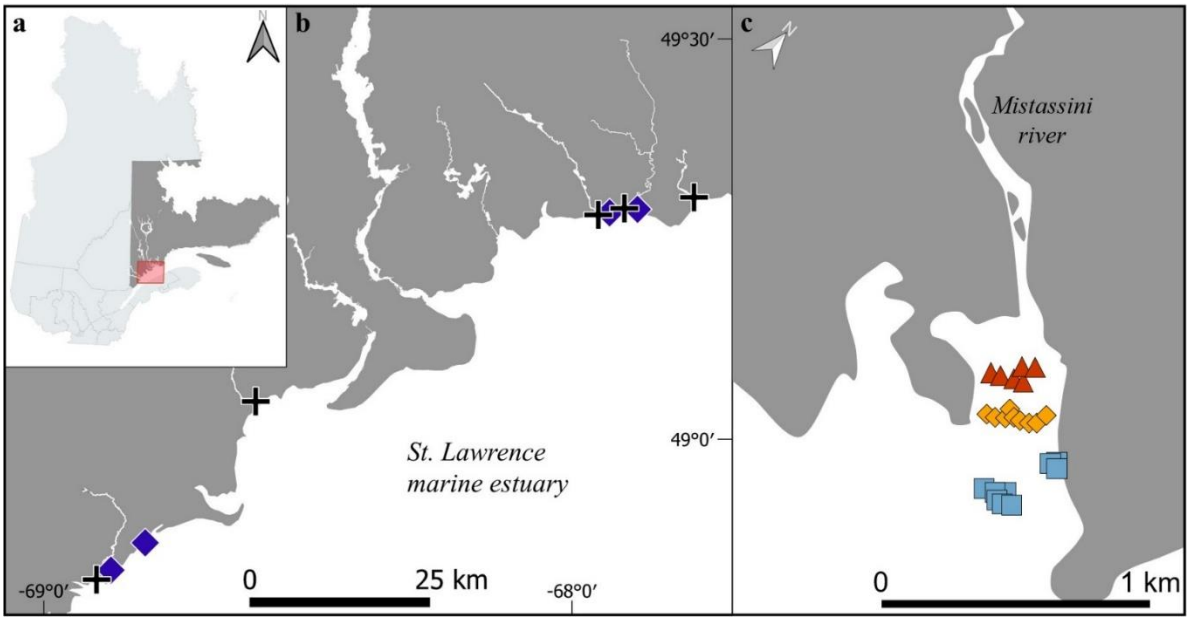


Figure 12. Maps showing (a) Quebec, Canada, with the study area locations in the red rectangle; (b) the location of estuaries (black crosses, from left to right: Cap-Colombier, Barthelemy, Mistassini, Franquelin and St. Nicolas) and marine sites (blue lozenges) sampled; (c) quadrats' repartition in Mistassini estuary (red triangles: high FI – freshwater input, orange lozenges: medium FI, blue square: low FI), as an example of the system used. See Figure A.1 for the detailed quadrats repartition in all studied estuaries.

1.2.5.2 Experimental design

In order to measure the impact of freshwater input (FI) on estuarian communities, we defined three FI zones in each estuary under study ("high", "medium" and "low" FI, see **Figure 12** and **Table A.2**) that formed a stress gradient for the marine species communities inhabiting the intertidal zone. To do so, we measured the salinity from the fully freshwater river zone upstream along a transect all the way down to the SLME on the shore every 50 to 200 m at mid-tide with a CTD (CastAway®-CTD, Sontek, San Diego, CA, USA) in September 2019. The zone with the highest FI was defined as the "high" FI zone, with salinity between 1 and 10. The "medium" FI zone had salinity between 11 and 19 while the "low" FI zone, located at the edge of the SLME, had the smallest freshwater intake with salinity between 20 and 27 (**Figure 12**; **Table A.2**). In addition to these three zones, a marine zone

with four sites was defined as the "null" FI zone with measured salinity constantly above 27 (usual salinity values for this section of the SLME) (**Figure 12**). These marine sites were located within the SLME, outside the plume of influence of freshwater from any estuary. Due to limited access to the shore in the region for sites meeting these criteria, the same marine site was used for both Franquelin and Mistassini, as it was located at an equal distance from both estuaries.

From September 28th to October 3rd, 2019, we sampled 5 to 9 quadrats (25 x 25 cm, average n = 8) of the macrobenthic (> 1 mm) community in each FI zone within each estuary and marine site. Each quadrat position on hard substrate was chosen randomly (> 5 m distance among quadrats) and were required to have > 5% of macroalgae canopy species cover. All quadrats were sampled within the same tidal elevation (*i.e.*, approximately between 1.5 and 2 m above the sea level), to reduce the effects of stresses linked to the vertical gradient (Scrosati and Heaven, 2007; Stephenson and Stephenson, 1949). In some zones/sites, the number of quadrats number was lower (n = 5 to 6) due to lack of hard substrate with abovementioned suitable criteria.

1.2.5.3 Sampling protocol and specimen identification

All macrobenthic organisms (*i.e.*, macroalgae and macroinvertebrates) were collected and brought to the laboratory where each individual was identified to the lowest taxonomic level possible, usually species, using local guides and taxonomic keys. They were then counted and weighed by taxon (± 0.01 g, analytical balance PG2002-S, Mettler Toledo, Columbus, OH, USA).

1.2.5.4 Approaches used for the functional trait analyses

A total of six functional traits (*i.e.*, adult mobility, lifespan, maximum potential size, trophic type, larval dispersal potential, and spawning seasons), each containing between two and five modalities for a total of 19 modalities, were selected to describe the community (**Table 1**). These traits were used to investigate difference in life strategies (*e.g.*, lifespan,

larval dispersal potential) or to express a species contribution to functions of the ecosystem (*e.g.*, trophic type) (Bremner *et al.*, 2006; Wahl, 2009). They can also describe both algae and invertebrates and had at least two modalities represented in several species in this study. Using the "fuzzy coding" approach (Chevenet *et al.*, 1994), we created a 'Species x Trait score' matrix that describes the affinity of a species to trait modalities: for each trait, each species was given a total score of 1 that could be distributed between the modalities, with "1" showing a high affinity and "0" an absence of affinity to a given category (**Table A.5**). The trait scores were collected for each species from multiple published sources: *e.g.*, a number of published papers and online databases such as BIOTIC (MarLIN, 2006). The Community Weighted Mean (CWM) was then calculated using the species relative abundance and the 'Species x Trait score' matrix. Since our traits are categorical, the CWM represents the proportion of each modality in the community. As we counted both very large (*e.g.*, macroalgae) and very small (*e.g.*, macroinvertebrates) individuals, we used a log transformed biomass data to reduce the effect of dominant taxa with large biomass values and to be able to detect changes in the distribution of modalities assumed by smaller species.

Table 1. Description of the six functional traits used to categorise each species in this study, and their 19 modalities.

Traits	Modalities
Adult mobility	Attached
	Crawler
Lifespan	Short (< 5 y)
	Medium (5-10 y)
	Long (> 10 y)
Maximum potential size	Very small (< 2.5 cm)
	Small (2.5 - 5 cm)
	Medium (5 - 10 cm)
	Large (10 - 100 cm)
	Very large (> 100 cm)
Trophic type	Suspension feeder
	Grazer
	Predator
	Photoautotroph
Larval dispersal potential	Limited
	Long distance
Spawning season	Spring
	Summer
	Fall

1.2.5.5 Response variables considered

Using biomass data, three variables were estimated in each quadrat: total biomass, taxonomic richness and diversity. The diversity was estimated using Simpson's index (D_1), which expresses the probability that any two individuals drawn at random from an infinitely large community belong to the same species. Furthermore, two functional diversity indices were chosen to describe the community: functional richness (FRic) and Rao's quadratic entropy (RaoQ). The functional richness (FRic) represents the volume of the functional space occupied by the community independently from the species abundance and was standardized by the maximal FRic to be constrained between 0 and 1 (Villéger *et al.*, 2008). Rao's quadratic entropy (RaoQ) expresses the mean distance between two selected individuals, taking into account the functional richness and abundance, and is a generalized form of Simpson's index (Botta-Dukát, 2005; Lepš *et al.*, 2006).

In addition to potential traits used in the functional analyses (*e.g.*, maximum adult size), we measured realized traits (*i.e.*, traits measured directly on individuals) in term of size class structure (*i.e.*, size class proportion of biomass) for numerical dominant invertebrates and morphological parameters (*i.e.*, individual weight, maximum length, and thallus area) for macroalgae. Individual size has been proposed as an alternative to taxonomic-based approaches for assessing changes in transitional water communities (Mouillot *et al.*, 2006), as it has been shown to vary along environmental gradient (Donadi *et al.*, 2015). Hence, for each quadrat, we weighted the invertebrates *per* taxa *per* size class: each taxon was divided into three to four size-classes based on the maximum adult size of its species (**Table A.3**). When the biomass was < 1g, we used the mean number of individuals *per* size class, the mean length *per* size class and regressions based on length calculated in previous studies to estimate the biomass (

Table A.4). For the algae morphological measurements, we randomly took five individuals to be measured (maximum length) and weighed individually. Three of these five were randomly selected for thallus area measurement. This was done by capturing an image

of the flat part of the algae on a graduated white sheet and then estimating the surface area automatically using ImageJ (version 1.52q) computer software.

1.2.5.6 Statistical analyses

In order to investigate the effect of salinity gradients on community taxonomic and functional diversity, we used a two-factor permutational analyses of variance (Anderson *et al.*, 2008; Clarke and Gorley, 2015) with the factors *Freshwater Input* (hereafter 'FI', four levels, fixed) and the *Sites* ('Site', five levels, random) on biomass, two taxonomical diversity indices (*i.e.*, richness and diversity), two functional diversity indices (*i.e.*, FRic and RaoQ) and three macroalgal morphological variables (*i.e.*, individual weight, maximum length and thallus area). For the analyses of the macroalgae morphological parameters, we included the *Identity of Quadrat* as additional random factor (nested in 'FI x Site') to the abovementioned design. The biomass, individual weight and thallus area data were log transformed prior to the analyses to limit the effect of outliers.

We compared the taxonomic (biomass data) and functional structure (CWM data) of the communities using the same design with a permutational multivariate analyses of variance (PERMANOVA, Anderson *et al.*, 2008) applied on a Bray-Curtis similarity matrix (biomass) and Gower distance matrix (CWM) (permutation of residuals under a reduced model, sums of squares type III and 9999 permutations). The Bray-Curtis similarity is the most commonly used coefficient for biological community analysis, as it is sensitive to differences in abundance between species and gives more weight to abundant species than to rare species (Clarke and Gorley, 2006; Ricotta and Podani, 2017). The Gower similarity is more appropriate for functional analyses as it allows the use of fuzzy coded traits and variable weights – *i.e.*, traits can be given the same weight regardless of the number of modalities (Laliberté and Legendre, 2010; de Bello *et al.*, 2021a). The same PERMANOVA design was used on size class structure data of dominant invertebrate taxa, applied on Euclidean similarity matrix. Prior to the multivariate analysis, biomass data were dispersion-weighted by species (at the 'FI x Site' level; Clarke *et al.*, 2014) and log-transformed according to the shade plot method (K. R. Clarke *et al.*, 2013).

When significant differences were found, either in univariate or multivariate realms, pairwise post-hoc permutational *t*-tests (9999 runs) were used to identify differences among FI zones. For morphological variables, numbers of quadrats did not have data, thus along with the abovementioned designs, we proceeded to planned pairwise contrasts across FI zones. We performed percentage similarity analyzes (SIMPER) to determine which species were responsible for taxonomic structure differences (Anderson *et al.*, 2008; Clarke *et al.*, 2014). For the functional structure, a SIMPER analysis could not be performed – since it cannot be weighted by number of modalities *per* trait; instead, for each modality of functional traits, a two-factor PER-ANOVA was performed on a Euclidian similarity matrix to detect changes among FI zones (9999 runs). Subsequently, to visualize the data patterns, we used Principal Coordinate Analysis (PCO) ordinations (Clarke *et al.*, 2014).

We used a significance level of $\alpha = 0.05$ for all statistical analyses. The "vegan" package (Oksanen, 2017) was used to calculate the traditional indices and the "FD" package (Laliberté *et al.*, 2014) for the functional indices, in RStudio (version 4.2). The data analyses were performed on Primer-PERMANOVA (version 6.1.12).

1.2.6 Results

1.2.6.1 Effect of freshwater input on community diversity variables

Eight macro invertebrate taxa and five macroalgae taxa were observed in our samples (**Table A.6**). Two macroinvertebrate phyla were represented, with a majority of Molluska taxa (65 %; *Mytilus* spp. represented 60 % of all invertebrate biomass) followed by Arthropoda (35 %). The macroalgae were dominated by *Ascophyllum nodosum* (49 %), followed by *Fucus vesiculosus* (33 %) and *Fucus distichus subsp. edentatus* (12 %). *Mytilus* spp. could not be identified to the species level due to the co-occurrence of *M. edulis* and *M. trossulus* in the St. Lawrence estuary. All macroalgae were identified to the species or subspecies level. Biomass, taxonomic richness, FRic and RaoQ decreased with increasing freshwater input (**Table 2**; **Figure 13**; pairwise results in **Table A.7**). For these four indices, the salinity stress explained between 21 and 41 % of the total variance observed. The total biomass was reduced to 20 % compared to the more marine sections of the estuaries (mean ± SE: 544.14 ± 62.98 g) to the lowest salinity zones (107.31 ± 19.78 g), while the richness decreased from 5.4 ± 0.5 to 3.5 ± 0.4 species (**Figure 13a**, **b**). FRic and RaoQ decreased from 0.56 ± 0.03 and 0.14 ± 0.01 in the marine zones to 0.26 ± 0.04 and 0.08 ± 0.01 in the highest osmotic stress level (**Figure 13d, e**). The taxonomic diversity was similar along the salinity gradient (**Table 2c**; **Figure 13c**). For all the response variables, except the taxonomic diversity, the effect of the freshwater input varied between estuaries, as indicated by the presence of a significant interaction between the terms ‘FI’ and ‘Sites’, which explained between 12 and 21 % of the variance (**Table 2**). However, the freshwater input caused biological responses that were similar among sites.

Table 2. Summary of the results of the PER-ANOVA tests showing the effects of the freshwater input ('FI', fixed factor), site ('Site', random factor) and their interaction on the (a) biomass, (b) taxonomic richness, (c) taxonomic diversity; (d) functional richness (FRic) and (e) Rao's quadratic entropy (RaoQ) of intertidal benthic communities. Significant values are in bold. V % stands for estimate of variance components.

Source	df	Pseudo-F	p-value	V
(a) Biomass (log)				
FI	3	14.33	**0.0001**	41
Site	4	2.86	**0.0289**	4
FI x Site	12	2.59	**0.0052**	12
Residuals	130			49
Total	149			
(b) Richness				
FI	3	6.55	**0.0073**	21
Site	4	15.21	**0.0001**	21
FI x Site	12	3.13	**0.0006**	13
Residuals	130			45
Total	149			
(c) Diversity				
FI	3	0.55	0.6456	1
Site	4	1.73	0.1513	5
FI x Site	12	1.09	0.3836	9
Residuals	130			85
Total	149			
(d) Functional richness				
FI	3	11.04	**0.0015**	32
Site	4	5.62	**0.0003**	10
FI x Site	12	2.30	**0.0123**	12
Residuals	112			50
Total	131			
(e) Rao's quadratic entropy				
FI	3	4.62	**0.0273**	16
Site	4	6.35	**0.0001**	11
FI x Site	12	2.81	**0.0021**	14
Residuals	130			55
Total	149			

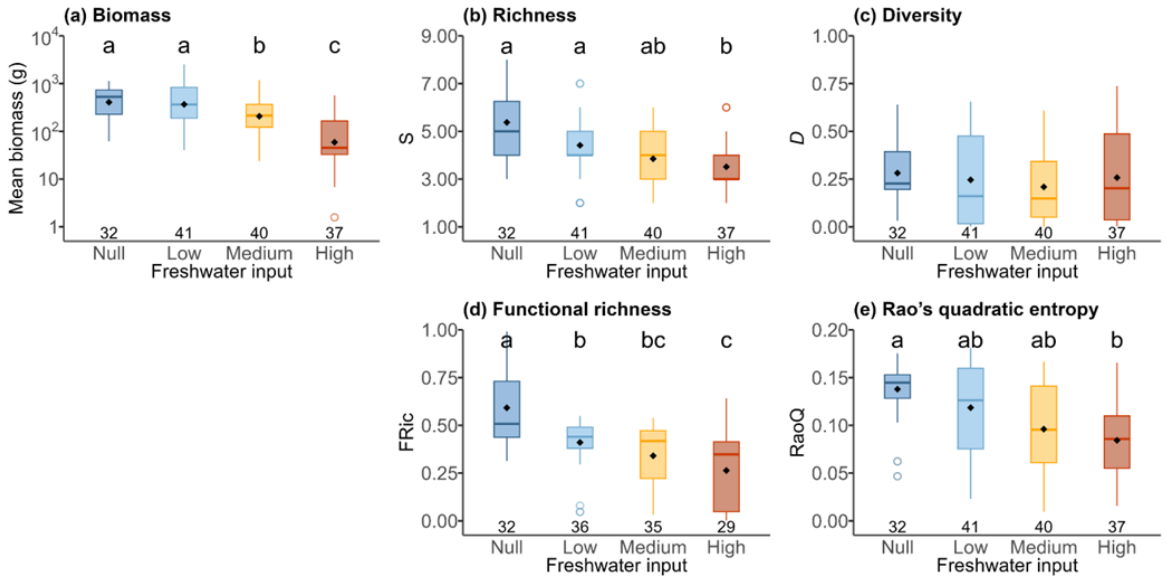


Figure 13. Effect of the freshwater input on intertidal benthic communities (a) biomass (presented with a logarithmic scale), (b) taxonomic richness, (c) taxonomic diversity, (d) functional richness (FRic), and (e) Rao's quadratic entropy (RaoQ). Boxplots show the 75th percentile, median, 25th percentile and the lowest and largest 1.5 times interquartile range. Mean indicated by black diamonds. Different letters indicate significant mean differences; n is indicated below each boxplot. Circles represent outliers.

1.2.6.2 Effect of freshwater input on the community structure

The taxonomic and functional traits structures were both significantly influenced by the freshwater input (

Table 3; **Figure 14**; **Table A.8**), although it explained a limited amount of the total variance: 11 and 13 %, respectively. Its effect varied among sites, with a significant interaction that explained 20 and 21 % of the variance (

Table 3). Most species (such as *L. obtusata*, *A. nodosum*, *F. vesiculosus* and *Mytilus* spp.) were more abundant in higher salinities, while *L. saxatilis* was the only species with higher biomass where the freshwater input was high (**Figure 14**; **Table A.9**). The proportion of suspension feeders (Pseudo-$F_{3,130}$ = 4.01; p = 0.038) and long-distance dispersers (Pseudo-

$F_{3,130}$ = 4.62; p = 0.026) decreased significantly with increasing freshwater input (**Figure 15**; **Table A.10**).

Table 3. Summary of the results for the PER-MANOVA tests showing the effects of the freshwater input ('FI', fixed factor), site ('Site', random factor) and their interaction on the community (a) taxonomic and (b) functional traits structure. Significant values are in bold. V% stands for estimate of variance components.

(a) Taxonomic structure

Source	df	Pseudo-F	p-value	V%
FI	3	2.19	**0.0215**	11
Site	4	4.97	**0.0001**	9
FI x Site	12	3.64	**0.0001**	20
Residuals	130			59
Total	149			

(b) Functional trait's structure

Source	df	Pseudo-F	p-value	V%
FI	3	2.38	**0.0397**	13
Site	4	8.44	**0.0001**	13
FI x Site	12	4.67	**0.0001**	21
Residuals	130			50
Total	149			

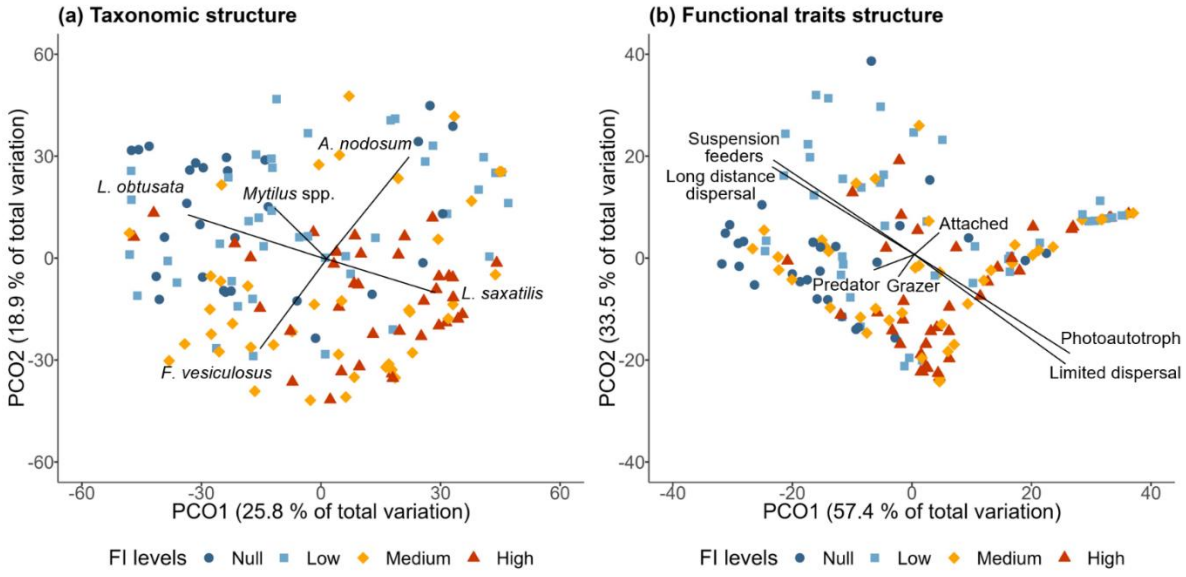


Figure 14. Principal Coordinate Analysis (PCO) plots of (a) taxonomic structure and (b) functional trait's structure. Vector length represents Pearson correlation with the biomass of important species or modality of functional traits identified from SIMPER analyses.

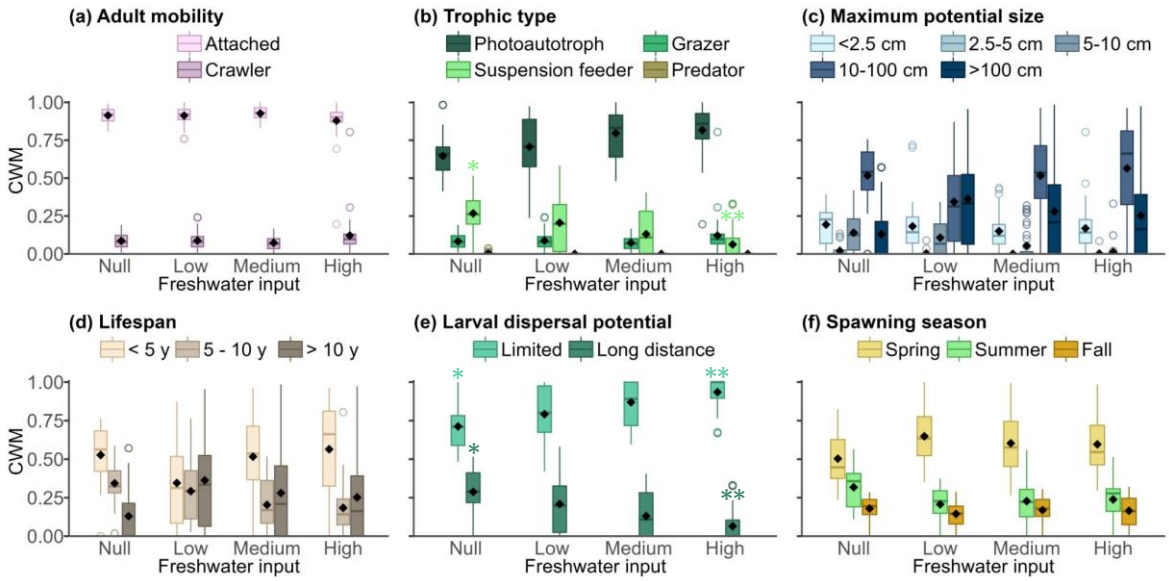


Figure 15. Effect of the freshwater input on the community-weighted mean (CWM) of each functional trait modality (n_{null} = 32, n_{low} = 41, n_{medium} = 40, n_{high} = 37). See **Figure 13** for box plot description. Mean indicated by black diamonds; n is indicated below each boxplot. Circles represent outliers. Asterisks indicate significant mean differences, between the high and null FI for suspension feeders, and both larval dispersal potential modalities.

1.2.6.3 Effect of freshwater input on observed realized traits

Mytilus spp. was the only invertebrate for which the freshwater input had a significant effect on size class structure ($F_{3,72}$ = 2.90, p = 0.025): only very small (< 1 cm) and large (> 3 cm) individuals were present close to the river, while small and medium size individuals (1-3 cm) represented 50 % of the marine mussels (**Table A.11**; **Figure 16**). *Littorina obtusata* size class structure was only marginally affected by freshwater input ($F_{3,74}$ = 2.59, p = 0.057), with bigger individuals found when the freshwater input was null or low (**Table A.11**; **Figure 16**). The full results for the other species are in **Table A.11**.

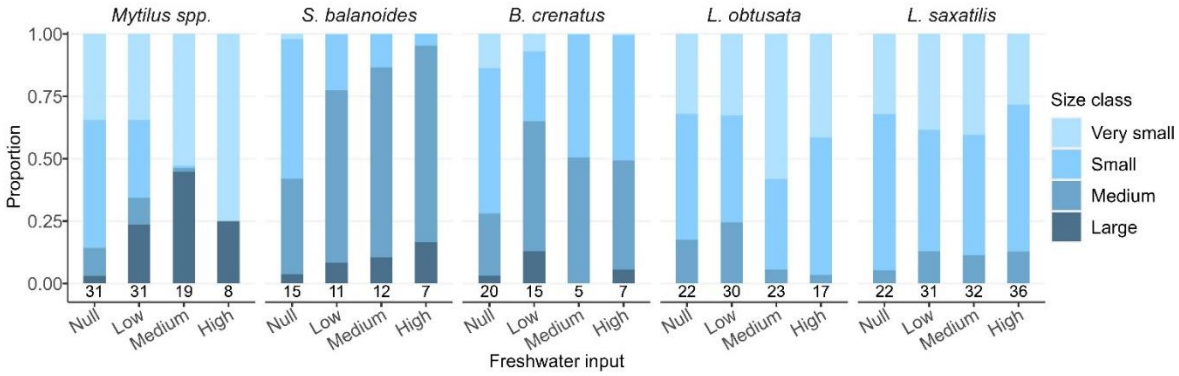


Figure 16. Effect of the freshwater input on the proportion size class structure of macroinvertebrates taxa investigated (*Mytilus* spp., *Semibalanus balanoides*, *Balanus crenatus*, *Littorina obtusata* and *L. saxatilis*). Bar plots show the proportion of biomass *per* size class *per* species. Sample numbers are indicated below each boxplot. Size classes for each taxon in **Table A.3**.

Fucus vesiculosus showed decreasing length (Pseudo-$F_{3,207}$ = 8.47; p = 0.001) and individual weight (Pseudo-$F_{3,207}$ = 3.31; p = 0.047) with increasing freshwater input, with bigger individuals in the Null FI zone than in the High FI zone (**Table A.12**, **Figure 17**; full pairwise results in **Table A.13**). While the main analysis of variance showed no effect of the freshwater input on *A. nodosum* morphological parameters (**Table A.12**), planned contrast indicated that *A. nodosum* length was also smaller in the higher stress level compared to the other three levels, and its weight was lower in the High than in the Null FI zone (**Table A.13**, **Figure 17**). The mean thallus area was unaffected by the freshwater input for both species. The effect of the freshwater input on the morphological measurements varied among sites, with an interaction that explained between 9 and 14 % of the variance (**Table A.12**).

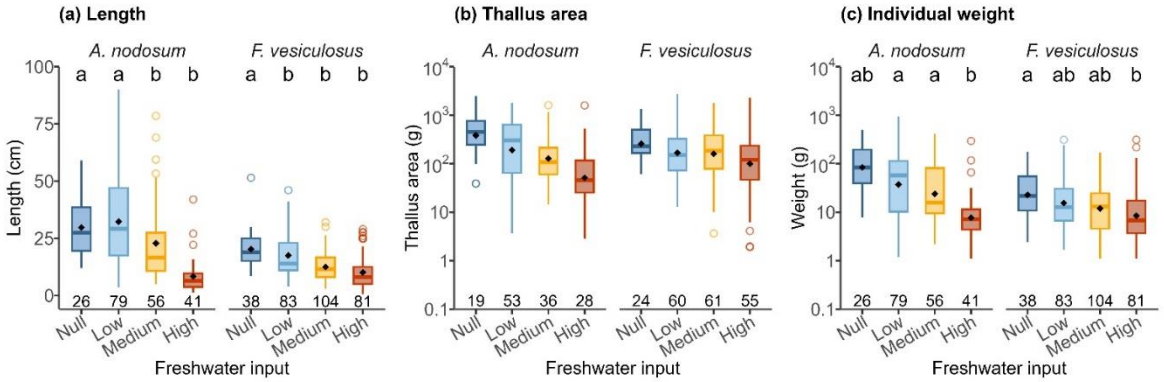


Figure 17. Effect of the freshwater input on algae morphological parameters: (a) length, (b) thallus area and (c) weight for *Ascophyllum nodosum* and *Fucus vesiculosus.* The thallus area and individual weight are presented with a logarithmic scale. See **Figure 13** for box plot description. Mean indicated by black diamonds. Different letters show significant mean differences; sample size (n) is indicated below each boxplot. Circles represent outliers.

1.2.7 Discussion

Our study provides first evidence that the freshwater input strongly drives the taxonomical and functional composition of subarctic marine benthic communities in small hard-substrate estuaries. We show that the freshwater input results in a reduction of both taxonomic and functional richness and biomasses of these intertidal rocky marine community, as well as a decrease in the size (length and individual biomass) of macroalgae. Some of the important ecosystem services from the estuarine community may be negatively affected, in particular the filtration of suspended matter by filter-feeders. Contrary to one of our initial hypotheses, there is no clear trend between the freshwater input and the body size of invertebrates or thallus area of macroalgae investigated. Our results also emphasize that functional-based indices are effective to detect changes in the community composition and loss of functions (*e.g.*, loss of filter-feeders), therefore they constitute a useful tool for conservation and management and should be integrated to taxonomic biodiversity analyses.

1.2.7.1 Loss of taxonomic and functional richness with freshwater input

The gradient of freshwater input acts as an important environmental filter that causes an increasing loss in biomass, taxa number and functions for hard-substrate communities, which is consistent to patterns shown in estuarian soft sediment habitats (McGovern *et al.*, 2020; Medeiros *et al.*, 2021; Sroczyńska *et al.*, 2021; van der Linden *et al.*, 2016). The decrease of functional richness of the benthic hard-substrate community from the marine sites to the entrance of the estuaries (low freshwater input) is caused by the loss of three species with unique traits combinations (*i.e.*, *Tectura testudinalis* and *Littorina littorea* are the only small-size and short-lived invertebrates, while *Onchidoris bilamellata* is the only predator; **Figure A.2**) that does not impact the taxonomic richness. The community then loses more taxa and functions with increasing freshwater input within the estuaries, with decline of suspension feeders (*i.e.*, *Mytilus* spp., *Balanus crenatus*, *Semibalanus balanoides*), and becomes primarily composed of macroalgae (*i.e.*, *A. nodosum* and *F. vesiculosus*) and grazers (*L. saxatilis*). Our results suggest that functional indices can be more sensitive to salinity gradient than taxonomic ones due to their sensitivity to the addition or loss of rare

species with rare combination of traits. These results are in line with other studies in estuarine habitats that are often characterised by a reduced number of taxa (Morais *et al.*, 2019; Nunes de Souza *et al.*, 2021; van der Linden *et al.*, 2016). The limited taxonomic richness we observed (only 13 identified taxa across all samples) can be attributed to our position in the mid-high intertidal zone and by the subarctic climate. Indeed, the marine mid-high intertidal zone remains a stressful environment under multiple abiotic constraints (Scrosati and Heaven, 2007; Stephenson and Stephenson, 1949), compounded by low temperature and seasonal ice cover and scouring in subarctic conditions (Burrows *et al.*, 2020; Gutt, 2001; Scrosati and Heaven, 2007).

While it is difficult to discern a clear pattern, given the low taxonomic richness in our estuaries, some functional redundancy (*i.e.*, several species within the community perform the same functions) is present in the low freshwater input part of the estuaries, but such redundancy vanishes at high freshwater input (**Table A.14**; **Figure A.3**). The lack of functional redundancy in estuarian habitats could be detrimental to their resilience, as it limits their ability to recover from disturbances and their tolerance over time (Biggs *et al.*, 2020).

1.2.7.2 Abiotic factors influencing the community composition

Macroalgae distribution follows patterns already observed along other natural salinity gradients. Specifically, *A. nodosum* and *F. vesiculosus*, which are present all along the estuaries, are known to inhabit brackish waters with salinity as low as 3 (Chock and Mathieson, 1979; Torn *et al.*, 2006), while *F. distichus* subsp. *edentatus*, *F. distichus* subsp. *evanescens* and *F. spiralis*, mostly present at higher salinities only (Doty and Newhouse, 1954). The later species distribution might result from the species sensibility to low salinity conditions at their early life stages (Wikström *et al.*, 2002), rather than at the adult stage (Romoth *et al.*, 2019). Similarly, estuarian invertebrate species are often tolerant to low salinity at their adult stage (Riisgård *et al.*; Sokolova *et al.*, 2000a; 2013; Sundell *et al.*, 2019), while their larvae are vulnerable to these conditions (Bhatnagar et Crisp, 1965; Pruett *et al.*, 2021, 2022; Sokolova, 1995). In addition to reducing salinity, freshwater input is likely to modify a number of physicochemical parameters, such as temperature (generally higher in

rivers than in marine sites in the summer, with an inverse pattern in the winter), pH, dissolved oxygen and turbidity, which could also influence the observed distribution patterns. However, several studies tend to show that salinity is the driver with the greatest influence on community composition (Morais *et al.*, 2019; Van Der Linden *et al.*, 2012).

Additional abiotic factors (*e.g.*, substrate availability, bathymetry) may interact with freshwater inputs and potentially influence the community composition in the rocky intertidal zone. These factors may explain the observed differences between sites, despite our efforts to select estuaries with similar substrates and geomorphology. The availability of hard substrate could influence the community composition, as boulder density can influence species richness (Franz *et al.*, 2021). Indeed, the estuary with the lowest taxonomic richness (Barthelemy) is also the one with the lowest hard-substrate availability (Loiseau *pers. obs.*). Additionally, hard substrates are often less frequently found closer to the river mouth, probably due to fine sediments accumulation (Dyer, 1995), which could also have contributed to the richness pattern. Finally, the bathymetry of estuaries, with lower depth at the river mouth when compared to the marine section of the estuaries, could also influence the community composition along the salinity gradient. Mobile species that are more abundant in the low intertidal, due to their sensitivity to desiccation (*e.g.*, *O. bilamellata* – Todd, 1979 and *T. testudinalis* – Wolcott, 1973), can at times venture in the high intertidal. Therefore, while they can occur in marine sites, they might not inhabit the shallower mouth of estuaries.

1.2.7.3 Biotic factors influencing the community composition

Interactions between species (*e.g.*, facilitation, predation, competition, grazing) can influence their occurrence and abundance along the salinity gradient we investigated. In particular, the decreasing macroalgae biomass and size we report could limit their facilitation role as foundation species. Foundation species provide spatial refuge from predation and/or physical stresses like heat and desiccation (Bertness *et al.*, 1999; Bruno and Bertness, 2001), and they promote enhanced recruitments of benthic community (Lemieux and Cusson, 2014) and resilience (Cimon and Cusson, 2018). For instance, *A. nodosum* can have a positive effect

on mussels' and barnacles' settlement in the high intertidal and can facilitate their own recruitment, while *Fucus* spp. are more able to invade clear surfaces (Bertness *et al.*, 1999). Some invertebrate species, like *L. obtusata*, are also associated with fucoids (Crisp and Southward, 1958) and their recruitment can depend on the availability of *Fucus vesiculosus* (Kozminsky, 2013). Our original experimental design does not allow us to discriminate the facilitation effect of macroalgae across our freshwater input levels, as macroalgae are present in all quadrats (see Methods). Investigating these aspects would indeed be of great interest in future studies. On the other hand, certain negative biotic interactions (*e.g.*, predation, competition for food, grazing pressure) may be suppressed under increasing levels of stress as predicted by the *Environmental Stress Gradient* hypothesis (Menge and Sutherland, 1976). Indeed, the only predator (*O. bilamellata*) in our surveys was found at high salinities which concurs with limited predation by invertebrate and fish at low salinities in other estuaries (Jurgens *et al.*, 2022; Posey *et al.*, 2005). Additionally, the absence of *L. littorea* at low salinities can limit its impact on both the abundance of *L. obtusata* (Putnam and Peckol, 2018) and algal recruitment (Bertness *et al.*, 1999).

Limited dispersal potential of propagules and larvae plays a key role in community composition within the estuaries, whereas marine community had more species with larvae that spent longer periods in the water column. Parental care and modified life cycles, such as brooding or direct development, may enhance marine invertebrates' survival in stressful habitats compared to species with pelagic larval development (Lucey *et al.*, 2015), which would explain their dominance in zones closer to freshwater inputs. Additionally, larval dispersion is particularly complex in estuaries due to changing currents with tides and depth (Bilton *et al.*, 2002), which could limit the ability of planktonic larvae to reach the high freshwater input zones. The greater sensibility of the larval stage to low salinities (Bhatnagar and Crisp, 1965; Pruett *et al.*, 2021a) would also limit settlement potential, in particular during spring flooding. Species with low dispersal potential would be expected to show stronger regional adaptation but species with both direct development and planktonic larvae have been shown to possess a greater local adaptation capability (Sanford and Kelly, 2011).

1.2.7.4 Freshwater input impacts on realized traits - size class structure and algae morphology

Increasing freshwater input induces a reduction in macroalgae length and biomass − probably due to its impact on photosynthetic activity (Kirst, 1990), but does not impact the size class structure of most invertebrate species. Indeed, only *L. obtusata* has a tendency to have a smaller size with decreasing salinity, a pattern consistent with numerous studies showing diminished growth rates and size at low salinities (Almada-Villela, 1984; Anger, 2003; Nasrolahi *et al.*, 2013), possibly due to increasing expenditure in osmoregulation (Podbielski *et al.*, 2022a). *Mytilus* spp., however, shows a different size-class pattern, with the presence of only very small or few large individuals in the high freshwater input sites, while all sizes are represented in the marine sites. Only few mussel individuals are seen in the medium and high freshwater input zones (8 out of 37 quadrats, approx. 22 % only) and their biomass was very low (*i.e.*, less than 5 g). Very large individuals, although very rare, represent a large proportion of the total mussel biomass in these zones. It is possible that these large individuals might have been transported by currents, drifting macroalgae or ice raft (Cusson and Bourget, 2005; Fraser *et al.*, 2011; Pacheco *et al.*, 2013) and settled there at their adult stage. *Mytilus edulis* has been shown to live and reproduce at mean salinities as low as 6 in the Baltic Sea, where it has locally adapted to these conditions (Johannesson *et al.*, 1990; Knöbel *et al.*, 2021), though it induces dwarfism (Westerbom *et al.*, 2002). However, *M. edulis* and *M. trossulus* from Atlantic Canada show very high mortality at salinities below 15, with reproductive adults (2.5-3 cm) being more vulnerable than juvenile (0.4-0.6 cm) or post-spawning adults to low salinities (Qiu *et al.*, 2002) which is more similar to the pattern observed in our estuaries. While local adaptation to salinity conditions have been shown to occur in estuaries (Bilton *et al.*, 2002; Eierman et Hare, 2013), *M. edulis* has a long pelagic larval stage that might promote mixing with coastal areas (Hilbish *et al.*, 2003), and therefore limits their potential for local adaptation.

1.2.7.5 Future implications for estuaries in a changing climate

Salinity-driven changes, such as earlier snowmelts and increased frequency and intensity of flooding, are anticipated with climate change in estuaries, with implications for the future of estuarine communities (Clavet-Gaumont *et al.*, 2017; Tabari, 2020). Snowmelt events are expected to occur earlier in the spring (Tabari, 2020), decreasing the salinity during a crucial period of development for many species, which phenology has evolved to optimise development and maximise their survival under a different set of environmental conditions (Philippart *et al.*, 2014; Gregory *et al.*, 2023). Warmer winters and earlier spring runoffs may additionally induce earlier phytoplankton bloom in estuaries (Laliberté and Larouche, 2023), or even lead to their disappearance in the spring (Nixon *et al.*, 2009). This can induce mismatches between estuarine organisms and their food, leading to smaller recruitment of bivalves (Philippart *et al.*, 2003) or reduced overlap time between predators and their prey (Chevillot *et al.*, 2017). Additionally, frequent and intense flooding events may decrease the ability of some species to remain within estuaries by limiting retention and pushing larvae seaward (Kim *et al.*, 2013), as wind, tide and currents drive larval dispersion and retention from the riverine sections into estuaries (Robins *et al.*, 2013).

The provision of several ecosystem functions or services could also be weakened by recurrent and prolonged low salinity conditions. In particular, the reduction in size and total biomass of macroalgae could impact their role as foundation species (Cimon and Cusson, 2018; Watt and Scrosati, 2013), as well as their services as carbon sink and nursery habitat (Schmidt *et al.*, 2011). A decrease in the abundance of filter feeders such as mussels could also have major impacts in the estuary ecosystem, as they are important preys of numerous predators (from gastropod to birds, Dame, 2012), and can act as foundation species by increasing habitat complexity (Norling and Kautsky, 2007; Palomo *et al.*, 2007). They are also of great importance in maintaining a good water quality through the filtration of suspended matter (Petersen *et al.*, 2014) and to redistribute these nutrients to the substrate or to upper tropic levels (Menge *et al.*, 1997). Similarly, extreme events (*e.g.*, flooding, droughts) can drastically reduce (and or change) ecosystem functioning (Sabater *et al.*,

2023), and long-term studies of both functional diversity and realized trait in these environments are needed to better evaluate their ability for resilience or resistance over time (Greenop *et al.*, 2021). Indeed, the low functional redundancy we observed in this work implies that small estuaries may be vulnerable and possess low resilience following a disturbance (Biggs *et al.*, 2020). Acquiring a more in-depth critical understanding of how these ecosystems changes following a hyposaline disturbance will allow us to create climate-smart conservation strategies (Patrick *et al.*, 2022; Stein *et al.*, 2014).

1.2.8 Concluding remarks

Our study reveals that freshwater input alters the structure of the macroalgae and macroinvertebrates fraction of hard-substrate subarctic estuarine communities, leading to decreased biomass, taxonomic, and functional richness. Filter-feeders and long-distance dispersers are notably absent at low salinities. Such loss of functions and low functional redundancy indicate a higher vulnerability of communities inhabiting areas with high freshwater input. Furthermore, our function-based indices are more sensitive to low salinities compared to taxonomic ones, highlighting their importance as a complement to traditional taxonomical indices in assessing community responses to environmental changes. While this study showed the strong influence of freshwater inputs on hard-substrate communities, it cannot discriminate between the effect of mean salinity or flooding events. Therefore, the comparative analysis of subarctic ecosystems at the community, species, and individual levels, before and after flooding events, across different seasons, is an important avenue of research, especially given the critical role of snow/rain precipitation dynamics in these regions.

1.2.9 CRediT author statement / Contribution

Valentine Loiseau: Conceptualization, methodology, formal analysis, investigation, data curation, writing – original draft, visualization; **Mathieu Cusson**: Conceptualization, methodology, resources, Writing - Review & Editing, Supervision; **Piero Calosi**: Conceptualization, methodology, resources, Writing - Review & Editing, Supervision; **Yanick Gendreau**: Conceptualization, methodology, resources, Writing - Review & Editing, Supervision, Project administration, Funding acquisition.

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1.2.12 Data availability

Loiseau V, Calosi P, Gendreau Y, Cusson M (2021): Inventory of macroalgae and benthic macroinvertebrates along a hypoosmolarity stress gradient in Barthelemy Bay and the Colombier, Mistassini, Franquelin and Saint-Nicolas rivers of the Upper North Shore, Quebec. v1. Fisheries and Oceans Canada. [Dataset]. https://doi.org/10.26071/OGSL-4BB77D86-B94E

CHAPITRE 2
L'EXPOSITION A UN GRADIENT DE DUREE DE PULSES D'EAU DOUCE IMITANT DES INONDATIONS FREQUENTES REVELE DES SEUILS DE SENSIBILITE SPECIFIQUES A L'ESPECE DANS UN ASSEMBLAGE DE MOLLUSQUES BENTHIQUES CLES

2.1 RESUME EN FRANÇAIS DU DEUXIEME ARTICLE

Les communautés estuariennes fournissent de nombreux services écosystémiques et sont très vulnérables aux changements globaux. Les modifications nocives dans l'utilisation des terres et les précipitations intenses augmentent la fréquence et l'intensité des inondations, provoquant des changements brusques dans les conditions abiotiques estuariennes. Ces épisodes hydrologiques extrêmes pourraient également conduire à des ouvertures plus fréquentes et prolongées des barrages et évacuateurs de crues. Par conséquent, les organismes marins sont plus souvent exposés à des conditions d'eau douce pendant plusieurs jours après les inondations. Bien que les organismes estuariens soient capables de prospérer dans des salinités fluctuantes, leurs réponses à un stress hypoosmotique intense et prolongé peuvent différer. Il est crucial de comprendre leurs réponses, car la variabilité de salinité est un facteur clé dans la distribution des espèces dans les estuaires. Les changements dans le cycle hydrologique se produisent beaucoup plus rapidement dans les environnements des hautes latitudes, pourtant les communautés estuariennes subarctiques sont rarement étudiées. Cette étude examine donc la sensibilité de trois espèces de macroinvertébrés benthiques marins clés habitant les estuaires subarctiques (*Littorina saxatilis*, *Macoma balthica* et *Mytilus* spp.) à différentes durées de pulses d'eau douce. Dans des conditions de laboratoire, les mollusques ont été exposés pendant six semaines à un gradient de 12 pulses d'eau douce, allant de 0 à 9 jours, entrecoupées de 24 h d'exposition à l'eau de mer. La mortalité et les traits individuels (c.-à-d. la masse corporelle et la croissance, ainsi que le contenu énergétique de *Mytilus* spp.)

ont été comparés après deux, quatre et six semaines d'exposition à l'aide de modèles linéaires mixtes et d'analyses de points de rupture. Les trois espèces ont montré une tolérance aux pulses d'eau douce de courte durée (moins de 2 jours) répétés pendant plusieurs semaines. *Littorina saxatilis* présentait la sensibilité la plus élevée, la mortalité augmentant sous des pulses d'eau douce de plus de 2 jours après deux semaines. *Macoma balthica* présentait un seuil comparable, mais après quatre semaines. *Mytilus* spp. a montré la plus grande tolérance, avec un seuil détectable seulement après six semaines d'exposition et une mortalité croissante dans les traitements avec des impulsions d'eau douce de plus de 5 jours. De plus, la croissance de la coquille et la masse corporelle diminuaient avec l'augmentation de la durée des pulses d'eau douce chez *L. saxatilis*, tandis que seule la masse corporelle était affectée négativement chez *M. balthica*. Ni la masse corporelle ni la croissance n'ont été affectées pour *Mytilus* spp. Le contenu énergétique chez *Mytilus* spp. variait en fonction de la durée et du temps de l'impulsion, le contenu énergétique le plus élevé étant détecté dans les pulses d'eau douce les plus longs, suggérant des réponses physiologiques complexes au stress hypoosmotique. Dans l'ensemble, notre étude indique l'existence de différences très spécifiques à l'espèce en matière de sensibilité à l'exposition à l'eau douce parmi les macroinvertébrés benthiques marins habitant les estuaires subarctiques. Nos résultats soulignent l'importance d'utiliser des gradients de niveaux de stresseurs pour identifier des seuils écologiquement pertinents, ce qui aide à la prévision et à la gestion d'événements climatiques extrêmes tels que les inondations fluviales sur les communautés estuariennes. Notre étude fournit de précieuses recommandations pour la gestion des barrages et la conservation de la biodiversité dans les écosystèmes estuariens.

Cet article, intitulé « *Exposure to a gradient of freshwater pulse durations mimicking frequent floodings reveals species-specific vulnerability thresholds in an assemblage of key benthic mollusks* », a été soumis en octobre 2024 dans la revue *Journal of Experimental Marine Biology and Ecology*, où il est actuellement en révision. Tous les auteurs ont participé à la conceptualisation du projet et de sa méthodologie et à la révision et à l'édition de l'article. En tant que première auteure, je me suis chargée de la mise en place du système expérimental, de la collecte et de l'analyse des données, ainsi que la rédaction de l'ébauche originale. Dr.

Yanick Gendreau, Prof. Piero Calosi et Prof. Mathieu Cusson ont contribué à la supervision du projet, à la gestion des ressources, à l'administration du projet et à l'acquisition de financement. Dr. David Drolet a également participé à la construction du système expérimental. Une version abrégée de l'article a été présentée à la Réunion Scientifique Annuelle de Québec-Océan à Rivière-du-Loup (CA) en hiver 2021 sous forme de présentation orale. Les résultats ont aussi été présenté à la Conférence Annuelle de la *Society for Experimental Biology* à Montpellier (France) en été 2021 sous forme d'une affiche, en ligne.

Loiseau, V., Calosi, P., Drolet, D., Cusson, M. et Gendreau, Y. (2024). Exposure to a gradient of freshwater pulse durations mimicking frequent floodings reveals species-specific vulnerability thresholds in an assemblage of key benthic molluscs. *Journal of Experimental Marine Biology and Ecology*, en revision.

2.2 EXPOSURE TO A GRADIENT OF FRESHWATER PULSE DURATIONS MIMICKING FREQUENT FLOODINGS REVEALS SPECIES-SPECIFIC VULNERABILITY THRESHOLDS IN AN ASSEMBLAGE OF KEY BENTHIC MOLLUSKS

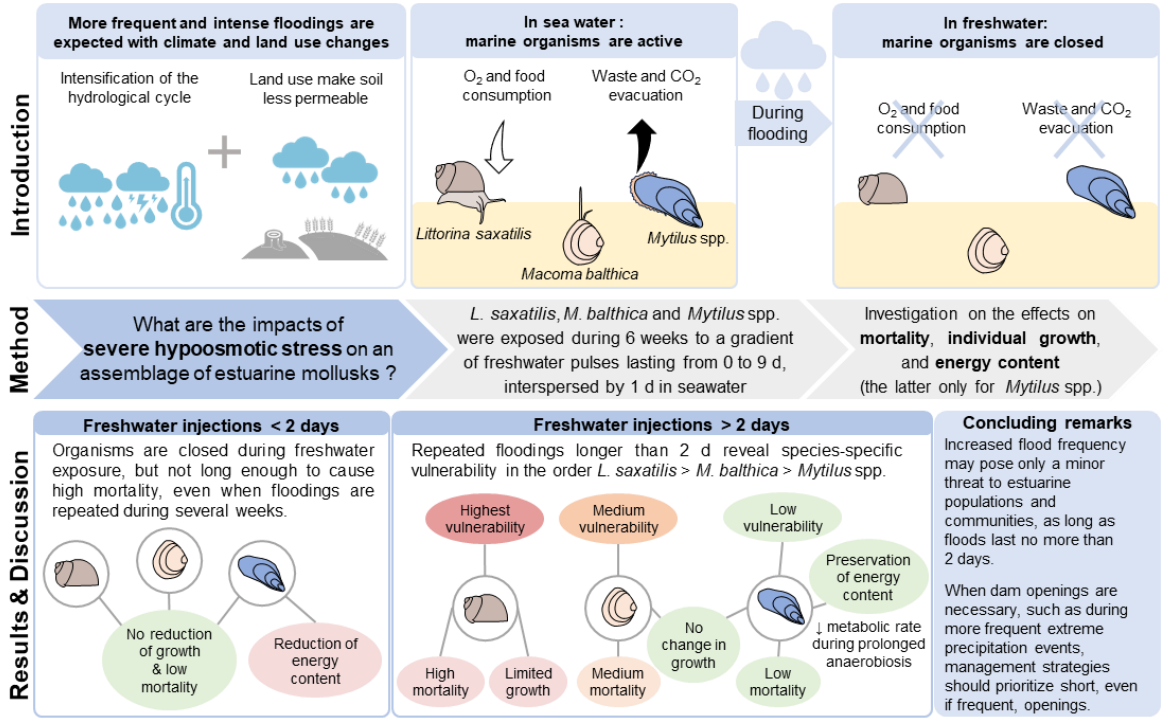
2.2.1 Abstract

Estuarine communities provide many ecosystem services and are highly vulnerable to global change. Detrimental changes in land use and intense rainfall events increase the frequency and intensity of flooding, causing abrupt changes in estuarine conditions. These extreme hydrological events could also lead to more frequent and prolonged openings of dams and spillways. As a result, marine organisms are more often exposed to freshwater conditions for several days after flooding. While estuarine organisms are able to thrive under fluctuating salinities, their responses to intense and prolonged hypoosmotic stress may differ. Understanding these responses is crucial as salinity variability is key to species distribution. Changes in hydrological regimes are occurring much faster in high latitudes environments, yet subarctic estuarian communities are rarely studied. This study investigates the sensitivity of three key marine benthic macroinvertebrates inhabiting subarctic estuaries (*Littorina saxatilis*, *Macoma balthica* and *Mytilus* spp.) to different durations of freshwater exposure. In laboratory conditions, mollusks were exposed during six weeks to a gradient of 12 freshwater pulse durations, ranging from 0 to 9 d, interspersed with 24 h of exposure to sea water. Mortality and individual traits (*i.e.*, body mass and growth, as well as energy content for *Mytilus* spp.), were compared after two, four and six weeks of exposure using linear mixed models and break-point analyses. All three species demonstrated tolerance to short-duration freshwater pulses (less than 2 d) repeated over several weeks. *Littorina saxatilis* exhibited the highest vulnerability, with mortality increasing under freshwater pulses longer than 2 d after two weeks. *Macoma balthica* displayed a comparable threshold but after four weeks. *Mytilus* spp. displayed the greatest tolerance, with a threshold only detectable after six weeks of exposure and increasing mortality in treatments with freshwater pulses longer than 5 d. In addition, shell growth and body mass decreased with increasing duration of freshwater pulse in *L. saxatilis*, whilst only body mass was negatively affected in *M. balthica*. Neither body mass nor growth were affected for *Mytilus* spp. Energy content in *Mytilus* spp.

varied according to pulse duration and time, with the highest energy content being detected in the longer freshwater exposure periods, suggesting complex physiological responses to hypoosmotic stress. Altogether, our study indicates the existence of highly species-specific differences in freshwater vulnerability among marine benthic macroinvertebrates inhabiting subarctic estuaries. Our findings highlight the importance of using gradients of stress scenarios to identify ecologically relevant thresholds, helping in the prediction and management of extreme climate events like river floods on estuarine communities. Our study provides valuable recommendations for dam management and biodiversity conservation in estuarine ecosystems.

Keywords: stress gradient, hypoosmotic stress, Molluska, estuaries, subarctic environments

2.2.2 Visual abstract



2.2.3 Highlights

- Study reveals species-specific differences in mollusk vulnerability to freshwater exposure.
- Short-term freshwater exposure does not cause significant mortality or growth reduction.
- *Littorina saxatilis* is the most vulnerable to longer-term freshwater exposures.
- *Mytilus* spp. is the most tolerant to longer-term freshwater exposures.
- Dam management should prioritize water releases < 2 days to minimize mollusk mortality.

2.2.4 Introduction

Estuaries support highly productive marine communities that provide many ecosystem services, for instance as nursery habitats for numerous marine species (Vasconcelos *et al.*, 2011) and natural water filtration systems (zu Ermgassen *et al.*, 2013). They are naturally stressed environments, as the river inflow causes great variability in the environmental physico-chemical characteristics (Elliott and Quintino, 2007). Freshwater inputs can increase during extreme rainfall events, which are predicted to become more intense and frequent as the hydrological cycle intensifies with global warming (IPCC, 2023b; Jong *et al.*, 2023; Tabari, 2020), in particular in polar and sub-polar environments (Constable *et al.*, 2023). Indeed, the atmosphere can hold about 7 % more water vapor with each degree of warming, which intensifies water fluxes and the frequency and intensity of floods (Allan *et al.*, 2020). In addition, land surfaces are becoming less permeable due to the expansion of agricultural lands and forest clearances, promoting runoffs and flooding (Mao and Cherkauer, 2009; Bathurst *et al.*, 2020). These extreme climatic and environmental events can shift estuaries' saline gradient seaward, causing salinity drops toward zero even in typically marine sites that can last for several days during extreme flooding (Fernandez *et al.*, 2006; Voynova *et al.*, 2016). As precipitation regimes continue to shift, it is highly likely that dam spillways will need to be opened more frequently and for longer durations than under current conditions (Lin *et al.*, 2021), also leading to more frequent abrupt drops in estuarine salinity (Linhoss *et al.*, 2023). Short-duration floods (less than 7 d) are the most common floods in North America, accounting for about 60 % of the total number of floods each year, followed by moderate-duration floods (8 to 20 d, 30 % of total events), and long-duration floods (more than 20 d, 10 % of total events) (Najibi and Devineni, 2018).

Hyposaline conditions can induce extensive mortality in estuaries (McFarland *et al.*, 2022), and alter community composition by reducing or locally eradicating more sensitive species (Loiseau *et al.*, 2024; Marshall *et al.*, 2019). Salinity has historically been considered the main biogeographic determinant of marine species distribution along estuaries (Kinne, 1971; Lu *et al.*, 2008; Vilas *et al.*, 2009), and its variability has been shown to negatively

affect macroinvertebrate diversity (Van Diggelen and Montagna, 2016). Estuarian macroinvertebrates tolerance to salinity variations depends on several factors, such as their genetic heritage and their developmental stage (Eierman et Hare, 2013; Kinne, 1966; Pruett *et al.*, 2022). In addition, gastropods and bivalves can modify their behavior during intense hypoosmotic stress (*i.e.*, exposure to a low salinity environment) by withdrawing into their shell to limit the osmo-ionic exchanges with the external environment (Sokolova *et al.*, 2000a; Woodin *et al.*, 2020). When the stress persists, the isolated state limits the organism's access to external oxygen, and mortality increases depending on its ability to survive hypoxemia (*i.e.*, extracellular fluid low levels of oxygen) (Berger and Kharazova, 1997; Sokolova *et al.*, 2000a).

Most of the studies reported to date on species hypoosmotic stress tolerance have focused on natural distributions along salinity gradients (Loiseau *et al.*, 2024) and transplant experiments (Jansena *et al.*, 2009; Vilas *et al.*, 2009), long-term exposure to typically a few salinity conditions within a species known tolerance range (Riisgård *et al.*, 2012; Podbielski *et al.*, 2022a) or single, short-term exposure to freshwater to investigate physiological processes (Sokolova *et al.*, 2000a; Veiga *et al.*, 2015). These studies, cumulatively, depict the large degree of variation in hypoosmotic stress tolerance among species. For instance, the rough periwinkle *Littorina saxatilis* (Olivi, 1792) lives constantly below 15 of salinity in the White Sea (Sokolova and Berger, 2000), and can survive freshwater exposure for at least 3 d (Sokolova *et al.*, 2000a). The blue mussel *Mytilus edulis* (Linnaeus, 1758) is found in salinities as low as 5, although specimens chronically exposed to these conditions display extreme reductions in size (Westerbom *et al.*, 2002). They have been found to survive up to 14 days in freshwater (Riley *et al.*, 2022). Finally, the Baltic clam *Macoma balthica* (Linnaeus, 1758) is able to live, grow and reproduce at salinities as low as 3 (Jansena *et al.*, 2009).

However, the multiplication of extreme flooding events already occurring with climate change makes it crucial to acquire a critical understanding of the impacts of repeated and prolonged exposure to freshwater conditions, as they will influence species distribution

(Wethey *et al.*, 2011). Extreme events can also act as strong directional selective drivers (Gutschick and BassiriRad, 2003), which could therefore become important biogeographical drivers (Bozinovic *et al.*, 2011). Due to the stochasticity of these events, their effects have rarely been studied in nature, except for a few long-term monitoring studies (Dittmann *et al.*, 2015; Neto *et al.*, 2010) and before-and-after studies of artificial dam openings or removals (Gladstone *et al.*, 2006; Rubin *et al.*, 2017b).

The aim of our work was to test the relative sensitivity of three key subarctic marine benthic mollusks found in estuaries to freshwater exposure. To achieve this, we used mesocosms with a 15 levels gradient of periodic pulses of increasing duration lasting from 0 to 9 d. We measured survival, body mass and growth rates, as well as energy content in *Mytilus* spp., as indicators of physiological performance, and evaluated both the effect of hypoosmotic stress on these metrics and the presence of sensitivity thresholds along the gradient (Suding and Hobbs, 2009). The three species we selected for our experiment, two bivalves (*Mytilus* spp. and *Macoma balthica*) and one gastropod (*Littorina saxatilis*), form an important part of the benthic communities they inhabit in the intertidal habitats of the North Atlantic coasts (Dexter, 1947; Khaitov, 2013). We hypothesized that (i) the negative effects of exposure to hypoosmotic conditions will cause a decrease in survival, body mass and shell growth and in energy content (done for the mussels only) with increasing duration of freshwater pulses; (ii) these negative effects will intensify with the duration of freshwater pulses and (iii) species- and trait-specific thresholds (corresponding to the duration of the freshwater pulses) will be observed. Based on the literature, we expect the tolerance to hypoosmotic stress to increase, for all traits, in the order: *L. saxatilis* < *Mytilus* spp. < *M. balthica.*

2.2.5 Material and methods

2.2.5.1 Study species

The rough periwinkle *Littorina saxatilis* is a small-size gastropod (up to 18 mm in height and 14 mm wide) that is typically found on any hard surfaces and within macroalgae, from the upper intertidal zone down to the subtidal fringe. They graze on benthic micro- and macroalgae. *Littorina saxatilis* is a dominant species in the high intertidal zone in estuaries (Dexter, 1947) and a model species for studying colonization and local adaptation (Johannesson, 2016). The blue mussel *Mytilus* spp. (composed of *Mytilus edulis*, *M. trossolus*, and their hybrids, hereafter referred to as *Mytilus* spp. − see Moreau *et al.*, 2005) is a large-size bivalve (5 to 10 cm in length at maturity) found from the high intertidal to the shallow subtidal zone, where it is attached to suitable substrate and conspecifics with the fibrous byssus threads it produces. It is an active suspension feeder, feeding on phytoplankton, but also on bacteria, detritus, and dissolved organic matter. Mussels are habitat-forming species (Arribas *et al.*, 2014) and highly efficient filter feeders that improve water quality (Timmermann *et al.*, 2019), and are farmed for human consumption (Petersen *et al.*, 2014). Both *M. edulis* and *M. trossolus* share similar responses to decreasing salinity (Sokolova *et al.*, 2024). The Baltic clam *Macoma balthica* is a small bivalve (maximum length of 18-20 mm for fully grown individuals), which, unlike the other two species, lives a few centimetres below the seafloor in sand, mud and muddy sand bottoms, from the upper regions of the intertidal to the subtidal (Budd and Rayment, 2001). This species can filter food particles suspended in the overlying water by holding its siphon in a fixed vertical position, or actively extend and move its siphon around on the sediment to consume deposited food particles (Skilleter and Peterson, 1994). Clams provide an important link between the water and sediments through intense bioturbation activity that improve oxygen and nutrient fluxes (Michaud *et al.*, 2005, 2006).

2.2.5.2 Specimen collection, acclimation, and preparation

Between July 20th and July 24th 2020, 500 adult indiv. of each selected species were collected in three out of four subarctic estuaries on the North shore of the St. Lawrence estuary (Quebec, Canada, **Figure A.4).** We collected the indiv. from several estuaries to mitigate the potential effects of adaptation/long-term acclimatisation to different environmental regimes (including differences in freshwater inputs) that could vary among estuaries (Bible and Sanford, 2016; Marshall *et al.*, 2021). The mussels and periwinkles were collected in Mistassini (49° 17' N, 67° 56' W), Franquelin (49° 17' N, 67° 53' W) and St. Nicholas (49° 18' N, 67° 47' W) estuaries and the clams in Mistassini, St. Nicholas and Barthelemy (49° 02'N, 68° 35'W) estuaries. These estuaries flow into the St. Lawrence marine Estuary, where surface waters have a mean annual salinity of approximately 28 (ranging from 20.9 to 29.1) and weekly average temperatures that vary from -1 °C in February to 12 °C in July (Galbraith *et al.*, 2022). The semidiurnal tide in the sampling area ranges between 3 and 3.5 m (Government of Canada, 2023). No clam was found in the Franquelin estuary due to the scarcity of muddy substrate, whereas there were only few periwinkles and mussels in the Barthelemy estuary due to the limited presence of hard substrate. To limit size variation effects, collected specimens were 0.5–1.0 cm for periwinkles, 0.5–1.5 cm for clams, and 1.5–2.5 cm for mussels. During the multi-day collection, organisms were kept in submerged mesh bags at the Baie-Comeau marina. They were transported to the laboratory (Maurice Lamontagne Institute, 48° 38' N, 68° 09' W, Mont-Joli, QC, CA) on July 24th within 6 h, in seawater-wetted bags placed in coolers kept under 9 °C. Less than 1 % mortality was observed in the days following arrival.

Once in the laboratory, the specimens were quarantined for 2 d in an outdoor pool (1000 L), under conditions similar to that of the St. Lawrence, then placed in three indoor tanks (425 L, one *per* estuary of origin) supplied with a continuous flow of filtered seawater delivered directly from the St. Lawrence estuary, where they were kept for three months for acclimation to laboratory conditions. The temperature and salinity were not controlled during this part of the acclimation and followed natural fluctuations, with the temperature decreasing

steadily from a maximum of 13.0 °C to the minimum of 8.0 °C (mean ± SE: 10.6 °C ± 0.2), and the salinity varying from 25.2 to 29.1 (27.3 ± 0.1). In each tank, the mussels and periwinkles were placed in submerged mesh containers to prevent them from escaping, while the clams were divided into three 100 L submerged open containers with 5 cm of sediment in which they buried themselves. These sediments were collected from a small estuary near the laboratory and had been passed through 0.5 mm sieves to remove all macroinfauna. All specimens were individually tagged with beekeeper numbers (Queen Marking Number Kits, Dancing Bee Equipment, Port Hope, ON, Canada), photographed with a high-resolution digital microscope (VHX-7000, Keyence, Mississauga, ON, CA), and weighed with a high-precision scale (XPE205, Mettler Toledo, Mississauga, ON, CA). One week prior to the experiment, specimens were divided into 30 mesocosms (5 L buckets, height 15cm, diameter 21 cm), each containing 8 indiv. *per* estuary of origin (a total of 24 indiv. for each species). The bottom of each mesocosm had been filled with 5 cm of sediment (same origin and treatment as previously described) to enable the clams to bury themselves. The periwinkles were placed in small (8 cm diam. and 5 cm height) submerged meshed containers to prevent them from reaching to the surface and avoiding treatments conditions, while the mussels were placed on top of the sediment at the bottom of the mesocosms.

2.2.5.3 Experimental design, system, and protocol

To test the impacts of the increasing duration of periodic exposure to freshwater pulses, whilst also identifying the presence of thresholds, on the survival and individual traits of an estuarine mollusk assemblage, we constructed a gradient of increasing hypoosmotic stress composed of 15 treatments. Each treatment corresponded to a freshwater pulse duration ranging from 0 (as control) to 9 d (*i.e.*, 0, 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5, 6, 7, 8, 9 d), interspersed with 24 h in seawater during a continuous period of six weeks (**Figure 18**). These flood scenarios reflected the most common flood durations in North America (Najibi and Devineni, 2018).

The experimental system comprised two 250 L head tanks, one filled with filtered seawater supplied directly from the St. Lawrence (salinity 27.2 ± 0.06, 13.4 °C ± 0.20), and the second filled with dechlorinated freshwater (salinity 0.5 ± 0.02, 13.1 °C ± 0.10) supplied by the town of Price. Precise control over freshwater and seawater exposure for each treatment was achieved using actuated three-way ball-valves controlled by a timer, ensuring a consistent flow of 0.7 L min^{-1} in two mesocosms (**Figure A.5**). We considered these mesocosms as independent replicates in our analyses, as there was no water exchange between them. The transition from 100 % freshwater to 100 % seawater (and *vice versa*) was completed within 15 min. The water temperature was controlled by mean of heat pumps (Gell'Air, Mont-Joli, Canada) so that the freshwater and sea water reached a similar temperature in the mesocosms. The water temperature was set at 13 °C, to replicate summer conditions we measured using calibrated probes (DST CTD, Star Oddi, Gardabaer, Iceland) in the estuaries where the organisms were sampled. The temperature was gradually increased from the acclimation tank temperature (9 °C) to the target temperature (13 °C) at a rate of 1 °C d^{-1} once the organisms were put in the experimental set-up, to reach the selected temperature 3 d before the start of the experiment (Clements *et al.*, 2018; Lasota *et al.*, 2018). During the acclimation period, the mortality rates stabilized around 3 % $week^{-1}$ for the periwinkles and < 1 % $week^{-1}$ for the clams and the mussels.

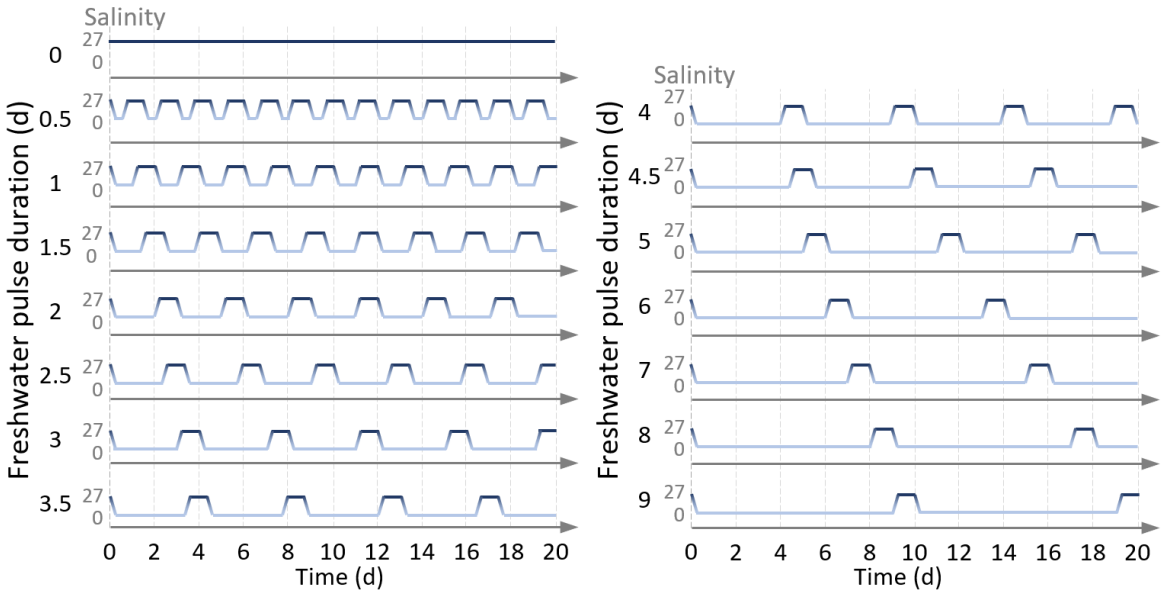


Figure 18. Schematic representation of the experimental design used. Each line represents the salinity in one treatment, with freshwater pulses (pale blue) ranging from 0 to 9 d, interspersed by 1 d in sea water (dark blue). Only the first 20 d are shown here but the experience lasted six weeks.

The experiment took place between October 23rd and December 4th, 2020. Survival was checked daily, and every dead specimen was removed to maintain good water quality levels, and replaced with spare marked indiv. in order to maintain indiv. density. The replacement individuals were not included in mortality and growth measurements.

The periwinkles were fed *ad libitum* with boiled lettuce *Lactuca sativa* that was changed every 2 d. The mussels and clams were fed with a concentrated mix of five marine microalgae (Shellfish Diet 1800®, Reed Mariculture Inc., Campbell, CA, USA) once a day, following the recommendation of 0.06 mL of Shellfish Diet 1800 *per* gram of wet meat weight for conditioning and fattening. The feeding always started at the same time, one hour after the water shifted from freshwater to saltwater and *vice versa*. The water flow was stopped for one hour, to allow time for mussels and clams to feed without allowing changes in abiotic parameters (*i.e.*, temperature, dissolved oxygen and pH). The temperature and salinity were checked daily in each mesocosm, while the pH (freshwater 8.3 ± 0.1, sea water 8.0 ± 0.1) was checked twice a week, with a multimeter (Water Quality Meter, HI98194,

Hanna instruments, Woonsocket, RI, USA). Dissolved oxygen (freshwater 82.4 % sat. ± 0.2, sea water 83.0 % sat. ± 0.4) was measured once a week with an oxygen meter (FireSting GO2, Pyroscience, Aachen, Germany). The abiotic parameters measured in each mesocosm throughout the experiment are in **Table A.15**.

One third of the indiv. were collected from each mesocosm after two, four and six weeks to investigate changes in growth rates and energy content over time across all freshwater pulse durations, and replaced with surplus indiv. to keep density constant. However, by the end of the fourth week, all periwinkles were either dead or sampled in nine out of 15 treatments. Since keeping them until six weeks would have left us with too few indiv. for reliable regression analysis, we decided to remove the remaining periwinkles at four weeks. Within minutes of extraction from the water, the individuals were promptly frozen at -85 °C, ensuring rapid euthanasia and optimal preservation of tissue parameters. In the following weeks, photos of the mollusks were taken with the same digital microscope mentioned above, then the specimens were weighted and dissected. Mussel soft tissues were preserved in microtubes of 1.5 mL at - 85 °C to be used later for the energy content.

2.2.5.4 Characterisation of behaviour

Behaviour was checked each day at the same time as mortality, and the salinity at the time of the observation was noted. Periwinkles were recorded as 'active' if they were moving outside their shells, and 'inactive' if they were tightly enclosed in their shells: *i.e.*, the operculum didn't move when lightly pushed. If the periwinkle was outside its shell but did not respond to any stimuli, or inside its shell but the operculum completely caved in at the slightest pressure without response, it was recorded as 'dead'. Mussels were marked as 'inactive' if tightly closed, 'active' if open and responding to touch (*i.e.*, closing), and 'dead' if open and unresponsive. As the clams live in the sediment, this behaviour could not be monitored. The organisms were identified as dead when their empty shells surfaced on the sediment.

2.2.5.5 Determination of morphometric traits

To quantify the effect of the freshwater pulse duration on the growth rate of organisms, we measured the whole organism body mass, and shell length, width and height (**Figure A.6**) before and after the experiment. Measurements were taken on three indiv. *per* mesocosm (one *per* estuary of origin whenever it was possible) collected after two, four and six weeks (except for periwinkle) of treatment, which enabled us to test for the effect of freshwater on growth over time. The morphometric parameters were measured from the photos captured with the high-resolution digital microscope using ImageJ software. Growth values were normalised by the number of days elapsed between the start of the experiment and the day of collection, and by the initial size of the organism to give a rate of change in % body mass/length/height/height d^{-1}. Finally, we calculated the difference in aspect ratio (shell width / shell length) to detect changes in the mollusks' shape.

2.2.5.6 Determination of calorimetric value of Mytilus spp. tissues

To determine the effects of freshwater pulse duration and of the time (*i.e.*, two, four or six weeks) on the energy content of *Mytilus* spp. we used a semi-microbomb calorimeter (6725, Parr Instrument Co., Moline, IL, USA), a precision thermometer (6772, Parr Instrument) and an oxygen bomb (1109A, Parr Instrument) following to the protocol of Siddon *et al.* (2013). In more detail, the whole soft tissues of three mussels *per* estuary of origin *per* mesocosm were used, for a total of 270 indiv. Only individuals of *Mytilus* spp. were used as our equipment was suitable only for samples larger than 0.025 g, which excluded periwinkles and clams from the analysis. Mussels' soft tissues were dried at 65 °C for 24 h (GO1340A-1 Lindberg / Blue M, Thermofisher Scientific, Waltham, USA) and weighed (precision scale, 225AC − precision 0.01 mg, VWR, Bridgewater, USA) to determine the dry weight. Because most of the samples did not meet the calorimeter's minimum weight requirement of 0.025 g, each sample was mixed with a predetermined amount of benzoic acid and subsequently pressed into pellets weighing between 0.05 g and 0.08 g using a pellet press (2811, Parr Instrument). Every 20 measurements, a 0.05 g benzoic pellet (made from 0.2 g benzoic acid pellets, 3418, Parr Instrument) was used for the

standardization of the energy equivalent value of the bomb and as a quality control. Rinse water from 10 randomly chosen samples was titrated with NaOH (Sodium Hydroxide Solution 0.1 N, Fisher Chemical, Thermo Fisher Scientific, Ottawa, ON, CA) to control for the heat potentially emitted by the nitric acid obtained from the nitrogen in the bomb. The heat emitted by the benzoic acid, the fuse wire and the nitric acid was subtracted from the total energy of combustion to determine the tissue energy of dry weight in kJ g^{-1}.

2.2.5.7 Statistical analysis

We analyzed each species independently, as preliminary analyses showed a significant effect and strong interactions involving the term *Species*. For each species, we used linear mixed models to assess the effect of the fix terms *Pulse duration* (*i.e.*, duration of the freshwater pulses, continuous), *Time* (three levels) and their interactions, and the random term *Estuary of origin* (three levels) on the mortality percentage and growth rates. The same design was used for the energy content, which was only measured for the mussel. We also added the *Replicate* (*i.e.*, incubation mesocosm) as a random factor for the individual traits (*i.e.*, growth rates and energy content). For the growth rates, we added the initial size (*i.e.*, shell length / width / height or body weight) as a covariate. We selected the best model using the Akaike Information Criterion (AIC), choosing the one that included either one or both of the random factors but keeping the fixed factors, based on parsimony and likelihood. Diagnostic plots were used to check for multicollinearity of fixed effects, the homogeneity of variances and normality of residuals for each model (Montgomery, 2012). We used the "lme4" package in R Studio (version 2024.4.0.735) to perform the linear mixed models. Additionally, when the effect of *Pulse duration* was significant, we performed break-point analyses to estimate the presence of thresholds (*i.e.*, where the relationship between the treatments and the measurements changed) along the gradient of freshwater exposure pulses. We used the "segmented" package (Muggeo, 2008) to detect the presence of thresholds, performed Davies tests (Davies, 1987) to determine the significance of the difference in slopes before and after each threshold, and use AIC values to select the best model (with 0, 1 or 2 thresholds). When a significant interaction between *Pulse duration* and *Time* was

detected, and no breakpoint was identified for any *Time* level (indicating a linear relationships), a t-test was performed to detect significant differences between the slopes using the "emmeans" package.

Finally, we displayed the mortality rates using Kaplan-Meier curves, and conducted Cox proportional hazard models, with death serving as the 'event', and time since the beginning of the experiment as the 'time until an event' with the "survival" package (Lumley *et al.*, 2024) to assess the relationship between mortality rates and the freshwater pulse durations, estuary of origin, and individual body mass. We estimated hazard ratios (HR) for each explanatory variable, indicating the risk of mortality: HR > 1 represent an increased risk of mortality and HR < 1 a decreased risk of mortality. When diagnostics plots suggested that the effect of a factor varied over time, we divided the data into intervals at two weeks to examine how its impact changed over time. We used a significance level of $\alpha = 0.05$ for all statistical analyses. We applied no corrections to *P*-values to our planned contrasts.

2.2.6 Results

2.2.6.1 Behaviour

Both mussels and periwinkles were always active in seawater and inactive (*i.e.,* closed) in freshwater, so no statistical analyses were performed. They stayed closed in freshwater even in the presence of food. The switch from 100 % seawater to 100 % freshwater was too fast (*i.e.*, 15 min) to determine the exact salinity at which the organisms closed their shells, which was not the purpose of the experiment.

2.2.6.2 Mortality

Time (*i.e.*, two, four and six weeks) significantly magnified the impact of the freshwater pulse duration on the mortality percentage of all species investigated, as indicated by the significant interactions between the time and the freshwater pulse duration (**Table 4**, **Figure 19**). In addition, the gradient of freshwater pulse duration produced non-linear responses that were highly species-specific; in fact, *Littorina saxatilis* showed the highest mortalities, with

mortality rising markedly after just two weeks of exposure, particularly when the freshwater pulse lasted longer than the identified threshold of 1.8 d (± 0.5). At four weeks, the threshold occurred at shorter freshwater pulses, as mortality increased at pulses of 1.3 d (± 0.2), reaching 100 % for pulses surpassing 3.8 d (± 0.2). At two weeks, *Macoma balthica* exhibited a steady linear increase in mortality with increasing duration of freshwater pulse, and no threshold was detected. However, at four weeks, mortality increased starting from freshwater pulse of 2.2 d (± 0.4), plateauing for pulses longer than 6 d (± 0.6) with comparable thresholds at six weeks (*i.e.*, 2.3 d ± 0.5 followed by a plateau starting at 6 d ± 0.5). *Mytilus* spp. showed the greatest tolerance, with mortality ratios surpassing 50 % only for freshwater pulse exceeding 5 d. Thresholds were identified at freshwater pulses lasting 4.0 d (± 1.3) at four weeks and 5.4 d (± 1.0) at six weeks, but no plateau was observed.

The survival proportion dropped below 50 % after just 10 d for *L. saxatilis*, while it took 20 d for *M. balthica* and 30 d for *Mytilus* spp. during the longest freshwater pulses (8–9 d depending on the species) (**Figure 20**). Mortality rates for all three species increased with longer freshwater pulse durations, with varying effects over time. Each additional day of freshwater pulse increased the mortality risk for *L. saxatilis* by approximately 44 % in the first two weeks ($p < 0.001$) and 78 % in the third and fourth weeks ($p < 0.001$) and for *M. balthica* by 34 % in the first two weeks ($p < 0.001$), 56 % in the third and fourth weeks ($p < 0.001$) and 14 % in the fifth and sixth weeks ($p = 0.002$). It increased *Mytilus* spp. mortality risk during the first two periods (51 % and 64 %, respectively; $p < 0.001$) but not in the last two weeks ($p = 0.225$). In addition, during the first two weeks, higher body mass significantly increased survival for *L. saxatilis* (HR = 0.007, $p = 0.003$), whereas smaller *M. balthica* had a higher chance of survival (HR = 94.22, $p < 0.001$). Body mass had no significant effect in the later weeks or on *Mytilus* spp. mortality (HR = 1.03, $p = 0.848$). Finally, inter-population variation was observed: *L. saxatilis* from Mistassini were more vulnerable than those from Franquelin (HR = 0.76, $p = 0.031$), and *M. balthica* from St. Nicholas were more vulnerable than those from Barthelemy (HR = 0.72, $p = 0.020$). Visual representation of the hazard ratios is available in the supplementary materials (**Figure A.7**).

Table 4. Summary of the ANOVA showing the effects of the freshwater pulse duration ('Pulse duration'), 'Time', and their interaction on the mortality ratios of (a) *Littorina saxatilis*, (b) *Macoma balthica* and (c) *Mytilus* spp. Significant values are given in bold. The goodness of fit (R^2) represents the variance explained by the fixed effects only (R^2m) and by the fixed and random effects (R^2c). The best model for *L. saxatilis* included only the 'Mesocosm' as a random factor, and included both the 'Mesocosm' and the 'Estuary of origin' for *M. balthica* and *Mytilus* spp.

Source of variation	df_1	df_2	Mean square	F ratio	*P* value
a. *Littorina saxatilis*: R^2m: 0.72, R^2c: 0.84					
Pulse duration	1	30	2.9760	110.90	**<0.0001**
Time	1	150	0.2734	10.18	**0.0017**
Pulse duration:Time	1	150	0.6379	23.76	**<0.0001**
b. *Macoma balthica*: R^2m: 0.59, R^2c: 0.76					
Pulse duration	1	29	2.5290	102.50	**<0.0001**
Time	2	225	0.0197	0.80	0.4516
Pulse duration:Time	2	228	0.9316	37.76	**<0.0001**
c. *Mytilus* spp.: R^2m: 0.38, R^2c: 0.51					
Pulse duration	1	28	0.7121	43.60	**<0.0001**
Time	2	234	0.0757	2.32	0.1010
Pulse duration:Time	2	234	0.6542	20.03	**<0.0001**

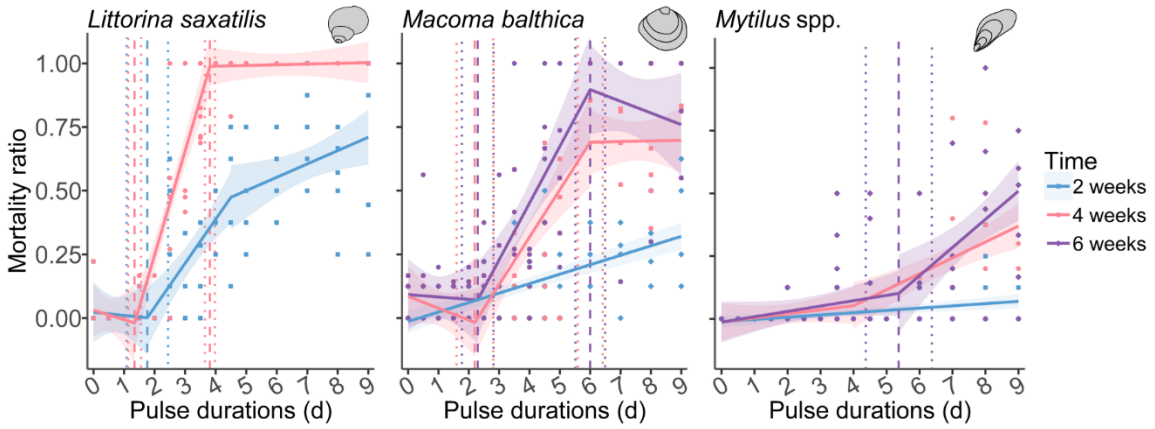


Figure 19. Relationship between the freshwater pulse duration and the mortality ratio of three mollusk species (*L. saxatilis*, *M. balthica*, and *Mytilus* spp.). Solid lines (with 95% confidence interval shaded areas) depict the optimal segmented regression models at two (blue), four (pink), and six weeks (purple). Data points illustrate the mortality percentage *per* estuary of origin *per* replicate. Dashed vertical lines represent significant ($p < 0.05$) thresholds, with dotted lines at the 95 % confidence interval. No thresholds were detected for *M. balthica* and *Mytilus* spp. at two weeks, hence linear models are depicted instead.

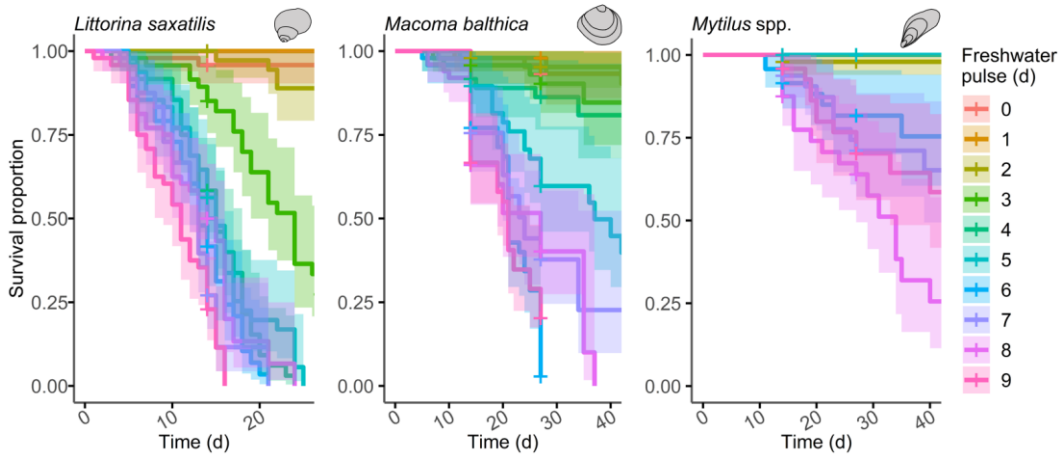


Figure 20. Survival probability curves over time for the three mollusk species investigated (*L. saxatilis*, *M. balthica*, and *Mytilus* spp.). Solid broken lines represent surviving curve for each freshwater pulse duration, with 95% confidence intervals depicted by shaded coloured areas. Crosses represents events where indiv. were taken out of the study (at two, four and six weeks). For better clarity, note that the x-axis stops at 27 d for *L. saxatilis* and 43 d for *M. balthica* and *Mytilus* spp., and that only 10 treatments (out of 15 used in our study) were represented.

2.2.6.3 Changes in body mass and shell length, height and width

Longer freshwater pulses reduced the growth of *L. saxatilis*, as well as *M. balthica* and *Mytilus* spp. after four weeks (**Table 5**, **Table 6**). In particular, *L. saxatilis* was most affected by long freshwater pulses, and the duration of freshwater pulse had a stronger negative effect after four weeks, as demonstrated by the presence of a significant interaction between the time and the pulse duration for the change in body mass (**Table 5**, **Figure 21**; the results of the contrast between slopes are provided in **Table A.16**), shell length and height (**Table 6**, **Figure 22**). The time also significantly interacted with the freshwater pulse duration for the changes in body mass for *M. balthica*, as after four weeks, they regained their initial body mass in the shorter duration but not in the longer exposure periods (**Table 5**, **Figure 21**, **Table A.16**). *M. balthica* shell growth was not affected by the pulse duration, though it was influenced by the time as some growth was only detected after four weeks (**Table 6**, **Figure 22**). *Mytilus* spp. showed decreasing body mass with increasing freshwater exposer only after

four and six weeks, when the opposite trend was observed after two weeks (**Table 5**, **Figure 21**, **Table A.16**). The pulse duration had no effect on any of the shell growth parameters we investigated, although they changed across time (**Table 6**, **Figure 22**). A certain degree of body mass loss was detected only at two weeks (**Figure 21**, **Table A.16**), length and width growths were smaller at two weeks while height growth was smaller at six weeks (**Figure 22**). The freshwater input duration did not influence the aspect ratio for neither species (**Table A.17**).

Table 5. Summary of the ANOVA showing the effects of the freshwater pulse duration ('Pulse duration'), 'Time', their interaction, and the initial body mass on the changes in body mass of (a) *L. saxatilis*, (b) *M. balthica* and (c) *Mytilus* spp. Significant values are in bold. The goodness of fit (R^2) represents the variance explained by the fixed effects only (R^2m) and by the fixed and random effects (R^2c). For *L. saxatilis*, the best model included only the 'Replicate' as a random factor, but included both the 'Replicate' and the 'Estuary of origin' for *M. balthica* and *Mytilus* spp.

Source of variation	df_1	df_2	Mean square	F ratio	*P* value
L. saxatilis: R^2m: 0.14, R^2c: 0.17					
Pulse duration	1	43	0.00021	15.73	**0.0003**
Time	1	260	0.00007	5.21	**0.0233**
Pulse duration:Time	1	93	0.00020	15.01	**0.0002**
Initial body mass	1	337	0.00043	32.65	**<0.0001**
M. balthica: R^2m: 0.31, R^2c: 0.41					
Pulse duration	1	33	0.00005	6.93	**0.0128**
Time	2	482	0.00028	43.05	**< 0.0001**
Pulse duration:Time	2	473	0.00005	7.48	**0.0006**
Initial body mass	1	479	0.00004	5.98	**0.0149**
Mytilus spp.: R^2m: 0.41, R^2c: 0.59					
Pulse duration	1	30	0.00001	0.41	0.5265
Time	2	612	0.00360	158.00	**< 0.0001**
Pulse duration:Time	2	617	0.00027	11.90	**< 0.0001**
Initial body mass	1	629	0.00021	9.15	0.0026

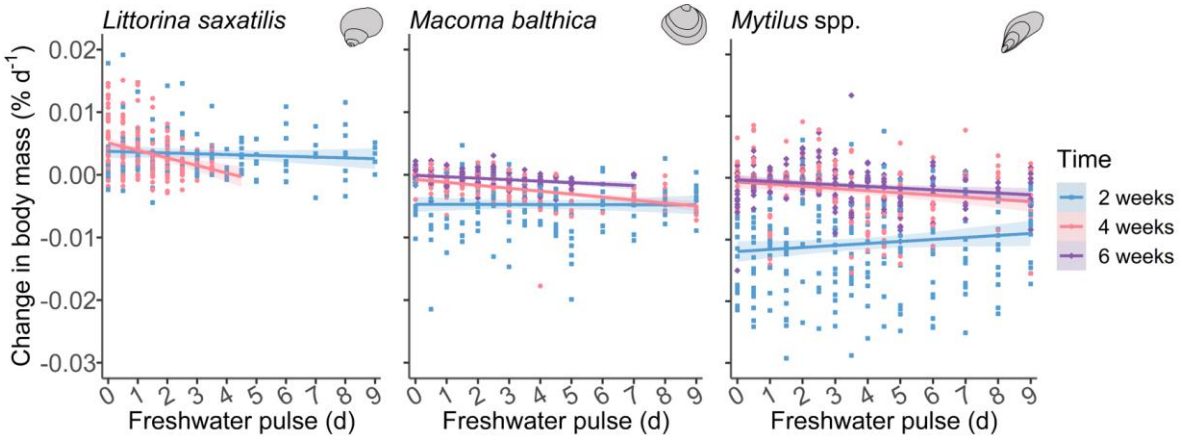


Figure 21. Relationship between the freshwater pulse duration and the individual daily percentage change in body mass of three mollusk species (*Littorina saxatilis*, *Macoma balthica*, and *Mytilus* spp.). Data points illustrate the indiv. measurements (three indiv. *per* mesocosm). Solid lines depict the linear regression at two (blue), four weeks (pink) and six weeks (purple), with 95 % confidence intervals illustrated in shaded colors. No breakpoint was detected for any relationship. Some values for *L. saxatilis* at six weeks are not represented because all the indiv. were dead or removed from the system during sampling.

Table 6. Summary of the ANOVA showing the effects of the freshwater pulse duration ('Pulse duration'), 'Time', their interaction and the initial weight on the individual morphometric parameters percentage change *per* day for (a) *L. saxatilis*, (b) *M. balthica* and (c) *Mytilus* spp. Significant values are in bold. The goodness of fit (R^2) represents the variance explained by the fixed effects only (R^2m) and by the fixed and random effects (R^2c).

	Source of variation	df_1	df_2	Mean square	F ratio	*P* value
a. *Littorina saxatilis*						
Shell length growth *	**Pulse duration**	1	70	0.0782	17.12	**0.0001**
R^2m: 0.46, R^2c: 0.54	**Time**	1	156	0.2745	60.09	**0.0000**
	Pulse duration:Time	1	156	0.0439	9.61	**0.0023**
	Initial length	1	159	0.0373	8.16	**0.0049**
Shell width growth **	Pulse duration	1	153	0.0350	3.05	0.0829
R^2m: 0.35, R^2c: 0.37	**Time**	1	152	0.3209	27.95	**0.0000**
	Pulse duration:Time	1	152	0.0254	2.21	0.1393
	Initial width	1	153	0.2665	23.21	**0.0000**
Shell height growth *	**Pulse duration**	1	69	0.0595	10.08	**0.0022**
R^2m: 0.33, R^2c: 0.42	**Time**	1	150	0.2292	38.81	**0.0000**
	Pulse duration:Time	1	148	0.0560	9.48	**0.0025**
	Initial height	1	152	0.0576	9.75	**0.0022**
b. *Macoma balthica*						
Shell length growth *	Pulse duration	1	43	0.0011	0.40	0.5305
R^2m: 0.26, R^2c: 0.35	**Time**	2	196	0.0468	17.75	**0.0000**
	Pulse duration:Time	2	207	0.0007	0.26	0.7682
	Initial length	1	209	0.0176	6.67	**0.0105**
Shell width growth *	Pulse duration	1	35	0.0020	0.70	0.4087
R^2m: 0.24, R^2c: 0.37	**Time**	2	191	0.0324	11.43	**0.0000**
	Pulse duration:Time	2	204	0.0003	0.12	0.8844
	Initial width	1	208	0.0091	3.21	0.0746
Shell height growth *	Pulse duration	1	37	0.0015	0.41	0.5257
R^2m: 0.04, R^2c: 0.19	Time	2	189	0.0008	0.22	0.7999
	Pulse duration:Time	2	203	0.0021	0.56	0.5712
	Initial height	1	205	0.0110	2.98	0.0860
c. *Mytilus* spp.						
Shell length growth ***	Pulse duration	1	29	0.0000	0.00	0.9902
R^2m: 0.18, R^2c: 0.28	**Time**	2	229	0.0389	14.64	**0.0000**
	Pulse duration:Time	2	231	0.0025	0.95	0.3893
	Initial length	1	250	0.0044	1.64	0.2010
Shell width growth **	Pulse duration	1	254	0.0000	0.01	0.9140
R^2m: 0.08, R^2c: 0.16	**Time**	2	254	0.0363	8.83	**0.0002**
	Pulse duration:Time	2	254	0.0076	1.84	0.1606
	Initial width	1	256	0.0050	1.21	0.2722
Shell height growth **	Pulse duration	1	252	0.0019	0.16	0.6883
R^2m: 0.21, R^2c: 0.24	**Time**	2	252	0.1065	9.24	**0.0001**
	Pulse duration:Time	2	252	0.0170	1.48	0.2307
	Initial height	1	247	0.0778	6.75	**0.0099**

* the best model included only 'Mesocosm' as a random factor

** the best model included only the 'Estuary of origin' as a random factor

*** the best model included both the 'Mesocosm' and the 'Estuary of origin' as random factors

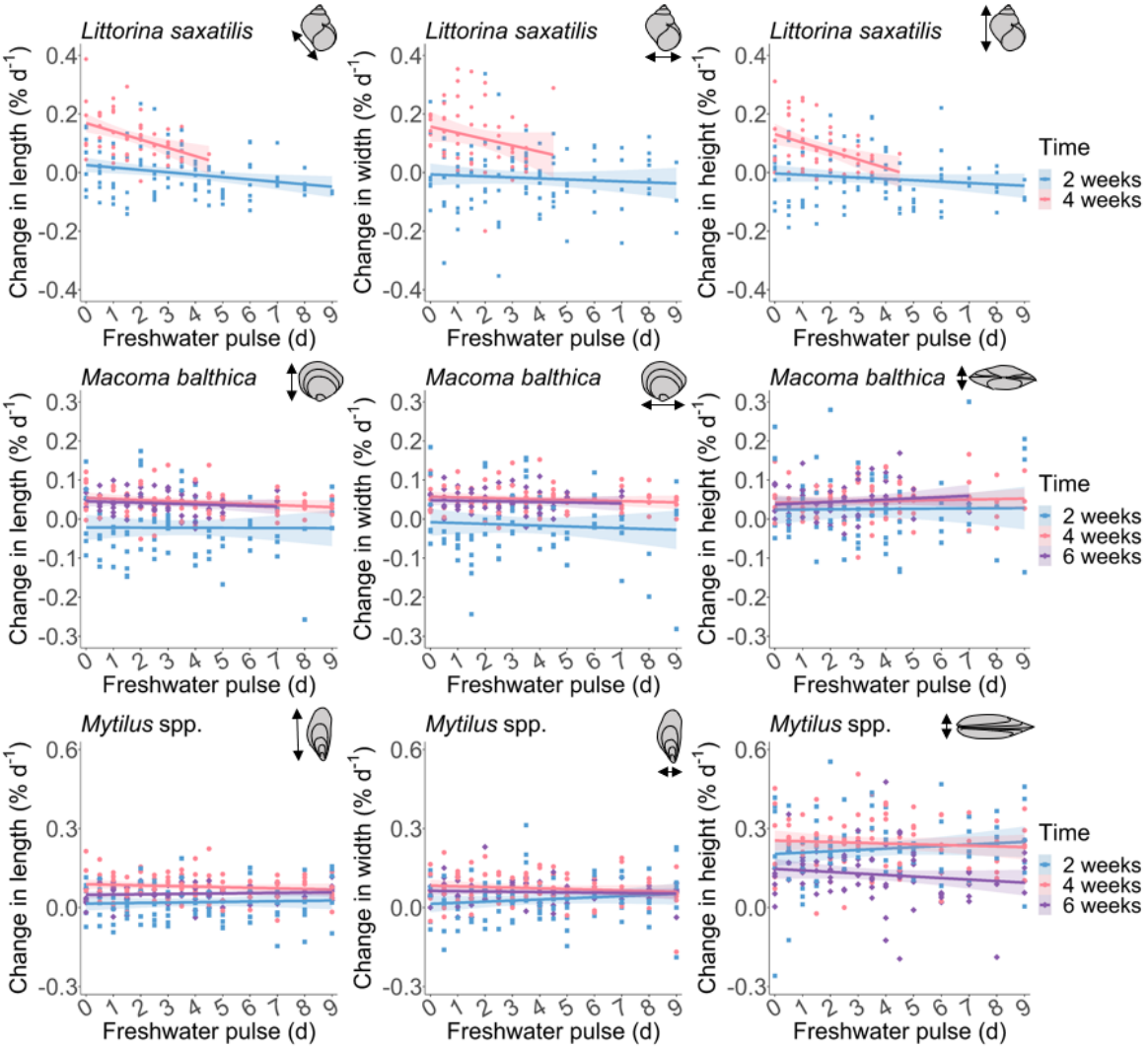


Figure 22. Relationship between the freshwater pulse duration and morphometric parameters percentage change *per* day of *L. saxatilis* (upper), *M. balthica* (middle) and *Mytilus* spp. (bottom), for the length (left), the width (middle), and the height (right). Data points illustrate the individual measurements (3-4 indiv. *per* mesocosm). Solid lines depict the linear regression at two (blue), four (pink) and six weeks (purple), with 95% confidence intervals illustrated in shaded colors. No breakpoint was detected for any relationship. At four weeks, all indiv. of *L. saxatilis* were dead in the treatments longer than 4.5 d so the growth rates could not be measured.

2.2.6.4 *Mytilus* spp. energy content

Time altered the response of *Mytilus* spp. energy content to the increasing duration of freshwater pulses, as indicated by a significant interaction (**Table 7**, **Figure 23**) and significantly different slopes between the second and sixth week (p = 0.003, **Table A.18**). Specifically, the energy content decreased between the second and the sixth week in the shorter freshwater pulses, but remained constant in treatments in the longer freshwater pulses (**Table 7**, **Figure 23**).

Table 7. Summary of the results of the ANOVA tests showing the effects of the freshwater pulse duration ('Pulse duration'), 'Time', and their interaction on energy content of *Mytilus* spp. Significant values are in bold. The goodness of fit (R^2) represents the variance explained by the fixed effects only (R^2m) and by the fixed and random effects (R^2c). The model included only the 'Mesocosm' as a random factor.

Source of variation	df_1	df_2	Mean square	F ratio	*P* value
R^2m: 0.19, R^2c: 0.19					
Pulse duration	1	28	259.0	28.33	**<0.0001**
Time	2	237	129.6	14.18	**<0.0001**
Pulse duration:Time	2	241	50.0	5.47	**0.0048**

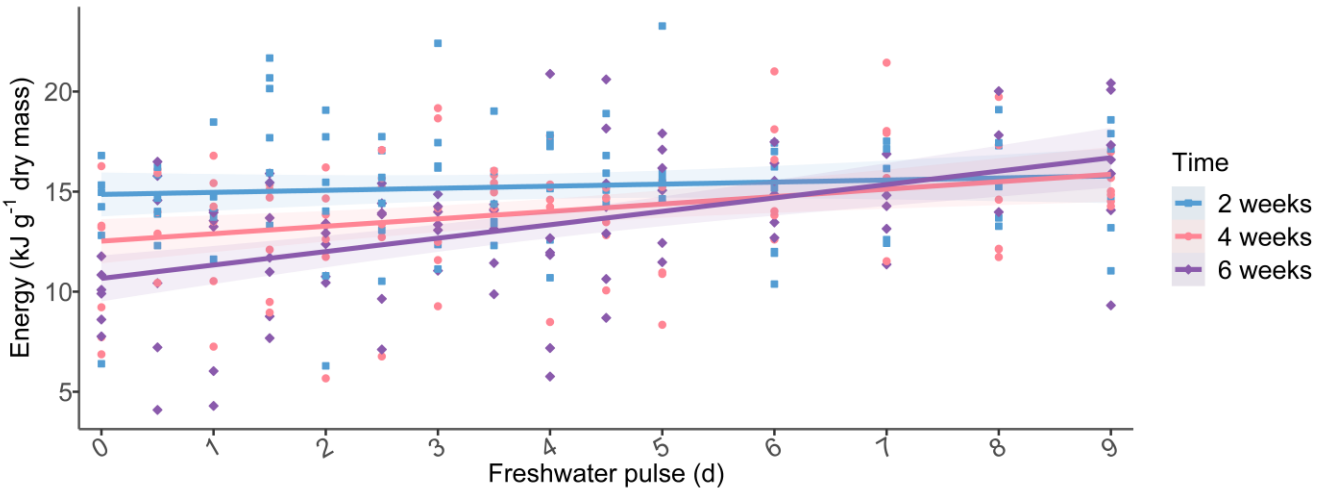


Figure 23. Relationship between the freshwater pulse duration and the energy content of *Mytilus* spp. Solid lines depict the linear regression at two (blue), four weeks (pink) and six weeks (purple), with 95% confidence intervals illustrated in shaded colors. Data points illustrate individual measurements (3 indiv. *per* mesocosm).

2.2.7 Discussion

Our study, by investigating periodic flooding scenarios along a intensity gradient at different time scales, reveals for the first time significant species-specific differences in the vulnerability to freshwater exposure among dominant marine mollusk assemblage in subarctic estuaries. As predicted, the results showed that *Littorina saxatilis* was the most vulnerable species to freshwater exposure, whilst again our prediction *M. balthica* is more vulnerable than *Mytilus* spp. Our findings also indicate that flood duration, rather than frequency, is the main driver of mortality in the three investigated species. Using a gradient design, we identified species-specific differences in thresholds for mortality proportion, as well as a gradual reduction in body mass (*L. saxatilis* and *M. balthica)* and morphometric traits (*L. saxatilis*) in response to increased hypoosmotic stress. However, we did not predict the increase in tissue energy content in *Mytilus* spp. along the same gradient. We discuss our results within the context of the potential consequences of extreme climatic events, such as riverine floods, of natural or anthropogenic origin, on estuarine macroinvertebrate assemblages and from the perspective of developing recommendations for dam management and biodiversity conservation.

2.2.7.1 Mollusks are tolerant to short-term exposure to freshwater but display species-specific vulnerability to prolonged exposure

For the three mollusk species investigated, we unveil for the first time a noteworthy tolerance to periods of exposure to freshwater shorter than two days repeated over several weeks. Many estuarian invertebrates, in particular mollusks, are osmoconformers (*i.e.*, they maintain their internal medium isosmotic to that of the environment (Rivera-Ingraham and Lignot, 2017). When challenged by osmotic stress outside their tolerance range, their first line of defence is behavioural: *i.e.*, they withdraw into their shell to avoid (or at least limit) exposure to external stress, minimizing water and salt exchange with the environment (Shick *et al.*, 1988). Such behaviour was observed in our experiment, as all organisms closed their shell when exposed to freshwater, even with food present. Once back in sea water, they

opened up, allowing them to access ambient oxygen and evacuate toxic wastes, explaining their survival during short periods of extreme hypoosmotic stress.

Isolation from the external environment becomes detrimental when the environmental stress persists, as the organisms lose access to oxygen, must resort to anaerobic metabolism, and cannot excrete their wastes (Shick *et al.*, 1988). This can lead to hypercapnia (*i.e.*, the accumulation of CO_2 in the tissues), acidosis caused by the buildup of toxic wastes and finally death (Shick *et al.*, 1988; Sokolova *et al.*, 2000a, 2000c). The vulnerability observed for *L. saxatilis* is consistent with findings from previous studies, where mortality began after 3 d of exposure to freshwater (Sokolova *et al.*, 2000a, 2000b). The low vulnerability of *Mytilus* spp. also aligns with Riley *et al.* (2022) where it survived for 14 d in freshwater. To the best of our knowledge, there has been no studies on freshwater exposure lasting several days for *M. balthica*. Studies have been conducted on their tolerance to anoxic conditions, which, similar to freshwater, cause them to retreat into their shells and resort to anaerobic metabolism (Babarro and De Zwaan, 2008; De Zwaan and Babarro, 2001; Wang and Widdows, 1993). Bivalves are usually excellent performers in anoxic conditions (De Zwaan and Eertman, 1996), with *M. balthica* exhibiting higher sensibility when compared to *Mytilus* spp. (Babarro and De Zwaan, 2008). When they use anaerobic metabolism, periwinkles (Sokolova *et al.*, 2000a, 2000b) and mussels (Isani *et al.*, 1995) exhibited ATP depletion and succinate accumulation, indicative of a transition from aerobic to anaerobic metabolism, as well as a decrease in internal pH due to toxic waste accumulation. The species-specific tolerance found in our study could therefore be linked to the species ability to better reduce their metabolic and ATP turnover rates during prolonged anaerobiosis and their efficiency to regulate their internal pH, as suggested in previous comparative studies (de Zwaan *et al.*, 1991; Sokolova *et al.*, 2000a, 2000b).

2.2.7.2 Energy budget under severe hypoosmotic stress

Longer periods of periodic exposure to freshwater lead to a reduction in growth and body mass in *L. saxatilis*, as well as body mass in *M. balthica*, while not affecting *Mytilus* spp. Our finding agrees with those by Sokolova (2000), who showed that fluctuating salinities

negatively affect juvenile *L. saxatilis*' shell growth rates. The high mortality and reduced growth observed with prolonged freshwater exposure suggest that facing durable hypoosmotic conditions represent an extreme challenge for *L. saxatilis*, which likely impose an adjustment to its energy allocation. During extended freshwater exposure and subsequent isolation, *L. saxatilis* likely reallocates energy from non-essential processes like growth to maintain acid-base regulation (Sokolova *et al.*, 2000b), damage repair (Kültz, 2005) and sustain energic homeostasis (Sokolova, 2021). Under extreme stress, organisms can enter a state of metabolic depression (Calosi *et al.*, 2013; Reipschläger and Pörtner, 1996), reducing energy requirements for maintenance and repair, and increasing the chances of survival while other non-essential processes are suspended (Sokolova *et al.*, 2012). Low salinity can also induce higher mineralization costs associated with diminished aragonite saturation (Sanders *et al.*, 2018). In contrast, growth is less affected by hypoosmotic stress in the two bivalve species investigated. This difference may partly be due to the structural differences between species; while the operculum of *L. saxatilis* has been shown to be an effective barrier for osmoregulation (Todd, 1964), it may not be as effective as the more robust valves of *M. balthica* and *Mytilus* spp. in withstanding prolonged freshwater exposure. *Macoma balthica* exhibits only a slight reduction in body mass at four weeks of prolonged freshwater exposure, while *Mytilus* spp. shows no significant growth reduction. Previous studies have documented growth reductions under constant low salinities in mussels (Westerbom *et al.*, 2002) and clams (Jansena *et al.*, 2009). It is intriguing that shell growth was not affected by freshwater exposure in both species, considering the likely higher cost of mineralization in undersaturated conditions (Sanders *et al.*, 2018). However, trade-offs in shell thickness or composition may explain the lack of changes in shell growth (Clark *et al.*, 2020). Short and frequent flooding, like in our scenarios, require organisms to open and close their shells more frequently and to spend more energy on osmo-regulation due to salinity fluctuations (Erk *et al.*, 2011). This could partially explain why mussels' energy content decreases over time under short but frequent freshwater exposure. In addition, it is likely that individuals with lower energy reserves died earlier in the prolonged freshwater exposures, which would have contributed to the higher mean energy content observed in surviving individuals. This would

suggest that only mussels with greater energy reserves were able to withstand the more extreme conditions. Finally, although bivalves were fed once a day, they did not have access to food *ad libitum*, contrary to the periwinkles, as suspended matter could not be properly contained in the open-flow system. This may have resulted in some food limitation for the bivalve species tested here, thus limiting the amount of energy available for repair, maintenance, shell growth and storage even in the control treatment.

The limited or null impact of freshwater exposure on the growth of clams and mussels, respectively, coupled with their relatively high survival levels, suggest that they are far better equipped to cope with extended periods of isolation within the shell, when compared to *L. saxatilis*. Mussels are very efficient in reducing their metabolic rate during stressful periods (Isani *et al.*, 1995), and can reduce their energy utilization rate under anoxic conditions to less than 5 % (De Zwaan and Eertman, 1996). Other processes can also reduce energy expenditure, like the use of alternative metabolic pathways (*e.g.*, the production of alternative end products to lactic acid to limit acid buildup) and more efficient enzymatic strategies (Larade and Storey, 2002).

Finally, it is worth noting that individuals in our experiment were kept fully submerged throughout the six-week period, thereby eliminating regular exposure to air that would normally occur during low tide in their natural intertidal habitat, also during floodings. In this sense, this constant submersion represents an ecologically relevant but extreme scenario, simulating conditions during prolonged freshwater inflow events when water levels remain persistently high. During emersion at low tide, intertidal molluscs are able to conduct (to some degree) gas exchanges (Sandison, 1966; Simpfendörfer *et al.*, 1995) which may help alleviate O_2 depletion and CO_2 buildup during low salinity events. The absence of aerial exposure in our design may have intensified the physiological stress experienced by molluscs, especially under prolonged freshwater conditions. Future studies could incorporate tidal simulation during phases of exposure to sea water to explore how periodic access to air may mitigate the impacts of hypoosmotic stress.

2.2.7.3 Potential consequences for estuarine communities under climate change

While Najibi and Devineni (2018) showed that the most frequent floods in North America last less than 7 d, there is a lack of studies analyzing the average duration and frequency of floods, whether past, present or future. An increase in the frequency of flooding in the St. Lawrence region has also been observed over the past 100 years (Saint-Laurent *et al.*, 2010), and this trend is expected to continue in the next century (Turcotte *et al.*, 2020; Verhaar *et al.*, 2011). In particular, summer floods caused by intense precipitation on drier and less permeable soils are expected to increase in occurrence (Grenier *et al.*, 2024). However, floods caused by intense and short events such as heavy precipitation (Kendon *et al.*, 2014; Zeeb *et al.*, 2024) and rain-on-snow events (Bonsal *et al.*, 2019), are predicted to increase in frequency as climate change progresses. These extreme climatic events can lead to salinity drops to zero in typically marine parts of estuaries for several days *(Fernandez et al.*, 2006; Voynova *et al.*, 2016). Conversely, longer-term events (*i.e.*, snowmelt) are expected to become shorter due to reduced accumulation of snow in winter and earlier snowmelt (Burn and Whitfield, 2016). Moreover, shifting precipitation regimes are likely to require more frequent and prolonged openings of dam spillways (Lin *et al*., 2021), contributing to increasingly recurrent drops in estuarine salinity (Linhoss et al., 2023). Our study showed that estuarine mollusks tolerate short-duration floodings, even when repeated over several weeks. As such, increased flood frequency may pose only a minor threat to estuarine communities, as long as floods last no more than 2 d. Even though short-time floods may not cause strong mortality in mollusks species, the stress from these conditions may reduce energy investment in processes like reproduction, which could ultimately affect population dynamics in the long term (Sokolova *et al.*, 2012). In addition, the larval stages of estuarine species have been shown to be more vulnerable to hypoosmotic stress than adult stages (Bhatnagar and Crisp, 1965; Pruett *et al.*, 2021, 2022; Sokolova, 1995), so the increase frequency of summer flooding may be particularly detrimental to species that release larvae into the water column during this season. On the other hand, species like *L. saxatilis*, which are ovoviviparous and do not have a larval stage, can produce numerous offspring and rapidly recolonize with just a few individuals (Blakeslee *et al.*, 2021; Wilhelmsen, 1998). This

reproductive strategy may explain the species' persistence in estuarine areas with significant freshwater input where mussels are less present (Loiseau *et al.*, 2024), as direct and modified life history strategies were indicated as better adapted to tolerate extreme environmental conditions when compared to those with larval stages (Lucey *et al.*, 2015).

Finally, our study focused exclusively on complete freshwater injections (salinity 0), whereas salinity stress in natural systems can be far more complex. Factors such as the intensity and frequency of flooding events (*i.e.*, mean and variance in salinity and the fact that they occur as isolated events every so many months or years) can influence community structure (Kinne, 1971; McFarland *et al.*, 2022; Van Diggelen and Montagna, 2016). Flooding events also alter other water parameters, including dissolved oxygen, turbidity, and pH (Doretto *et al.*, 2019; Nichols, 1977; Voynova *et al.*, 2016). Although these stressors have been studied individually, their combined effects remain poorly understood (cf. Pruett *et al.*, 2021, 2022; Loiseau, 2025).

2.2.8 Conclusions and recommendations

In conclusion, based on the non-linear mortality responses of the mollusk assemblage to flooding scenarios, we show that repeated floodings shorter than 2 d do not appear to pose a significant risk to our studied mollusk assemblage, whereas longer freshwater exposure can become a threat. Therefore, under scenarios where dam openings are necessary, such as during extreme precipitation events, management strategies should prioritize short, even if frequent, openings. The species-specific responses we observed highlight the significant differences in vulnerabilities among estuarine species within the same phylum, emphasizing the importance of comparative studies like ours in developing more accurate ecosystem conservation strategies. Furthermore, we observed that individual size can influence survival, with "bigger is better" proving true for periwinkles but not for clams. This suggests avenues for further research that incorporate allometric approaches. Looking forward, it is crucial that future studies incorporate multiple stressors to better reflect the complexity of environments, as marine communities face increasing anthropogenic pressures.

2.2.9 CRediT author statement / Contribution

Valentine Loiseau: Conceptualization, methodology, formal analysis, investigation, data curation, writing – original draft, visualization; **Piero Calosi**: Conceptualization, methodology, resources, Writing - Review & Editing, Supervision; **David Drolet**: Conceptualization, methodology, Writing - Review & Editing; **Mathieu Cusson**: Conceptualization, methodology, Writing - Review & Editing, Supervision; **Yanick Gendreau**: Conceptualization, methodology, resources, Writing - Review & Editing, Supervision, Project administration, Funding acquisition.

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CHAPITRE 3
LES CONDITIONS D'INONDATION PRINTANIERE AMPLIFIENT LA SENSIBILITE AU STRESS HYPOOSMOTIQUE DES MOLLUSQUES D'ESTUAIRES SUBARCTIQUES

3.1 RÉSUMÉ EN FRANÇAIS DU TROISIÈME CHAPITRE

Les estuaires sont des écosystèmes dynamiques façonnés par l'interaction entre les eaux douces des rivières et les eaux salées des marées océaniques. Ils abritent des communautés biologiques diversifiées et fournissent des services écologiques essentiels, tels que le transfert des nutriments et la création d'habitats pour de nombreuses espèces. Cependant, les estuaires sont de plus en plus menacés par les changements globaux, car l'intensification du cycle hydrologique accroît le risque d'événements extrêmes, tels que les inondations. Les crues printanières, en particulier, provoquent des changements brusques dans les conditions abiotiques des estuaires, notamment une diminution de la salinité et du pH, ainsi qu'une augmentation de la turbidité. Malgré de nombreuses recherches sur ces facteurs de stress individuels, leurs effets combinés restent peu étudiés, en particulier dans le contexte des estuaires subarctiques et des cours d'eau acides de ces régions. Cette étude examine les effets des conditions de crues printanières (c.-à-d. acidification côtière et augmentation des solides en suspension totaux) le long d'un gradient de durées de pulses d'eau douce sur trois espèces marines clés présentes dans les estuaires subarctiques *: Littorina saxatilis, Macoma balthica* et *Mytilus* spp. Nous émettons l'hypothèse que des pulses d'eau douce prolongées augmenteront la mortalité et réduiront la croissance de toutes les espèces en fonction de seuils de sensibilité spécifiques à chacune. De plus, nous prévoyons que les conditions de crue printanières exacerberont ces effets négatifs en abaissant les seuils de sensibilité à la faible salinité de manière spécifique à chaque espèce. Nous anticipons également que les conditions de crue entraîneront une dissolution des

coquilles, bien que le ratio des coquilles devrait rester inchangé face au stress hypoosmotique ou aux conditions de crue. Enfin, nous supposons que la sensibilité globale des espèces augmentera dans l'ordre suivant : *Mytilus* spp. < *M. balthica* < *L. saxatilis*. Pendant cinq semaines, des spécimens ont été exposés en laboratoire à de l'eau douce en l'absence de conditions de crue (salinité 0, pH 7,7, turbidité 0 mg L^{-1}) et à de l'eau douce simulant une « crue printanière » (salinité 0, pH 5,7, turbidité 325 mg L^{-1}) selon un gradient de 12 durées de pulses allant de 0 à 9 jours, entrecoupées de 24 h d'exposition à l'eau de mer (salinité 28, pH 7,8, turbidité 0 mg L^{-1}). La mortalité, la croissance des coquilles, le ratio des coquilles et leur dissolution ont été comparés après 2,5 et 5 semaines d'exposition à l'aide de modèles mixtes linéaires et d'analyses de points de rupture. Les résultats ont montré des réponses hautement spécifiques aux espèces, *L. saxatilis* affichant la mortalité la plus rapide et la plus élevée, atteignant 100 % après 5 semaines sous des pulsations d'eau douce prolongées en présence de conditions de crue. En revanche, *M. balthica* et *Mytilus* spp. ont montré une plus grande tolérance, bien que la mortalité ait augmenté dans les deux espèces avec la durée des pulsations d'eau douce, en particulier dans des conditions de crue. La dissolution des coquilles de *L. saxatilis* augmentait avec la durée des pulsations en conditions de crue printanière, tandis que la croissance des coquilles et le ratio des coquilles étaient marginalement affectés. *Macoma balthica* et *Mytilus* spp. n'ont montré aucune dissolution des coquilles et peu, voire pas, de changements de croissance. Nos résultats soulignent la nécessité d'étudier les facteurs de stress combinés pour une gestion efficace des écosystèmes estuariens, car les conditions d'inondation printanière augmentent fortement la mortalité lorsqu'elles sont combinées à l'exposition à l'eau douce. Les réponses spécifiques aux espèces suggèrent que la composition et les fonctions des communautés pourraient changer avec des précipitations extrêmes et des inondations plus fréquentes dues au changement climatique. La gestion des conditions abiotiques des rivières, en particulier le pH et la turbidité, sera essentielle pour préserver la biodiversité et les fonctions des écosystèmes dans un contexte de changements globaux.

Cet article, intitulé « S*pring flood conditions differently amplify species-specific hypo-saline vulnerability in subarctic estuarine mollusks* » sera soumis au journal *Limnology and*

Oceanography lorsque les analyses d'alcalinité auront été faites sur les échantillons d'eau. Tous les auteurs ont participé à la conceptualisation du projet et de sa méthodologie et à la révision de l'article. Comme première auteure, je me suis chargée de la mise en place du système expérimental, de la collecte et de l'analyse des données, ainsi que la rédaction de l'ébauche originale. Dr. Yanick Gendreau, Prof. Piero Calosi et Prof. Mathieu Cusson ont contribué à la supervision du projet, à la gestion des ressources, à l'administration du projet et à l'acquisition de financement. Dr. David Drolet a également participé à la construction du système expérimental. Une version abrégée de l'article a été présentée à la Réunion Scientifique Annuelle de Québec-Océan à Rivière-du-Loup (CA) en hiver 2023 sous forme d'affiche. Les résultats ont aussi été présenté à la Conférence Annuelle de la *Society for Experimental Biology* à Édimbourg (Royaume-Uni) en été 2023 sous forme d'une présentation orale, et à Prague (République Tchèque) en été 2024 sous forme de présentation oral et d'affiche.

3.2 SPRING FLOOD CONDITIONS DIFFERENTLY AMPLIFY SPECIES-SPECIFIC HYPO-SALINE VULNERABILITY IN SUBARCTIC ESTUARINE MOLLUSKS

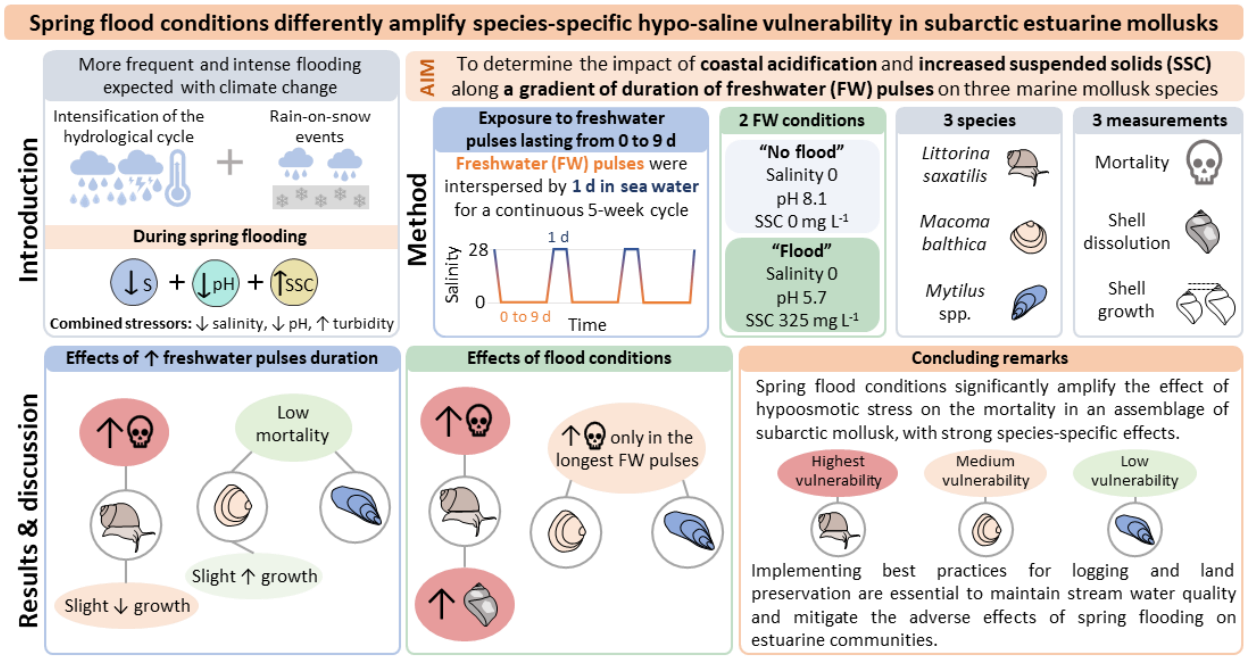
3.2.1 Abstract

Estuaries are dynamic ecosystems shaped by the interaction of freshwater from rivers and saltwater from oceanic tides. They support diverse biological communities and provide essential ecological services, such as nutrient cycling and the provision of habitats for numerous species. However, estuaries are increasingly threatened by climate change, as the intensification of the hydrological cycle increases the risk of extreme events such as flooding. Spring floods in particular cause abrupt changes in estuaries' abiotic conditions, including decreasing in salinity and pH and increasing turbidity. Despite extensive research on these individual stressors, their effects in combination remain understudied, especially in the context of subarctic estuaries and acidic subarctic streams. This study examines the effects of spring flood conditions (*i.e.*, coastal acidification and increased total suspended solids) along a gradient of freshwater pulse durations on three key marine species found in subarctic estuaries: *Littorina saxatilis*, *Macoma balthica* and *Mytilus* spp. We hypothesise that longer freshwater pulses will increase mortality and reduce growth in all species, according to species-specific sensitivity thresholds. In addition, we expect that flood conditions will exacerbate these negative effects by advancing sensitivity thresholds to low salinity in a species-specific manner. We also anticipate that flood conditions will lead to shell dissolution, but that shell aspect ratio (*i.e.*, the relation between shell height and shell width) will remain unaffected by hypoosmotic stress or flood conditions. Furthermore, we expect that the overall vulnerability of species to increase according to the order: *Mytilus* spp. < *M. balthica* < *L. saxatilis*. For 5 weeks, specimens were exposed under laboratory conditions to freshwater in the absence of flood conditions (salinity 0, pH 7.7, turbidity 0 mg L^{-1}) and to 'spring flood' freshwater (salinity 0, pH 5.7, turbidity 325 mg L^{-1}) along a gradient of 12 freshwater pulse durations lasting between 0 and 9 d, interspersed with 24 h exposure to sea water (salinity 28, pH 7.8, turbidity 0 mg L^{-1}). Mortality, shell growth, shell aspect ratio and shell dissolution were compared at 2.5 and 5 weeks of exposure using linear mixed models

and break-point analyses. Results showed highly species-specific responses, with *L. saxatilis* exhibiting the fastest and highest mortality, reaching 100 % at 5 weeks under longer freshwater pulses in the presence of flooding conditions. In contrast, *M. balthica* and *Mytilus* spp. showed greater tolerance, although mortality increased in both species with the increasing duration of freshwater pulses, particularly under flooding conditions. Shell dissolution increased with freshwater pulse duration under spring flood conditions in *L. saxatilis*, whilst shell growth and aspect ratio were only marginally affected. *Macoma balthica* and *Mytilus* spp. displayed no shell dissolution, and little to no changes in growth. Our findings underscore the critical need to investigate combined stressors for estuarine ecosystems effective management, as flood conditions strongly increased mortality when combined to freshwater exposure. Species-specific responses suggest that community composition and functions may shift with more extreme precipitation and flooding due to climate change. Managing river abiotic conditions, especially pH and turbidity, will be crucial for maintaining biodiversity and ecosystem functions under global changes.

Keywords: hypoosmotic stress, coastal acidification, multiple stressors, global change, turbidity, interaction, combined stress, bivalve, gastropod

3.2.2 Visual abstract



3.2.3 Highlights

- Flood conditions (low pH, high turbidity) and hypoosmotic stress had strong species-specific effects.
- Flood conditions amplified the effect of hypoosmotic stress on mortality.
- *Littorina saxatilis* showed the highest vulnerability to hypoosmotic stress and flood conditions.
- Flood conditions induced shell dissolution only in *L. saxatilis*, contributing to its vulnerability.
- *Mytilus* spp. was the most tolerant species to hypoosmotic stress and flood conditions.

3.2.4 Introduction

Estuaries are among the most complex and productive ecosystems, characterized by a unique interplay of conditions driven by the cyclic input of freshwater from rivers, and saltwater from marine tides (Broadley *et al.*, 2022). These environments support diverse biological communities and offer significant ecological and economic services, such as nutrient cycling and carbon sequestration, and provide habitats for numerous species, including commercially important fish and invertebrates (Savage *et al.*, 2012). The productivity and ecological significance of estuaries stem from their dynamic nature, where abiotic factors such as salinity, pH and turbidity fluctuate cyclically and stochastically along discrete gradients (Broadley *et al.*, 2022). Species inhabiting these dynamic environments have evolved adaptations that allow them to cope with and thrive under such extreme and variable conditions (Elliott and Quintino, 2007). These adaptations include efficient osmoregulatory mechanisms (Freire *et al.*, 2003), osmotic-stress avoidance behavioural strategies (Castellano *et al.*, 2018), and life-cycle adjustments to optimize survival and reproduction (Charmantier *et al.*, 2001). However, with ongoing anthropogenically driven environmental changes, including climate change and pollution, future extremes may exceed the current environmental tolerance windows of these species (Röthig *et al.*, 2023). As a result, the resilience of estuarine species and ecosystems is increasingly under threat (Bindoff *et al.*, 2019), requiring a deeper understanding of how these organisms will respond to the compounded effects of multiple stressors in a rapidly changing climate (Côté *et al.*, 2016; Stockbridge *et al.*, 2020).

Human-induced climate changes are leading to an increase in extreme climatic events, such as heavy rainfall, which are expected to continue intensifying (IPCC, 2023b; Jong *et al.*, 2023; Tabari, 2020). In northern latitudes, the hydrological regime is also expected to shift from a snow- to a rain-dominated one in the next century, with earlier snow-melt and an increase in rain-on-snow events that can cause floodings (Boyer *et al.*, 2010). Additionally, agricultural land expansion and deforestation make surfaces less permeable, also favoring runoff and flooding (Mao and Cherkauer, 2009; Bathurst *et al.*, 2020). Floodings cause

abrupt shifts in key environmental conditions in estuarine waters. Salinity can drop drastically and take up to two months to return to usual values throughout the estuary (Nichols, 1977; Voynova *et al.*, 2016). Very high suspended sediment concentrations can be observed for over a week (Nichols, 1977), to values that differ greatly among rivers and estuaries, influenced by, among other factors, land use, rainfall patterns, soil moisture and hydrology (Vercruysse *et al.*, 2017). Finally, the acidification of surface water can naturally occur in subarctic streams during spring floodings, due to the flushing of organic acids and dissolution of base cations, a phenomenon which is defined as "coastal acidification" (Alexander *et al.*, 2017). This process can be exacerbated by acidic rainfall or pre-existing acidic deposition, leading to more severe episodes of decrease in water pH lasting from days to weeks (Marty *et al.*, 2021). Clear-cut logging can also contribute to streams acidification, as whole-tree harvesting depletes the soil of base cations (*e.g.*, Ca and Mg), reducing the buffering capacity of soils and increasing the risk of acidification of surface waters (Akselsson *et al.*, 2007).

Exposure to low salinity, low pH, and high turbidity each separately imposes significant physiological stress on marine invertebrates. Hypoosmotic stress forces organisms to reallocate energy towards osmo-ionic-regulation, often reducing growth, reproduction, and survival (Podbielski *et al.*, 2022a; Sokolova, 2000; Tan *et al.*, 2023). Estuarine acidification can lead to tissue damage and reduced survival rates (Dove and Sammut, 2007a; Proum *et al.*, 2017), as well as shell dissolution due to calcium carbonate dissolution (Marshall *et al.*, 2008). Aragonite and high-Mg calcite are affected to an higher degree under more corrosive waters (*i.e.*, under low saturation conditions) when compared to low-Mg calcite as they are more soluble, hence mollusks that rely on them for their shells may experience a greater challenge in maintaining shell's integrity (Findlay *et al.*, 2009; Morse *et al.*, 2007; Ries *et al.*, 2009). Finally, high turbidity often results in sedimentation, which negatively impacts invertebrate communities by increasing mortality, particularly in sessile species unable to avoid burial (Thrush *et al.*, 2003). However, an increase in turbidity can also be beneficial for filter-feeding organisms, if it is associated to a greater availability of suspended organic matter (Hawkins *et al.*, 1996; Rubin *et al.*, 2017).

Marine mollusks show some osmoregulatory capacity when expose to low salinity (Medeiros *et al.*, 2020) or low pH (Melzner *et al.*, 2009; Whiteley, 2011). Sessile or low-mobility species, which cannot displace themselves from environment conditions outside of their tolerance range, can also use behavioral mechanisms to respond to these stressors. For example, marine gastropods and bivalves retreat into their shells, reducing tissue contact with the external environment during freshwater exposure (Sokolova *et al.*, 2000a; Woodin *et al.*, 2020) or when the pH drops drastically (Proum *et al.*, 2017). However, this "isolation" strategy can lead to hypoxemia and hypercapnia, and increased mortality, due to limited access to oxygen, disrupted homeostasis and buildup of toxic waste (Berger and Kharazova, 1997; Sokolova *et al.*, 2000a). If the shell's integrity is compromised, organisms isolation from environmental factors is also compromised, making them more vulnerable to environmental challenges and more exposed to predation risks (Dove and Sammut, 2007b; Amaral *et al.*, 2012).

While each of these stressors in isolation has been well studied, there is an important gap in our critical understanding of their combined effects (*c.f.*, Pruett *et al.*, 2021, 2022). This gap is particularly critical as these stressors often occur simultaneously in nature during spring flooding, and the combined effects of multiple stressors can lead to ecological surprises (*i.e.*, non-additive and non-multiplicative responses), which are not predictable from the effects of each stressor alone (Côté *et al.*, 2016; Stockbridge *et al.*, 2020). Additionally, when using a gradient of a given environmental driver to investigate a species' tolerance, introducing other factors can increase the species' vulnerability, revealing new thresholds or shifting existing ones to lower levels along the first factor gradient (Carrier-Belleau *et al.*, 2023). Using both gradients and realistic combination of cooccurring stressors is therefore crucial for predicting ecological impacts and informing conservation efforts, by identifying critical thresholds where intervention may be most effective and determining which stressor to target to minimize negative effects (Carrier-Belleau *et al.*, 2022). In fact, despite their importance, studies investigating the combined effects of multiple stressors along a gradient of conditions remain scarce in estuaries (Carrier-Belleau *et al.*, 2022). In addition, studies using values of sea water pH corresponding to estuarine/coastal acidification (reduction in at least 1 pH unit

caused mostly by sulfuric or organic acids) rather than ocean acidification (reduction in ≈ 0.5 pH unit by century end, driven by CO_2 (Caldeira and Wickett, 2005, 2003), are scarce and investigate most often species from tropical climate (Dove and Sammut, 2007b; Proum *et al.*, 2017). These gaps in knowledge hinders our ability to develop effective management strategies to enhance the tolerance and resilience of subarctic estuarine ecosystems in the face of global changes.

The aim of our study was to determine the sensitivity of an assemblage of intertidal macroinvertebrates to spring flood conditions (*i.e.*, estuarine acidification and increasing turbidity) along a gradient of hypoosmotic stress. We hypothesize that: (i) longer durations of freshwater pulses will increase mortality and reduce shell growth whilst not affecting shell integrity and shell ratio; (ii) spring flood conditions will cause a greater level of mortality and shell dissolution whilst not affecting shell ratio; (iii) spring flood conditions will amplify the effect of freshwater exposure, by increasing its negative effects and / or by advancing tipping points to shorter freshwater pulse durations, and (iv) species- and trait-specific tipping points will be observed. Based on the literature and our previous experiment (**chapter 2**), we expect the tolerance to hypoosmotic stress to increase, for all traits, in the following order: *L. saxatilis* < *M. balthica* < *Mytilus* spp. Based on shell composition and known structure, we also expect the tolerance to flood conditions (*i.e.*, corrosive waters) to increase in the order: *M. balthica* (aragonite shell) < *L. saxatilis* (aragonite and low-Mg calcite shell) < *Mytilus* spp. (aragonite and low-Mg calcite shell and *periostracum*). In combined treatments of long freshwater exposure and flood conditions, we therefore expect *L. saxatilis* to be the most vulnerable species, and *M. balthica* and *Mytilus* spp. to be more tolerant.

3.2.5 Material and Methods

3.2.5.1 Study species

Three mollusk species were selected for our study: the blue mussel *Mytilus* spp. (Linnaeus, 1758, either *M. edulis* or *M. trossulus* or their hybrids in the St. Lawrence − see Moreau *et al.*, 2005), the rough periwinkle *Littorina saxatilis* (Olivi, 1792) and the Baltic clam *Macoma balthica* (Linnaeus, 1758). These species form a major part of the benthic communities they inhabit in the intertidal habitats of the North Atlantic coasts (Dexter, 1947; Khaitov, 2013). They all very frequently cooccur in river estuaries although clams live in soft sediments, while the other two species are found on hard substrates (Khaitov, 2013). *Littorina saxatilis* feeds on both micro- and macroalgae and is a dominant species in the intertidal zone in estuaries (Dexter, 1947; Loiseau *et al.*, 2024). *Macoma balthica* is both a filter and a deposit feeder that can use its siphon in a fixed position or actively extend and move it around on the sediment to collect deposited food particles (Skilleter and Peterson, 1994). It plays a crucial role in connecting the water and sediments by engaging in intense bioturbation activity, which enhances the flow of oxygen and nutrients (Michaud *et al.*, 2005, 2006). *Mytilus* spp. actively filters suspended matter (*i.e.*, phytoplankton, bacteria, detritus and dissolved organic matter), and is highly efficient at improving water quality (Timmermann *et al.*, 2019).

3.2.5.2 Specimen collection, acclimation, and preparation

Between September 7th and 9th, 2021, 900 indiv. of each species were collected in three out of four river estuaries (Mistassini, Franquelin, St. Nicolas and Barthelemy) on the North shore of the St. Lawrence marine estuary (QC, Canada, **Figure A.8**). We collected specimens from several estuaries to mitigate the possible effects of adaptation to freshwater input regimes that could vary among estuaries (Bible and Sanford, 2016; Marshall *et al.*, 2021). Mussels and periwinkles were collected in Mistassini (49° 17’ N, 67° 56’ W), Franquelin (49° 17’ N, 67° 53’ W) and St. Nicolas (49° 18’ N, 67° 47’ W) and clams in Mistassini, St. Nicolas and Barthelemy (49° 02’N, 68° 35’W), since no clam was found in the Franquelin estuary, whereas there was very few periwinkles and mussels in the Barthelemy estuary. To

limit the effect for difference in sizes during the experiment, the collected specimens were to measure between 0.5 to 1.0 cm for the periwinkles, 0.5 to 1.5 cm for the clams, and 1.5 to 2.5 cm for the mussels. As the collection lasted 3 d, the organisms were placed at the end of each day in submerged mesh bags at the Baie-Comeau marina. They were brought back to the laboratory (Maurice-Lamontagne Institute, Mont-Joli, QC, CA) in less than 6 h, in bags wetted in seawater placed in coolers where the temperature was kept at the same temperature as the seawater (9 °C). Less than 1 % mortality was observed during the week following their arrival.

At the laboratory, the organisms were first quarantined for 2 d in a 1000 L outdoor pool, then placed in three indoor tanks (425 L, one *per* estuary of origin) supplied with a continuous flow of unfiltered sea water supplied directly from the St. Lawrence marine estuary. Prior to their arrival, the clams' tanks were filled with sediments collected from a small estuary near the laboratory. To remove all macroinfauna, the sediments were sieved through 0.5 mm mesh using freshwater, left to dry for 3 d, then sieved again, prior to being placed in the mesocosms. The mussels and periwinkles were placed in separate mesh containers that allow the water to flow through. The organisms were maintained under laboratory conditions for 8.5 months, until the beginning of the experiment. Temperature and salinity followed natural fluctuations during this part of the acclimation, with the temperature decreasing steadily from a maximum of 10.8 °C to the minimum of 1.5 °C (mean ± SE: 5.6 °C ± 0.3), and the salinity varying from 24.6 to 30.6 (27.0 ± 0.1). During this period, the periwinkles were fed *ad libitum* with boiled lettuce *Lactuca sativa*, while the mussels and the clams were fed every 2 d with a concentrated mix of five marine microalgae (Shellfish Diet 1800®, Reed Mariculture Inc., Campbell, CA, USA), following the recommendation of 0.06 mL of Shellfish Diet 1800 *per* gram of wet meat weight for conditioning. The mortality was checked every 2 d and was around 1.5 % w^{-1} for the periwinkles and < 1 % w^{-1} for the clams and mussels for most of the 8.5 months. During the first three weeks of October, we observed a high mortality in the periwinkles (300 indiv. from St. Nicolas, 155 indiv. from Mistassini, and 109 indiv. from Franquelin) but we were not able to assess the cause, despite verifying multiple factors: *i.e.*,

oxygen level, ammonia concentration, temperature, pH, presence of a parasite outbreak. The mortality rates returned to previous mortality rates after this 3-week period.

Each specimen was tagged with a bee marking number (Queen Marking Number Kits, Dancing Bee Equipment, Port Hope, ON, Canada), photographed with a high-resolution digital microscope (VHX-7000, Keyence, Mississauga, ON, CA), and weighed with a high-precision scale (XPE205, Mettler Toledo, Mississauga, ON, Canada). Fourteen days prior to the beginning of the experiment, eight indiv. *per* species and estuary of origin were distributed into 48 mesocosms (5 L buckets, height 15 cm, diam. 21 cm, two replicates *per* treatment). The bottom of each mesocosm had been filled with 5 cm of sediment (same origin and handling as previously described) for the clams to bury themselves (Reading and McGrorty, 1978; Zwarts *et al.*, 1994). The periwinkles and mussels were placed in separated submerged meshed containers to prevent them from reaching the surface and escape from treatments' conditions. Three days after they were placed in the mesocosms (*i.e.*, 11 d before the beginning of the experiment), the temperature was slowly raised from the temperature of the acclimation tank (2.2 °C) to the experimental temperature (5.7 °C) at a rate of 0.5 °C d^{-1} (Clements *et al.*, 2018; Lasota *et al.*, 2018). During the 14 d of exposure to experimental conditions in the system, the mortality rates stabilized around 1.5 % w^{-1} for the periwinkles and clams, and < 1 % w^{-1} for the mussels. Dead indiv. were replaced by surplus indiv. that were subjected to the same exposure process and conditions.

3.2.5.3 Experimental design

To investigate if freshwater exposure and spring flood conditions affect the mortality, growth and shell integrity of mollusks, we exposed specimens to one of 12 levels of freshwater pulse duration ranging from 0 to 9 d (*i.e.*, 0, 1, 2, 3, 3.5, 4, 4.5, 5, 6, 7, 8 and 9 d), interspersed with 24 h of exposure to sea water (**Figure 24**), during a continuous cycle of five weeks, with or without "spring flood" conditions (*i.e.*, low pH and high turbidity, hereafter "flood conditions"). To determine ecologically relevant and realistic pH and temperature values to use in our study, we compiled monthly data from 2017 to 2019 collected by Réseau-Rivière for seven rivers near the sampling sites, including the Franquelin River where mussels and

periwinkles were sampled (Ministère de l'environnement, de la lutte contre les changements climatiques, 2019). In May, the mean pH was of 6.2 (min 5.7, max 6.6) and the temperature of 5.7 °C (min 5.3 °C, max 5.9 °C). As floods usually cause a decrease in pH (Voynova *et al.*, 2016), we used the lowest value registered (*i.e.*, pH 5.7) for our experiment. For the suspended sediment content (SSC), we used a concentration of 350 mg L^{-1} for our study, as it was frequently found during flooding and snowmelt events in rivers and estuaries (Oeurng *et al.*, 2010; Beltaos and Burrell, 2016; Le Gall *et al.*, 2017). To assess the effect of flood conditions across all freshwater pulse durations, we conducted parallel freshwater pulses in the absence of flood conditions, using untreated freshwater ("no flood conditions": salinity 0, pH 7.7, turbidity < 1 mg L^{-1}). [*To the members of the jury: we will be analysing* $\Omega_{aragonite}$ *and* $\Omega_{calcite}$ *prior to the submission of the article, but the water samples could not be analyzed before the thesis submission due to shortage in standards necessary for the analyses*]

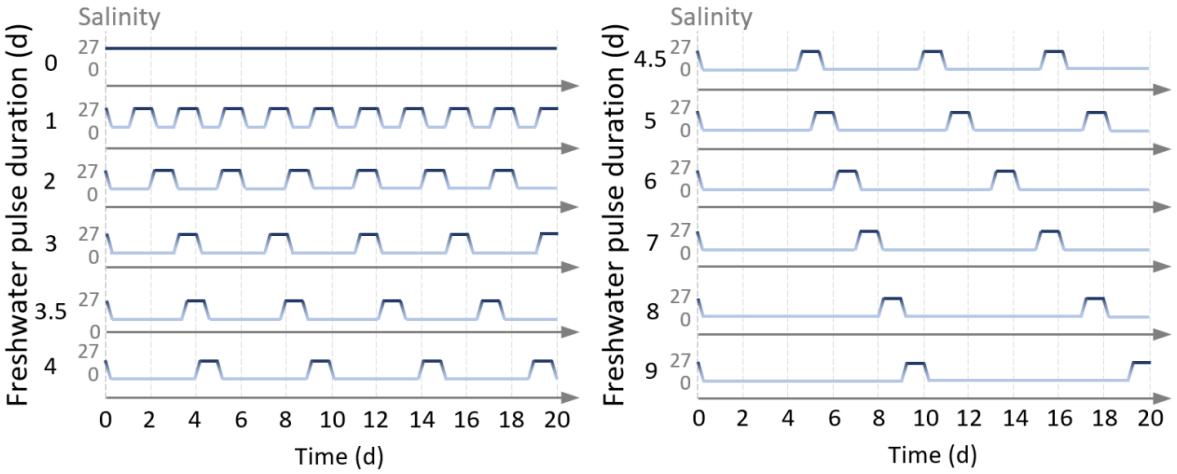


Figure 24. Schematic representation of the experimental design used, for the "flood" and "no flood" conditions. Each line represents the salinity in one treatment, with freshwater pulses (pale blue) ranging from 0 to 9 d in duration, interspersed by 1 d in sea water (dark blue). Only the first 20 d are represented here to achieve a greater clarity, but the experience lasted 5 weeks.

3.2.5.4 Experimental system and protocol

The experimental system consisted of three 250 L head tanks. The first one was filled with filtered sea water supplied directly from the St. Lawrence and the second with drinkable

municipal freshwater (*i.e.*, the "no flood" freshwater). In each of these two tanks, the temperature was controlled using a heat pump (Gell'Air, Mont-Joli, QC, Canada). The third tank contained the "spring flood freshwater" (*i.e.*, low pH and high turbidity, hereafter "flood" freshwater) and was supplied with freshwater coming from the second tank (**Figure A.9**). In the "flood" freshwater tank, the pH was controlled with an automatic system (IKS aquastar, IKS Computer System, Karlsbad, Germany) that allowed a 0.05 variation in pH values using a 10 % sulfuric acid aqueous solution (Bamber, 1987; Calosi *et al.*, 2007) delivered by a peristaltic pump. Sulfuric acid was used as low pH values found during flood events are often linked to acidic deposition (Lacoul *et al.*, 2011; Fuss *et al.*, 2015; Riscassi *et al.*, 2019). The accuracy of the pH electrode was tested every day using pH 4.01 and 7.01 buffers, and it was calibrated once a week, or on any occasion that it was found to deviate from expected values. The suspended sediment content was adjusted manually daily, based on the water volume coming out of the tank and on the turbidity measured in the head tank every minute by a turbidity sensor (ECO FLNTU, Sea-Bird Electronics, Bellevue, WA, USA) mounted on a CTD profiler (SBE 19plus V2 SeaCAT Profiler CTD, Sea- Bird Electronics). The suspended sediments were composed of 90 % of inorganic mater (kaolin clay) and 10 % of organic matter (organic *Spirulina* powder, Organika, Vancouver, CA), to simulate spring flood conditions (McConnachie and Petticrew, 2006). They were delivered in the header tank with a peristaltic pump (Masterflex 7553-20, Cole Parmer Instrument Co., Vernon Hills, IL, USA) from a 60 L reservoir where the sediments were highly concentrated (50 g L^{-1}, mixed every 45 s for 15 s, emptied and refilled every 2 to 3 d with 50 L of water, 2 700 g of kaolin clay and 300 g of *Spirulina* powder).

For each treatment, precise control over freshwater and seawater exposure was achieved using actuated three-way ball-valves connected to the seawater tank and one of the freshwater tanks (*i.e.*, either the "no flood" or the "flood" freshwater tank) and controlled by a timer. It allowed only seawater or only freshwater to pass into two replicates, at a flow of 0.7 L min^{-1} (**Figure A.10**), allowing a complete change from freshwater to sea water (and *vice versa*) in 15 min.

The experiment took place from 15 March 2022 to 20 April 2022. The mortality and behaviour of the studied mollusks species were verified daily for periwinkles and mussels, and the dead specimens were taken out and replaced by spare indiv. to maintain a constant density and ensure good water quality levels. Periwinkles were categorized based on their activity level: they were recorded as 'active', if they were moving outside their shells, or 'inactive', if they were tightly enclosed in their shells, with the operculum not moving when gently pressed with forceps. If the periwinkle was outside its shell, but did not respond to multiple gentle stimuli, or if it was inside its shell with the operculum collapsing under a slight pressure without response, it was recorded as 'dead'. Mussels were marked as 'inactive' if they were tightly closed, 'active' if they were open and responding to touch by closing, and 'dead' if they were open and unresponsive. As clams live buried in the sediment, their behavior could not be observed, so indiv. were noted as dead and replaced when empty shells appeared on the sediment surface.

In each mesocosm, the temperature, pH and salinity were measured daily with a multimeter (Water Quality Meter, HI98194, Hanna instruments, Woonsocket, RI, USA). The dissolved oxygen was measured once a week with an oxygen meter (FireSting GO2, Pyroscience, Aachen, Germany). Once a day, 1 L of water was taken from each water line (“flood” freshwater, “no flood” freshwater, and sea water) and the sediment content was measured for both freshwater lines by filtering 200 mL of untreated water and 50 mL of “flood” freshwater in a 45 μm mesh and by weighting the dried (total SSC) and burned (inorganic SSC) residues (**Figure A.11**).

The pH and suspended sediment levels were significantly distinct between “flood” and “no flood” freshwater during the entire duration of the experiment (**Table 8**, **Figure A.12**). However, despite our best efforts, there was a minimal but significant difference in temperature between the treatments (**Table A.**, **Figure A.12**). The “flood” freshwater reached the 5.7 °C as wanted, as it was the mean temperature in May (see previous section) whilst the mean temperature of 5.2 °C that was measured in the “no flood” freshwater and in

the sea water (**Table 8**, **Table A.**, **Table A.19**) is still in the range of realistic temperature that

can be measured in May in the same rivers. We strongly believe that these differences in the mean temperature did not influence our results, based on (i) the ability of the selected species to live in the intertidal zone, where abiotic parameters largely vary hourly, daily and seasonally, (ii) the fact that both 5.2 and 5.7 °C are well within the thermal tolerance range of the three species (Sokolova and Pörtner, 2003; Jansen *et al.*, 2007), and (iii) within the temperature rang found in the St. Lawrence (weekly mean temperature of -1 °C in February to 12 °C in July (Galbraith *et al.*, 2022). Similarly, the dissolved oxygen was lower in the "no flood" freshwater (**Table 8**, **Figure A.12**), but still falling under high levels of oxygen saturation that should not represent a stress for the three species.

Table 8. Summary of mean values (± SE) for the physico-chemical parameters controlled under the two scenarios.

Treatment	"Flood" freshwater	"No flood" freshwater	Sea water
Salinity	0.47 (± 0.62)	0.40 (± 0.41)	26.79 (± 1.36)
pH	5.74 (± 0.25)	7.71 (± 0.11)	7.83 (± 0.06)
Temperature (°C)	5.68 (± 0.25)	5.17 (± 0.24)	5.24 (± 0.59)
Dissolved oxygen (% of sat.)	90.18 (± 4.61)	84.70 (± 6.58)	91.60 (± 4.42)
Total suspended sediment (mg L^{-1})	323.77 (± 36.52)	0.01 (± 0.01)	-
Inorganic matter (mg L^{-1})	304.04 (± 35.25)	0.01 (± 0.01)	-
Organic matter (mg L^{-1})	19.73 (± 1.36)	0.01 (± 0.03)	-

After two and a half and five weeks, four indiv. of each species and mesocosm were promptly dissected and the shells were placed in individual containers in a cold room at - 20 °C until they were photographed using the digital microscope mention above (VHX-7000, Keyence).

3.2.5.5 Determination of shell dissolution, growth, and aspect ratio

To measure the effect of the freshwater pulse duration and spring flood conditions on the shell growth rate, shell dissolution and shell aspect ratio of mollusks, we compared the shell

dimensions and shell dissolution before and after the experiment. We used four indiv. collected in each replicate after two and half and five weeks in each mesocosm, which enabled us to test for the effect of freshwater pulse duration and flood conditions over time. Pictures taken with the high-resolution digital microscope (VHX-7000, Keyence) were put in random order before measurement to avoid perception biases by the observer. We outlined the total shell surface and the dissolved area of each specimen by using the ImageJ software (Abràmoff *et al.*, 2004). Only the areas that had completely lost at least the first layer of the shell were considered as "dissolved", which was either grey or black in *L. saxatilis*, grey in *M. balthica* and grey or pale pink in *Mytilus* spp. (**Figure 25**; method adapted from Gazeau *et al.*, 2014). The area covered by the number tag was considered as not dissolved. We calculated the shell dissolution as the difference of % shell dissolved before and after treatment relative to the total shell area. We measured the shell height (SH) and width (SW) on the same pictures and calculated the shell aspect ratio as SH / SW (**Figure 25**). Growth values were standardised by the number of days elapsed between the start and end of the experiment and by the initial size of the organism to give % change in length or width d^{-1}.

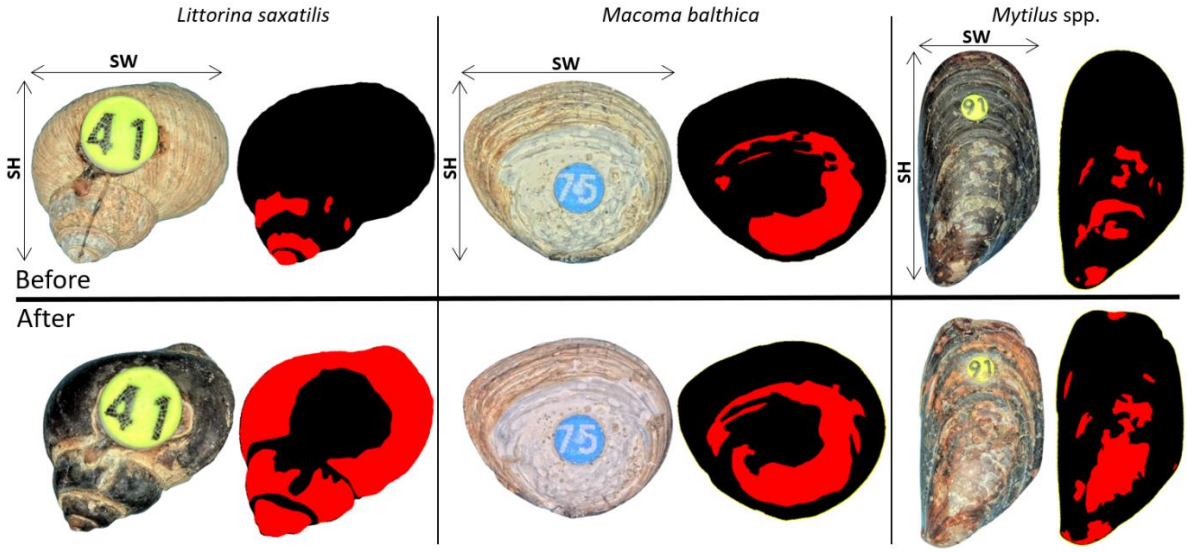


Figure 25. Examples of shell dissolution quantification for *Littorina saxatilis*, *Macoma balthica* and *Mytilus* spp. before (upper panel) and after (lower panel) 5 weeks of exposure to 9-day freshwater pulses under flood conditions. Total shell areas are in black and partly dissolved areas are in red. The shell height (SH) and shell width (SW) were measured on the

same pictures. Bee-keepers number measured 2 mm in diameter and were used as a reference scale to measure shell parameters.

3.2.5.6 Statistical analysis

We used linear mixed models to test the effects of the *Freshwater pulse duration* (*'Pulse duration'*, continuous), the *Flood conditions* (two levels: "no flood" or "flood"), the *Time* (two levels: 2.5 or 5 weeks), the *Species* (three levels), all set as fix terms, and their interaction on the mortality percentages, shell dissolution, shell growth rates and shell aspect ratio. Following preliminary analyses, given the significant effects of the term *Species*, in isolation and combined with other terms, we analyzed each species independently, and separately for the 2.5 and 5-week periods to evaluate the effects of *Pulse duration* and *Flood conditions* in isolation and combined. The random effects of *Mesocosm* and the *Estuary of origin* of the specimens were accounted for in the analyses, and the best model was selected for each species and trait using the Akaike information criterion (AIC). For shell growth rates, we added the initial size (*i.e.*, shell width or height) as a covariate (as in Melatunan *et al.*, 2013). We used the "lme4" package in RStudio (version 2024.4.0.735) to perform the linear mixed models. Diagnostic plots were used to check for the homogeneity of variance and normality of residuals for each model (Montgomery, 2012).

Additionally, when we detected a significant effect of the *Pulse duration* or a significant interaction between the *Pulse duration* and *Flood conditions*, break-point analyses were performed to estimate the presence of tipping-points (*i.e.*, an abrupt change in the slope, *sensu* Toms and Villard, 2015) along the gradient of freshwater pulse duration, using the "segmented" package (Muggeo, 2008). The best model (*i.e.*, with 0, 1 or 2 breakpoints) was chosen using the AIC. Davies tests (Davies, 1987) were performed to determine the significance of the difference in slopes before and after each breakpoint.

Finally, we displayed the mortality rates using Kaplan-Meier curve, and conducted Cox proportional hazard model, with death serving as the 'event', and time since the beginning of the experiment as the 'time until event' with the "survival" package (Lumley *et al.*, 2024) to assess the relationship between mortality rates and the freshwater pulse durations, flood conditions, initial individual body mass, and estuary of origin. The resulting hazard ratio (*HR*) of each explanatory variable estimates the risk of mortality: $HR > 1$ represent an

increased risk of mortality and *HR* < 1 a decreased risk of mortality. When diagnostics plots suggested that the effect of a factor varied over time, we divided the data into intervals of 2.5 weeks to examine how its impact changed over time. We used a significance level of α = 0.05 for all statistical analyses. We applied no corrections to *P* values to our planned contrasts.

3.2.6 Results

3.2.6.1 Mortality

In all species investigated, spring flood conditions (*i.e.*, low pH and high turbidity) significantly amplified the impact of the freshwater pulse duration on mortality ratios, and its effect varied long the gradient of freshwater pulse durations, as indicated by the presence of significant interactions between the two stressors for all species (**Table 9**, **Figure 26**). In addition, the superimposition of flood conditions to hypoosmotic stress exerted highly species-specific effects, which could manifest in three ways: (1) a consistently higher mortality across all pulse durations (*i.e.*, no interaction, as with *L. saxatilis* at 2.5 weeks); (2) a more pronounced increase in mortality in the longer freshwater pulses (*i.e.*, presence of an interaction, marked by significant differences in linear regression slopes or the emergence of a threshold, as with *M. balthica*); and/or (3) a shift of the onset of high mortality to shorter freshwater pulses (*e.g.*, with *L. saxatilis*). These negative effects also intensified over time.

Littorina saxatilis was the most vulnerable species, with mortality ratios significantly increasing after just 2.5 weeks, driven by both increasing freshwater pulse duration and flood conditions (**Table 9a**, **Figure 26A**). At this time point, the interaction between the stressors was not significant, indicating that the effect of exposure to flood conditions is consistent across the freshwater pulse duration gradient. Under flood conditions, mortality plateaued at around 60 % when freshwater pulses lasted more than the tipping point of 4.0 d (± 0.6). In the absence of flood conditions, mortality increased linearly with the freshwater pulse duration, reaching approximately 50 % at the longest pulse duration. At 5 weeks, the interaction between flood conditions and freshwater pulse duration became significant,

indicating a varying effect of flood conditions across the pulse duration gradient (**Table 9a**, **Figure 26B**). Under flood conditions, mortality exceeded 75 % once pulse durations surpassed the threshold of 1.3 d (± 0.1). Mortality remained low in the absence of flood conditions when specimens were exposed to freshwater pulses shorter than the threshold of 3.2 d (± 0.5), but then sharply increased until reaching a plateau at around 60 % of mortality for pulses longer than 5.3 d (± 0.6).

Flood conditions triggered the emergence of a threshold along the gradient of pulse duration in *M. balthica* at 2.5 weeks, with mortality increasing only for freshwater pulses longer than 7.6 d (± 0.5), which is also supported by a significant interaction between the stressors (**Table 9b**; **Figure 26A**). At 5 weeks, flood conditions amplified the negative effect increasing freshwater pulse duration, causing increasing mortality with longer freshwater pulses that was not observed in the absence of flood conditions (**Table 9b**; **Figure 26B**). However, no breakpoints were detected in the presence or absence of flood conditions at this time.

Finally, *Mytilus* spp. did not show significant changes in mortality at 2.5 weeks, regardless of the freshwater pulse duration or the presence / absence of flood conditions (**Table 9c**; **Figure 26A**). However, at 5 weeks, flood conditions increased mortality when the freshwater pulses were longer than 4.5 d (± 1.2), which was confirmed by the presence of a significant interaction between the freshwater pulse duration and flood conditions (**Table 9c**; **Figure 26B**).

Table 9. Summary of the results of the ANOVA tests showing the effects of the duration of freshwater pulses ('Pulse duration'), 'Flood conditions', and their interaction on the mortality ratios of (a) the rough periwinkle *Littorina saxatilis*, (b) the Baltic macoma *Macoma balthica* and (c) the blue mussel *Mytilus* spp. at 2.5 (left) and 5 weeks (right). Significant values are given in bold. The goodness of fit (R^2) represents the variance explained by the fixed effects only (R^2m) and by the fixed and random effects (R^2c). For all sources of variation, $df_1 = 1$.

	After 2.5 weeks					After 5 weeks			
Source of variation	**df_2**	**MS**	**F ratio**	***P* value**	**Source of variation**	**df_2**	**MS**	**F ratio**	***P* value**
a. *Littorina saxatilis*	R^2m: 0.56, R^2c: 0.70*					R^2m: 0.67, R^2c: 0.79***			
Pulse duration	44	2.2910	93.78	**<0.0001**	**Pulse duration**	44	2.3240	99.51	**<0.0001**
Flood conditions	44	0.3030	12.40	**0.0010**	**Flood conditions**	44	0.8733	37.39	**<0.0001**
Interaction	44	0.0471	1.93	0.1719	**Interaction**	44	0.1262	5.40	**0.0248**
b. *Macoma balthica*	R^2m: 0.15, R^2c: 0.19**					R^2m: 0.26, R^2c: 0.50***			
Pulse duration	138	0.0439	7.71	**0.0062**	**Pulse duration**	44	0.2085	18.65	**0.0001**
Flood conditions	138	0.0026	0.46	0.4968	Flood conditions	44	0.0034	0.30	0.5861
Interaction	138	0.0445	7.81	**0.0059**	**Interaction**	44	0.0791	7.08	**0.0109**
c. *Mytilus* spp.	R^2m: 0.02, R^2c: 0.02***					R^2m: 0.24, R^2c: 0.30*			
Pulse duration	140	0.0012	2.36	0.1270	**Pulse duration**	44	0.1728	31.31	**<0.0001**
Flood conditions	140	0.0001	0.20	0.6571	Flood conditions	44	0.0038	0.68	0.4132
Interaction	140	0.0003	0.62	0.4314	**Interaction**	44	0.0249	4.51	**0.0393**

* The best model included the 'Mesocosm' and 'Estuary of origin' as random factors

** The best model included only the 'Estuary of origin' as a random factor

*** The best model included only the 'Mesocosm' as a random factor

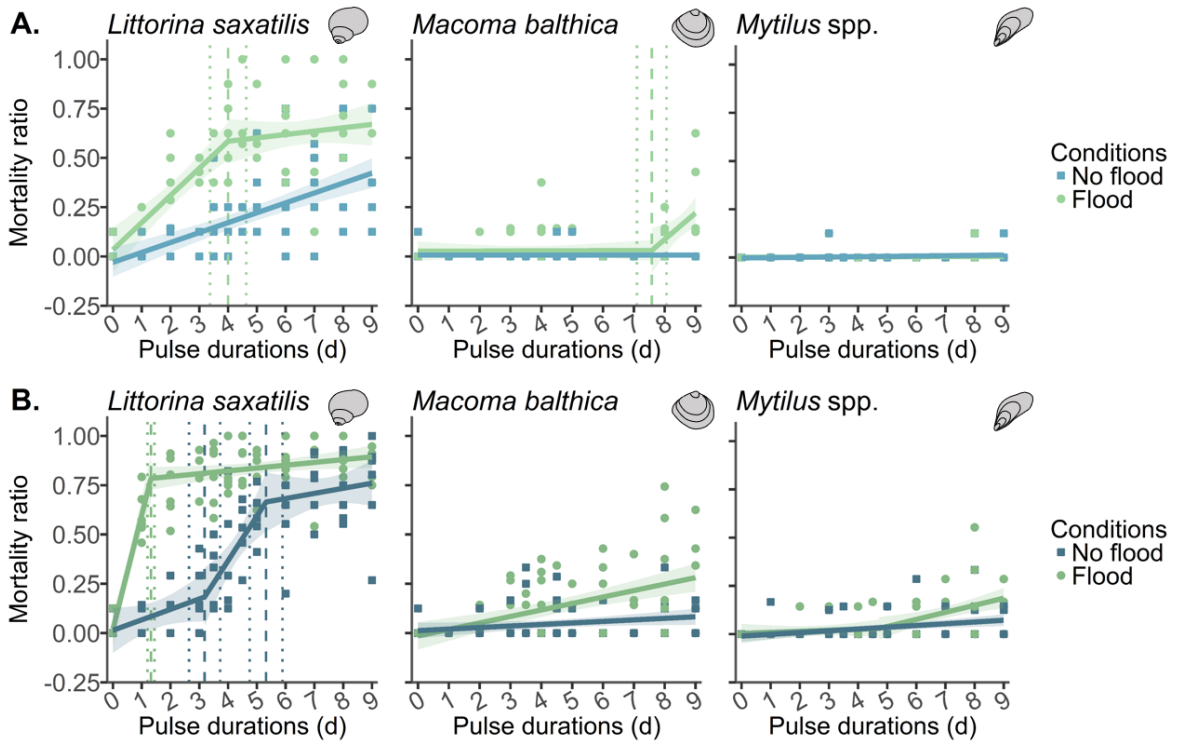


Figure 26. Relationship between the freshwater pulse duration and the mortality ratio of *L. saxatilis*, *M. balthica*, and *Mytilus* spp. at 2.5 (A) and 5 (B) weeks. Solid lines depict the optimal segmented or linear regression models without (blue) and with flood conditions (green), with 95% confidence intervals depicted by the shaded areas around the solid lines. Data points illustrate the mortality ratio measured *per* estuary of origin *per* mesocosm. Dashed vertical lines represent significant ($P < 0.05$) tipping points, with dotted lines at the 95 % confidence interval. When no tipping point was detected, linear models were depicted instead.

Survival probability significantly decreased under flood conditions for *L. saxatilis*, *M. balthica* and *Mytilus* spp. with an increase in mortality risk of 288 % ($HR = 3.88$, $P < 0.001$), 472 % ($HR = 5.72$, $P < 0.001$) and 121 % ($HR = 2.21$, $P = 0.011$) respectively (**Figure A.13**, **Figure A.14**). Freshwater pulse duration played a crucial role for the three species, each additional day in the freshwater pulse duration increasing mortality risk by 32 % ($HR = 1.32$, $P < 0.001$), 28 % ($HR = 1.28$, $P < 0.001$) and 41 % ($HR = 1.41$, $P < 0.001$) for *L. saxatilis*, *M. balthica* and *Mytilus* spp., respectively. Survival differed significantly among estuaries for the three species, but the most tolerant origin varied among species (see full results in **Figure A.13**). Finally, for *L. saxatilis* and *Mytilus* spp., larger individuals were more tolerant,

as each 0.1 g increase in initial body mass significantly reduced mortality risk by 51 % (*HR* = 0.48, *P* < 0.001) and 12 % (*HR* = 0.88, *P* = 0.001) (**Figure A.13**).

3.2.6.2 Shell dissolution and growth

Flood conditions caused shell dissolution of *L. saxatilis*, and its effect was consistent along the freshwater pulse duration gradient at 2.5 weeks, as indicated by the absence of a significant interaction between the freshwater pulse duration and flood conditions (**Table 10a**, **Figure 27**). However, at 5 weeks, the effect of the flood conditions gradually increased with increasing freshwater pulse duration, as indicated by the presence of a significant interaction between both stressors, though no thresholds were detected (**Table 10a**, **Figure 27**). There was no significant effect of the flood conditions or the freshwater pulse duration on the shell dissolution of *M. balthica* and *Mytilus* spp. (**Table 10bc**, **Figure 27**). For the three species, no shell dissolution was detected in the absence of flood conditions, even under the longest freshwater pulses (**Figure 27**).

Table 10. Summary of the results of the ANOVA tests showing the effects of the duration of freshwater pulses ('Pulse duration'), 'Flood conditions' and their interaction on the shell dissolution in (a) *L. saxatilis*, (b) *M. balthica* and (c) *Mytilus* spp. at 2.5 (left) and 5 weeks (right). Significant values are given in bold. The goodness of fit represents the variance explained by the fixed effects only (R^2m) and by the fixed and random effects (R^2c). For all sources of variation, $df_1 = 1$.

Shell dilution	**At 2.5 weeks**				*Shell dilution*	**At 5 weeks**			
Source of variation	**df_2**	**MS**	**F ratio**	***P* value**	**Source of variation**	**df_2**	**MS**	**F ratio**	***P* value**
a. *Littorina saxatilis*		R^2m: 0.40, R^2c: 0.50 *					R^2m: 0.52, R^2c: 0.67 ***		
Pulse duration	37	0.01784	1.15	0.2904	**Pulse duration**	35	0.03821	11.22	**0.0020**
Flood conditions	37	0.17800	11.48	**0.0017**	**Flood conditions**	27	0.02381	6.99	**0.0136**
Interaction	36	0.03249	2.10	0.1564	**Interaction**	35	0.03971	11.66	**0.0016**
b. *Macoma balthica*		R^2m: 0.02, R^2c: 0.28 **					R^2m: 0.52, R^2c: 0.52 **		
Pulse duration	139	0.00002	0.01	0.9319	Pulse duration	170	0.00550	1.63	0.2036
Flood conditions	138	0.00512	1.53	0.2183	Flood conditions	169	0.00424	1.26	0.2641
Interaction	138	0.00024	0.07	0.7894	Interaction	169	0.00012	0.03	0.8536
c. *Mytilus* spp.		R^2m: 0.02, R^2c: 0.06 **					R^2m: 0.06 , R^2c: 0.19 **		
Pulse duration	170	0.00005	0.03	0.8532	Pulse duration	181	0.00041	0.14	0.7104
Flood conditions	170	0.00243	1.80	0.1814	Flood conditions	182	0.00286	0.95	0.3300
Interaction	170	0.00012	0.09	0.7668	Interaction	181	0.00335	1.12	0.2914

* The best model included the 'Mesocosm' and 'Estuary of origin' as random factors
** The best model included only the 'Estuary of origin' as a random factor
*** The best model included only the 'Mesocosm' as a random factor

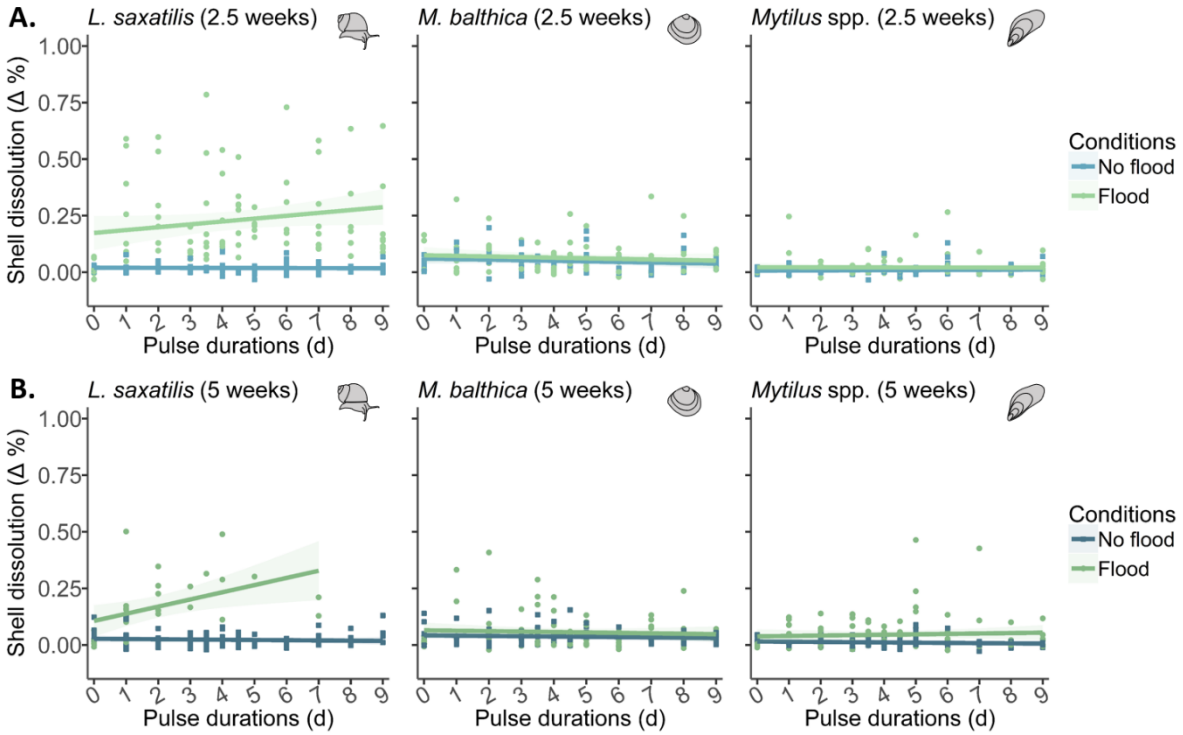


Figure 27. Relationship between the freshwater pulse duration and the shell dissolution of *L. saxatilis*, *M. balthica*, and *Mytilus* spp. at 2.5 (A) and 5 (B) weeks. Data points illustrate the shell dissolution of indiv. mollusks, with four indiv. *per* mesocosm. Some freshwater pulses levels are not represented because all the indiv. were dead or removed from the system, *e.g.*, *L. saxatilis* at 5 weeks in the flood conditions.

The effects of the flood conditions and freshwater pulse duration on shell growth and shell aspect ratio were limited and varied much among species and across time (**Table 11**). Although some effects were statistically significant, the goodness of fit of the fixed factors (R^2m) of the models were usually very low (between 0.02 and 0.13), suggesting that they explained only a small proportion of the variance observed. Therefore, these findings should be taken with caution, as the predictability of the statistical model is relative speaking low to very low.

In *L. saxatilis* at 2.5 weeks, increasing freshwater pulse duration had a positive effect on shell height growth in the absence of flood conditions, but a negative effect under flood conditions, as indicated by a significant interaction between pulse duration and flood conditions (**Table 11a**, **Figure 28A**). More precisely, in the absence of flood conditions, shell height growth

decreased until the threshold of 7.1 d (± 0.9 d), after which it increased, while the decrease was linear under flood conditions across the entire freshwater pulse gradient tested (**Figure 28A**). No significant changes were detected for shell height growth at 5 weeks, nor for the width growth at 2.5 weeks (**Table 11a**, **Figure A.15**). At 5 weeks, the width growth decreased with longer freshwater pulses, regardless of the conditions (**Table 11a**, **Figure 28B**). *Macoma balthica* exhibited the inverse trends, as its height growth increased with freshwater pulse duration at 2.5 weeks (**Table 11b**, **Figure 28A**). Increasing freshwater pulse duration also increased width growth in *M. balthica*, until the threshold at 5 d (± 1.0 d) after which it decreased slightly (**Table 11**, **Figure 28B**). Neither the freshwater pulse duration or flood conditions had a significant effect on width growth (**Table 11b**, **Figure A.15**). For *Mytilus* spp., flood conditions induced a slight decrease in shell height growth at 2.5 weeks (**Table 11c**, **Figure 28A**) but no difference was detected at 5 weeks or at either time for the shell width growth (**Table 11c**, **Figure A.15**). Full representation of the results is provided in the supplementary material (**Figure A.15**).

Finally, the shell shape did not appear to be affect by the freshwater pulse duration, flood conditions or the time (**Table A.20**, **Figure A.16**). Only *M. balthica* became slightly more elongated under flood conditions with increasing freshwater pulse duration at 5 weeks ($F_{1,167}$ = 4.34, P = 0.039, R^2m = 0.02) (**Table A.20**, **Figure A.16**).

Table 11. Summary of the results of the ANOVA showing the effects of the duration of freshwater pulses ('Pulse duration'), the 'Flood conditions' and their interaction, together with the initial size on the metrics tested, on shell height growth (upper part) and shell width growth (lower part) of (a) *L. saxatilis*, (b) *M. balthica* and (c) *Mytilus* spp. at 2.5 (left) and 5 (right) weeks. Significant values are in bold. The goodness of fit (R^2) represents the variance explained by the fixed effects only (R^2m) and by the fixed and random effects (R^2c). For all sources of variation, $df_1 = 1$.

Shell height growth st 2.5 weeks

Source of variation	df_2	MS	F ratio	*P* value
a. *L. saxatilis*		R^2m: 0.09, R^2c: 0.24 *		
Pulse duration	39	0.00083	0.157	0.6942
Flood conditions	42	0.00936	1.774	0.1901
Interaction	39	0.03355	6.362	**0.0159**
Initial height	147	0.01262	2.393	0.1241
b. *M. balthica*		R^2m: 0.13, R^2c: 0.13 *		
Pulse duration	135	0.01071	9.474	**0.0025**
Flood conditions	135	0.00037	0.326	0.5691
Interaction	135	0.00032	0.284	0.5947
Initial height	135	0.01098	9.713	**0.0022**
c. *Mytilus* spp.		R^2m: 0.04, R^2c: 0.11 *		
Pulse duration	45	0.00002	0.024	0.8771
Flood conditions	48	0.00434	4.333	**0.0428**
Interaction	45	0.00387	3.861	0.0556
Initial height	160	0.00069	0.686	0.4089

Shell height growth at 5 weeks

Source of variation	df_2	MS	F ratio	*P* value
		R^2m: 0.03, R^2c: 0.03 *		
Pulse duration	102	0.00093	0.296	0.5875
Flood conditions	102	0.00062	0.198	0.6570
Interaction	102	0.00331	1.049	0.3081
Initial height	102	0.00356	1.132	0.2900
		R^2m: 0.04, R^2c: 0.05 **		
Pulse duration	166	0.00094	1.206	0.2737
Flood conditions	166	0.00047	0.601	0.4391
Interaction	166	0.00063	0.800	0.3724
Initial height	166	0.00182	2.327	0.1290
.		R^2m: 0.09, R^2c: 0.20 *		
Pulse duration	46	0.00113	2.597	0.1140
Flood conditions	44	0.00006	0.146	0.7047
Interaction	46	0.00175	4.028	0.0507
Initial height	180	0.00002	0.049	0.8245

Shell width growth at 2.5 weeks

Source of variation	df_2	MS	F ratio	*P* value
a. *L. saxatilis*		R^2m: 0.10, R^2c: 0.19 *		
Pulse duration	37	0.00249	0.702	0.4075
Flood conditions	41	0.00090	0.253	0.6176
Interaction	37	0.00790	2.220	0.1442
Initial width	149	0.03647	10.270	**0.0017**
b. *M. balthica*		R^2m: 0.06, R^2c: 0.08 **		
Pulse duration	129	0.00413	3.967	**0.0485**
Flood conditions	135	0.00090	0.862	0.3547
Interaction	165	0.00028	0.271	0.6033
Initial width	130	0.00411	3.955	**0.0488**
c. *Mytilus* spp.		R^2m: 0.02, R^2c: 0.10 *		
Pulse duration	44	0.00004	0.024	0.8769
Flood conditions	45	0.00073	0.415	0.5228
Interaction	43	0.00301	1.701	0.1990
Initial width	163	0.00171	0.964	0.3275

Shell width growth at 5 weeks

Source of variation	df_2	MS	F ratio	*P* value
		R^2m: 0.10, R^2c: 0.19 *		
Pulse duration	37	0.00704	4.624	**0.0382**
Flood conditions	23	0.00057	0.376	0.5457
Interaction	100	0.00210	1.380	0.2429
Initial width	36	0.00319	2.094	0.1565
		R^2m: 0.11, R^2c: 0.13 *		
Pulse duration	43	0.00001	0.015	0.9034
Flood conditions	45	0.00159	3.781	0.0582
Interaction	44	0.00035	0.832	0.3667
Initial width	167	0.00489	11.640	**0.0008**
		R^2m: 0.09, R^2c: 0.17 *		
Pulse duration	45	0.00079	1.017	0.3187
Flood conditions	44	0.00091	1.176	0.2841
Interaction	45	0.00212	2.737	0.1050
Initial width	179	0.00464	5.992	**0.0153**

* The best model included only the 'Mesocosm' as a random factor

** The best model included only the 'Estuary of origin' as a random factor

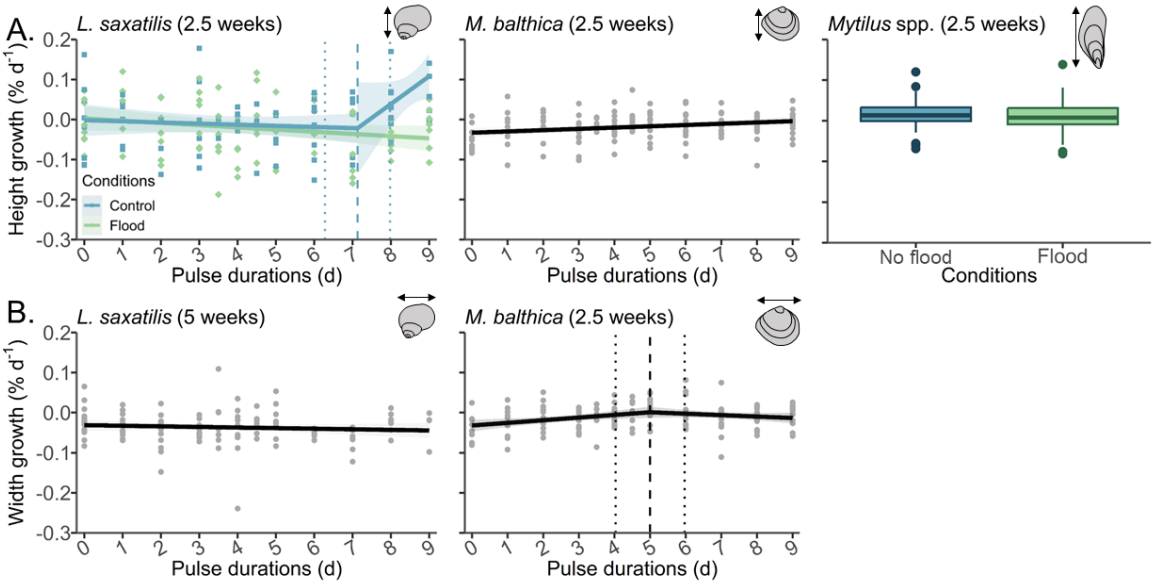


Figure 28. (A) Relationship between the freshwater pulse duration and the height growth of *L. saxatilis* and *M. balthica* at 2.5 weeks and effect of flood conditions on shell height growth of *Mytilus* spp. at 2.5 weeks, and (B) relationship between the freshwater pulse duration and shell width growth of *L. saxatilis* at 5 weeks and *M. balthica* at 2.5 weeks. Flood conditions are represented in green and the absence of flood conditions in blue, with 95 % CI depicted by the shaded areas around the solid lines and data points illustrate the individual growth of mollusks with four indiv. *per* mesocosm. Dashed vertical lines represent significant ($P < 0.05$) tipping points, with dotted lines at the 95 % CI. When no tipping points were detected, linear models were depicted instead. Boxplots show the 75th percentile, median, 25th percentile and the lowest and largest 1.5 times interquartile range, whilst circles represent outliers.

3.2.7 Discussion

In this study, we demonstrated for the first time that spring flood conditions (*i.e.*, high turbidity and low pH) significantly amplify the effect of hypoosmotic stress on the mortality in an assemblage of subarctic mollusk, with strong species-specific effects. As predicted, the results showed that the rough periwinkle *Littorina saxatilis* was the most vulnerable species to freshwater exposure, in particular under spring flooding, followed by the Baltic clam *Macoma balthica* and finally the blue mussel *Mytilus* spp., which displayed very limited mortality. The elevated mortality in *L. saxatilis* appears to be linked to severe shell dissolution under spring flood conditions, which was not observed in the two more tolerant species. In addition, the three species were unaffected by freshwater pulses shorter than three days, even after five weeks, but only under favourable freshwater conditions: *i.e.*, pH 7.7, turbidity 0 mg L^{-1}. Contrary to our hypotheses, neither hypoosmotic stress nor spring flood conditions consistently reduced shell growth in all species. We focus our discussion on how flood-associated stressors impact estuarine communities by amplifying sensibility to hypoosmotic stress with highly species-specific responses, which could induce changes in the community structure with global changes. Finally, we will explore the physiological mechanisms behind these varied responses, and conclude with management recommendations to protect subarctic estuaries communities.

3.2.7.1 Flood-associated stressors strongly amplify the negative effects of hypoosmotic stress

Our study demonstrates that the superimposition of stressors occurring during spring flooding (*i.e.*, low pH and high turbidity) amplifies the negative effects of hypoosmotic stress. More specifically, spring flood conditions increased mortality levels in the three investigated species but also unveiled new mortality thresholds for *M. balthica* and *Mytilus* spp. while shifting the threshold to shorter freshwater exposure in *L. saxatilis*.

Investigating the effects of realistic combinations of stressors is crucial to acquire a critical understanding of the complex dynamics of ecosystems under realistic conditions (Côté *et al.*, 2016). Since flooding inherently involve decreased salinity, the stressors associated with

spring floods (*i.e.*, low pH / high turbidity) were not investigated in isolation and our experimental design did not aim to ascertain whether the combination of the flood conditions and hypoosmotic stress had additive, synergistic of antagonistic effects (*sensus* Côté *et al.*, 2016). However, the elevated mortality in *M. balthica* and *Mytilus* spp., as well as the high shell dissolution in *L. saxatilis* seemed to be dominated by the effect of low pH / high turbidity, as nearly no mortality or shell dissolution was observed in the absence of these additional stressors. The effect of hypoosmotic stress *vs*. low pH / high turbidity are harder to disentangle regarding *L. saxatilis* mortality. The latter seem to either dominate or act in synergy with the hypoosmotic stress on the mortality response under shorter freshwater pulses (*i.e.*, large difference with or without flood conditions). However, the hypoosmotic stress seems dominant in longer freshwater pulses (*i.e.*, comparable mortality with or without flood conditions).

Additive effects of flood-associated stressors (*i.e.*, coastal acidification, hyposalinity, and hypoxia) on the survival of the eastern oyster *Crassostrea virginica* have been observed by Pruett *et al.* (2022), although these effects were mainly driven by salinity. In contrast, in our study, long freshwater exposure by itself did not cause mortality in *Mytilus* spp. and *M. balthica*. While also investigating flood associated stressors (*i.e.*, OA, hyposalinity, warming and low food availability), Cole *et al.* (2016) found that OA did not change the response to salinity stress and did not exert a significant effect on the mortality of eastern oyster larvae, though mortality increased with hypoosmotic stress. However, Cole *et al.* (2016) and Pruett *et al.* (2022) used pH "stress" levels between 7.2 and 7.8, that are a lot higher than the pH level used in our experiment to simulate spring flooding in subarctic estuaries (5.7), most likely explaining why the effect of decreasing pH was weaker when compared to our study. Pruett *et al.* (2022) also found an additive negative effect of salinity and coastal acidification on the growth of earlier life-stage individuals of the eastern oyster, an effect that adult mollusks in our study do not show. These differences may stem from the greater tolerance of adult mollusks, which can better withstand stressors that impact younger life stages (Pandori and Sorte, 2019).

3.2.7.2 Flood conditions cause dissolution of *L. saxatilis* shells and inhibit its protective function

Molluskan shells are an organo-mineral composite that protects their soft bodies from desiccation and predation and limit tissue contact with the outside environment reducing costs for homeostasis (Sokolova *et al.*, 2000a, 2000b; Marin *et al.*, 2007). Additionally, the shell provides a refuge from environmental stressors under hyaline or pH conditions outside of the species' tolerance range, as mollusks close their valves (bivalves) or *operculum* (snails) to minimise the exchange of water and salts with the environment (Shick *et al.*, 1988), in turn minimising energy costs to maintain a positive homeostasis (Sokolova *et al.*, 2000a). This isolation behaviour was observed during our experiment in the three species during freshwater exposure, under both control and flood conditions (*pers. obs.*). However, extended periods of isolation in the shell can lead to mortality, as organisms lose access to oxygen and accumulate toxic wastes, leading to hypoxemia, hypercapnia and acidosis (Shick *et al.*, 1988; Sokolova *et al.*, 2000b, 2000c). The ability of *M. balthica* and *Mytilus* spp. to survive isolated into their shell for prolonged periods has been previously demonstrated (Babarro and De Zwaan, 2008; De Zwaan and Eertman, 1996; Riley *et al.*, 2022), and concurs with the very low mortality observed in our experiment, even under the longest freshwater exposure. On the other hand, *L. saxatilis* mortality has been shown to increase after just three days in freshwater (Sokolova *et al.*, 2000a, 2000b), which is consistent with the freshwater pulse duration threshold that emerged after five weeks in the absence of flood conditions (*i.e.*, three days).

The high mortality of *L. saxatilis* under coastal acidification is most likely due to the dissolution (and subsequent perforation) of its shell, which impedes its protective role (Zhao *et al.*, 2020). The differences in the proportion in high-Mg calcite (more soluble), aragonite, and low-Mg calcite (less soluble) in the shells of the three studied species could explain their different vulnerability, as aragonite and high-Mg calcite are more prone to dissolution in corrosive (*i.e.*, low Ω/low pH) conditions (Ries *et al.*, 2009b). *Littorina saxatilis* and *Mytilus* spp. both built their shells with an outer calcite layer and an inner aragonite layer (Bourgoin, 1988; Taylor and Reid, 1990). *Mytilus* spp. uses low-Mg calcite, and its shell is also covered

by a thick *periostracum* (25-100 µm), an organic sheet that protects the shell surface from dissolution and contributes to the species' tolerance to corrosive conditions (Clarck, 1976; Telesca *et al.*, 2019). The type of calcite used in the shells of *L. saxatilis* (*i.e.*, low-Mg or high-Mg) could not be found in the literature, though another periwinkle, *L. littorea*, also uses low-Mg calcite (Ries, 2011). *Macoma balthica* uses exclusively aragonite (Sturesson and Reyment, 1971) making it potentially more vulnerable to dissolution than *L. saxatilis*, which contradicts our observations. Whilst *L. saxatilis* and *M. balthica* also produce a *periostracum*, it has been less studied and is often described as "thin" (Bubel, 1973; Richard and Prezant, 2021).

The depth of dissolved areas in *Mytilus* spp. seemed to increase under flood conditions (*pers. obs.*), suggesting that effect on shell strength/resistance could be affected and that perforation could happen after longer exposure. Shell dissolution could also occur from the inside of the organism, as internal fluid pH decreases when mollusks stay isolated inside their shell to avoid stressful environmental conditions (Cole *et al.*, 2016). In addition, internal shell dissolution has been observed under ocean acidification in the blue mussel (Melzner *et al.*, 2011). Since in *M. balthica* it was challenging to measure shell's dissolution, due to its white and powdery nature (*i.e.*, the shell did not show clear changes in color as the other species), and since shell dissolution seems to play a major role in the survival of mollusks, it would be valuable to investigate further changes in the "strength" of the shells, particularly since individuals' shells exposed to flood conditions broke more easily during manipulation across all three species (*pers. obs.*). A quantification of shells strength would be valuable to help predict the vulnerability of estuarine community, as weaker shells leave mollusks more vulnerable to other sources of stress, such as predation (Amaral *et al.*, 2012). Additionally, pH gradients found in acidic sulfate soil estuaries or near CO_2 vents showed that coastal or ocean acidification is a powerful driver of community structure, with calcifying organisms disappearing at low pH leading to loss of ecosystem functions (OA: Kroeker *et al.*, 2011, Teixidó *et al.*, 2018; coastal acidification: Hossain *et al.*, 2019), a pattern confirmed also under control laboratory conditions (Christen *et al.*, 2013).

3.2.7.3 Strong species-specific vulnerability may lead to shift in community structure

Our study reveals strong negative species-specific responses to repeated hypoosmotic stress, especially in the presence of additional stressors associated with spring flooding (*i.e.*, low pH and high turbidity), which further amplify its negative effects. While *L. saxatilis* is severely affected by both freshwater exposure and spring flood conditions, *M. balthica* and *Mytilus* spp. experience increased mortality only under spring flood conditions during prolonged freshwater pulses.

The highest sensibility of *L. saxatilis* to flood conditions compared to the other species could lead to substantial shifts in community structure within subarctic estuarine ecosystems, especially considering that *L. saxatilis* is the main grazer in these environments (Loiseau *et al.*, 2024). However, *L. saxatilis*' ability to produce a relative high number of offspring and rapidly recolonize hard substrate habitats thanks to their direct development life-history strategy, with just a few individuals (Blakeslee *et al.*, 2021; Wilhelmsen, 1998) may allow it to settle back following prolonged flooding events. Direct and modified-development life-history strategies, as in *L. saxatilis*, were shown as better adapted to tolerate extreme environmental conditions when compared to those with larval stages (Lucey *et al.*, 2015). Conversely, the apparent tolerance of filter feeders such as *Mytilus* spp. and *M. balthica* to flooding indicate they may keep their function in subarctic estuaries in a changing climate as foundation species, enhancing habitat complexity (Norling and Kautsky, 2007; Palomo *et al.*, 2007), but also supporting numerous predators (from gastropods to birds; Dame, 2012) and maintaining water quality through their filtration of suspended particles (Petersen *et al.*, 2014). Additionally, filter feeders play an essential role in nutrient cycling, redistributing nutrients to the substrate or to higher trophic levels (Menge *et al.*, 1997). However, as mentioned earlier, their early life stages might be more vulnerable to hypoosmotic stress than adults, in particular as both species have larvae that spend a long time in the water column during the spring (Caddy, 1969; Seed, 1969).

Spring-like flooding most likely drives significant seasonal changes in ecosystem functions by decreasing taxonomic and functional diversity, and by affecting some taxa more than

other, which has been observed in temperate estuaries (Grilo *et al.*, 2011). Therefore, with climate change, shifts in the timing and intensity of spring flooding (Boyer *et al.*, 2010) could further alter estuarine communities, not only due to adult vulnerability but also through changes in spawning timing as warmer air and ocean temperatures may trigger earlier spawning (Asch *et al.*, 2019). This could potentially expose larvae to flood conditions when they are more vulnerable and when food sources are not yet available, creating a mismatch in environmental conditions (Asch *et al.*, 2019; Dijkstra *et al.*, 2011; Edwards and Richardson, 2004; Thackeray *et al.*, 2010).

3.2.8 Conclusions and recommendations

Our results reinforce the notion that using combined stressors in laboratory experiments can help identify which factors have the most detrimental effects, thereby informing more effective management and conservation strategies. Estuaries are unique ecosystems to protect, as management strategies must be applied to both marine waters and land, depending on the issue (Saunders *et al.*, 2017). To improve the tolerance and resilience of estuarine communities, it is crucial to manage the landscape surrounding the catchment of estuaries, to ensure maintaining sufficient stream water quality before it arrives in the marine portion of estuaries. For example, coastal landscapes with a high proportion of land protected natural areas optimize water quality and reduce terrestrial runoff, which in turn enhances the diversity and abundance of coastal fish (Goodridge Gaines *et al.*, 2024). We demonstrated that flood conditions increase mortality for all three mollusk species we investigated, while even the longest hypoosmotic stress tested by itself does not cause significant mortality of *M. balthica* and *Mytilus* spp. Therefore, protection plans for subarctic estuaries should include advice on best practices for logging (Akselsson *et al.*, 2007), urbanization and agriculture (Stets *et al.*, 2020), and natural land preservation, as these activities can influence stream acidity, turbidity and overall water quality (Goodridge Gaines *et al.*, 2024). In our study however, high turbidity did not cause sufficient sedimentation to cause burial during the experiment, likely due to the small size of the sediment particles used, therefore its effect on mortality was probably low. Lakes and rivers are slowly recovering from the acidic

deposition caused by unrestrained industrialisation in the beginning of the century (Marty *et al.*, 2021b), thanks to global policies regulating air pollution (Watmough and Eimers, 2020), though the efforts are mostly limited to North-America and Europe (Grennfelt *et al.*, 2020). Nonetheless, studies investigating freshwater invertebrates communities have shown that recovery can be long following acidification and recovery of lakes due to acid rain (Szkokan-Emilson *et al.*, 2010) and of streams following the abandonment of mining activities (Bae *et al.*, 2023). Furthermore, our study used the lowest pH value recorded during spring flooding, meaning that our results may represent a worst-case scenario for most subarctic estuaries in terms of low pH and alkalinity conditions. However, future studies should investigate the impact of summer flooding, in particular in addition to marine heat waves, as hypoosmotic stress can reduce the thermal tolerance of invertebrates (Farias *et al.*, 2024). Given the increasing frequency of extreme events due to climate change, understanding the effects of different flooding scenarios that include seasonality, pH, temperature, and salinity is essential for developing effective conservation strategies.

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CONCLUSION GÉNÉRALE

Ma thèse avait pour objectif principal d'approfondir nos connaissances sur la vulnérabilité des communautés benthique des estuaires subarctiques face à la multiplication des inondations dans le contexte des changements globaux. Le **premier chapitre** visait à décrire la composition et diversité taxonomique et fonctionnelle des communautés benthiques de substrat dur retrouvées le long du gradient de salinité dans de petits estuaires de la Côte-Nord. Les résultats ont dévoilé une perte de biomasse et de richesses taxonomique et fonctionnelle avec une augmentation de l'apport en eau douce. L'apport en eau douce a également considérablement façonné les structures taxonomiques et fonctionnelles des communautés, notamment en diminuant la proportion de filtreurs et d'espèces dont les propagules peuvent être transportés sur de grandes distances. De plus, la littorine des rochers *Littorina saxatilis* était la seule espèce retrouvée en plus grande abondance proche des rivières, les autres espèces (p. ex. la moule bleue *Mytilus* spp.) étant plus abondantes près du milieu marin. Enfin, les macroalgues étaient plus petites à de faibles salinités mais ce patron n'a pas été détecté chez les espèces d'invertébrés, possiblement à cause d'une méthodologie moins précise (c.-à-d. taille individuelle pour les algues *vs.* classe de taille pour les invertébrés).

En se basant sur l'analyse des patrons de répartition des espèces le long des gradients de salinité, nous avons ensuite choisis trois espèces de mollusques (c.-à-d. *L. saxatilis*, la macoma baltique *Macoma balthica* et *Mytilus* spp.) pour évaluer leur sensibilité face à des inondations intenses plus ou moins prolongées dans le **deuxième chapitre**, en utilisant un gradient d'exposition à des pulses d'eau douce durant de 0 à 9 jours. L'application de ce gradient de stress hypoosmotique, couplée à des analyses de seuils, a permis de déterminer que les inondations de deux jours ou moins, même répétées sur plusieurs semaines, ne posent pas de risque majeur pour l'assemblage de mollusques étudié. Cependant, au-delà de ce seuil, *L. saxatilis* s'est avérée être l'espèce la plus vulnérable, suivie de *M. balthica*; *Mytilus* spp.

était la plus tolérante, affichant une mortalité très faible même après six semaines. De plus, une diminution de la masse corporelle et de la croissance de la coquille avec l'augmentation de la durée des pulses d'eau douce a été observé chez *L. saxatilis*, mais seule la masse corporelle était affectée négativement chez *M. balthica*. Ni la masse corporelle ni la croissance n'ont été affectées pour *Mytilus* spp. mais son contenu énergétique variait en fonction de la durée du pulse d'eau douce et du temps. En effet, contrairement à ce qui était attendu, le contenu énergétique le plus élevé a été détecté dans les pulses d'eau douce les plus longs, suggérant des réponses physiologiques complexes au stress hypoosmotique.

La sensibilité au stress hypoosmotique propre à chaque espèce contrastant avec la distribution de ces espèces dans les estuaires, nous avons exploré dans le **troisième chapitre** si les conditions des inondations printanières pouvaient modifier cette sensibilité en ajoutant une diminution du pH et une augmentation de la turbidité aux pulses d'eau douce. Les résultats de cette seconde expérience ont confirmé une sensibilité croissante selon l'ordre *L. saxatilis* > *M. balthica* > *Mytilus* spp., avec une sensibilité accrue des trois espèces aux conditions d'inondations printanières. *Littorina saxatilis* était particulièrement vulnérable en conditions d'inondation, probablement en raison de la dissolution accrue de sa coquille, qui n'a pas été détectée chez les autres espèces.

Les trois chapitres mettent donc en lumière la vulnérabilité des communautés benthiques face à la multiplication des inondations dans le contexte des changements globaux, car l'apport en eau douce entraîne une diminution de la biomasse et de la richesse taxonomique et fonctionnelle des communautés benthiques en milieu naturel (**chapitre 1**), et provoque une mortalité qui diffère entre chaque espèce pouvant déséquilibrer la structure des communautés (**chapitres 2** et **3**). Toutefois, les descriptions fonctionnelles et taxonomiques des communautés le long des gradients naturels de salinité, bien qu'informatives, ne suffisent pas à elles seules pour formuler des recommandations de gestion, car elles ne permettent pas toujours d'identifier précisément quelle composante de l'apport en eau douce constitue un stress (p. ex. moyenne ou minimum de salinité ou de pH, quantité de sédiments en suspension). En revanche, les expériences de ma thèse en milieu contrôlé ont permis de

déterminer des seuils de sensibilité et d'exposer les réponses complexes des espèces à l'eau douce et aux conditions d'inondations printanières. Cependant, ces expériences se concentraient uniquement sur un stade de vie (c.-à-d. les adultes) et ne pouvaient ni reproduire fidèlement les conditions naturelles ni représenter la complexité du milieu et de ses communautés naturelles.

Ma conclusion générale vise donc d'abord à résumer les recommandations de gestion environnementale issues des différents chapitres pour préserver les communautés estuariennes dans le contexte des changements globaux. Ensuite, j'aborderai les avantages et les limites des approches employées, puis je proposerais des perspectives de recherche pour améliorer nos pratiques scientifiques, toujours dans une perspective de gestion.

1. RECOMMANDATIONS DE GESTION DES PETITS ESTUAIRES SUBARCTIQUES DANS LE CONTEXTE DES CHANGEMENTS GLOBAUX

Les connaissances sur l'influence des régimes de flux de l'eau douce sur les communautés estuariennes restent faibles comparées à celles sur les écosystèmes fluviaux et les plaines inondables, malgré les liens avec des processus clés tels que l'hydrodynamique, la régulation de la salinité, la dynamique des sédiments, le cycle des nutriments, le transfert trophique et la connectivité (Chilton *et al.*, 2021). Mes différents chapitres illustrent la vulnérabilité des écosystèmes subarctiques estuariens face à des inondations plus fréquentes. Par conséquent, une gestion holistique, allant du bassin versant au milieu côtier marin, est essentielle pour atténuer les risques liés aux changements globaux, tout en trouvant un équilibre entre les besoins socio-économiques et écosystémiques (Arthington *et al.*, 2018; Van Niekerk *et al.*, 2019; Chilton *et al.*, 2021).

1.1 Qualité de l'eau des estuaires

Les taux élevés de mortalité observés chez les trois espèces en conditions d'inondations printanières soulignent l'importance de promouvoir des mesures de conservation visant à

maintenir la qualité de l'eau dans les rivières, notamment en aspirant à un pH neutre ou moins acide, à une alcalinité élevée et à une faible turbidité (**chapitre 3**). Dans ce contexte, les estuaires peu anthropisés, c.-à-d. où la présence de l'Homme dans l'ensemble du bassin versant est négligeable, pourraient être moins à risque que ceux où les sols, en particulier, sont modifiés. En effet, un grand nombre d'activités anthropiques diminue la qualité de l'eau des rivières par une augmentation de la quantité de matières en suspension, comme la modification des sols pour l'urbanisation et l'agriculture (Stets *et al.*, 2020), ou les coupes à blanc pour la sylviculture (Palviainen *et al.*, 2014). La création de zones de protection du milieu naturel dans le bassin versant (p. ex. préservation de végétation résiduelle dans les terres anthropisées, créations d'aires de conservation) peut avoir un effet tampon et aider à maintenir une meilleure qualité de l'eau (Goodridge Gaines *et al.*, 2024). De plus, des actions comme la réduction des surfaces imperméables ou l'installation de jardins peuvent aider à retenir l'eau des pluies intenses en milieu urbain tout en diminuant l'apport excessif de nutriments et de toxines et l'installation d'espèces invasives (McGrane, 2016; Zevenbergen *et al.*, 2018).

En Amérique du Nord et en Europe, les lacs et les rivières se remettent lentement des dépôts acides causés par l'industrialisation effrénée du début du siècle (Grennfelt *et al.*, 2020; Marty *et al.*, 2021; Whelan *et al.*, 2022) grâce aux politiques mondiales de régulation de la pollution de l'air (Watmough and Eimers, 2020). Néanmoins, des études ont montré que le rétablissement des communautés d'invertébrés d'eau douce peut être long après l'acidification des lacs en raison des pluies acides (Szkokan-Emilson *et al.*, 2010) et des cours d'eau à la suite de l'abandon des activités minières (Bae *et al.*, 2023). Dans certaines régions de l'Est du Canada, la roche granitique du Bouclier canadien a de faibles capacités tampons acides (Clair *et al.*, 2002). Dans ces régions où les inondations printanières seront vraisemblablement longtemps associées à une acidification saisonnière des cours d'eau, et en présence de pollution (p. ex. exploitation des sables bitumineux), il serait pertinent de s'inquiéter de la vulnérabilité des organismes aux métaux lourds et aux hydrocarbures, ceux-ci devenant plus mobiles en condition acides (Alexander *et al.*, 2017). Cependant, au Canada, une mauvaise qualité de l'eau est majoritairement due à l'utilisation des terres pour

l'agriculture et la foresterie (Environnement et changement climatique Canada, 2023). Entre 2002 et 2022, la qualité de l'eau a par ailleurs diminuée dans 41 % des cours d'eau suivis par Environnement et changement climatique Canada (2023), ce chiffre montant à 46 % dans la région de l'Océan Atlantique et 67 % dans celle des Grands Lacs et du Fleuve Saint-Laurent. L'étude des effets des stresseurs s'accumulant dans les estuaires situés à proximité des exploitations forestières ou des zones agricoles sur les communautés benthiques estuariennes serait particulièrement pertinente et pourrait être comparée aux conditions observées dans des estuaires peu anthropisés.

Enfin, bien que notre étude se soit concentrée sur la diminution du pH et l'augmentation de la turbidité, il est important de noter que les flux d'eau douce peuvent apporter d'autres facteurs de stress dans les milieux estuariens. Par exemple, l'apport massif en carbone et en azote par les cours d'eau, notamment en présence d'agriculture intensive, peut entrainer une prolifération du microbiome pouvant être suivi non seulement d'une diminution du pH mais aussi d'une eutrophisation des eaux estuariennes (Hudon *et al.*, 2017). L'impact d'autres facteurs de stress associés aux changements globaux, comme par exemple la hausse des températures marines et du niveau de la mer, se font aussi ressentir dans les estuaires (Scanes *et al.*, 2020; Colombano *et al.*, 2021). Pourtant, les milieux estuariens restent bien moins suivis que les milieux marins concernant l'impact des changements globaux, puisqu'ils ne représentent que 9 % des études à ce sujet (Biguino *et al.*, 2023).

1.2 Gestion des barrages et évacuateurs de crue

Les barrages homogénéisent les débits des rivières et réduisent les débits maximaux annuels au printemps (Assani *et al.*, 2006). Cela pourrait potentiellement favoriser la richesse et la biomasse des communautés benthiques des estuaires harnachés en comparaison au estuaires d'eau libre, puisque ces indices sont plus élevés à des niveaux d'apport en eau douce plus faibles (**chapitre 1**). Cependant, l'intensification du cycle hydrologique avec les changements globaux pourrait nécessiter des ouvertures des évacuateurs de crues de plus en plus fréquentes et prolongées (Lin *et al.*, 2021). Advenant ce cas, les deux expériences en

laboratoire (**chapitre 2** et **3**) permettent de recommander aux gestionnaires de favoriser des ouvertures des déverseurs des barrages et d'évacuateurs de crue pour des durées de deux jours maximums, même si les opérations doivent être répétées pendant plusieurs semaines. En effet, les inondations de plus longues durées causent des mortalités plus élevées chez les espèces étudiées dans l'ordre suivant : d'abord chez la littorine des rochers *Littorina saxatilis*, puis chez la macoma baltique *Macoma balthica* et enfin chez la moule bleue *Mytilus* spp.

Aucune recommandation de ce type ne semble avoir été émise en climat tempéré ou subarctique, malgré la forte présence de barrages en Amérique du Nord. Mes recommandations s'enlignent cependant avec celles émises par Loveridge *et al.* (2021) pour protéger les populations de la méduse mosaïque *Catostylus mosaicusi* dans un estuaire anthropisé en Australie. Leur étude recommande ainsi de libérer de plus petits volumes d'eau sur une base plus régulière afin d'atténuer les fluctuations de salinité dans l'estuaire (Loveridge *et al.*, 2021). Il est intéressant de noter que, au contraire, l'ouverture des barrages a été proposée par Amorim *et al.* (2018) comme outil pour limiter la présence de méduses pouvant devenir problématique (c.-à-d. impacts négatifs sur la pêcherie et le tourisme) dans certaines zones côtières de la péninsule ibérique.

Il est par ailleurs important de souligner que les relâches d'eau douce sont nécessaires pour permettre le transport de la matière en suspension provenant des rivières et ainsi éviter l'appauvrissement et l'érosion des estuaires et écosystèmes côtiers avoisinants (Syvitski and Kettner, 2011; Chilton *et al.*, 2021; Wolanski and Hopper, 2022). De plus, en représentant des fluctuations naturelles, ces relâches permettent de maintenir une plus grande biodiversité phytoplanctonique et d'éviter l'eutrophisation des estuaires ainsi que la prolifération d'algues nuisibles (Ketchum, 1954; Ferreira *et al.*, 2005). Une limitation excessive des flux naturels d'eau douce peut aussi déséquilibrer les paramètres physico-chimiques de l'eau, favorisant ainsi les espèces non indigènes au détriment des espèces natives (Scott *et al.*, 2016). Enfin, les relâches saisonnières par les barrages sont aussi utiles en régions arides ou semi-arides, dans les estuaires à faible débit, car elles aident à maintenir la connectivité des écosystèmes

et stimulent les migrations de frai des poissons entre les habitats d'eau douce et estuariens (Adams *et al.*, 2023).

2. COMBINER DES INVENTAIRES SUR LE TERRAIN ET DES EXPERIENCES EN LABORATOIRE POUR EVALUER LA VULNERABILITE DES COMMUNAUTES BENTHIQUES

Dans cette thèse, nous avons adopté deux approches complémentaires pour évaluer la vulnérabilité des communautés benthiques estuariennes à un apport en eau douce : d'abord une étude de la composition des communautés le long d'un gradient de salinité en milieu naturel, puis l'exposition de trois espèces clefs à des inondations intenses en conditions contrôlées. Les résultats révèlent une inéquation entre la répartition des espèces dans le gradient de salinité observée sur le terrain et leur sensibilité à l'eau douce dans des conditions contrôlées en laboratoire. Cette section de la discussion commencera par l'exploration des mécanismes pouvant expliquer cette divergence, tout en mettant en lumière les limites propres à chacune des approches (terrain et laboratoire) et les perspectives de recherche permettant de combler ces lacunes. Ensuite, l'importance de combiner différents facteurs de stress et d'explorer des gradients de stresseurs sera abordée, accompagnée de recommandations sur les priorités de recherche à considérer à l'avenir. Pour finir, les avantages et inconvénients des indices fonctionnels et taxonomiques seront brièvement discutés, et leur utilité dans les plans de conservation et de suivi des écosystèmes sera abordée.

2.1 Différences entre les répartitions sur le terrain et les vulnérabilités observées en laboratoire

Les stratégies de reproduction et la vulnérabilité associée au stade larvaire de chacune des espèces étudiées pourraient expliquer pourquoi *Mytilus* spp. semble vulnérable à l'apport en eau douce dans son milieu naturel (**chapitre 1**) bien qu'elle soit l'espèce la plus tolérante aux simulations d'inondations en laboratoire (**chapitres 2** et **3**). Il est fort probable que sa plus grande vulnérabilité au stade larvaire face à de faibles salinités (Pruett *et al.*, 2021)

limite son potentiel de peuplement. À l'inverse, *L. saxatilis* était la seule espèce présente en plus grande abondance proche de l'apport en eau douce sur le terrain, malgré une grande vulnérabilité aux inondations en laboratoire. Puisqu'il s'agit d'une espèce ovovivipare, sans stade larvaire, et pouvant produire une progéniture nombreuse, *L. saxatilis* est capable de recoloniser rapidement son milieu avec seulement quelques individus (Blakeslee *et al.*, 2021; Wilhelmsen, 1998), ce qui expliquerait en partie sa capacité à recoloniser les milieux proches des rivières après des inondations et donc son patron de répartition sur le terrain. Les soins parentaux et les cycles de vie modifiés, comme la couvaison ou le développement direct, peuvent améliorer la survie des invertébrés marins dans les habitats stressants par rapport aux espèces dont le développement larvaire est pélagique (Lucey *et al.*, 2015) ce qui expliquerait leur dominance dans les zones plus proches des apports d'eau douce.

De plus, les simulations d'inondation en laboratoire n'ont pas imité les périodes d'exondation associées aux marées dans la zone intertidale qu'occupe les trois espèces étudiées. En milieu naturel, ces périodes d'exondation représentent habituellement un certain stress pour les espèces marines, entre autres à cause de la dessication, à l'exposition aux rayons UV et aux variations de température qui y sont associées (Chapman et Underwood, 1996; Kaiser *et al.*, 2020; Lubchenco et Menge, 1978; Underwood et Denley, 1984). Dans le cadre des inondations, elles peuvent cependant permettre de limiter leur exposition aux stresseurs associés au milieu aquatique (c.-à-d. diminution de la salinité, du pH et de l'alcalinité et hausse de la turbidité). Les espèces mobiles, comme *L. saxatilis*, pourraient par ailleurs chercher à se déplacer à la recherche de conditions plus favorables. Cependant, ce mouvement pourrait être limité par leur isolation dans la coquille en présence d'eau douce.

2.1.1 Perspective 1 : intégrer les réponses de tous les stades de vie et examiner les effets intergénérationnels des stress environnementaux

Pour mieux comprendre la résilience des populations marines face aux perturbations climatiques, il est essentiel d'intégrer l'étude de différents stades de vie des organismes estuariens. Les taxons d'invertébrés marins benthiques présentent généralement des cycles

de vie biphasiques complexes qui comprennent des stades larvaires pélagiques souvent microscopiques, libres et dispersifs qui résident dans un environnement pélagique (Thorson, 1950). Ces stades pélagiques peuvent être affectés différemment que les stades adultes, et sont fréquemment plus sensibles qu'eux face aux stresseurs environnementaux (Bhatnagar et Crisp, 1965; Charmantier *et al.*, 2001; Pruett *et al.*, 2021, 2022). Par exemple, Pruett *et al.* (2022) ont montré que les larves et les juvéniles de l'huitre américaine *Crassostrea virginica* n'étaient pas affectés de la même manière lorsqu'elles sont exposées à des stresseurs associées aux inondations. Ainsi, une diminution de la salinité réduisait la croissance et l'établissement des larves ainsi que la survie et la croissance des juvéniles (Pruett *et al.*, 2022). L'hypoxie en revanche était plus stressante pour les larves d'huîtres que pour les juvéniles, tandis qu'un faible pH avait des effets négatifs sur la croissance des juvéniles uniquement (Pruett *et al.*, 2022). De plus, certains stress subis au stade larvaire peuvent avoir des effets latents, qui ne se manifestent qu'après la métamorphose (voir synthèse par Pechenik, 2006).

Enfin, les inférences tirées d'expériences de courte durée relativement à la vie de l'organisme sont potentiellement limitées, car elles peuvent fréquemment surestimer ou sous-estimer les impacts du changement climatique (Cripps *et al.*, 2014). Ainsi, l'inclusion d'un suivi sur plusieurs générations permet de prendre en compte les effets transgénérationnels, soit lorsqu'un signal environnemental subi par une génération influence le phénotype de plusieurs générations successives (Mousseau, 1998; Bell and Hellmann, 2019). Ces effets peuvent survenir avant la fécondation (p. ex. Jensen *et al.*, 2014), pendant l'embryogenèse (p. ex. Giménez et Anger, 2003) ou après l'éclosion et la libération de la progéniture (p. ex. Chaparro *et al.*, 2014). Malgré leur rôle majeur dans les fonctions écosystémiques, les mollusques sont peu représentés dans les études portant sur les effets transgénérationnels (Fallet *et al.*, 2020), et rares sont les études portant sur les stress de salinité (mais voir Z. Zhang *et al.*,2023 et Griffiths *et al.*, 2021). Ainsi, l'intégration de l'étude des différents stades de vie et des effets transgénérationnels des stress environnementaux liés aux inondations permettrait de mieux anticiper la résilience et l'adaptabilité des populations marines face aux pressions croissantes du changement climatique.

2.1.2 Perspective 2 : utilisation de multiples espèces clés pour se rapprocher d'une approche écosystémique

Les réponses aux stress environnementaux, tels que ceux causés par les inondations et les variations de salinité, varient considérablement entre les espèces, même lorsqu'elles appartiennent au même embranchement, comme c'est le cas ici avec les mollusques. Cette variabilité souligne l'importance de s'éloigner des études centrées sur une seule espèce pour adopter une approche plus « écosystémique », où plusieurs espèces clés sont incluses afin de représenter la diversité des réponses physiologiques et comportementales.

En laboratoire, la reproduction d'une communauté en incluant plusieurs espèces permet d'observer des interactions interspécifiques, telles que la compétition pour les ressources et la prédation, qui influencent directement la résilience des communautés face aux stress environnementaux (Goldenberg *et al.*, 2017, 2018). L'inclusion d'une espèce fondatrice, comme l'huitre, peut aussi permettre de minimiser certains stress, comme le réchauffement, sur d'autres espèces d'invertébrés (McAfee *et al.*, 2018). Ainsi, la reproduction d'une communauté complexe en laboratoire permet d'observer des dynamiques compensatoires inhérentes à la complexité des écosystèmes pouvant atténuer les impacts des changements globaux sur les espèces et leurs communautés (Stewart *et al.*, 2013; Goldenberg *et al.*, 2018). Le cycle des marées (Pansch *et al.*, 2016) ou de la variabilité des paramètres physico-chimiques (Pansch and Hiebenthal, 2019) peuvent aussi être simulés en laboratoire afin de reproduire plus fidèlement les conditions naturelles (Kraufvelin *et al.*, 2010).

Une approche « écosystémique », en considérant les communautés dans leur ensemble, permet ainsi d'acquérir une vision plus complète de la résilience écologique (Stewart *et al.*, 2013). En observant non seulement les réponses spécifiques aux espèces, mais aussi leurs interactions et la manière dont elles modifient les réponses aux stress, on peut mieux comprendre les impacts à long terme des perturbations climatiques sur les réseaux trophiques, la structure des habitats et, ultimement, les services écosystémiques fournis par ces milieux. La taille et les coûts liés à l'inclusion de nombreuses espèces et paramètres

abiotiques limitent cependant la possibilité pour une grande réplication et répétabilité (Stewart *et al.*, 2013).

2.2 Utiliser un gradient de stresseurs et des conditions réalistes pour mieux représenter l'environnement et formuler des recommandations de gestion appropriées

Elliott et Quintino (2007) ont nommé le « Paradoxe de la qualité des estuaires » (*Estuarine Quality Paradox*) l'observation selon laquelle, malgré la dégradation apparente des conditions environnementales dans de nombreux estuaires (p. ex. pollution, apports en nutriments, changements hydrologiques), les indices de biodiversité et de productivité n'y diminuent pas toujours, et peuvent même y rester élevés. La grande variabilité retrouvée dans les conditions environnementales des estuaires rend également l'étude de ces milieux particulièrement complexe, puisqu'il est difficile de discriminer l'effet des stresseurs naturels (p. ex. variations journalière et saisonnière de la salinité, du pH et de l'oxygène dissout) avec ceux d'origines anthropiques (p. ex. pollution, modification du climat) (Elliott et Quintino, 2007). Bien que de nombreux changements des conditions environnementales sont observés durant des inondations, nous avons d'abord choisi de cibler la vulnérabilité de notre assemblage de mollusques au stress hypoosmotique, puisqu'il s'agit d'un stresseur inhérent aux inondations, et que la salinité est considérée comme le principal déterminant de la distribution des espèces dans les estuaires (Kinne, 1971; Lu *et al.*, 2008). L'utilisation d'un gradient de durée des pulses d'eau douce a permis d'identifier un seuil de vulnérabilité, les trois espèces montrant une mortalité très faible lorsque les pulses d'eau douce étaient inférieurs à deux jours. Afin d'étudier plus spécifiquement l'impact des inondations printanières, nous avons ensuite ajouté un second facteur de stress (conditions d'inondations printanières, c.-à-d. baisse du pH et hausse de la turbidité). L'ajout de ce second stresseur a augmenté le risque de mortalité chez toutes les espèces, a déplacé les points de bascule vers

des durées de pulses d'eau (premier stresseur) plus courtes chez *L. saxatilis* ou a fait apparaitre des seuils non détectés en conditions de contrôle chez *M. balthica* et *Mytilus* spp.

Mes résultats soulignent donc l'importance d'utiliser autant que possible des combinaisons de stresseurs représentants au mieux les conditions rencontrées par les communautés dans leur milieu naturel. Mon plan expérimental n'a pas cherché à déterminer si la combinaison des conditions d'inondations printanières (c.-à-d. diminution du pH et hausse de la turbidité) et du stress hypoosmotique avait des effets additifs, synergiques ou antagonistes puisque nous nous sommes concentrés sur des scénarios réalistes. En effet, une diminution de la salinité sans baisse de pH et hausse de la turbidité pourrait être observés dans certains estuaires, tandis qu'une diminution du pH aussi bas que 5,7 ne peut arriver sans une diminution de la salinité dans ces milieux. Sans avoir étudié l'impact de la diminution du pH et de l'augmentation de la turbidité en isolation, il semble tout de même que la mortalité élevée chez *M. balthica* et *Mytilus* spp. ainsi que la dissolution élevée de la coquille chez *L. saxatilis* semblent être dominées par l'effet des conditions d'inondation, car presque aucune mortalité ou dissolution de la coquille n'a été observée en l'absence de ces stresseurs supplémentaires. Dans l'ensemble, ces résultats permettent de souligner la nécessité de stratégies de gestion visant à protéger les communautés estuariennes subarctiques en réduisant les mauvaises pratiques agricoles et sylvicoles (p. ex. : coupe à blanc, suppression de la végétation riveraine) qui exacerbent l'acidification et la turbidité des cours d'eau.

Enfin, en comparant la mortalité observée dans les chapitres 2 et 3, après 2 semaines d'exposition à des pulses identiques d'exposition à l'eau douce, on peut observer que la mortalité est plus élevée dans la première que dans la seconde expérience (**Erreur ! Source du renvoi introuvable.**). Les organismes ont été prélevés dans les mêmes estuaires, et ont vécu des conditions de transport, de stabulation et d'exposition similaires, il semblerait donc que ce soit la température plus élevée (13,1 °C dans la première expérience vs. 5,7 °C dans la seconde) qui semble provoquer une mortalité accrue chez les trois espèces. En utilisant des analyses de modèle linéaire mixte pour les facteurs fixes « Expérience – Température » (deux niveaux, « Exp. 1 – 13,1 °C » et « Exp. 2 – 5,7 °C »), « Durée des pulses d'eau douce » et

leur interaction, cette dernière ressort par ailleurs significative pour les trois espèces (**Table A.21**), indiquant que la température semble augmenter la mortalité dans les pulses d'eau douce les plus longs.

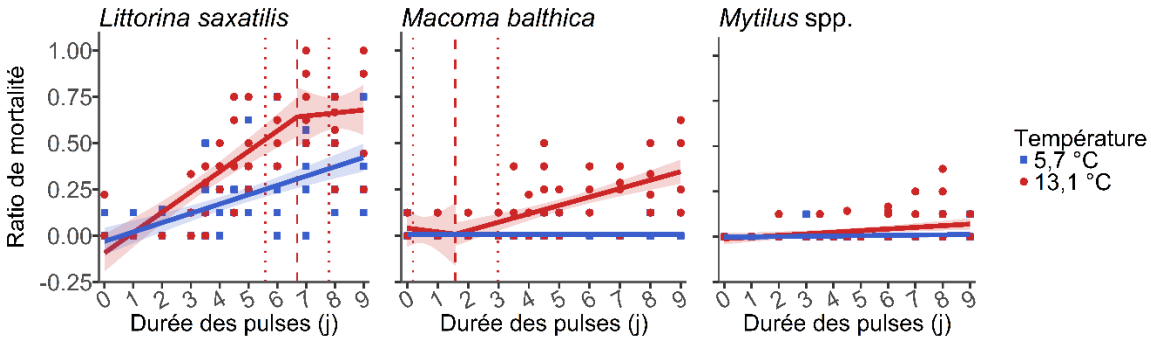

Figure 29. Relation entre la durée du pulse d'eau douce et le taux de mortalité de trois espèces de mollusques (*L. saxatilis*, *M. balthica* et *Mytilus* spp.). Les lignes continues (avec des zones ombrées d'intervalle de confiance à 95 %) représentent les modèles de régression segmentée optimaux à 5,7 °C (expérience 2, bleu, à 2.5 semaines) et à 13,1 °C (expérience 1, rouge, à 2 semaines). Les points de données illustrent le pourcentage de mortalité par estuaire d'origine et par réplicat. Les lignes verticales pointillées représentent des seuils significatifs ($p < 0,05$), avec des lignes pointillées à l'intervalle de confiance de 95 %.

2.2.1 Perspectives 3 : effet de la température et de la saisonnalité des inondations sur la vulnérabilité des écosystèmes estuariens

Avec le réchauffement global, les températures moyennes augmentent depuis le début de l'ère industrielle (Calvin *et al.*, 2023). Les vagues de chaleur marines, définies comme des anomalies de température durant au moins cinq jours au-dessus du 90ème centile des valeurs historiques (Hobday *et al.*, 2016), deviennent de plus en plus fréquentes et intenses à l'échelle mondiale (Frölicher *et al.*, 2018; Holbrook *et al.*, 2020). Comme la salinité, la température est un facteur déterminant dans l'organisation des communautés marines, car elle influence les réactions biochimiques et les taux métaboliques des organismes ectothermes (Clarke and Fraser, 2004). En combinaison, ces facteurs peuvent influencer la répartition et le recrutement des espèces dans les estuaires (Wooldridge et Deyzel, 2009;

Peck *et al.*, 2015). De plus, une faible salinité associée à un réchauffement peut réduire la fenêtre thermique des invertébrés (Farias *et al.*, 2024) et peut agir de manière synergique et induire un stress oxydatif et des dommages aux macromolécules tissulaires, déclenchant une réponse cellulaire au stress et une diminution des réserves énergétiques, signe d'une stratégie de compensation métabolique (Madeira *et al.*, 2021). Il serait donc pertinent d'étudier l'impact du réchauffement en combinaison avec les conditions d'inondations, surtout dans le cas d'une inondation accompagnée d'une vague de chaleur.

Les changements globaux entrainent aussi un décalage des périodes de crues de printemps, qui surviennent plus tôt dans l'année en raison de la hausse des température (Hodgkins *et al.*, 2003), et une augmentation de la fréquence des épisodes de pluies intenses, qui peuvent survenir à diverses saisons (Clavet-Gaumont *et al.*, 2017; Tabari, 2020). Il est donc pertinent de se demander si les inondations ont des impacts différents et plus ou moins prononcés selon les saisons sur les populations estuariennes, non seulement en raison des variations de température, mais aussi de l'état physiologique des organismes. En effet, les réserves énergétiques des organismes peuvent varier selon les saisons (Robinson *et al.*, 1981; Thompson et MacDonald, 1990; Brockington et Clarke, 2001), influençant leur capacité à résister aux stress (Sokolova, 2021; Sokolova, 2013). La disponibilité de nourriture peut aussi varier de façon saisonnière (Selleslagh *et al.*, 2012; Young *et al.*, 2021) et influencer la vulnérabilité des macroinvertébrés estuariens (Delorme *et al.*, 2020; Jeno and Brokordt, 2014). Pour les gestionnaires d'écosystèmes, l'acquisition de connaissance concernant la vulnérabilité des communautés estuariennes en fonction des saisons, mais aussi des périodes de reproduction et de croissance des espèces permettrait par exemple de pouvoir cibler les meilleurs périodes pour ouvrir les évacuateurs de crues en cas de nécessité.

2.3 Avantages et inconvénients des approches taxonomiques et fonctionnelles

Les approches taxonomiques et fonctionnelles ont toutes deux été efficaces pour détecter que l'apport en eau douce influence la composition et la structure des communautés estuariennes dans les estuaires subarctiques, en causant notamment une diminution de la

biomasse totale, et de la richesse fonctionnelle et taxonomiques. L'approche fonctionnelle a été plus efficace pour repérer ces changements de composition, puisque la diminution de la richesse fonctionnelle a été détectée à un niveau de stress plus faible que pour la diminution de la richesse taxonomique. Ces résultats concordent avec d'autres études menées dans des habitats estuariens, souvent caractérisés par une faible diversité taxonomique (van der Linden *et al.*, 2016; Morais *et al.*, 2019; Nunes de Souza *et al.*, 2021).

La perte de biodiversité observée avec les changements globaux et une pression anthropique croissante (Butchart *et al.*, 2010; Cardinale *et al.*, 2012) a conduit à explorer les relations complexes entre la diversité des communautés et les fonctions des écosystèmes (Barnes *et al.*, 2018; Lindegren *et al.*, 2018; Worm *et al.*, 2006). Cependant, tandis que certaines études ont mis en évidence une relation positive entre diversité et fonction (Danovaro *et al.*, 2008; Lefcheck and Duffy, 2015; Rodrigues-Filho *et al.*, 2023), d'autres n'ont pas trouvé de schémas cohérents (Baldrighi *et al.*, 2017; Leduc *et al.*, 2013; Witman *et al.*, 2008). Ces divergences pourraient être liées au type de traits fonctionnels analysés, à la complémentarité et redondance des espèces (Henderson *et al.*, 2020; Hooper *et al.*, 2005b). Dans notre étude, un fort apport en eau douce entraine la disparition des espèces filtreuses du substrat dur des estuaires subarctiques (*Mytilus* spp., *Balanus crenatus*, *Semibalanus balanoides*), entrainant donc une perte de fonction en raison du faible nombre d'espèces (**chapitre 1**). Il serait intéressant d'étudier si cette fonction, perdue sur substrat dur, continue d'être soutenue par la biodiversité présente en substrat mou.

2.3.1 Perspectives 4 : suivis continus des communautés benthiques estuariennes

Le nombre de barrages ne cesse d'augmenter à l'échelle mondiale pour répondre aux besoins d'une population humaine croissante à la recherche d'énergies renouvelables comme alternative aux énergies fossiles, ainsi que pour constituer des réserves d'eau destinées à l'agriculture et à l'approvisionnement en eau potable (Grill *et al.*, 2015). Pourtant, leurs influences sur les communautés benthiques estuariennes restent relativement peu connues, la plupart des études portant sur les modifications dans l'hydrologie et le transport de sédiment

(p. ex. Assani *et al.*, 2006; Wolanski et Hopper, 2022), les communautés d'eau douce (p. ex. Doretto *et al.*, 2019) ou de poissons (p. ex. Chícharo *et al.*, 2006), ou encore des comparaisons avant/après le retrait des barrages (p. ex. Morley *et al.*, 2020; Rubin *et al.*, 2017). Cette thèse soutient le concept que les analyses fonctionnelles permettent d'évaluer à la fois les causes et les conséquences des changements dans la structure et la composition des communautés (Lam-Gordillo *et al.*, 2020). Similairement à ce qui a été proposé dans la section 2.2.1 pour les expériences en laboratoire, il serait donc intéressant de faire un suivi de la composition fonctionnelle communautés estuariennes tout au long de l'année, en particulier à des moments clefs comme avant et après les inondations printanières.

Puisque l'identification à l'espèce (ou au minimum à un niveau taxonomique supérieur comme le genre ou la famille) est nécessaire pour les analyses fonctionnelles, nous conseillons de poursuive l'utilisation des analyses taxonomiques parallèlement aux analyses fonctionnelles. Les analyses taxonomiques permettent notamment de cibler de possibles espèces *sentinelles* ou *bioindicatrices*, c.-à-d. des espèces qui, par leur présence ou leur relative abondance, indiquent de possibles déséquilibres dans le milieu environnant ou des perturbations dans les fonctions des communautés (Dauvin *et al.*, 2012; Serrano *et al.*, 2022). Une espèce sentinelle optimale peut aussi avoir une réponse mesurable, comme l'accumulation d'un polluant dans les tissus, et une vulnérabilité au stresseur pris en compte (Multisanti *et al.*, 2022). Les milieux benthiques, qui supportent un grand nombre d'espèces sessiles incapables de fuir des stresseurs, sont particulièrement adaptés pour l'utilisation d'espèces sentinelles (García-Gómez *et al.*, 2020). *Mytilus* spp. est fréquemment utilisée comme espèce sentinelle, en raison de ses caractéristiques biologiques et écologiques: c'est une espèce sessile (donc qui fournit des informations spécifiques à un emplacement), de taille moyenne (un individu peut fournir suffisamment de tissu pour une analyse chimique), et formant des bancs en eaux peu profondes, ce qui facilite sa récolte (Beyer *et al.*, 2017). Cette espèce est aussi facile à maintenir en culture, ce qui la rend adaptée aux études écotoxicologiques en laboratoire ainsi qu'aux analyses in situ (Beyer *et al.*, 2017). Dans nos estuaires, son abondance augmentait avec la diminution de l'apport en eau douce, faisant

possiblement d'elle une bonne espèce sentinelle pour le stress hypoosmotique, et les autres stresseurs y étant associés (p. ex. variation du pH, de l'alcalinité et de la turbidité).

3. CONTRIBUTIONS ET RETOMBEES

Ma thèse met en lumière la vulnérabilité des communautés benthiques des estuaires subarctiques face à l'intensification du cycle hydrologique avec les changements globaux. Nos résultats apportent également une contribution essentielle à la description de ces communautés en milieu naturel, et apporte des recommandations de gestion pour limiter leur vulnérabilité face à la multiplication et à l'intensification des inondations.

En utilisant un gradient de durée d'exposition à des pulses d'eau douce, combiné à des conditions simulant les inondations printanières (baisse du pH et augmentation de la turbidité), notre recherche a permis d'identifier des seuils critiques de tolérance pour trois espèces clés de mollusques benthiques. Nous avons démontré que la mortalité des espèces étudiées augmente avec la durée de l'exposition au stress hypoosmotique, et que ce risque est intensifié sous des conditions typiques d'inondations printanières.

Les retombées de mon étude se traduisent en trois recommandations stratégiques pour les gestionnaires de barrages ou de bassins versants. Premièrement, afin de limiter les impacts négatifs des inondations sur les espèces estuariennes vulnérables, nous recommandons de ne pas excéder une durée de deux jours dans l'ouverture des évacuateurs de crue, au-delà de laquelle la mortalité commence à fortement augmenter. Deuxièmement, il est crucial de diminuer l'apport d'autres facteurs de stress lors des inondations printanières (p. ex. pH bas, turbidité élevée), car ils peuvent fortement aggraver les impacts du stress hypoosmotique sur les communautés estuariennes. Enfin, notre étude souligne la nécessité d'utiliser des facteurs de stress combinés pour représenter des conditions environnementales réalistes dans les études et les scénarios de gestion : l'utilisation de facteurs en isolation pourrait entrainer une sous-estimation des risques réels que les changements environnementaux imposent aux écosystèmes estuariens.

Enfin, pour améliorer nos connaissances et notre compréhension de l'impact des inondations sur les communautés estuariennes, nous recommandons de poursuivre la recherche selon quatre axes, à savoir (1) l'intégration de tous les stades de vie et l'étude des effets intergénérationnels, (2) l'étude des impacts de la température et de la saisonnalité des inondations, (3) l'utilisation de multiples espèces clés en laboratoire pour adopter une approche écosystémique et enfin (4) le suivi en continu des communautés benthiques estuariennes. Combiner ces approches permettrait de mieux évaluer la résilience des écosystèmes face aux changements globaux, offrant ainsi des pistes pour des stratégies de gestion plus efficaces.

ANNEXES

Table A.1. Summary of the coordinates, type of substrate and width for each study site.

Sites	Latitude	Longitude	Substrate	Width (m)
St-Nicolas	49.31589	-67.79173	Boulder	25
Marine 1	49.28627	-67.88047	Boulder	
Franquelin	49.29110	-67.89392	Boulder	50
Marine 2	49.28801	-67.92813	Boulder	
Mistassini	49.28718	-67.94943	Boulder	50
Barthelemy	49.04975	-68.59917	Bedrock	25
Marine 3	48.87671	-68.79431	Bedrock	
Marine 4	48.84018	-68.86902	Bedrock	
Cap-Colombier	48.82459	-68.90080	Bedrock	16

Table A.2. Summary of the mean (± SE) salinity measured in each estuary, for each of the freshwater input zone (n = 5).

Estuary	Null (Marine)	Low	Medium	High
Saint-Nicolas	29.86 (± 0.17)	24.64 (± 2.90)	11.14 (± 6.25)	6.50 (± 2.52)
Franquelin	29.64 (± 0.00)	23.38 (± 2.39)	17.83 (± 2.14)	4.66 (± 5.02)
Mistassini		24.29 (± 2.19)	14.50 (± 4.90)	8.25 (± 4.83)
Barthelemy	28.85 (± 1.74)	23.30 (± 4.57)	16.66 (± 4.22)	8.00 (± 2.45)
Cap-Colombier	27.20 (± 5.36)	24.21 (± 4.42)	16.75 (± 3.54)	7.38 (± 3.16)

Table A.3. Size classes used for each taxa group.

Taxon	A	B	C	D
Littorina spp.	< 0.5 cm	0.5 -1.0 cm	> 1 cm	
Balanidae	< 0.5 cm	0.5 -1.0 cm	1 - 2 cm	> 2 cm
Mytilus spp.	< 1.0 cm	1.0-2.0 cm	2 - 3 cm	> 3 cm

Table A.4. Summary of the empirical regression equations used to estimate the biomass (in g) for the invertebrate species. The length is in cm.

Species	**Regression**	**n**	**R^2**
Mytilus spp.[1]	$= 0.1016 \times length^{2.6861}$	54	0.9554
L. obtusata[1]	$= 0.3082 \times length^{2.9321}$	63	0.9769
L. saxatilis[1]	$= 0.2517 \times length^{2.5654}$	57	0.8514
B. crenatus and *S. balanoides*[2]	$= \frac{10^{(3.106 \times \log(length \times 10)) - 0.734}}{1000}$	204	0.981

[1]based on data collected by Sonia Morón and Mathieu Cusson (unpublished data), conducted in the same area in 2019.

[2](Spivey, 1989).

Table A.5. Weight given to each modality within trait for each species.

Traits	Modalities	*L. saxatilis*	*L. littorea*	*L. obtusata*	*O. bilamellata*	*T. testudinalis*	*Mytilus spp.*	*S. balanoides*	*B. crenatus*	*A. nodosum*	*F. vesiculosus*	*F. edentatus*	*F. evanescens*	*F. spiralis*
Adult mobility	Attached	0	0	0	0	0	1	1	1	1	1	1	1	1
	Crawler	1	1	1	1	1	0	0	0	0	0	0	0	0
Lifespan	Short	0	0	0	1	1	0	0	0	0	1	1	1	1
	Medium	1	1	1	0	0	1	1	1	0	0	0	0	0
	Long	0	0	0	0	0	0	0	0	1	0	0	0	0
Maximum potential size	Very small	1	0	1	0	0	0	1	1	0	0	0	0	0
	Small	0	1	0	1	1	0	0	0	0	0	0	0	0
	Medium	0	0	0	0	0	1	0	0	0	0	0	0	0
	Large	0	0	0	0	0	0	0	0	0	1	1	1	1
	Very large	0	0	0	0	0	0	0	0	1	0	0	0	0
Trophic type	Suspension feeder	0	0	0	0	0	1	1	1	0	0	0	0	0
	Grazer	1	1	1	0	1	0	0	0	0	0	0	0	0
	Predator	0	0	0	1	0	0	0	0	0	0	0	0	0
	Photoautotroph	0	0	0	0	0	0	0	0	1	1	1	1	1
Dispersal potential	Limited	1	0	1	0	0	0	0	0	1	1	1	1	1
	Long distance	0	1	0	1	1	1	1	1	0	0	0	0	0
Spawning season	Spring	0.4	1	0.8	1	0.5	0.2	1	0.4	1	0.4	0.3	0.6	0
	Summer	0.3	0	0.2	0	0.5	0.6	0	0.2	0	0.3	0.4	0.4	1
	Fall	0.3	0	0	0	0	0.2	0	0.4	0	0.3	0.3	0	0

Table A.6. List of taxa identified in this study with their mean biomass (g) (± SE) *per* freshwater input zone.

Species	**Null (n = 32)**	**Low (n = 41)**	**Medium (n = 40)**	**High (n = 37)**
Macroinvertebrate				
Mytilus spp. (Linnaeus, 1758)	18.06 (5.36)	36.1 (16.46)	4.64 (2.38)	0.46 (0.40)
Semibalanus balanoides (Linnaeus, 1767)	10.54 (4.87)	10.27 (3.94)	5.12 (2.92)	1.64 (1.16)
Balanus crenatus (Bruguière, 1789)	4.06 (1.52)	2.92 (1.38)	0.18 (0.09)	0.60 (0.33)
Littorina obtusata (Linnaeus, 1758)	1.20 (0.28)	0.87 (0.18)	0.26 (0.06)	0.17 (0.05)
Littorina saxatilis (Olivi, 1792)	0.39 (0.10)	0.52 (0.08)	0.68 (0.13)	0.73 (0.10)
Littorina littorea (Linnaeus, 1758)	0.24 (0.13)	0.02 (0.02)	0 (0.00)	0.01 (0.01)
Testudinalia testudinalis (O. F. Müller, 1776)	0.15 (0.07)	0.01 (0.01)	0 (0.00)	0 (0.00)
Onchidoris bilamellata (Linnaeus, 1767)	0.04 (0.02)	0 (0.00)	0 (0.00)	0 (0.00)
Macroalgae				
Ascophyllum nodosum (Linnaeus) Le Jolis, 1863	174.00 (60.67)	322.96 (78.38)	154.08 (46.85)	24.43 (9.42)
Fucus vesiculosus (Linnaeus, 1753)	104.20 (31.91)	161.21 (47.83)	136.40 (24.70)	60.91 (18.08)
Fucus distichus subsp. edentatus (Bachelot Pylaie) H.T.Powell, 1957	165.83 (42.86)	19.57 (9.22)	0.00 (0.00)	6.50 (5.45)
Fucus distichus subsp. evanescens (C.Agardh) H.T.Powell, 1957	48.76 (22.73)	4.88 (4.88)	1.37 (0.78)	8.84 (4.79)
Fucus spiralis (Linnaeus, 1753)	16.66 (9.97)	0.38 (0.38)	5.36 (4.20)	3.01 (2.55)

Table A.7. Summary of pairwise comparison between freshwater input zones by t-test: (a) biomass, (b) taxonomic richness, (c) functional richness (FRic), (d) Rao's quadratic entropy (RaoQ). Significant values are in bold.

	Groups	**t**	**P(perm)**
(a) Biomass (log)	High, Low	4.82	**0.0150**
	High, Medium	2.88	**0.0419**
	High, Null	3.89	**0.0248**
	Low, Medium	5.0	**0.0148**
	Low, Null	0.59	0.5837
	Medium, Null	2.85	**0.0506**
(b) Richness	High, Low	3.06	**0.0479**
	High, Medium	1.89	0.1316
	High, Null	4.31	**0.0186**
	Low, Medium	1.91	0.1312
	Low, Null	1.55	0.2144
	Medium, Null	2.40	0.0754
(c) Functional richness (FRic)	High, Low	3.36	**0.0101**
	High, Medium	2.03	0.1139
	High, Null	5.33	**0.0084**
	Low, Medium	2.18	0.1049
	Low, Null	2.48	**0.0414**
	Medium, Null	3.10	**0.0195**
(d) Rao's quadratic entropy (RaoQ)	High, Low	2.53	0.0760
	High, Medium	1.24	0.2816
	High, Null	5.11	**0.0119**
	Low, Medium	2.20	0.0937
	Low, Null	0.84	0.4687
	Medium, Null	1.99	0.1289

Table A.8. Summary of pairwise comparison between freshwater input zones by t-test: (a) taxonomic and (b) functional traits structure. Significant differences are in bold.

	Freshwater input zones	t	p-value
(a) Taxonomic structure	High - Low	2.05	**0.0131**
	High - Medium	1.65	0.0627
	High - Null	1.80	0.0570
	Low - Medium	1.87	0.0764
	Low - Null	0.75	0.6109
	Medium - Null	1.30	0.2301
(b) Functional traits structure	High - Low	2.23	0.0807
	High - Medium	1.41	0.1926
	High - Null	2.06	**0.0470**
	Low - Medium	1.61	0.1426
	Low - Null	1.08	0.3602
	Medium - Null	1.25	0.2634

Table A.9. Results of the SIMPER analysis for the taxonomic community among freshwater input zones.

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
High - Low	**High**	**Low**	**73.81**			
L. obtusata	0.14	0.49	13.78	0.98	18.67	18.67
A. nodosum	0.05	0.43	13.6	0.91	18.42	37.09
L. saxatilis	0.49	0.37	12.63	1.23	17.12	54.2
F. vesiculosus	0.21	0.39	12.4	0.94	16.8	71
Mytilus spp.	0.01	0.28	6.01	0.56	8.15	79.15
S. balanoides	0.04	0.18	5.29	0.55	7.16	86.31
B. crenatus	0.05	0.17	4.53	0.51	6.14	92.45
High - Medium	**High**	**Medium**	**66.32**			
L. saxatilis	0.49	0.43	17.22	1.34	25.96	25.96
F. vesiculosus	0.21	0.43	16.49	1.17	24.86	50.82
L. obtusata	0.14	0.2	9.69	0.92	14.61	65.43
A. nodosum	0.05	0.23	9.64	0.66	14.54	79.96
S. balanoides	0.04	0.09	4.11	0.51	6.19	86.15
Mytilus spp.	0.01	0.07	2.44	0.41	3.67	89.83
B. crenatus	0.05	0.02	2.08	0.42	3.14	92.97
Low - Medium	**Low**	**Medium**	**68.79**			
F. vesiculosus	0.39	0.43	13.25	1.17	19.26	19.26
A. nodosum	0.43	0.23	12.95	1.02	18.83	38.09
L. obtusata	0.49	0.2	11.92	1.03	17.33	55.41
L. saxatilis	0.37	0.43	11.4	1.18	16.57	71.98
Mytilus spp.	0.28	0.07	6.16	0.62	8.96	80.94
S. balanoides	0.18	0.09	5.58	0.64	8.12	89.06
B. crenatus	0.17	0.02	3.62	0.46	5.27	94.33
High - Null	**High**	**Null**	**80.29**			
L. obtusata	0.14	0.58	14.21	1.05	17.7	17.7
L. saxatilis	0.49	0.28	10.47	1.22	13.04	30.75
F. vesiculosus	0.21	0.3	9.01	1.04	11.22	41.97
F. distichus edentatus	0.02	0.34	7.97	0.83	9.93	51.89
A. nodosum	0.05	0.24	7.82	0.59	9.74	61.63
B. crenatus	0.05	0.25	5.99	0.6	7.47	69.1
Mytilus spp.	0.01	0.24	5.68	0.72	7.07	76.17
S. balanoides	0.04	0.18	5.31	0.65	6.62	82.79
F. distichus evanescens	0.03	0.13	3.66	0.48	4.56	87.34
L. littorea	0.01	0.13	3.08	0.39	3.84	91.18
Low - Null	**Low**	**Null**	**73.48**			
L. obtusata	0.49	0.58	12.14	1.15	16.52	16.52
A. nodosum	0.43	0.24	10.25	0.96	13.95	30.47
F. vesiculosus	0.39	0.3	8.88	1	12.08	42.55
L. saxatilis	0.37	0.28	7.13	1.14	9.71	52.26
Mytilus spp.	0.28	0.24	6.73	0.8	9.15	61.41
F. distichus edentatus	0.05	0.34	6.38	0.85	8.68	70.09
B. crenatus	0.17	0.25	5.96	0.67	8.11	78.21
S. balanoides	0.18	0.18	5.55	0.76	7.55	85.76
L. littorea	0.01	0.13	2.51	0.39	3.42	89.17
F. distichus evanescens	0.01	0.13	2.48	0.41	3.37	92.55
Medium - Null	**Medium**	**Null**	**76.58**			
L. obtusata	0.20	0.58	12.69	1.13	16.57	16.57
F. vesiculosus	0.43	0.3	10.24	1.27	13.37	29.94
L. saxatilis	0.43	0.28	9.36	1.11	12.22	42.16
A. nodosum	0.23	0.24	9.19	0.75	12	54.16
F. distichus edentatus	0.00	0.34	7.11	0.81	9.28	63.44

Mytilus spp.	0.07	0.24	5.53	0.77	7.22	70.66
S. balanoides	0.09	0.18	5.24	0.72	6.84	77.5
B. crenatus	0.02	0.25	5.08	0.57	6.64	84.14
F. distichus evanescens	0.01	0.13	2.81	0.41	3.67	87.81
F. spiralis	0.04	0.11	2.61	0.4	3.41	91.22

Table A.10. Summary of the PER-ANOVAs test used to investigate the effects of freshwater input on the Community Weighted Means (CWM). Significant values are in bold. V% stands for estimate of variance components.

Traits	**Modalities**	**df**	**Pseudo-F**	**p-value**	**% V**
Adult mobility	Attached	3	1.52	0.2598	10
	Crawler	3	1.52	0.2598	10
Lifespan	Short	3	2.44	0.1191	9
	Medium	3	2.04	0.1632	10
	Long	3	1.09	0.4057	6
Maximum potential	Very small	3	0.30	0.8396	1
	Small	3	2.29	0.0915	10
	Medium	3	2.89	0.0827	15
	Large	3	2.41	0.1112	9
	Very large	3	1.09	0.4046	6
Trophic type	Suspension	3	4.01	**0.0383**	19
	Grazer	3	1.60	0.2190	10
	Predator	3	2.45	0.1008	5
	Photoautotroph	3	2.25	0.1310	11
Dispersal potential	Limited	3	4.62	**0.0261**	21
	Long distance	3	4.62	**0.0281**	21
Spawning season	Spring	3	0.86	0.5079	5
	Summer	3	1.48	0.2654	7
	Fall	3	0.26	0.8549	1

Table A.11. Summary of PERMANOVAs showing the effects of freshwater input on the size class structure of the invertebrate species investigated: *Mytilus* spp., *Semibalanus balanoides*, *Balanus crenatus*, *Littorina obtusata* and *Littorina saxatilis*. Significant values are in bold. V% stands for estimate of variance components.

Species	Source	df	Pseudo-F	p-value	V%
Mytilus spp.	FI	3	2.90	**0.0246**	14
	Site	4	3.56	**0.0011**	11
	Site x FI**	9	2.23	**0.0032**	15
	Residual	72			54
	Total	88			
L. saxatilis	FI	3	1.22	0.3305	3
	Site	4	8.29	**0.0001**	20
	Site x FI	12	1.41	0.1046	10
	Residual	100			62
	Total	119			
L. obtusata	FI	3	2.59	0.0569	7
	Site	4	2.01	**0.0515**	8
	Site x FI**	9	0.99	0.4837	8
	Residual	74			70
	Total	90			
B. crenatus	FI	3	1.00	0.4751	10
	Site	4	1.36	0.2203	11
	Site x FI**	4	1.71	0.1092	14
	Residual	31			64
	Total	42			
S. balanoides	FI	3	1.22	0.3388	10
	Site	4	1.27	0.2794	8
	Site x FI**	8	1.94	0.0558	24
	Residual	29			46
	Total	44			

** Term had one or more empty cells, as the species was not present at each level of each site

Table A.12. Summary of PER-ANOVAs showing the effects of freshwater input ('FI'), the site ('Site'), their interaction and the quadrat on (a) the individual length, (b) thallus area and (c) weight of the macroalgae species investigated, *Ascophyllum nodosum* and *Fucus vesiculosus*. Significant values are in bold. V% stands for estimate of variance components. The site and the quadrat are random factors.

	(a) Length				**(b) Thallus area**				**(c) Weight**			
Source	**df**	**Pseudo-F**	**p-value**	**V%**	**df**	**Pseudo-F**	**p-value**	**V%**	**df**	**Pseudo-F**	**p-value**	**V%**
A. nodosum												
FI	3	2.22	0.1050	6	3	1.28	0.3026	4	3	2.16	0.1087	4
Site	4	0.48	0.7411	1	4	1.46	0.2262	3	4	0.87	0.4793	2
FI x Site	12	2.46	**0.0198**	12	11	2.35	**0.0240**	14	12	1.73	0.0902	9
Quadrat(FIxSite)	56	2.54	**0.0001**	30	50	0.99	0.5112	28	56	1.65	**0.0105**	30
Residual	126			27	67			38	126			40
Total	201				135				201			
F. vesiculosus												
FI	3	8.47	**0.0008**	15	3	1.19	0.3497	4	3	3.31	**0.0474**	8
Site	4	2.64	0.0508	4	4	1.95	0.1121	3	4	0.98	0.4284	2
FI x Site**	10	1.79	0.0966	6	10	3.18	**0.0036**	14	10	2.13	**0.0382**	9
Quadrat(FIxSite)	81	2.08	**0.0002**	33	79	1.03	0.4417	34	81	1.89	**0.0001**	36
Residual	207			40	103			43	207			49
Total	305				199				305			

**Term had one or more empty cells, as the species was not present at each level of each site

Table A.13. Pairwise results between freshwater input zones (FI) for the macroalgae morphological parameters: (a) length, (b) thallus area and (c) weight. Significant differences are in bold.

		(a) Length		(b) Thallus area		(c) Weight	
Species	**FI**	**t**	**p-value**	**t**	**p-value**	**t**	**p-value**
A. nodosum	High - Low	2.27	**0.0347**	1.21	0.261	2.16	**0.0473**
	High - Medium	2.26	**0.0299**	1.38	0.194	2.37	**0.0236**
	High - Null	2.57	**0.0519**	1.62	0.190	2.34	0.0623
	Low - Medium	0.86	0.4195	0.01	0.995	0.35	0.7379
	Low - Null	0.53	0.6220	0.94	0.416	0.74	0.4928
	Medium - Null	0.34	0.7591	0.98	0.396	1.16	0.3030
F. vesiculosus	Null - Medium	3.05	**0.0260**	1.27	0.288	2.11	0.1110
	Null - Low	2.09	0.1446	1.26	0.322	1.41	0.2754
	Null - High	4.53	**0.0221**	1.49	0.252	15.33	**0.0005**
	Medium - Low	3.19	**0.0117**	0.09	0.931	0.88	0.4218
	Medium - High	1.48	0.1880	1.31	0.240	1.30	0.2347
	Low - High	2.65	**0.0401**	0.87	0.435	1.51	0.1922

Table A.14. Results of (a) the analyse of covariance on the effect of taxonomical richness and freshwater input zones (FI) on the functional richness, and (b) pairwise analyses among freshwater input zones for the slope (interaction Richness x FI).

(a) Effects of taxonomic richness and FI on FRic

Source	**df**	**F-value**	**p-value**
Richness	1	205.04	< **0.001**
FI	3	8.70	< **0.001**
Richness x FI	3	2.92	**0.0368**
Residuals	124		

(b) Pairwise results of the interaction

Contrast	**t-ratio**	**p-value**
Null - Low	1.12	0.6783
Null - Medium	-1.29	0.5700
Null - High	-1.93	0.2230
Low - Medium	-2.11	0.1546
Low - High	-2.64	**0.0456**
Medium - High	-0.67	0.9102

Table A.15. Summary of mean (and standard error) for the abiotic parameters in each mesocosm during the 6-week experiment.

Exposure (d)	Mesocosm	Salinity		Temperature °C	pH	DO % sat.
0	29	Seawater	27.31 (0.2)	13.36 (0.05)	7.95 (0.05)	84.0 (1.0)
	30	Seawater	27.29 (0.2)	13.37 (0.05)	7.95 (0.05)	84.0 (1.0)
0.5	17	Freshwater	0.75 (0.27)	13.34 (0.05)	8.10 (0.20)	83.0 (2.0)
		Seawater	27.08 (0.27)			
	18	Freshwater	0.70 (0.28)	13.34 (0.05)	8.10 (0.20)	83.5 (0.5)
		Seawater	27.29 (0.23)			
1	7	Freshwater	0.45 (0.03)	13.19 (0.04)	8.00 (0.01)	82.0 (2.0)
		Seawater	27.34 (0.27)			
	8	Freshwater	0.45 (0.03)	13.21 (0.05)	7.95 (0.05)	83.5 (3.5)
		Seawater	27.27 (0.27)			
1.5	13	Freshwater	0.43 (0.02)	13.15 (0.04)	8.25 (0.35)	83.0 (0.1)
		Seawater	27.14 (0.34)			
	14	Freshwater	0.44 (0.02)	13.16 (0.05)	8.20 (0.20)	82.0 (1.0)
		Seawater	27.13 (0.32)			
2	5	Freshwater	0.44 (0.01)	13.21 (0.03)	8.10 (0.20)	82.0 (2.0)
		Seawater	27.25 (0.37)			
	6	Freshwater	0.49 (0.05)	13.20 (0.03)	8.10 (0.20)	80.0 (0.1)
		Seawater	27.32 (0.36)			
2.5	25	Freshwater	0.56 (0.12)	13.19 (0.04)	8.40 (0.10)	82.0 (1.0)
		Seawater	27.18 (0.28)			
	26	Freshwater	0.57 (0.12)	13.19 (0.04)	8.35 (0.15)	82.0 (1.0)
		Seawater	27.29 (0.31)			
3	9	Freshwater	0.42 (0.01)	13.14 (0.04)	8.50 (0.10)	82.0 (1.0)
		Seawater	27.01 (0.39)			
	10	Freshwater	0.42 (0.01)	13.15 (0.04)	8.50 (0.01)	83.0 (0.1)
		Seawater	26.83 (0.37)			
3.5	23	Freshwater	0.54 (0.12)	13.24 (0.03)	8.35 (0.05)	82.0 (1.0)
		Seawater	27.22 (0.38)			
	24	Freshwater	0.54 (0.12)	13.22 (0.03)	8.30 (0.01)	83.0 (0.1)
		Seawater	27.34 (0.38)			
4	27	Freshwater	0.53 (0.11)	13.15 (0.03)	8.15 (0.15)	83.5 (0.5)
		Seawater	27.24 (0.54)			
	28	Freshwater	0.66 (0.15)	13.21 (0.03)	8.15 (0.15)	83.5 (0.5)
		Seawater	27.31 (0.53)			
4.5	19	Freshwater	0.53 (0.11)	13.25 (0.04)	8.10 (0.20)	83.5 (0.5)
		Seawater	27.17 (0.53)			
	20	Freshwater	0.55 (0.11)	13.25 (0.04)	8.15 (0.15)	83.5 (0.5)
		Seawater	27.10 (0.52)			
5	11	Freshwater	0.41 (0.01)	13.14 (0.03)	8.15 (0.15)	81.5 (0.5)
		Seawater	27.18 (0.63)			
	12	Freshwater	0.41 (0.01)	13.15 (0.03)	8.20 (0.20)	82.5 (0.5)
		Seawater	27.30 (0.62)			
6	21	Freshwater	0.53 (0.11)	13.23 (0.04)	8.45 (0.15)	83.0 (0.1)
		Seawater	27.22 (0.36)			
	22	Freshwater	0.53 (0.11)	13.22 (0.03)	8.35 (0.05)	82.0 (1.0)
		Seawater	27.23 (0.38)			
7	3	Freshwater	0.43 (0.01)	13.20 (0.03)	8.20 (0.10)	80.5 (0.5)
		Seawater	27.10 (0.40)			
	4	Freshwater	0.44 (0.02)	13.19 (0.03)	8.25 (0.05)	81.5 (0.5)
		Seawater	26.90 (0.30)			
8	1	Freshwater	0.47 (0.04)	13.24 (0.04)	8.15 (0.05)	84.0 (0.1)
		Seawater	27.13 (0.63)			
		Freshwater	0.50 (0.07)			

	2	Seawater	26.43 (0.50)	13.21 (0.03)	8.20 (0.10)	81.5 (0.5)
9	15	Freshwater	0.42 (0.01)	13.13 (0.04)	8.20 (0.20)	84.0 (1.0)
		Seawater	26.40 (1.12)			
	16	Freshwater	0.41 (0.01)	13.13 (0.04)	8.20 (0.20)	83.5 (1.5)
		Seawater	27.10 (0.95)			

Table A.16. Summary of the contrast between slopes among time levels, for the relationships between the changes in body mass and the freshwater input duration in *Littorina saxatilis*, *Macoma balthica* and *Mytilus* spp.

Species	Contrast between slopes	Estimate	SE	df	t-ratio	*P* value
L. saxatilis	2 *vs*. 4 weeks	0.0012	0.0032	85	3.770	**0.0003**
M. balthica	2 *vs*. 4 weeks	0.0004	0.0001	476	3.752	**0.0006**
	2 *vs*. 6 weeks	0.0001	0.0001	454	0.579	0.8312
	4 *vs*. 6 weeks	-0.0003	0.0002	477	-2.115	0.0879
Mytilus spp.	2 *vs*. 4 weeks	0.0008	0.0002	613	4.37	**<0.0001**
	2 *vs*. 6 weeks	0.0007	0.0002	622	3.812	**0.0004**
	4 *vs*. 6 weeks	-0.0001	0.0002	615	-0.420	0.9072

Table A.17. Summary of the ANOVA showing the effects of the freshwater pulse duration ('Pulse duration'), 'Time' and their interaction on the changes in aspect ratio of (a) *Littorina saxatilis*, (b) *Macoma balthica* and (c) *Mytilus* spp. Significant values are in bold. The goodness of fit (R^2) represents the variance explained by the fixed effects only (R^2m) and by the fixed and random effects (R^2c). For *L. saxatilis*, the best model included only the 'Replicate' as a random factor, but only the 'Estuary' for *M. balthica* and *Mytilus* spp.

Source of	df_1	df_2	Mean	F ratio	*P* value
Littorina saxatilis (R^2m: 0.07, R^2c: 0.09)					
Pulse duration	1	68	4.74E-06	0.01	0.9438
Time	1	145	0.0002	0.23	0.6357
Interaction	1	127	0.0010	1.09	0.2994
Macoma balthica (R^2m: 0.06, R^2c: 0.10)					
Pulse duration	1	202	0.0011	2.44	0.1196
Time	2	201	0.0016	3.62	**0.0284**
Interaction	2	201	0.0002	0.56	0.5745
Mytilus spp. (R^2m: 0.14, R^2c: 0.17)					
Pulse duration	1	251	0.0004	0.76	0.3838
Time	2	251	0.0012	2.47	0.0869
Interaction	2	251	0.0011	2.16	0.1176

Table A.18. Summary of the contrast between slopes among time levels, for the relationships between the energy content and the freshwater input duration in *Mytilus* spp.

Contrast between slopes	Estimate	SE	df	t-ratio	*P* value
2 *vs*. 4 weeks	-0.268	0.169	235	-1.582	0.2552
2 *vs*. 6 weeks	-0.568	0.172	244	-3.303	**0.0031**
4 *vs*. 6 weeks	-0.300	0.172	243	-1.740	0.1924

Table A. Summary of the results of the ANOVA tests showing the effects of freshwater pulses ('Pulse duration'), 'Flood conditions', and their interaction on various abiotic parameters measured in the mesocosms during the 5-week experiment. Significant values are given in bold.

Parameter	Source of variation	Df	MS	F value	*P* value
pH*	**Flood conditions**	1	1133.75	321090.00	**< 0.0001**
	Pulse duration	10	0.00	0.20	0.9966
	Flood conditions:Pulse duration	10	0.01	2.24	**0.0136**
	Residuals	1144	0.00		
Salinity*	Flood conditions	1	1.70	0.02	0.8925
	Pulse duration	11	6167.60	66.27	**< 0.0001**
	Flood conditions:Pulse duration	11	6.70	0.07	1.0000
	Residuals	1554	93.10		
DO **	**Flood conditions**	1	1198.19	41.92	**< 0.0001**
(% sat.)	**Pulse duration**	11	100.98	3.53	**0.0001**
	Flood conditions:Pulse duration	11	87.22	3.05	**0.0007**
	Residuals	250	28.59		
Temperature **	**Flood conditions**	1	55.47	450.35	**< 0.0001**
(°C)	**Pulse duration**	11	1.08	8.75	**< 0.0001**
	Flood conditions:Pulse duration	11	3.36	27.27	**< 0.0001**
	Residuals	1553	0.12		

* Only the freshwater data were used

** Both the freshwater and the sea water data were used

Table A. Summary of mean (and standard error) for the abiotic parameters measured throughout the duration of the experiment in each mesocosm for the "flood" freshwater (FW) pulses.

Mesocosm	Pulse	Temperature	DO (SE)	Water	Salinity	pH (SE)
1	2	5.60 (0.34)	91.85 (4.58)	Flood FW	0.46 (0.05)	5.74 (0.04)
				Sea water	26.93 (1.01)	7.80 (0.11)
2	2	5.62 (0.32)	91.47 (4.84)	Flood FW	1.09 (3.09)	5.78 (0.18)
				Sea water	26.93 (1.04)	7.80 (0.09)
3	7	5.67 (0.26)	92.14 (4.01)	Flood FW	0.44 (0.02)	5.74 (0.04)
				Sea water	26.05 (0.76)	7.79 (0.04)
4	7	5.69 (0.27)	93.05 (3.52)	Flood FW	0.44 (0.02)	5.74 (0.04)
				Sea water	26.08 (0.77)	7.80 (0.04)
5	9	5.68 (0.26)	90.62 (4.88)	Flood FW	0.44 (0.03)	5.74 (0.04)
				Sea water	26.47 (1.59)	7.77 (0.03)
6	9	5.70 (0.25)	90.85 (4.62)	Flood FW	0.52 (0.43)	5.74 (0.04)
				Sea water	26.57 (1.64)	7.73 (0.02)
9	3	5.60 (0.33)	89.47 (4.29)	Flood FW	0.43 (0.01)	5.75 (0.04)
				Sea water	26.45 (1.70)	7.79 (0.07)
10	3	5.61 (0.34)	90.60 (4.96)	Flood FW	0.44 (0.03)	5.74 (0.04)
				Sea water	26.39 (1.74)	7.76 (0.13)
13	3.5	5.66 (0.28)	94.33 (3.38)	Flood FW	0.44 (0.01)	5.75 (0.04)
				Sea water	27.42 (0.64)	7.84 (0.02)
14	3.5	5.62 (0.28)	92.81 (4.08)	Flood FW	0.43 (0.01)	5.74 (0.03)
				Sea water	27.43 (0.65)	7.84 (0.01)
17	5	5.54 (0.35)	90.58 (4.47)	Flood FW	0.43 (0.01)	5.74 (0.03)
				Sea water	27.30 (1.02)	7.80 (0.07)
18	5	5.50 (0.36)	88.63 (5.88)	Flood FW	0.43 (0.01)	5.74 (0.03)
				Seawater	27.32 (1.02)	7.81 (0.05)
23	6	5.56 (0.32)	85.34 (5.04)	Flood FW	0.43 (0.01)	5.74 (0.03)
				Sea water	27.31 (1.91)	7.84 (0.03)
24	6	5.65 (0.33)	87.73 (6.33)	Flood FW	0.43 (0)	5.74 (0.03)
				Sea water	27.27 (1.97)	7.84 (0.03)
27	1	5.57 (0.47)	90.54 (4.12)	Flood FW	0.44 (0.02)	5.77 (0.05)
				Sea water	26.73 (1.5)	7.83 (0.05)
28	1	5.54 (0.47)	92.36 (4.02)	Flood FW	0.47 (0.1)	5.75 (0.04)
				Sea water	26.76 (1.49)	7.83 (0.05)
29	4.5	5.79 (0.53)	92.44 (3.24)	Flood FW	0.44 (0.04)	5.75 (0.04)
				Sea water	26.92 (1.6)	7.83 (0.04)
30	4.5	5.80 (0.48)	91.6 (4.01)	Flood FW	0.43 (0.01)	5.75 (0.04)
				Sea water	26.96 (1.63)	7.83 (0.04)
37	8	5.61 (0.24)	86.9 (4.54)	Flood FW	0.43 (0.01)	5.75 (0.03)
				Sea water	27.48 (0.63)	7.82 (0.01)
38	8	5.64 (0.24)	87.24 (4.60)	Flood FW	0.43 (0.01)	5.74 (0.03)
				Sea water	27.5 (0.58)	7.82 (0.01)
41	0	5.12 (0.52)	92.48 (4.33)	Sea water	26.8 (1.43)	7.86 (0.05)

42	0	5.07 (0.54)	94.42 (3.76)	Sea water	26.77 (1.43)	7.86 (0.05)
47	4	5.38 (0.38)	89.22 (5.38)	Flood FW	0.44 (0.02)	5.75 (0.04)
				Sea water	26.44 (1.62)	7.85 (0.06)
48	4	5.35 (0.41)	89.68 (4.57)	Flood FW	0.44 (0.02)	5.75 (0.04)
				Sea water	26.4 (1.62)	7.84 (0.04)

Table A.19. Summary of mean (and standard error) for the abiotic parameters measured during the duration of the experiment in each mesocosm for the "control" freshwater (FW) pulses.

Mesocosm	Pulse duration (d)	Temperature (SE)	DO (SE)	Water	Salinity (SE)	pH (SE)
7	8	5.36 (0.18)	85.95 (8.37)	Control FW	0.37 (0.03)	7.73 (0.06)
				Sea water	27.44 (0.59)	7.82 (0.01)
8	8	5.35 (0.19)	83.34 (5.25)	Control FW	0.37 (0.01)	7.73 (0.06)
				Sea water	27.45 (0.62)	7.83 (0.01)
11	0	5.61 (0.63)	93.17 (5.31)	Seawater	26.78 (1.43)	7.81 (0.09)
12	0	5.55 (0.63)	94.92 (5.32)	Sea water	26.81 (1.43)	7.82 (0.07)
15	6	5.30 (0.30)	88.77 (8.07)	Control FW	0.37 (0.01)	7.73 (0.08)
				Sea water	27.32 (1.92)	7.86 (0.05)
16	6	5.30 (0.30)	87.59 (8.34)	Control FW	0.37 (0.01)	7.73 (0.07)
				Sea water	27.32 (1.91)	7.86 (0.05)
19	7	5.20 (0.19)	88.15 (3.95)	Control FW	0.37 (0.01)	7.73 (0.06)
				Sea water	26.11 (0.69)	7.84 (0.04)
20	7	5.21 (0.19)	85.87 (5.61)	Control FW	0.37 (0.01)	7.72 (0.06)
				Sea water	26.09 (0.75)	7.84 (0.04)
21	2	5.24 (0.31)	81.90 (7.47)	Control FW	0.37 (0.01)	7.7 (0.05)
				Sea water	26.97 (1.06)	7.84 (0.05)
22	2	5.31 (0.30)	82.57 (5.14)	Control FW	0.38 (0.01)	7.70 (0.05)
				Sea water	26.88 (0.95)	7.86 (0.04)
25	5	5.15 (0.28)	88.88 (8.74)	Control FW	0.38 (0.02)	7.72 (0.06)
				Sea water	27.29 (0.96)	7.83 (0.05)
26	5	5.15 (0.26)	83.95 (8.48)	Control FW	0.37 (0.01)	7.72 (0.06)
				Sea water	27.34 (1.03)	7.84 (0.06)
31	3	5.13 (0.25)	88.58 (3.51)	Control FW	0.37 (0.01)	7.72 (0.06)
				Sea water	26.58 (1.55)	7.83 (0.06)
32	3	5.19 (0.26)	88.41 (4.55)	Control FW	0.39 (0.07)	7.63 (0.42)
				Seawater	26.62 (1.54)	7.84 (0.06)
33	4.5	5.13 (0.46)	85.61 (8.86)	Control FW	0.37 (0.01)	7.71 (0.07)
				Sea water	26.64 (1.52)	7.85 (0.04)
34	4.5	5.19 (0.44)	84.36 (4.32)	Control FW	0.37 (0.01)	7.71 (0.06)
				Sea water	26.65 (1.52)	7.85 (0.04)
35	3.5	5.13 (0.30)	81.45 (7.27)	Control FW	0.85 (1.77)	7.71 (0.09)
				Sea water	27.43 (0.57)	7.84 (0.05)
36	3.5	5.10 (0.27)	81.47 (6.76)	Control FW	0.39 (0.11)	7.72 (0.06)
				Sea water	27.42 (0.6)	7.85 (0.04)
39	4	5.12 (0.32)	85.26 (4.03)	Control FW	0.37 (0.01)	7.72 (0.08)
				Sea water	26.43 (1.6)	7.85 (0.03)

40	4	5.20 (0.37)	84.49 (4.91)	Control FW	0.37 (0.01)	7.71 (0.07)
				Sea water	26.43 (1.64)	7.86 (0.03)
43	9	4.97 (0.20)	87.55 (4.15)	Control FW	0.38 (0.02)	7.73 (0.10)
				Sea water	26.59 (1.62)	7.88 (0.06)
44	9	4.99 (0.22)	85.64 (7.11)	Control FW	0.37 (0.01)	7.73 (0.09)
				Sea water	26.92 (1.18)	7.85 (0.02)
45	1	4.83 (0.34)	89.38 (5.03)	Control FW	0.42 (0.09)	7.69 (0.07)
				Sea water	26.61 (1.39)	7.85 (0.04)
46	1	4.84 (0.32)	89.23 (5.00)	Control FW	0.59 (0.65)	7.69 (0.06)
				Sea water	26.65 (1.44)	7.86 (0.05)

Table A.20. Summary of the results of the ANOVA tests showing the effects of exposure to freshwater pulses ('Pulse duration'), 'Flood conditions' and their interaction on the shell aspect ratio in (a) *Littorina saxatilis*, (b) *Macoma balthica* and (c) *Mytilus* spp. at 2.5 (left) and 5 weeks (right). Significant values are given in bold. The goodness of fit represents the variance explained by the fixed effects only (R^2m) and by the fixed and random effects (R^2c). For all the sources of variation, $df_1 = 1$.

Shell aspect ratio	**Change in aspect ratio at 2.5 weeks**				*Shell aspect ratio*	**Change in aspect ratio at 5 weeks**			
Source of variation	**df_2**	**MS**	**F ratio**	***P* value**	**Source of variation**	**df_2**	**MS**	**F ratio**	***P* value**
a. *L. saxatilis*	R^2m: 0.03, R^2c: 0.26 *					R^2m: 0.02, R^2c: 0.02 *			
Pulse duration	36	0.00130	1.014	0.3207	Pulse duration	103	0.00232	1.020	0.3149
Flood conditions	39	0.00156	1.213	0.2776	Flood conditions	103	0.00116	0.512	0.4759
Interaction	36	0.00220	1.716	0.1984	Interaction	103	0.00008	0.035	0.8516
b. *M. balthica*	R^2m: 0.03, R^2c: 0.15 **					R^2m: 0.02, R^2c: 0.18 **			
Pulse duration	136	0.00060	1.869	0.1738	Pulse duration	168	0.00022	0.640	0.4248
Flood conditions	134	0.00012	0.371	0.5433	Flood conditions	167	0.00056	1.637	0.2025
Interaction	134	0.00046	1.424	0.2348	**Interaction**	167	0.00148	4.342	**0.0387**
c. *Mytilus* spp.	R^2m: 0.05, R^2c: 0.08 **					R^2m: 0.02, R^2c: 0.02 **			
Pulse duration	165	0.00006	0.345	0.5577	Pulse duration	180	0.00001	0.092	0.7622
Flood conditions	165	0.00069	3.852	0.0514	Flood conditions	181	0.00037	2.372	0.1253
Interaction	165	0.00006	0.310	0.5782	Interaction	180	0.00002	0.114	0.7356

* The best model included only the 'Mesocosm' as a random factor

** The best model included only the 'Estuary of origin' as a random factor

Table A.21. Summary of the ANOVA showing the effects of the freshwater pulse duration ('Pulse duration'), 'Temperature' (or experiment) and their interaction on the mortality ratios of (a) *L. saxatilis*, (b) *M. balthica* and (c) *Mytilus* spp. Significant values are in bold. For *L. saxatilis*, the best model included the 'Replicate' and 'Estuary' as random factors, but only the 'Estuary' for *M. balthica* and *Mytilus* spp.

Source of variation	df_2	Mean square	F ratio	*P* value
a. *Littorina saxatilis*				
Pulse duration	44	2.1960	109.3	< **0.0001**
Temperature	44	0.0008	0.039	0.8443
Interaction	44	0.1871	9.308	**0.0039**
b. *Macoma balthica*				
Pulse duration	138	0.3669	45.38	**0.0000**
Temperature	138	0.0069	0.8518	0.3576
Interaction	138	0.3685	45.57	**0.0000**
c. *Mytilus* spp.				
Pulse duration	138	0.0287	10.84	**0.0013**
Temperature	138	0.0007	0.2726	0.6024
Interaction	138	0.0135	5.086	**0.0257**

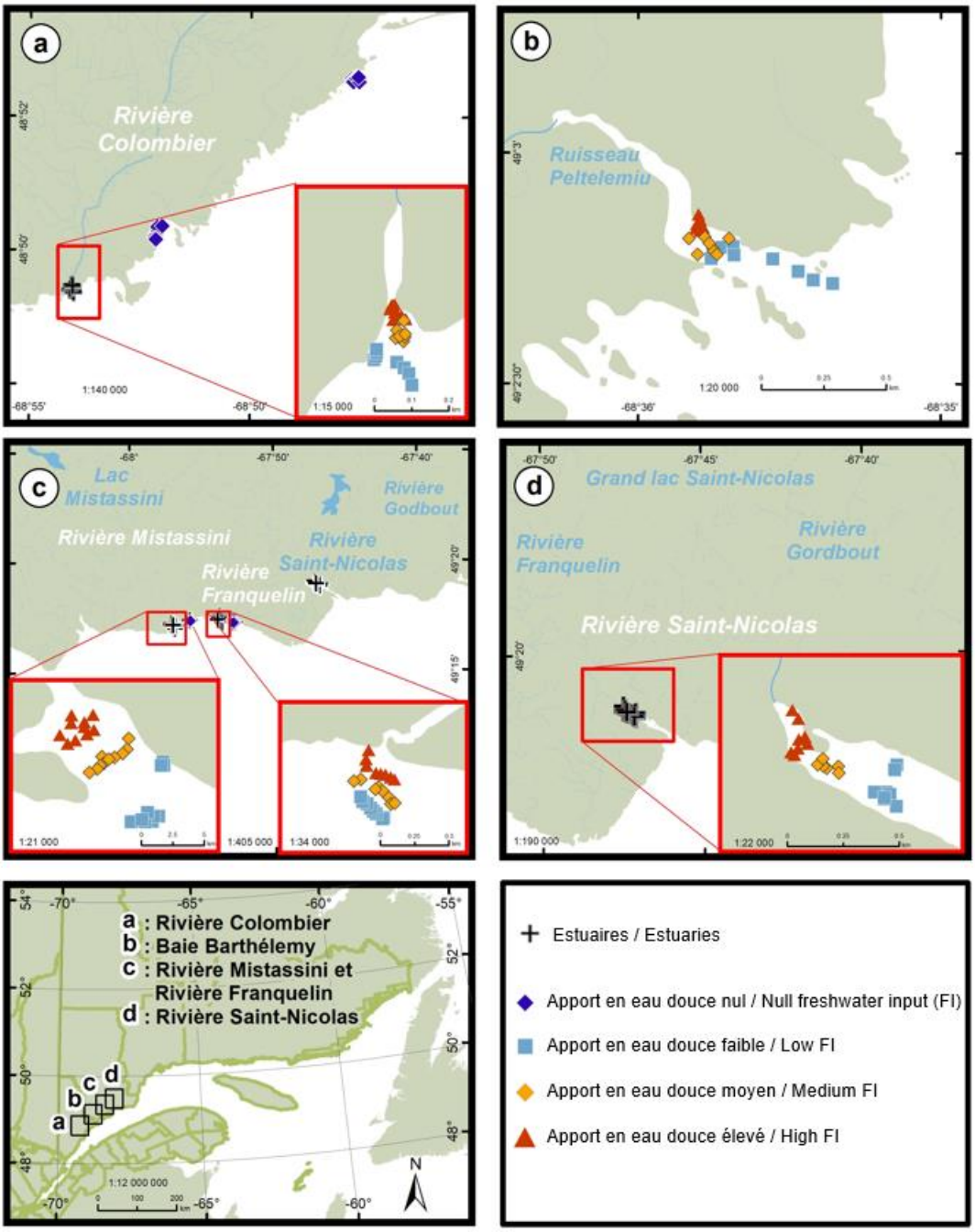

Figure A.1. Maps showing the repartition of the studied estuaries along the St.-Lawrence estuary (bottom left) and the quadrat repartition in every estuary. The map is available with the corresponding data on the website of the St. Lawrence Global Observatory (doi: 10.26071/ogsl-4bb77d86-b94e).

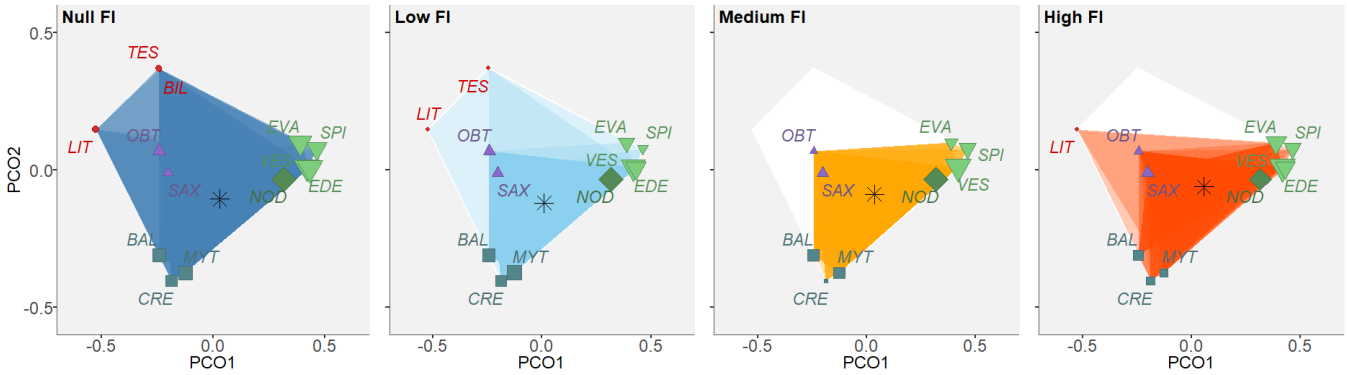

Figure A.2. Two-dimensional representation of the functional space filled by species in the communities in each freshwater input zones (FI). The name of each species is indicated by a three-letter code (SAX: *Littorina saxatilis*, LIT: *L. littorea*, OBT: *L. obtusata*, BIL: *Onchidoris bilamellata*, TES: *Testudinalia testudinalis*, MYT: *Mytilus spp.*, BAL: *Semibalanus balanoides*, CRE: *Balanus crenatus*, NOD: *Ascophyllum nodosum*, VES: *Fucus vesiculosus*, EDE: *F. edentatus*, EVA: *F. evanescens*, SPI: *F. spiralis*). The point size represents the mean biomass. The shape and color of the point represents the functional group (chosen a posteriori, using a dendrogram cut at 0.4 created with the dbFD function). The colored surface represents the functional richness in each single quadrat, therefore the denser colored area is representative of the mean FRic in each FI. The black star represents the gravity center of each FI zone. PCO1 and PCO2 explained 53.2% and 26.6% of total variation.

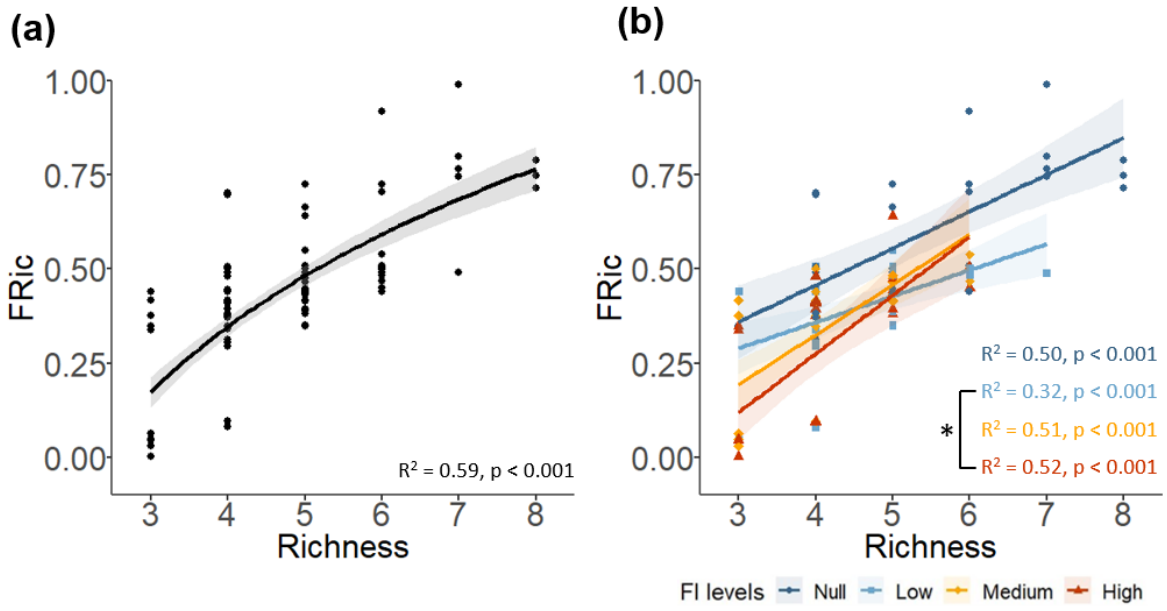

Figure A.3. Relationship between the taxonomic richness and the functional richness (FRic): (a) overall, across all freshwater input zones. The FRic depends on the taxonomical richness (logistical regression, $F_{1,130} = 183.87$, $p < 0.001$); and (b) separately, for each freshwater input zone. FRic increased with the richness across all FI zones ($p < 0.001$ for each linear regression, R^2 between 0.32 and 0.52), but the slopes significantly differed between the high and low freshwater input zones.

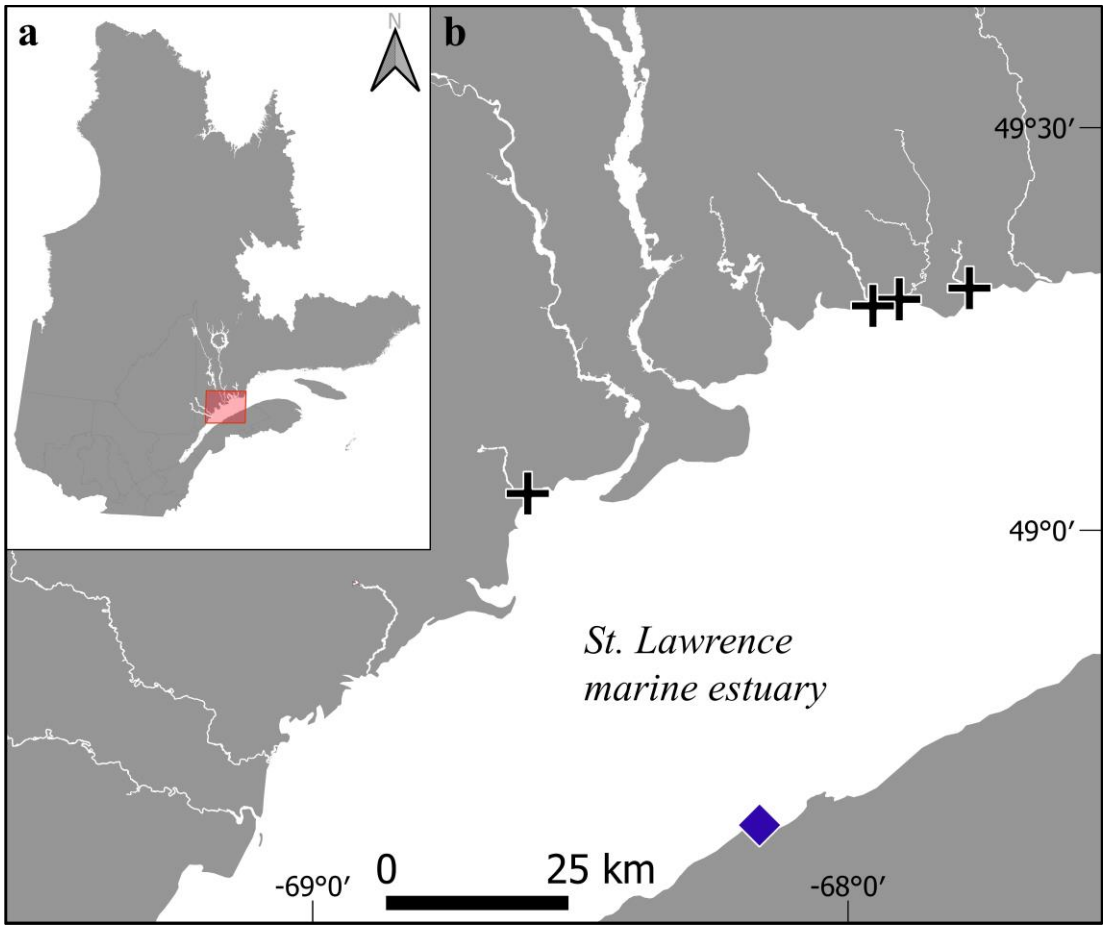

Figure A.4. Maps showing (a) Quebec, Canada, with the sampling locations in the red rectangle; (b) the location of estuaries where specimens were collected (black crosses, from left to right: Barthelemy, Mistassini, Franquelin and St. Nicholas) and the laboratory (Maurice-Lamontagne Institute) where the experiment took place (blue diamond).

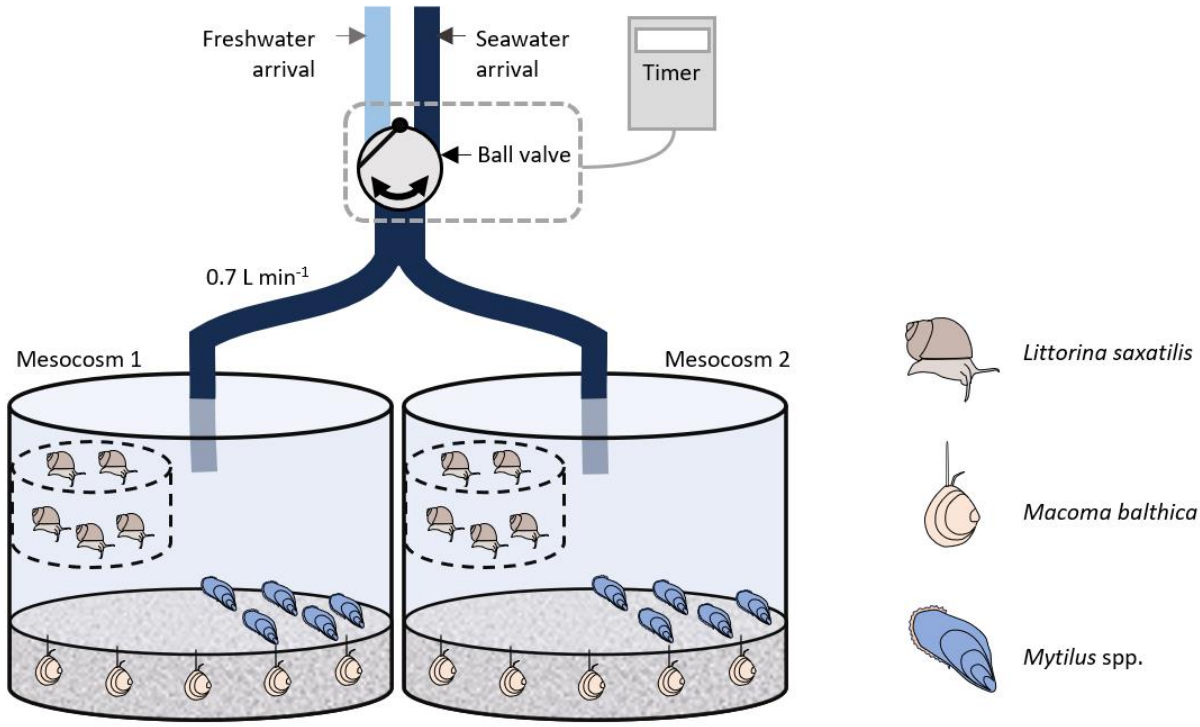

Figure A.5. Representation of the experimental set-up. Each mesocosm was a 5 L bucket. Doted line around *L. saxatilis* represent the mash-container they were kept in.

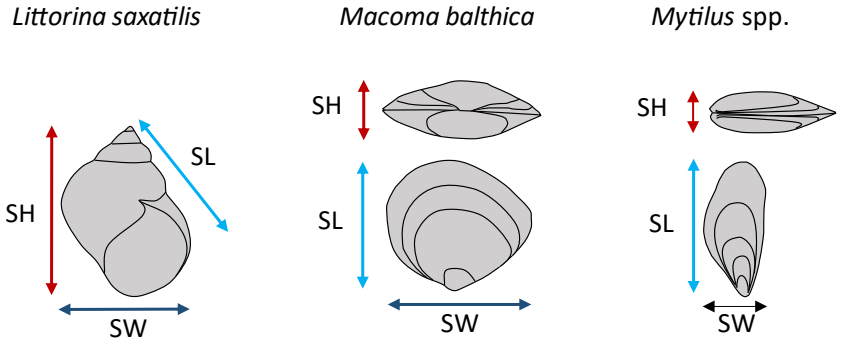

Figure A.6. Morphometric parameters measured for each species (SL: shell length; SW: shell width; SH: shell height) at the beginning and at the date of sampling.

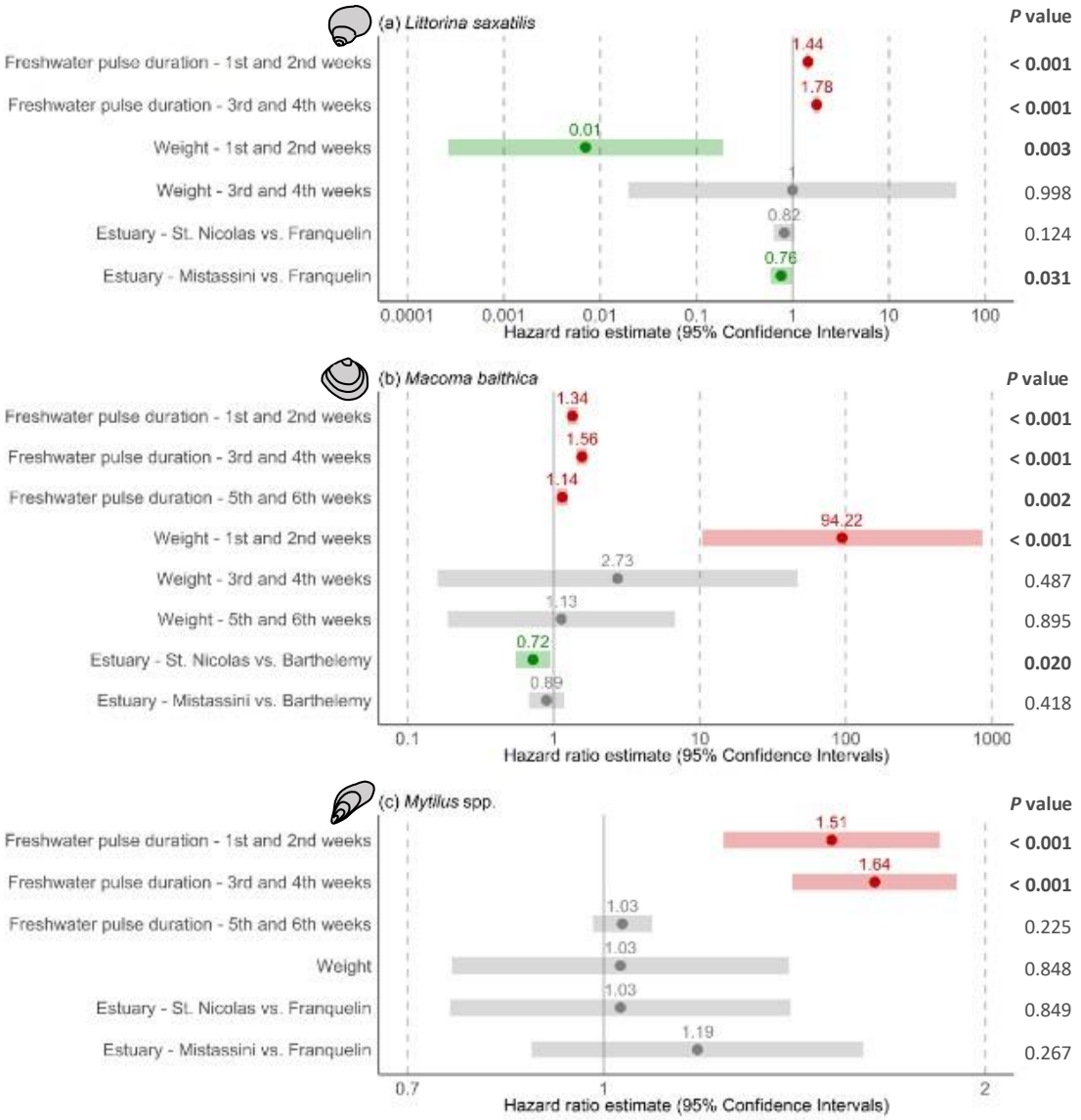

Figure A.7. Forest plots of Cox regression analyses with time variation for (a) *Littorina saxatilis*, (b) *Macoma balthica*, and (c) *Mytilus* spp. The plots include 95% confidence intervals (shaded lines) and *P* values displayed on the right. Factors that did not significantly vary across time (*e.g.*, the estuary of origin) were not split according to time. Factors with a significant hazard ratio > 1 increase the risk of death and are displayed in red. For instance, each additional day of freshwater pulse increases the risk of death of *L. saxatilis* by 41 % in the first week and 78 % in the second week. Factors with a significant hazard ratio < 1 decrease the risk of death and are displayed in green. For example, an increase of 1 g in individual weight in *L. saxatilis* decreases the risk of death by 99 %. Factors with a non-significant hazard ratio are in grey. The Estuary of origin is represented with Franquelin as the reference category.

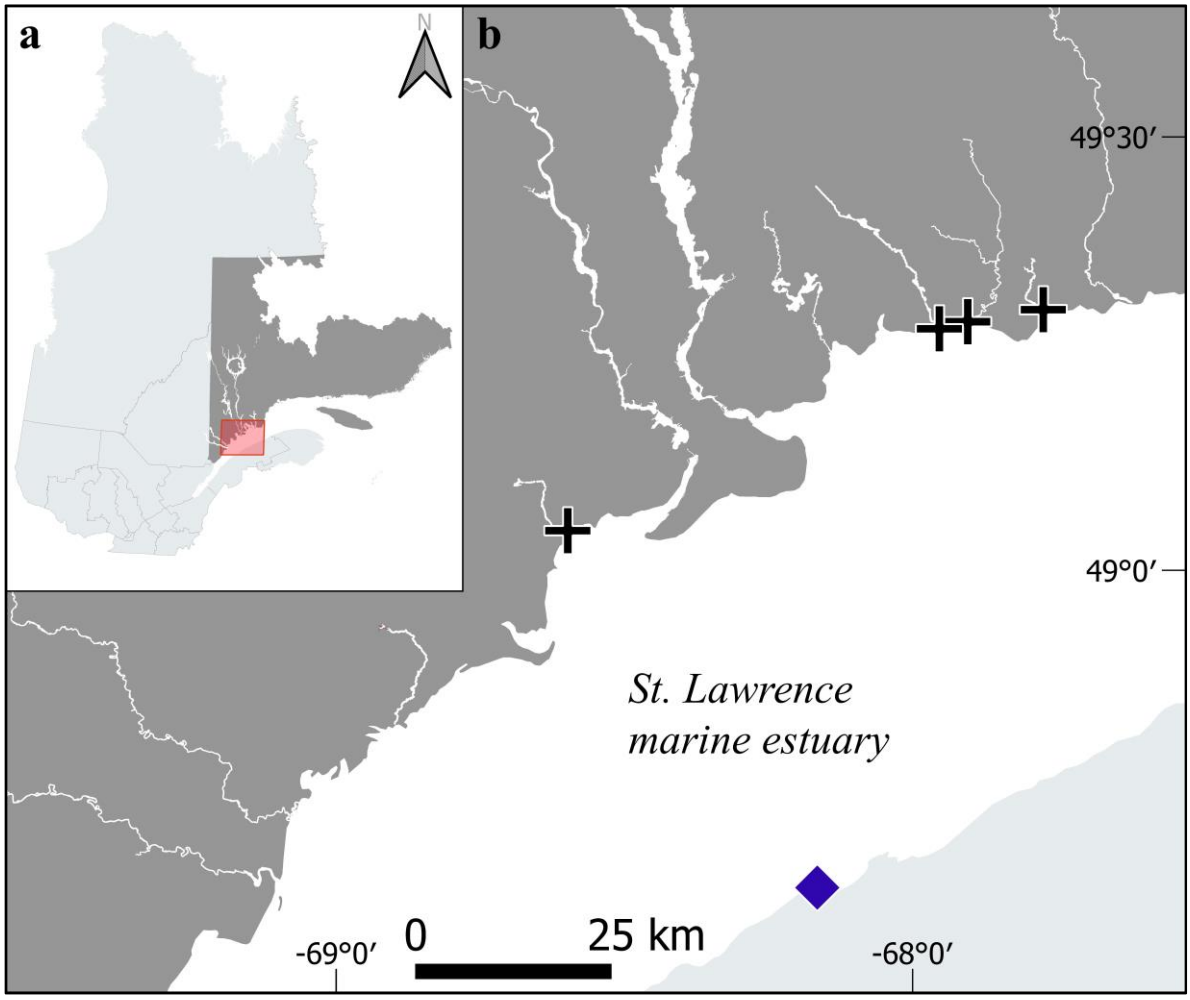

Figure A.8. Maps showing (a) Quebec, Canada, with the sampling locations in the red rectangle; (b) the location of estuaries where specimens were collected (black crosses, from left to right: Barthelemy, Mistassini, Franquelin and St-Nicolas) and the Maurice-Lamontagne Institute where the experiment took place (blue lozenge).

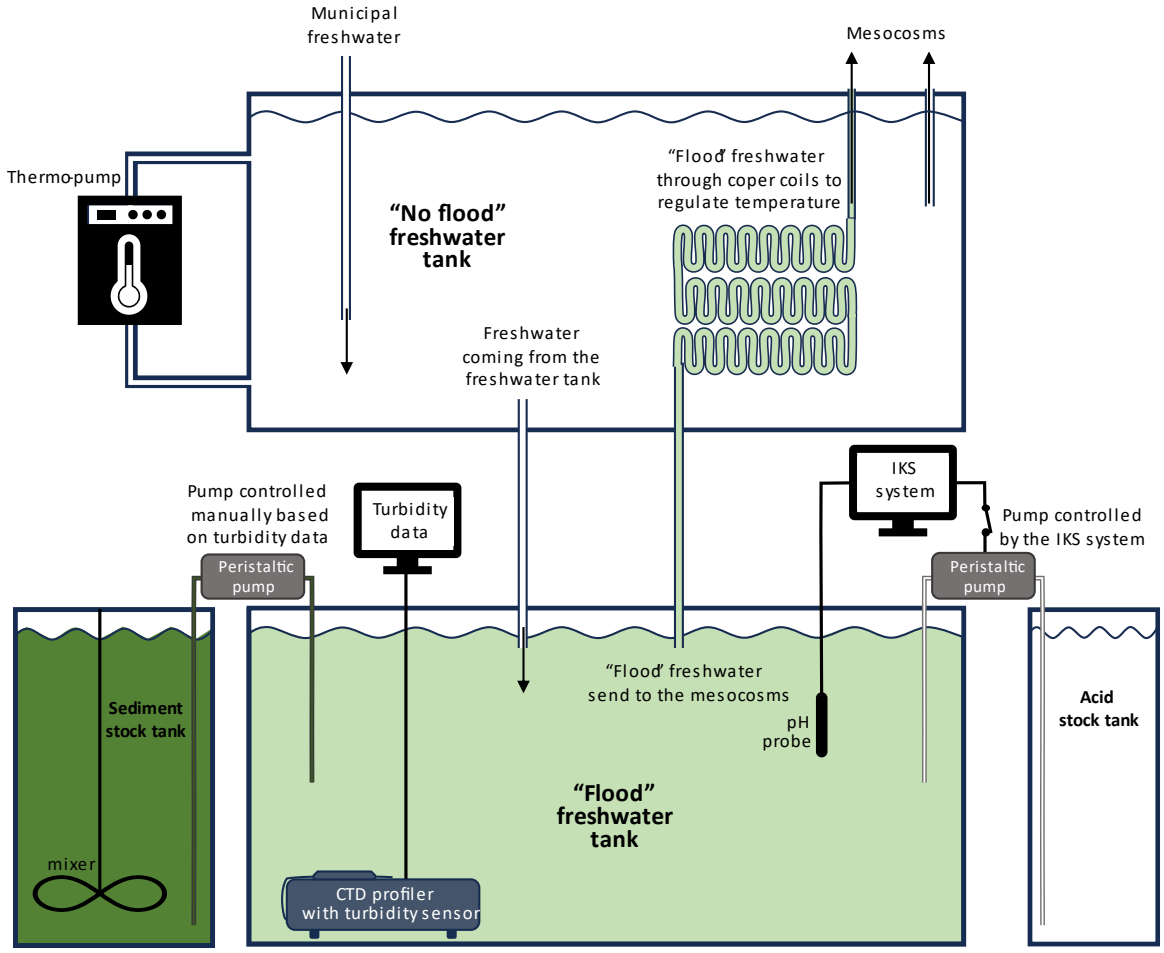

Figure A.9. Schematic representation of the experimental set up, with "no flood" and "flood" freshwater tanks set-up used in the experiment. The temperature was controlled in the "no flood" freshwater tank. The suspended sediment content and pH were controlled in the "flood" freshwater tank with two separate systems.

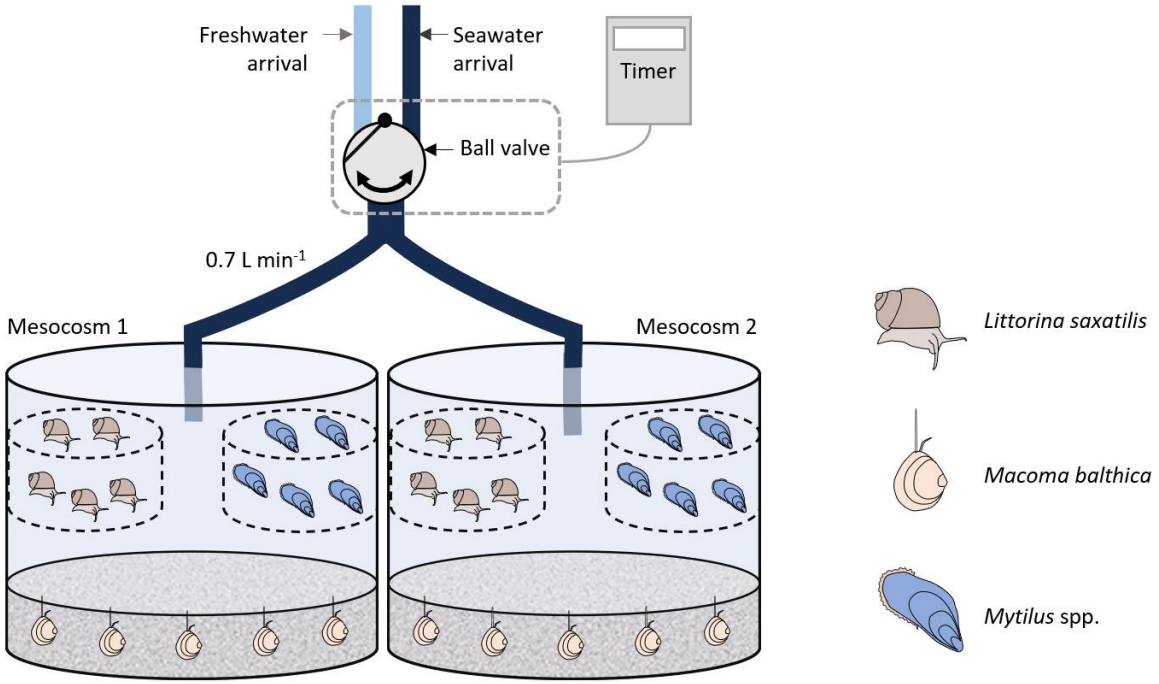

Figure A.10. Schematic representation of the experimental set-up, for one treatment. The "freshwater" comes either from the "flood" freshwater tank or from the "control" freshwater tank depending on the treatment. For clarity, there are only five indiv. *per* species represented but there were 24 indiv. *per* species during the experiment. Dotted line around *Littorina. saxatilis* and *Mytilus* spp. represent the mash-container they were kept in.

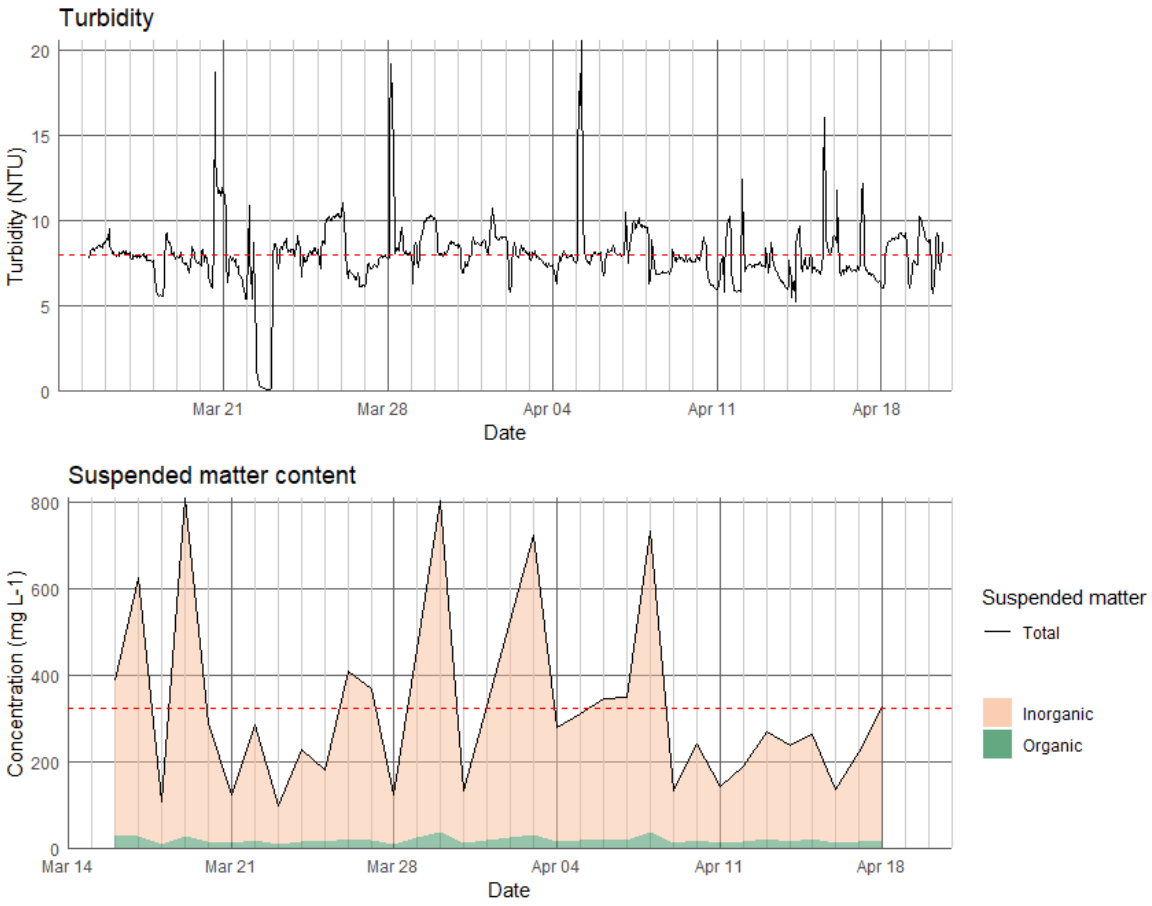

Figure A.11. Time-series representation of abiotic parameters in the "flood" head tank, with the turbidity (top) and the suspended matter content (bellow). The proportion of inorganic matter is in orange, and of organic matter is in green. The mean turbidity and the mean total suspended matter concentration are represented by red dashed lines.

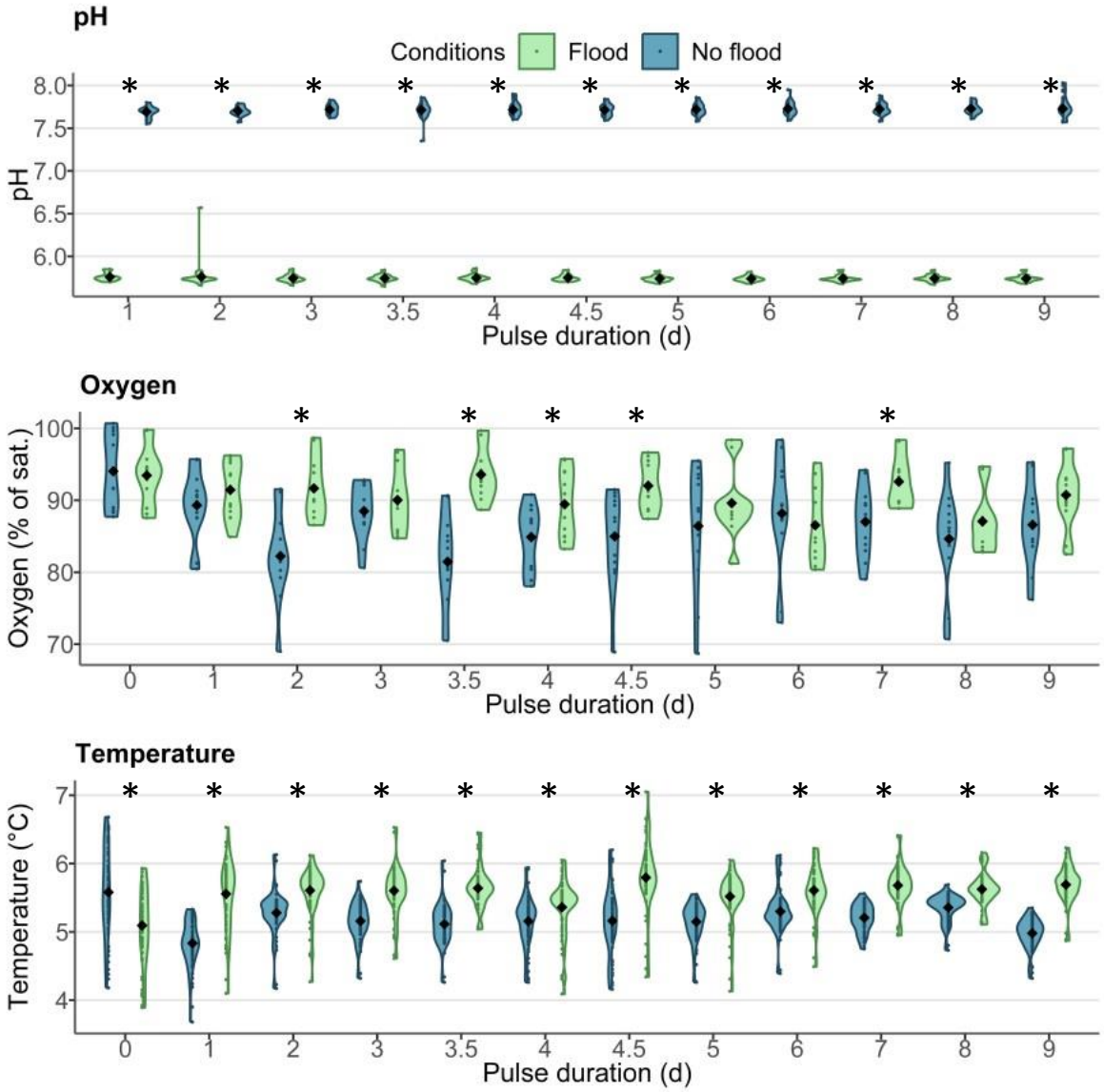

Figure A.12. Violin plot showing the abiotic parameters measured in each of the freshwater treatment, with the "flood" freshwater in green, and the "no flood" freshwater in blue. Mean indicated by black diamond. Significant differences between the "flood" and "no flood" freshwater of the same pulse duration are indicated by an asterisk.

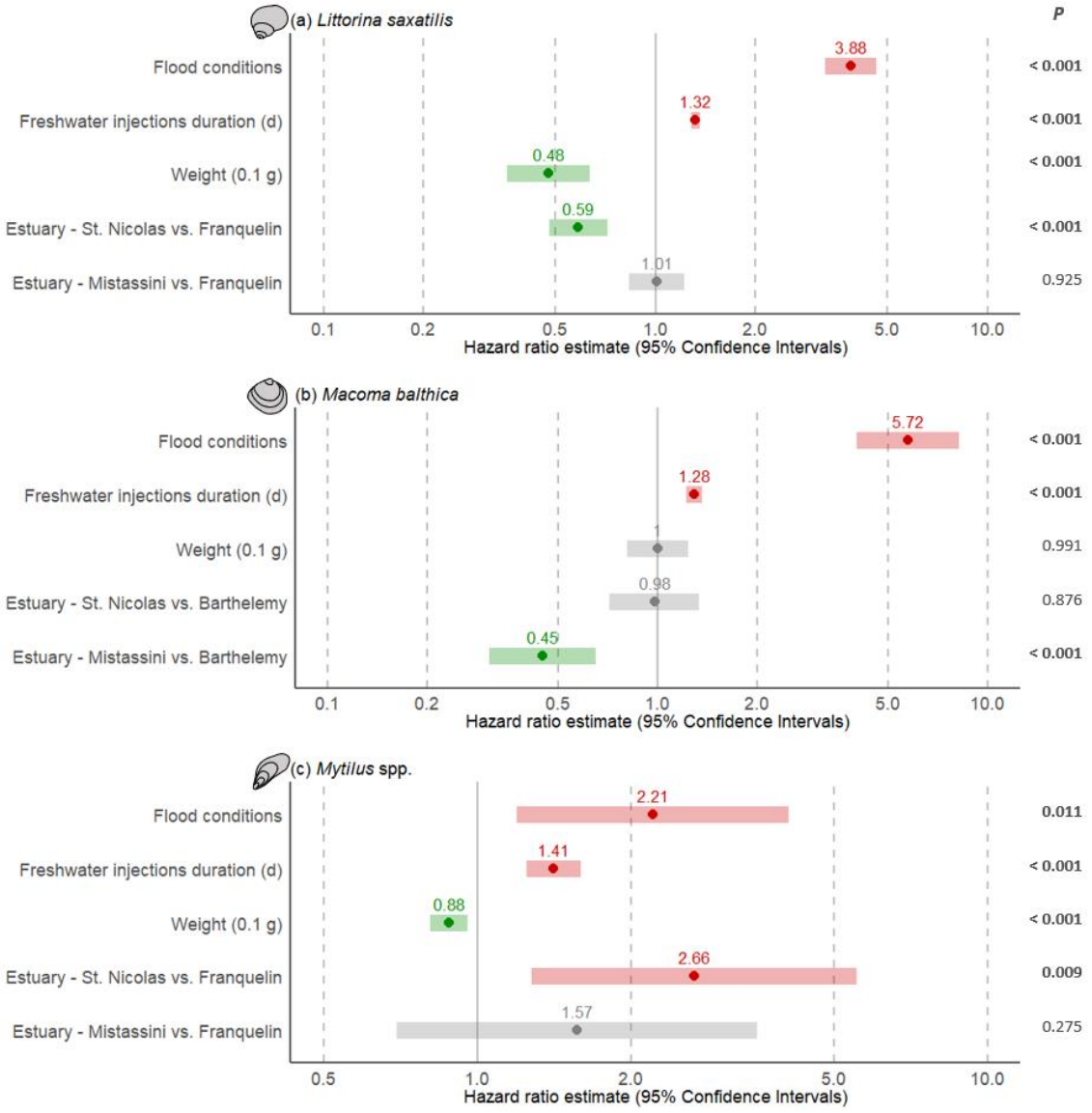

Figure A.13. Forest plots showing the hazard ratio of death for a. *L. saxatilis*, b. *M. balthica* and c. *Mytilus* spp. The plots include 95% confidence intervals (shaded lines) and *P* displayed on the right. Factors with a significant hazard ratio > 1 increase the risk of death and are displayed in red. For instance, each additional day of freshwater pulse increases the risk of death of *L. saxatilis* by 32 %. Factors with a significant hazard ratio < 1 decrease the risk of death and are displayed in green. For example, an increase of 0.1 g in individual weight in *L. saxatilis* decreases the risk of death by 52 %. Factors with a non-significant hazard ratio are in grey. The effect of the estuary of origin is represented with Franquelin or Barthelemy as the reference category.

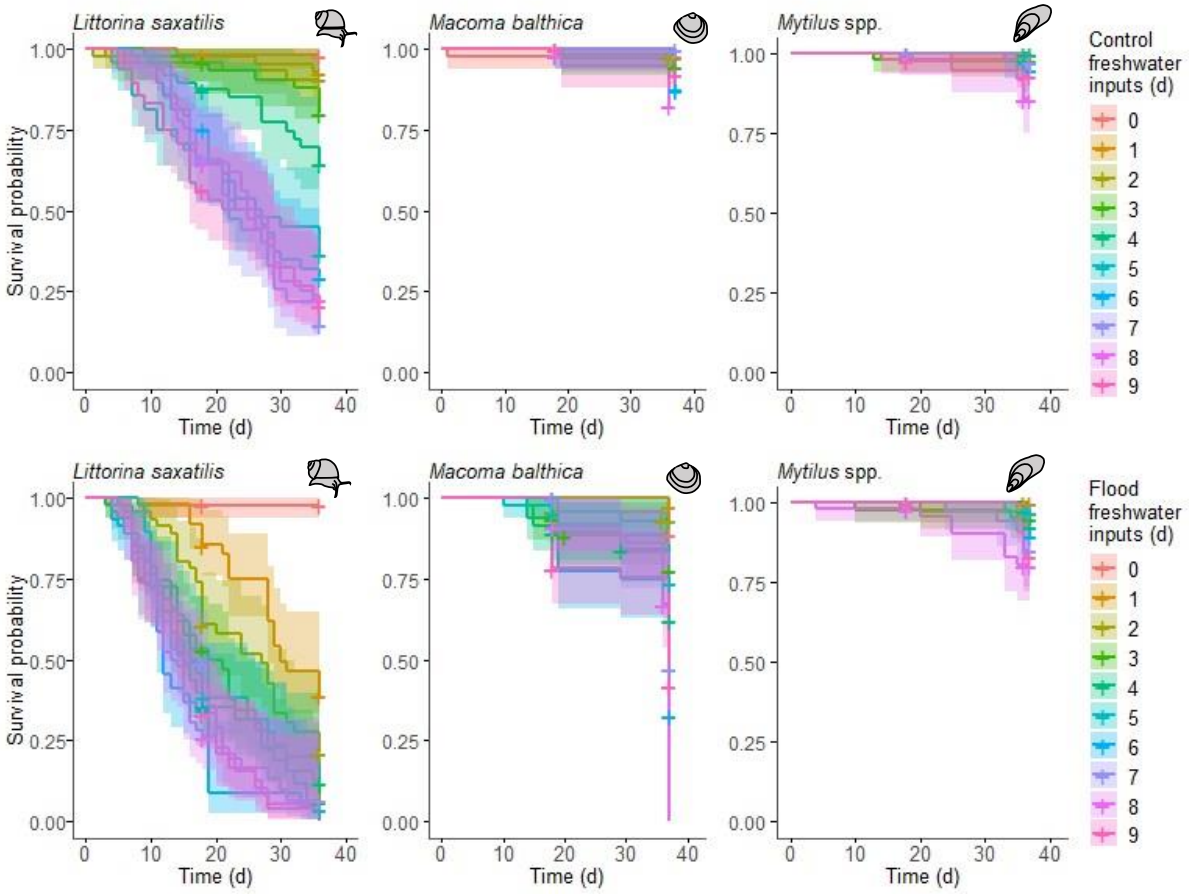

Figure A.14. Survival probability curves over time for the three mollusk species investigated (*L. saxatilis*, *M. balthica*, and *Mytilus* spp.), with control (top) and flood (bottom) freshwater pulses. Solid lines represent the Kaplan-Meier curve for each freshwater pulse duration, with 95% confidence intervals depicted by shaded coloured areas. Crosses represents events where indiv. were taken out of the study. Only 10 treatments (out of 12 used in our study) were represented for greater clarity.

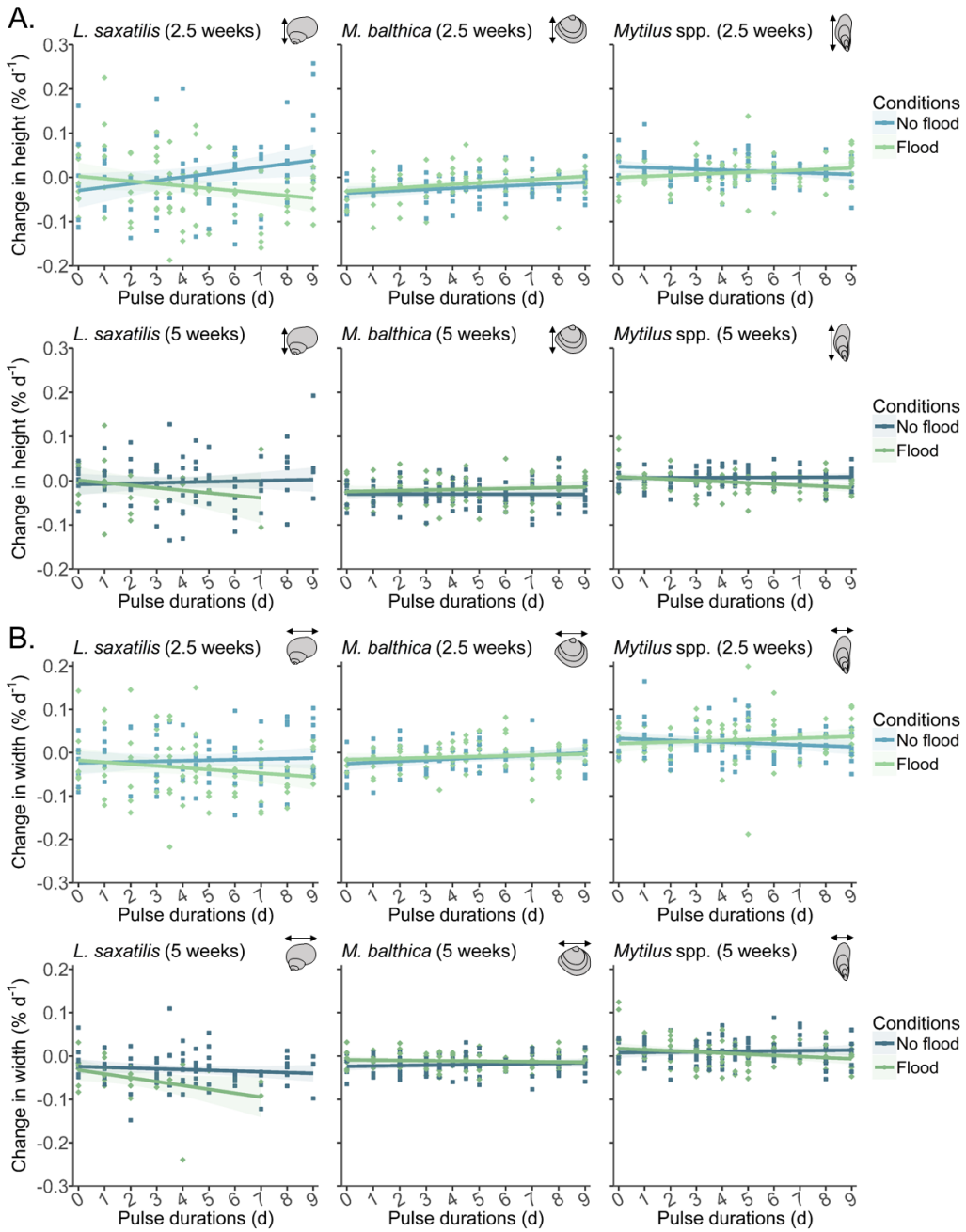

Figure A.15. Relationship between the freshwater pulse duration and the shell width growth (A) and height growth (B) of *L. saxatilis*, *M. balthica*, and *Mytilus* spp. at 2.5 (upper panels) and 5 (lower panels) weeks. Data points illustrate the individual growth of mollusks, with four indiv. *per* mesocosm. Some freshwater pulses levels are not represented because all the indiv. were dead or sampled, *e.g.*, *L. saxatilis* at 5 weeks in the flood conditions.

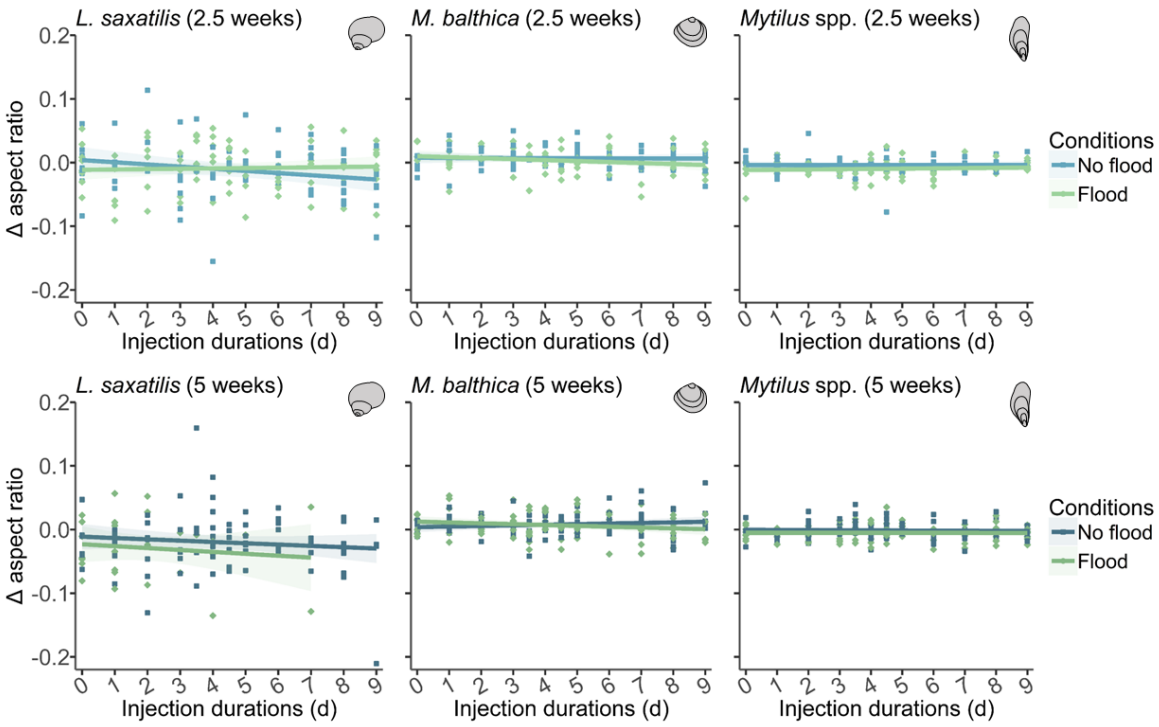

Figure A.16. Relationship between the freshwater pulse duration and change in aspect ration of *L. saxatilis*, *M. balthica*, and *Mytilus* spp. at 2.5 (upper panels) and 5 (lower panels) weeks. Data points illustrate the individual aspect ratio of mollusks, with four indiv. *per* mesocosm. Some freshwater pulses levels are not represented because all the indiv. were dead or removed from the system, *e.g.*, *L. saxatilis* at 5 weeks in the flood conditions.

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