Répercussions actuelles et futures du changement climatique sur les communautés benthiques dans l'Arctique Canadien

Thèse

Marie Pierrejean

Doctorat interuniversitaire en océanographie
Philosophiæ doctor (Ph. D.)

Québec, Canada

Résumé

L’océan Arctique est une des régions les plus touchées par les changements climatiques. Une importante augmentation de la température de ses eaux de surfaces et des précipitations y est attendue, entrainant une perte significative du couvert de glace et une augmentation des activités humaines. Causant des effets sur les paramètres physico-chimiques, ces changements devraient directement affecter les producteurs primaires (algues de glace et phytoplancton), et de ce fait limiter l’apport de matière organique vers les fonds marins. Il est ainsi admis que les changements climatiques affecteraient la distribution, la diversité et l’abondance des communautés benthiques, en raison de leur impact sur les paramètres environnementaux (couplage pélago-benthique et paramètres physico-chimiques), mais également sur les services et fonctions écosystémiques (par exemple la reminéralisation benthique). La diminution de l’étendue et de l’épaisseur de la glace de mer, la désalinisation des eaux de surface ou bien encore l’augmentation du trafic maritime dans les régions de la Baie d’Hudson et de l’est de l’Arctique Canadien, sont susceptibles d’être à l’origine de grands changements dans la structure des communautés benthiques et des habitats à structures biogéniques.

Les impacts des changements climatiques sur les écosystèmes benthiques arctiques étant jusqu’alors peu connus, les objectifs de cette thèse étaient de i) d’apporter une description plus complète et actualisée de la diversité et la distribution spatiale des communautés benthiques dans le complexe de la Baie d’Hudson ; ii) de comprendre les effets des changements climatiques sur la biodiversité et le fonctionnement des écosystèmes benthiques; et iii) d’enrichir les connaissances des écosystèmes benthiques et d’appuyer la désignation de zones d’intérêt écologique et biologique ainsi que des aires marines protégées. Les travaux réalisés pendant cette thèse nous ont permis de i) mettre à jour les données épibenthiques dans le complexe de la Baie d’Hudson ; ii) aider les gestionnaires dans la mise en place de zones d’importance écologique et biologique ainsi que de zones d’intérêts pour une future désignation d’aires marines protégées; et iii) mettre en évidence l’importance des coraux de bambous en milieu profond sur le fonctionnement de l’écosystème benthique.

Un total de 380 taxa a été dénombré dans 46 stations à travers le complexe de la Baie d’Hudson. Malgré une relativement faible couverture spatiale de notre échantillonnage, nous avons été en mesure d'estimer que ce recensement représentait 71 % des taxons présents dans le complexe de la Baie d'Hudson. Nous avons montré que la biomasse, l'abondance, la diversité ainsi que la distribution spatiale des communautés épibenthiques étaient fortement influencées par le substrat, la salinité, les ressources alimentaires et la couverture de glace. Nous avons aussi pu démontrer que la faible diversité, abondance et biomasse des communautés observées près des côtes étaient causées par les importants écoulements d'eaux douces. À l'inverse, les données récoltées dans les polynies situées plus au large montrent un fort couplage pélago-benthique se traduisant par une forte productivité en termes de biomasse, d'abondance et de diversité. L'utilisation d'un modèle de distribution des communautés a permis de démontrer l'importance de la présence de glace et indirectement des algues de glace associées à cet habitat sur les communautés épibenthiques occupant le centre de la Baie d'Hudson. La projection des communautés sous un scénario climatique RCP4.5 a révélé que le centre de la Baie ressortait, potentiellement, comme étant la zone la plus vulnérable aux changements climatiques puisqu'une perte de diversité liée à la diminution de la glace de mer est attendue. À l'inverse, les zones côtières pourraient possiblement servir de refuges en augmentant la diversité. En outre, notre étude a montré que la présence des structures biogéniques telles que les coraux bambous, dans les habitats profonds, améliore le piégeage des particules de matière organique menant à une plus forte densité d'espèces endofauniques dans ces milieux comparativement à des sédiments nus. Cet effet a également été constaté dans la reminéralisation benthique où les sédiments des structures biogéniques agissaient comme source de nitrates et d'ammonium. En revanche, nos travaux n'ont pu démontrer ces effets dans un habitat moins profond hébergeant des éponges.

En générant de nouvelles connaissances sur la répartition actuelle et future des communautés épibenthiques du complexe de la Baie d'Hudson ainsi que sur le fonctionnement de l'écosystème benthique dans les habitats à structures biogéniques, les résultats de cette thèse contribueront à désigner des zones d'importance écologique et biologique ainsi qu'à la mise en place d'aires marines protégées et de stratégies de conservation de la biodiversité arctique.

Abstract

The Arctic Ocean is emerging as one of the regions that is most affected by climate change. A significant increase in precipitation and sea surface water temperatures are expected and will undeniably lead to a significant loss of sea ice cover. Because of their effects on physico-chemical parameters, these changes are expected to directly impact the surface primary producers (sea ice algae and phytoplankton), thereby limiting organic matter input towards the seafloor. It is thus commonly accepted that climate change will affect the distribution, diversity and abundance of benthic communities, due to its impact on environmental parameters (pelagic-benthic coupling and physicochemical parameters), and on ecosystem services and functions (*e.g.*, benthic remineralization). As a consequence, the decrease in sea ice cover, the desalination of the surface layer or the increase in shipping traffic in the Hudson Bay Complex and in the eastern Canadian Arctic will likely lead to major changes in benthic community structure and biogenic structural habitats.

In this context and since the impacts of climate change on benthic arctic ecosystems were still poorly understood, the objectives of this thesis were to i) describe the diversity and distribution of epibenthic communities in the Hudson Bay Complex and ii) understand the effects of climate change on biodiversity and benthic ecosystem functioning. The outcomes of this thesis allowed us to i) provide the most recent survey on epibenthic organisms in the Hudson Bay Complex and their relationships with environmental variables; ii) identify diversity hotspots sensitive to climate change; and iii) document and compare benthic biodiversity and fluxes within biogenic structures and adjacent bare sediments in the Canadian Arctic.

A total of 380 taxa have been identified from 46 stations sampled across the Hudson Bay Complex. Despite the relatively low spatial coverage of our sampling, we estimated that our survey represented 71% of the taxa present in the Hudson Bay Complex. We showed that biomass, abundance, diversity and spatial distribution of epibenthic communities were strongly influenced by substrate, salinity, food supply and sea ice cover. We also showed that freshwater inputs were responsible for the lowest biomass, abundance and diversity observed along the coasts. In contrast, data collected from polynyas, further offshore, showed strong pelagic-benthic coupling resulting in high productivity in terms of biomass, abundance and diversity. Moreover, hierarchical modelling of species communities highlighted the influence of sea ice and indirectly of sea ice algae on the epibenthic communities occupying the central Hudson Bay. Projections of the structure of epibenthic communities under a RCP4.5 climate scenario revealed that the central Hudson Bay emerges as the most vulnerable area to climate change with a future diversity loss related to the decrease of sea ice. On the contrary, it would appear that coastal areas will serve as refuges and increase the diversity. In addition, our study showed that the presence of biogenic structures in deep habitats improved the trapping of organic matter, leading to a higher density of infauna in these environments compared to bare sediments. Their presence has also been found to enhance sediment nutrient release in the form of nitrates and ammonium. However, our study could not demonstrate these effects in a shallower sponge habitat.

By providing new knowledge on the current and future distribution of epibenthic communities in the Hudson Bay Complex and the benthic ecosystem functioning in habitats with biogenic structures, results obtained during this thesis will contribute to the designation of Ecologically and Biologically Significant Areas, as well as to the establishment of Marine Protected Areas and conservation strategies in the Arctic Ocean.

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Abréviations	**Anglais**	**Français**
ACT	Actiniaria	Actiniaria
ANOVA	Analysis of variance	Analyse de variance
AST	Asteridae	Asteridae
BAL	Balanidae	Balanidae
BaySys	Hudson Bay System study	-
BB	Baffin Bay	Baie de Baffin
B_{O2}	Bottom oxygen	Oxygène de fond
BriGHT	Bridging Global Change, Inuit Health and the Transforming Arctic Ocean project	-
BS	Bottom Salinity	Salinité de fond
B_T	Bottom temperature	Température de fond
CAISN	Canadian Aquatic Invasive Species Network	Réseau Canadien sur les Espèces Aquatiques Envahissantes
CCA	Canonical Correspondence Analysis	Analyse Canonique des Correspondances
CCGS	Canadian Coast Guard Ship	Navire de Garde Côtière Canadienne
CH_4	Methane	Méthane
CO_2	Carbon dioxyde	Dioxyde de carbone
CTD	Conductivity-Temperature-Depth	Conductivité-Température-Profondeur
CWM	Community-level weighted means of trait values	Moyennes pondérées des valeurs des traits au niveau communautaire
EBSA	Ecologically and Biologically Significant Area	-
FB	Frobisher Bay	Baie de Frobisher
Fe^{2+}	Ferrous ion	Ion ferreux
Fe^{3+}	Ferric ion	Ion ferrique
FEve	Functional Evenness	Régularité fonctionnelle
FRic	Functional Richness	Richesse Fonctionnelle
GORG	Gorgonocephalidae	Gorgonocephalidae
H_2S	Hydrogen Sulfide	Hydrogène sulfuré
HB	Hudson Bay	Baie d'Hudson
HBC	Hudson Bay Complex	Complexe de la Baie d'Hudson
HMSC	Hierarchical Modelling Species Communities	Modèle hiérarchique des communautés d'espèces

Abréviations	Anglais	Français
JSDM	Joint Species Distribution Model	Modèles joints de distribution des espèces
MERICA	-	MERs Intérieures du CAnada
Mn^{2+}	Manganese(II)	Manganèse(II)
Mn^{4+}	Manganese(IV)	Manganèse(IV)
N_2	Dinitrogen	Diazote
NEP	Nephtheidae	Nephtheidae
NH_4^+	Ammonium	Ammonium
NO_2^-	Nitrite	Nitrite
NO_3^-	Nitrates	Nitrates
NSERC	Natural Sciences and Engineering Research Council	Conseil de recherches en sciences Naturelles et en Génie
O_2	Oxygen	Oxygène
OM	Organic matter	Matière organique
OPHI	Ophiuridae	Ophiuridae
OREG	Oregonidae	Oregonidae
OW	Open water	Eaux libres
PC	Principal Component	Composante Principale
PCA	Principal Component Analysis	Analyses des composantes principales
PECT	Pectinidae	Pectinidae
PO_4^{3-}	Phosphate	Phosphate
POC	Particulate Organic Carbon	Carbone Organique Particulaire
POR	Porifera	Porifera
PP	Primary production	Production primaire
RCP	Representative Concentration Pathway	Profils représentatifs d’évolution de concentration
RDA	Redundancy Analysis	Analyse de redondance
ROV	Remotely Operated underwater Vehicle	Véhicule sous-marin téléguidé
SE	Standard Error	Erreur Standard
$Si(OH)_4$	Silicates	Silicates
SO_4^{2-}	Sulfate	Sulfate
SOD	Sediment Oxygen Demand	Demande d’oxygène des sédiments
SOLAS	Solasteridae	Solasteridae
STRONG	Strongylocentrotidae	Strongylocentrotidae
THOR	Thoridae	Thoridae
UCDC	Up and Down Conveyors	Convoyeurs inverses
YOLD	Yoldiidae	Yoldiidae
ZIEB	-	Zone d’intérêt écologique et biologique

« Une fois qu'elle vous a ensorcelé, la mer vous tient pour toujours dans son filet à merveilles »

Jacques-Yves Cousteau

« *Ces choses-là sont rudes. - Il faut pour les comprendre avoir fait des études.* »

Victor Hugo

« *Gouttelettes… miroirs de la joie de mon cœur.* »

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Marie Pierrejean

Avant-propos

La présente thèse a pour but d'exposer les résultats des travaux de doctorat en océanographie portant sur les répercussions actuelles et futures du changement climatique sur les communautés benthiques dans l'Arctique Canadien. Plus spécifiquement, cette thèse de doctorat comprend une introduction, trois articles scientifiques et une conclusion générale. L'introduction et la conclusion sont rédigées en français tandis que les chapitres 1 à 3 sont rédigés en anglais sous forme d'articles scientifiques dont voici les références :

Chapitre 1. **Spatial distribution of epifaunal communities in the Hudson Bay Complex: Patterns and drivers.** Marie Pierrejean, David Babb, Frédéric Maps, Christian Nozais, Philippe Archambault. Cet article a été soumis dans le numéro spécial « BaySys » du journal « Elementa : Science of Anthropocene » le 20 avril 2020 et accepté le 2 novembre 2020. Dans ce chapitre, j'ai dirigé la conception de l'étude, effectué les expériences et l'identification taxonomique, analysé les données, préparé les figures et les tableaux, rédigé et revu l'ébauche du document. D. Babb a effectué l'analyse de l'extraction de la glace de mer, a contribué à la rédaction et à la révision du manuscrit. P. Archambault, C. Nozais ont dirigé la conception de l'étude, a rédigé et revu l'ébauche du document. F. Maps a rédigé et revu l'ébauche du document.

Chapitre 2. **Modelling benthic communities in the Hudson Bay under current and future environmental conditions.** Marie Pierrejean, F. Guillaume Blanchet, Frédéric Maps, Christian Nozais, Philippe Archambault. Dans ce chapitre, j'ai dirigé la conception de l'étude, effectué les analyses, préparé les figures et les tableaux, rédigé et revu l'ébauche du document. F.G. Blanchet, P. Archambault, C. Nozais et F. Maps ont contribué à la rédaction et revu l'ébauche du document.

Chapitre 3. **Influence of deep-water corals and sponge gardens on infaunal community composition and ecosystem functioning in the Eastern Canadian Arctic.** Marie Pierrejean, Cindy Grant, Gwénaëlle Chaillou, Bárbara De Moura Neves, Evan Edinger, F. Guillaume Blanchet, Frédéric Maps, Christian Nozais et Philippe Archambault. Cet article a été soumis dans le journal « Frontiers in Marine Science » le 29 mai 2019 et accepté le 3 juin

2020. Cet article a été publié le 30 juin 2020. Dans ce chapitre, j'ai conçu l'étude, préparé les données, effectué les analyses et dirigé la rédaction du manuscrit. C. Grant a échantillonné l'endofaune, effectué les incubations benthiques et les analyses de l'ammonium. B. Neves a conçu des figures, rédigé et révisé le manuscrit. G. Chaillou, E. Edinger et F. Maps ont contribué à la rédaction et à la révision du manuscrit. F. G. Blanchet a révisé les analyses et le manuscrit. C. Nozais et P. Archambault ont contribuer à concevoir l'étude, la rédaction et la révision du manuscrit.

Les résultats de cette thèse ont fait l'objet de présentations orales et sous forme d'affiches scientifiques lors de conférences nationales et internationales au cours desquelles j'ai reçu une mention d'excellence. J'ai participé à un atelier scientifique du Secrétariat canadien de consultation scientifique (CSAS), le 5-6 décembre 2018, concernant l'île de Southampton « Ecological and Biophysical Overview of the Southampton proposed Area of Interest for the Southampton Island Ecologically and Biologically Significant Area (SI EBSA) ».

Listes des publications écrites issues de la thèse

Pierrejean M, Babb D, Maps F, Nozais C, Archambault P. *Accepted in Elementa : Science of Anthropocene*. Spatial distribution of epifaunal communities in the Hudson Bay Complex: Patterns and drivers.

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Pierrejean M, Grant C, Archambault P, Nozais C. 2019. Communities of Benthic invertebrates in the Hudson Bay Marine Region. In: From Science to Policy in the Greater Hudson Bay Marine Region: An Integrated Regional Impact Study (IRIS) of Climate Change and Modernization, eds. KA, Kuzyk and LM Candlish, ArcticNet, Québec City, 245-253.

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Pierrejean M, Blanchet G, Maps F, Nozais C, Archambault P (2019). Predicting benthic communities in the Hudson Bay Complex. CHEERS "Global changes in estuarine and coastal systems: innovative approaches and assessment tools", 4-8 novembre, Bordeaux, France.

Pierrejean M, Archambault P, Blanchet G, Nozais C, Maps F (2018). Epibenthic communities' baselines in the Hudson Bay Complex. ArcticNet, 10-14 décembre, Ottawa, Canada.

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Listes des présentations par affiches

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Pierrejean M, Archambault P, Maps F, Nozais C (2017). État des lieux des hotspots benthiques de la Baie d'Hudson. Réunion scientifique annuelle Québec-Océan, 13-15 novembre, Rivière du Loup, Canada. *Prix d'excellence pour la présentation par affiche.*

Pierrejean M, Archambault P, De Neves B, Edinger E, Nozais C (2016). Identification of benthic hotspot ecosystems in the Canadian Arctic. Réunion scientifique annuelle Québec-Océan, 8-9 novembre, Rimouski, Canada.

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Introduction

L’écosystème Arctique

Caractéristiques de l’océan Arctique

Avec une superficie de 14 millions de km^2 et une profondeur moyenne de 1038 m, l’océan Arctique est le plus petit et le moins profond des cinq océans mondiaux. Néanmoins, il est l’un des océans les moins explorés à ce jour en raison des conditions extrêmes qui y persistent. Ce dernier se compose du bassin océanique arctique et de mers arctiques connexes moins profondes. Ces mers comprennent les eaux de la marge continentale du Groenland, les plateaux eurasiens des mers de Kara, Laptev et de Sibérie orientale, la mer des Tchouktches, la mer de Barents, la mer de Béring ainsi que les plateaux arctiques américains de la mer de Beaufort et de l’Archipel Canadien (Figure 1).

Figure 1. Carte de l'océan Arctique et de ses mers connexes modifiée de Piepenburg (2005).

L’océan Arctique est caractérisé par de faibles températures et une importante variation saisonnière de la lumière. Ces dernières contribuent à la formation de banquise (pluriannuelle aux plus hautes latitudes et saisonnière à des latitudes plus basses) et conditionnent la production primaire (Carmack et Wassmann, 2006; Wassmann et Reigstad, 2011). Ainsi, l’hiver est caractérisé par une période d’obscurité quasi totale, une étendue importante du couvert de banquise et une faible activité biologique (Carmack et Wassmann, 2006; Wassmann et Reigstad, 2011). Le printemps et l’été sont, quant à eux, caractérisés par une importante période d’ensoleillement, associée à une faible couverture de glace et une forte activité biologique (Carmack et Wassmann, 2006; Wassmann et Reigstad, 2011). L’océan Arctique est aussi caractérisé par d’importants apports fluviaux, transportant d’importantes quantités de nutriments, de carbone organique, de sédiments et de métaux traces issus des bassins versants (Bring et al., 2016). Ces apports représenteraient environ 11% des débits fluviaux mondiaux (Dai et Trenberth, 2002) et 30 à 50% de la matière organique présente dans les écosystèmes côtiers et plateaux continentaux de l’Arctique (Naidu et al., 2000; Dunton et al., 2006). Ces caractéristiques uniques ont une profonde influence sur les processus physiques, biogéochimiques et sur la composition des communautés pélagiques et benthiques de l’Arctique.

La production primaire arctique

La production primaire arctique est principalement soutenue par les algues sympagiques au printemps (algues de glace) et pélagiques en été (phytoplancton; Figure 2), auxquelles s’ajoute une contribution moindre, mais non négligeable du microphytobenthos (microalgues benthiques) et des macroalgues dans les écosystèmes côtiers (Duarte et Cebrián, 1996).

Dans la banquise, la disponibilité en lumière au printemps dicte le début de la production des algues de glace, tandis que la disponibilité en nutriments conditionne l’étendue dans le temps de leur productivité (Cota et al., 1987; Smith et al., 1990; Leu et al., 2015). Cette communauté sympagique se développe principalement dans la partie inférieure de la banquise poreuse sous forme d’agrégats (Figure 2). C’est à l’interface avec l’eau de mer que cette communauté trouve un environnement relativement stable (pH, salinité, oxygène) ainsi qu’une disponibilité suffisante en lumière et en nutriments (Smith et al., 1990). Les algues de glace représentent la seconde principale source de production primaire en Arctique mais leur contribution à la production primaire des eaux arctiques reste relativement minime en comparaison à la communauté pélagique (Pabi et al., 2008). L'efflorescence sympagique se termine à la fin du printemps, lorsque l'augmentation progressive des températures atmosphériques entraîne la dégradation graduelle de la glace de mer et l'expulsion des algues sympagiques dans la colonne d'eau (Figure 2). La fonte estivale de la banquise et de la neige la recouvrant induit une augmentation drastique de la disponibilité en lumière dans l'océan de surface permettant ainsi une efflorescence des algues pélagiques en surface. Cette efflorescence se poursuit ensuite en profondeur à mesure que les nutriments viennent à être consommés en surface (Figure 2). Cette production pélagique est la principale source de production primaire en Arctique (Sakshaug, 2004; Ardyna et al., 2013; Matrai et al., 2013).

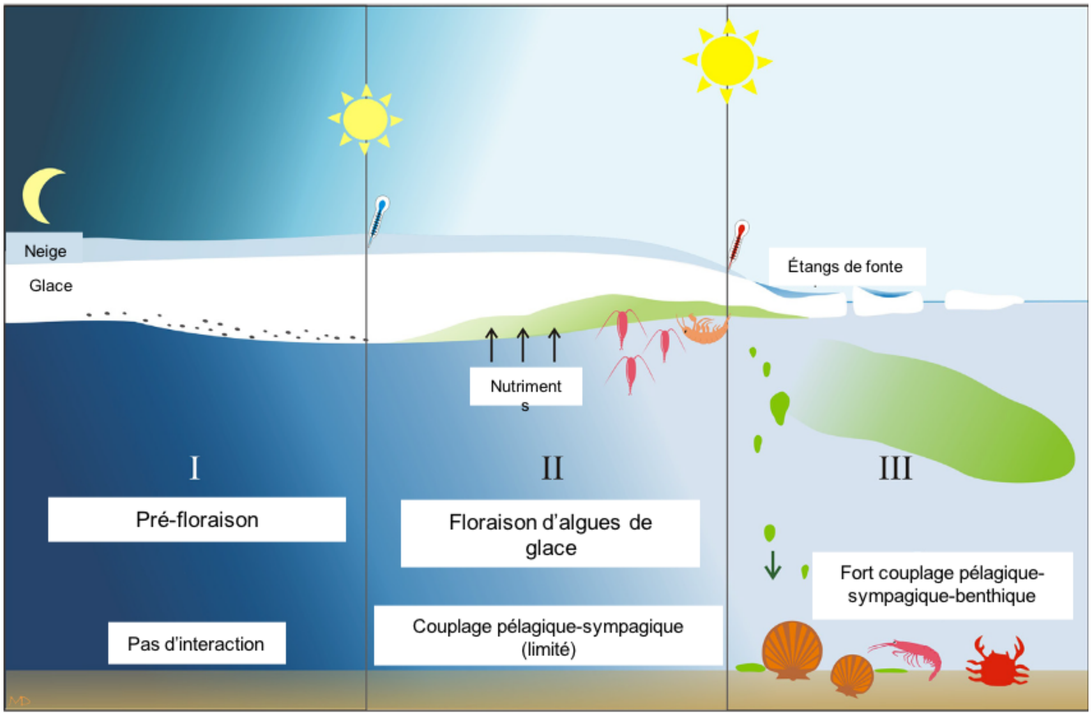

Figure 2. Schéma du développement des algues sympagiques et du phytoplancton durant la période hivernale (phase I), printanière (phase II) et estivale (phase III). Le passage de la phase I à II est dirigé par la lumière tandis que l'augmentation de la température conduit à la phase III. Illustration tirée de Leu et al. (2015).

Le couplage pélago-benthique décrit l'ensemble des échanges de matière organique entre la colonne d'eau (pélagos) et les fonds marins (benthos). L'intensité de ce couplage dépend à la fois de l'étendue de la productivité des algues (sympagiques ou pélagiques), mais aussi de leur potentiel à être exporté jusqu'au sédiment. Ainsi les algues sympagiques et pélagiques contribuent différemment à ce couplage. Les algues sympagiques y contribueraient grandement en raison de leur floraison précoce dans la saison et leur important taux de sédimentation, leur permettant généralement d'atteindre les fonds marins dans le jour suivant leur expulsion de la banquise (Renaud et al., 2007b; Boetius et al., 2013; Katlein et al., 2015). À l'inverse, les algues pélagiques contribueraient dans une moindre mesure à ce couplage, en raison de leur faible taux de sédimentation (Rutgers van der Loeff et al., 2002), qui a pour conséquence d'importantes dégradations biotiques (broutage zooplanctonique, reminéralisation par la boucle microbienne) et/ou abiotiques (photo-oxydation, auto-oxydation) dans la couche euphotique, puis tout au long de leur sédimentation relativement lent dans la colonne d'eau (Morata et Renaud, 2008; Roy et al., 2015a; Amiraux et al., 2017).

Écosystèmes benthiques arctiques : Structure et fonctionnement

Facteurs structurant les communautés

Les organismes benthiques représentent environ 90% des invertébrés marins (CAFF, 2013). Dans l'océan Arctique, ces derniers représentent près de 4900 taxa (Piepenburg et al., 2011). Ces organismes sont généralement catégorisés selon leur localisation dans le fond marin : on distingue les organismes endobenthiques vivant dans les sédiments et les organismes épibenthiques vivant à la surface des sédiments. Ayant une mobilité limitée voire nulle, il est généralement admis que la répartition des espèces benthiques reflète fortement l'influence des paramètres environnementaux. Parmi ceux-ci, la profondeur, la salinité et la température représentent les paramètres physico-chimiques connus pour avoir un impact direct sur la distribution des espèces et leur diversité (Grebmeier et al., 2006; Cusson et al., 2007; Roy et al., 2014). L'importance des apports de matière organique issus de la production primaire de surface vers le benthos (couplage pélago-benthique) ainsi que la qualité nutritionnelle de ces apports (c.-à-d. la composition élémentaire et biochimique) contribuent également à la répartition des communautés benthiques (Ambrose et Renaud, 1995; Piepenburg, 2005; Witman et al., 2008). Outre les paramètres physico-chimiques et les apports nutritifs, le type de substrat et la présence de structures biogéniques (Figure 3) permettraient d'augmenter la complexité des habitats benthiques et influenceraient les communautés benthiques (Freiwald et Roberts, 2005). Ces structures vivantes érigées sont composées d'espèces ingénieures telles que les cnidaires, éponges, bryozoaires et autres organismes sessiles (Jones et al., 1994; Buhl-Mortensen et al., 2010; Rossi, 2013a). La présence de ces structures modifie l'hydrodynamisme, influençant fortement les flux verticaux et horizontaux des particules en suspension près du fond. Ces changements de flux de la matière organique modifient ainsi la disponibilité des ressources pour les espèces avoisinantes (Gili et Coma, 1998; Rossi et al., 2012; Rossi, 2013a). Ces structures offrent également des habitats diversifiés fournissant des refuges contre les prédateurs, des surfaces d'attaches, des sites de frai et de nourricerie pour les poissons et les organismes benthiques (Jensen et Frederiksen, 1992; Costello et al., 2005; Roberts et al., 2006; Baillon et al., 2012). De par leur faculté à modifier l'environnement, ces structures génèrent ainsi une plus forte diversité et biomasse et représentent de véritables oasis de vie au sein des écosystèmes benthiques (Roberts et al., 2002; Cerrano et al., 2009; van Oevelen et al., 2009).

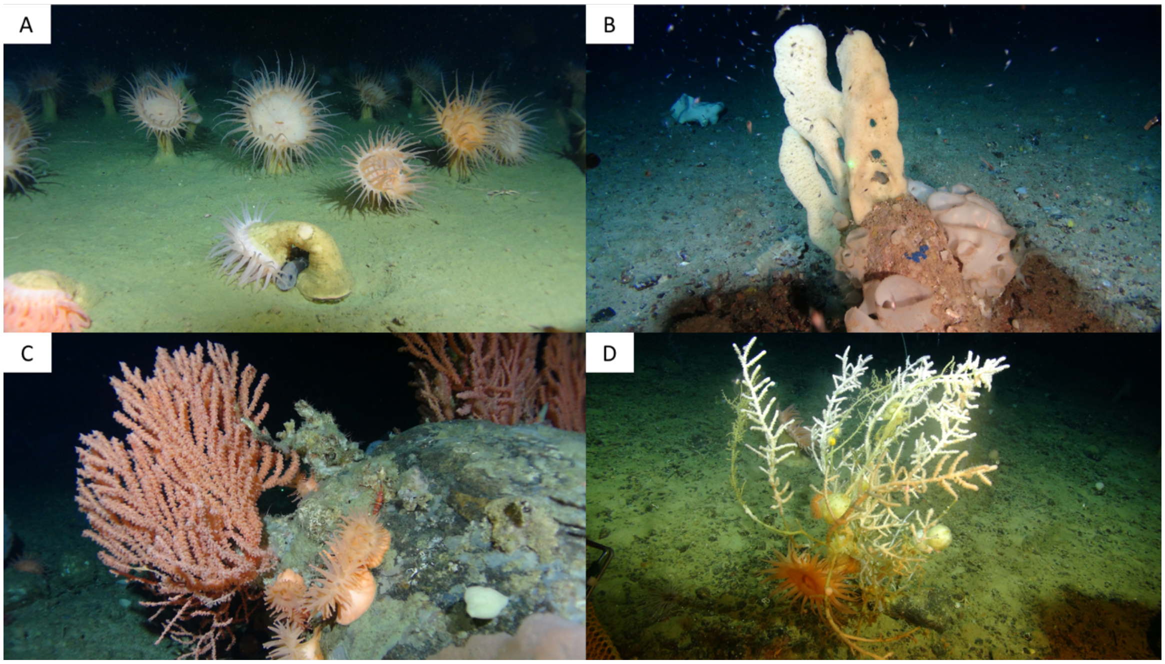

Figure 3. Exemples de structures biogéniques dans l'Arctique canadien. (A) Anémones de mer de la famille des Hormathiidae; (B) éponge rainurée, *Mycale (Mycale) lingua*; (C) coraux des résédas, *Primnoa reseadeformis*; et (D) éponge carnivore *Cladorhiza* sp. Crédits : ArcticNet-CSSF-DFO.

Fonctionnement de l’écosystème benthique

Dans les sédiments meubles, les organismes benthiques jouent un rôle majeur dans la reminéralisation de la matière. La minéralisation de la matière organique découle de l’action des micro-, méio- et macro-organismes benthiques, et est considérée comme une fonction écologique importante au sein des écosystèmes marins (Jahnke, 1996). Elle correspond à la régénération des nutriments et à leur diffusion du sédiment vers la colonne d’eau suite à la dégradation de la matière organique par la boucle microbienne (Figure 4). La matière est d’abord oxydée en surface par l’oxygène puis subit une cascade de réactions impliquant la réduction successive des nitrates, des oxydes de manganèse, des oxydes de fer, des sulfates et du dioxyde de carbone (Froelich et al., 1979). Les différentes réactions de minéralisation aérobie, utilisant l’oxygène comme oxydant, et anaérobie, utilisant les autres oxydants, conduisent à la libération de composés inorganiques dissous, tels que les nitrates, l’ammonium, le phosphate et les silicates. Ces produits issus de la dégradation s’accumulent dans le sédiment et peuvent subir des transformations chimiques (nitrification et dénitrification). Via la circulation thermohaline, ces composés alimentent le réservoir nutritif de surface nécessaire à la production primaire.

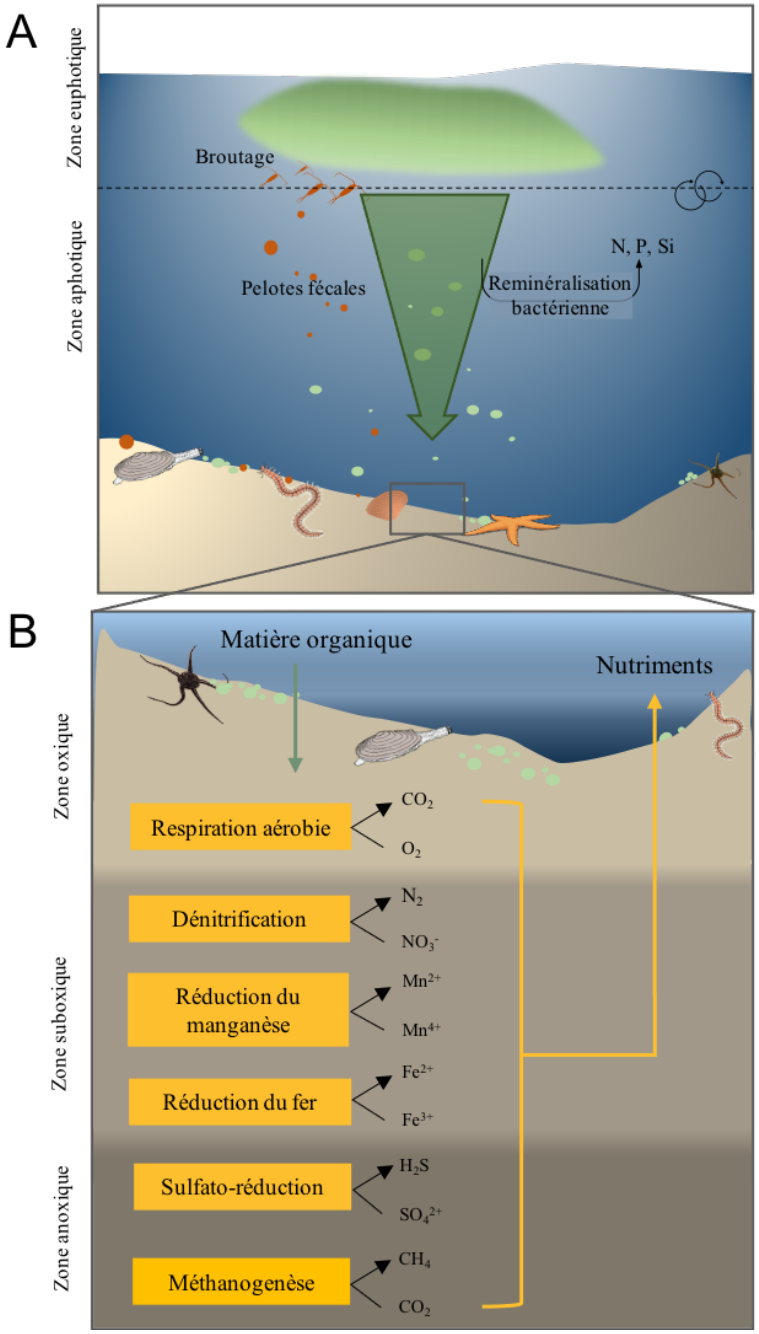

Figure 4. Représentation schématique des processus de sédimentation sur le fond marin (A); et des voies de transformation de la matière organique dans le sédiment (B; reminéralisation benthique), modifiée de Froelich et al. (1979).

L'intensité de la minéralisation dépend de nombreux facteurs dont la quantité et la qualité de la matière organique arrivant sur le sédiment et l'activité de bioturbation réalisée par les organismes benthiques (Sun et al., 2009; Link et al., 2011; Bourgeois et al., 2017). La bioturbation est définie comme l'ensemble des modifications physiques du sédiment et de la matière particulaire, produites lors des activités d'alimentation, de déplacement et/ou de création de terriers (Figure 5; Richter, 1936; Rhoads, 1974). Ainsi, les organismes benthiques influencent directement la disponibilité de l'oxygène, la séquestration et la distribution de la matière organique au sein des différentes couches de sédiments et l'orientation des flux des produits de dégradation à l'interface eau-sédiment.

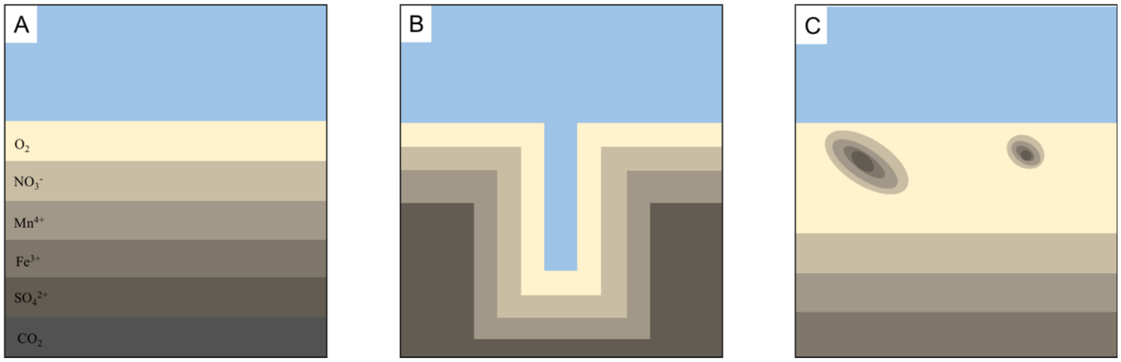

Figure 5. (A) Distribution théorique des principaux oxydants associés aux réactions d'oxydo-réductions de la matière organique dans le sédiment. (B) Variation de la distribution sous l'influence d'organismes bioturbateurs lors de la construction de galeries et (C) à l'intérieur de pelotes fécales déposées à la surface des sédiments. Adapté de Aller (1994).

Subissant tous les changements physiques au sein de leur écosystème, les organismes benthiques sont de fait des indicateurs pertinents de la santé des écosystèmes et peuvent être utilisés pour évaluer les changements à long terme du milieu marin (Snelgrove et Butman, 1994; McArthur et al., 2010). Un changement dans les paramètres environnementaux peut se refléter au niveau d'une espèce, mais également au niveau d'un groupe d'espèces et sur le fonctionnement de l'écosystème benthique.

Impact du changement climatique sur les communautés benthiques

L'amplification arctique

Depuis maintenant plusieurs années, la région arctique dans son ensemble émerge comme la région la plus touchée par le réchauffement de la planète comparativement aux régions tropicales et tempérées (Derksen et al., 2019). En agissant comme une barrière entre l'océan et l'atmosphère, la banquise contribue de façon cruciale à la singularité de l'océan Arctique. De par son important albédo (pouvoir réfléchissant), la banquise limite la quantité d'énergie solaire absorbée durant le printemps. L'augmentation actuelle de plus de 1.5°C des températures atmosphériques par rapport à la moyenne de 1971 à 2000 a provoqué une réduction drastique de l'étendue et de l'épaisseur de la glace saisonnière, et de ce fait, une réduction de son pouvoir réfléchissant (Overland et al., 2014; Walsh et al., 2017; Zhao et al., 2018; Derksen et al., 2019). L'océan qui forme une surface sombre absorbant efficacement le rayonnement solaire accumule donc en retour une plus grande part de l'énergie solaire. Ainsi, l'Arctique subit une rétroaction positive du réchauffement climatique : l'augmentation de la température provoque une intensification de la fonte de la neige et de la glace, favorisant d'une part l'absorption des radiations solaires et d'autre part la hausse des températures de l'eau de surface. En raison de ce phénomène, le couvert de glace a été réduit de près de 20% par décennie entre 1968 et 2016 dans de nombreuses régions de l'Arctique canadien (Figure 6), suggérant un été libre de glace d'ici l'année 2050 (Barnhart et al., 2016; Derksen et al., 2019).

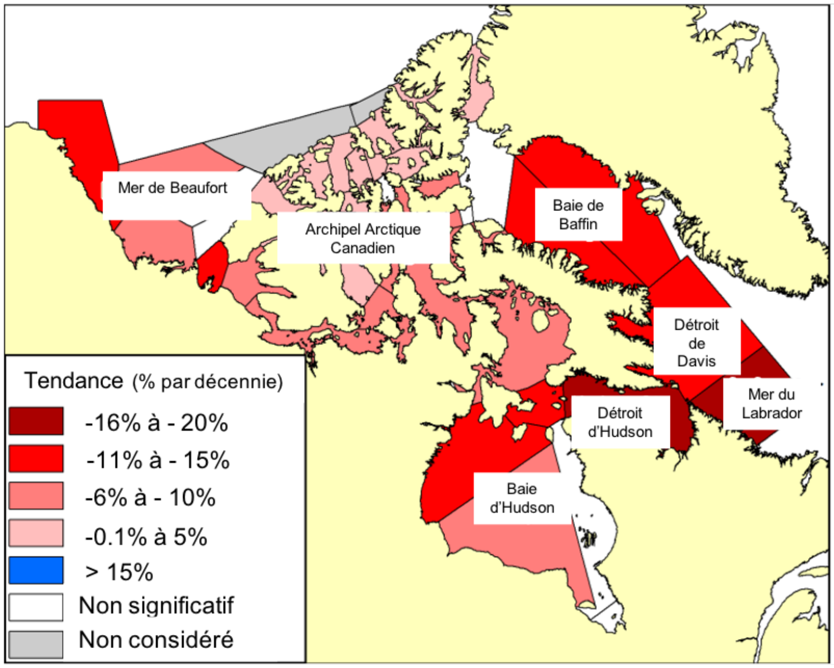

Figure 6. Tendance de la diminution de la glace totale estivale, exprimée en pourcentage, relevée en Arctique entre 1968 et 2016 (Derksen et al., 2019).

Des écosystèmes en changement

L'augmentation de températures des eaux arctiques affecte en premier lieu les espèces adaptées aux conditions froides actuelles. Il est ainsi estimé que plus de 95% des écosystèmes de coraux d'eaux froides et d'eaux profondes déclineraient sous l'effet d'un réchauffement de 1.5°C (IPCC, 2019). Outre l'augmentation des températures et la réduction du couvert de glace, l'Arctique pourrait être exposé, d'ici 2100, à une augmentation des précipitations de 15 à 65% selon les régions d'Arctique (Bintanja et Selten, 2014). Une des conséquences majeures de ce phénomène est l'intensification des apports d'eaux douces par les rivières pouvant entrainer une importante désalinisation des zones côtières. Depuis 1980, les débits annuels des rivières arctiques ont augmenté, passant en moyenne de 3900 ± 390 km^3 en 2000 à 4200 ± 420 km^3 en 2010 (Haine et al., 2015). Les simulations récentes montrent une tendance à l'augmentation des rejets des rivières de l'ordre de 25 à 50% dans les régions eurasiennes et canadiennes (Figure 7; Bring et al., 2017).

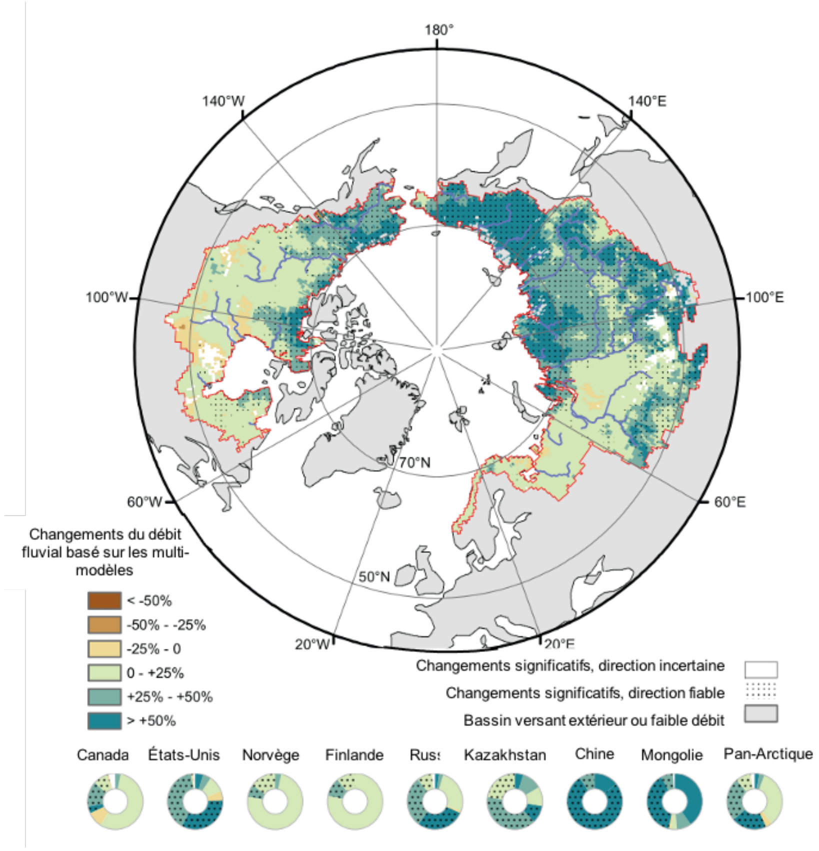

Figure 7. Projection des changements dans le débit des rivières à l'échelle Pan-Arctique de 1961-1990 à 2061-2090. Les graphiques circulaires montrent la distribution des changements par pays ainsi que pour la région Pan-Arctique (Bring et al., 2017).

Ainsi, la disparition graduelle de la banquise associée à une augmentation des précipitations devrait conduire à une plus forte stratification de la colonne d'eau dans le futur, tout en contribuant à une augmentation de la disponibilité en lumière pour les organismes photosynthétiques (Barber et al., 2015; Nummelin et al., 2016; Ardyna et al., 2017). Pour ces raisons, une augmentation de la production primaire de l'ordre de 57% a été observée entre 1998 et 2018 (Lewis et al., 2020). Néanmoins, cette augmentation semble résulter principalement de la composante autotrophe pélagique. Il est important de noter que la production pélagique sera de moins en moins susceptible d'être exportée vers l'océan profond du fait de l'accroissement de la stratification qui rend plus difficile les échanges entre la couche mélangée de surface et les profondeurs, ainsi que de la contribution croissante à la production primaire des algues pélagiques de petite taille à faible potentiel de sédimentation (Li et al., 2009). Le couplage pélago-benthique devrait ainsi être graduellement remplacé par un couplage phytoplancton-zooplancton, propre à la colonne d'eau (Piepenburg, 2005; Arrigo et al., 2008; Wassmann et Reigstad, 2011). Il est ainsi estimé que le changement climatique en Arctique devrait particulièrement affecter la distribution, la diversité et l'abondance des communautés benthiques, en raison de son impact sur les paramètres environnementaux (couplage pélago-benthique et paramètres physico-chimiques) mais également sur les services et fonctions écosystémiques (Piepenburg, 2005; Grebmeier et al., 2006; Renaud et al., 2008; Kędra et al., 2015).

Évolution des services écosystémiques

Les activités maritimes dans l'Arctique canadien reposent principalement sur le réapprovisionnement des communautés autochtones, les activités d'exploration minière, de tourisme et de pêche commerciale (Pizzolato et al., 2014, 2016). Depuis 2007, l'ensemble de ces activités montre une hausse d'environ 20%, concentrée principalement dans les régions du nord de la Baie d'Hudson, du détroit d'Hudson, du détroit de Davis, de la Baie de Baffin, du détroit de Lancaster et du sud de la mer de Beaufort (Pizzolato et al., 2014, 2016; Melia et al., 2016). Les augmentations observées dans le détroit d'Hudson, la Baie de Baffin, la mer de Beaufort et le passage du Nord-Ouest, ont été mises en relation avec l'intensification des explorations minières et des activités de pêche (Miller et Ruiz, 2014; Pizzolato et al., 2016; Tai et al., 2019). Le réchauffement climatique devrait entrainer une accessibilité accrue et une saison de navigation plus longue (Melia et al., 2016; Aksenov et al., 2017). La diminution de la glace de mer pluriannuelle est susceptible d'entrainer l'ouverture de nouvelles routes commerciales saisonnières par le passage du Nord-Ouest et la route maritime du Nord (Figure 8; Melia et al., 2016). Une connectivité accrue entre les eaux des océans Pacifique Nord et Atlantique occasionnera de plus nombreuses activités maritimes dans l'Arctique, représentant un vecteur d'espèces aquatiques envahissantes dans les eaux de ballast ou sur les coques (Goldsmit et al., 2017, 2019, 2020).

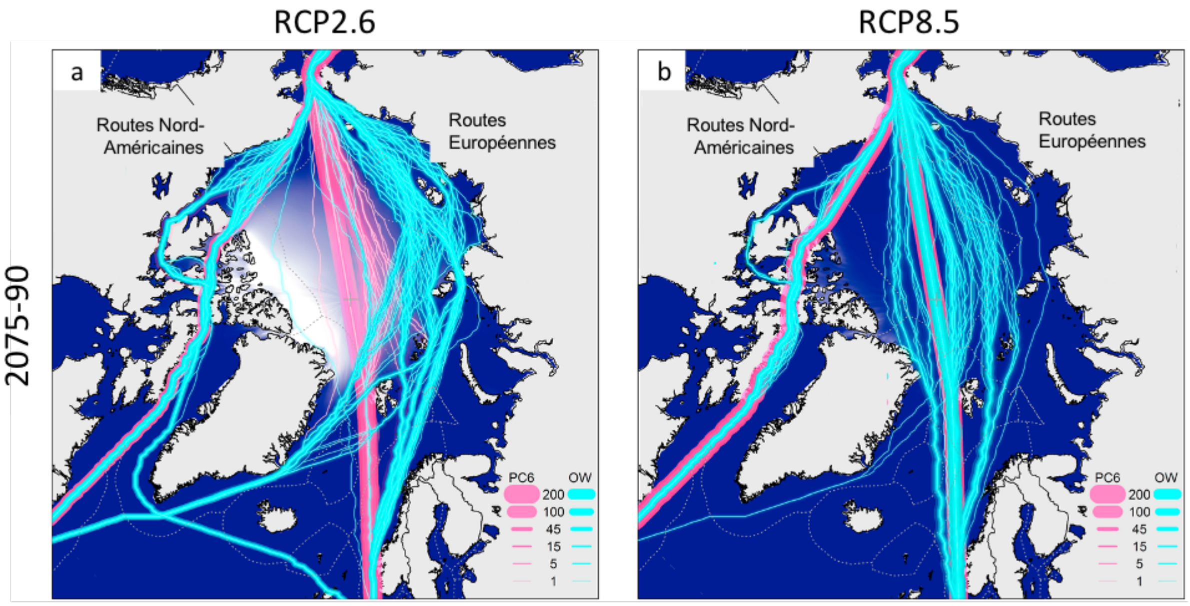

Figure 8. Projections des routes transarctiques les plus rapides sous un scénario RCP2.6 (a) et un scénario RCP 8.5 (b) pour la période de 2075 à 2090. Les lignes cyan représentent les navires en eau libre (OW) et la ligne rose représente les navires polaires de classe 6 (PC6); les épaisseurs de ligne indiquent le nombre de transits utilisant le même itinéraire. Les lignes grises en pointillés indiquent les zones économiques exclusives. Modifiée de Melia et al. (2016).

Les pêcheries constituent par ailleurs une grande part du marché canadien (Pêches et Océans Canada, 2020). Les principales prises sont les poissons de fond tels que le flétan du Groenland (*Reinhardtius hippoglossoides*), ainsi que les invertébrés benthiques comme la crevette nordique (*Pandalus borealis*). En raison d'un accès plus hâtif aux eaux arctiques (Melia et al., 2016), les prédictions de captures de ces espèces montrent une augmentation importante d'ici 2100 pouvant atteindre 6.95 (± 5.07) millions de tonnes sous un scénario RCP8.5 (+ 4.9°C d'ici 2100) dans l'Archipel Canadien (Tai et al., 2019). Le déploiement des engins de pêche comme les chaluts hauturiers et de fond induirait, entre autres, des perturbations au sein des écosystèmes benthiques telles que la remise en suspension de la matière organique et la destruction d'habitats vulnérables, comme les structures biogéniques (Mayer et al., 1991; Palanques et al., 2001; Thrush et Dayton, 2002). Ces changements pourraient induire un changement dans la composition des communautés benthiques et réduire considérablement leur diversité ainsi que modifier le fonctionnement de l'écosystème benthique (Thrush et Dayton, 2002).

Sites d'études

Les conséquences du changement climatique dans les régions de la Baie d'Hudson et de l'est de l'Arctique canadien, tels que la diminution de la glace de mer, la désalinisation ou bien l'augmentation du trafic maritime, sont susceptibles d'être à l'origine de destructions des habitats marins vulnérables et d'occasionner de grands changements dans la structure des communautés benthiques.

Diversité et distribution des communautés benthiques: cas du complexe de la Baie d'Hudson

Le complexe de la Baie d'Hudson, couvert de glace de mer entre 5 à 10 mois par an (Hochheim et Barber, 2014), est composé de 4 régions distinctes : le détroit d'Hudson, le bassin de Foxe, la Baie d'Hudson et la Baie James (Figure 9).

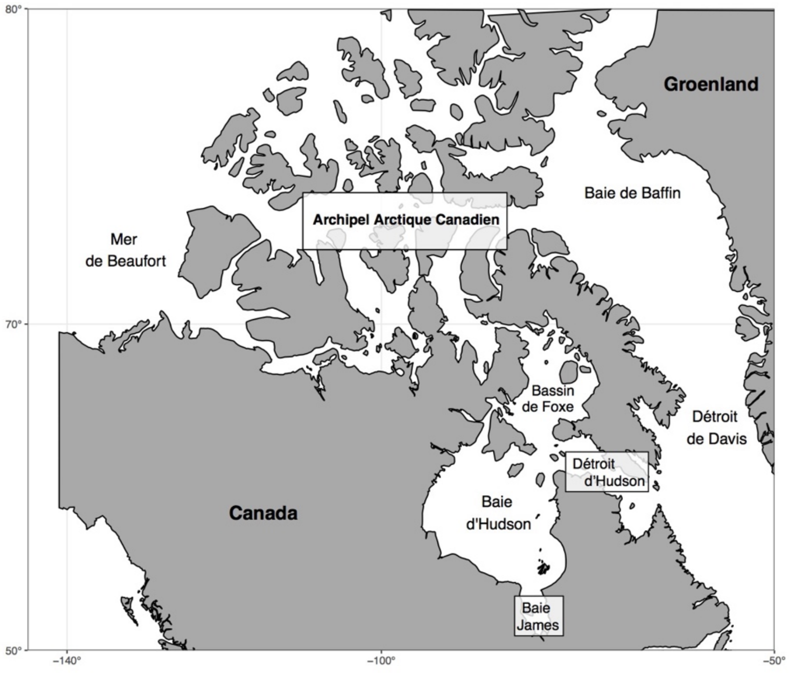

Figure 9. Zones d'études situées dans l'archipel canadien

Ce complexe est influencé par des entrées marines arctique provenant du bassin de Foxe et atlantique provenant de la mer du Labrador, ainsi que des entrées d'eaux douces provenant de 42 rivières majeures qui alimentent la baie d'Hudson. Celles-ci contribuent à plus de 70%

à l'apport annuel total d'eau douce dans le complexe (Déry et al., 2018). Les apports d'eaux douces par ces rivières présentent des fluctuations saisonnières et annuelles reliées aux précipitations et à la fonte des neiges au printemps (Déry et al., 2005, 2011, 2016). Ajoutée à ces fluctuations naturelles, la construction d'infrastructures hydroélectriques dans des rivières majeures, telles que les rivières Nelson, Churchill et La Grande Rivière, ont engendré des modifications dans leur décharge quotidienne, saisonnière et annuelle notamment en raison de la rétention d'eau durant le printemps et l'été et à l'évacuation ponctuelle des barrages durant l'hiver (Déry et al., 2016, 2018). Les importantes variations des apports d'eau douce par les rivières affectent ainsi directement les paramètres physico-chimiques (température, densité et salinité) et biologiques du système de la Baie d'Hudson (Prisenberg, 1986; Granskog et al., 2007). De plus, l'augmentation attendue des précipitations sous l'effet du réchauffement climatique aura pour effet d'augmenter le débit des rivières de l'ordre de 15% dans cette région, entrainant une forte désalinisation des côtes et des eaux de surface (Déry et al., 2016; Bring et al., 2017; MacDonald et al., 2018).

Parallèlement, le système de la Baie d'Hudson présente une des plus fortes diminutions de couverture de glace de mer estivale et automnale avec un allongement de la saison d'eaux libres de plus de 3 semaines (Figure 6; Hochheim et Barber, 2014; Derksen et al., 2019). Cette débâcle hâtive implique potentiellement une augmentation de la longueur de la saison de navigation dans des eaux libres de glace associée à une probable hausse des prises de pêche commerciale de crevettes nordiques dans le complexe (Andrews et al., 2018; Tai et al., 2019). Les connaissances des communautés benthiques dans le complexe de la Baie d'Hudson sont encore limitées à des données historiques (Wacasey et Atkinson, 1976; Atkinson et Wacasey, 1989a, 1989b; Cusson et al., 2007; Roy et Gagnon, 2016). Face à l'urgence climatique, de nouveaux projets scientifiques ont été mis en place depuis le début du siècle, pour comprendre les effets des changements climatiques sur l'environnement marin de la Baie d'Hudson (MERICA, ArcticNet, CAISN, BaySyS, BriGHT, GENICE William Kennedy). Une partie de ces études a mené à la désignation de zones d'importance écologique ou biologique (ZIEB) basée principalement sur les communautés mégabenthiques (coraux et éponges) et macrobenthiques (diversités et caractéristiques benthiques) (Kenchington et al., 2011). Cependant, malgré des densités relativement élevées d'éponges et de coraux dans le détroit d'Hudson et leur potentiel d'influence sur les communautés benthiques (Figure 10A), l'écologie (substrats d'attaches, formation d'agrégation) ainsi que les localisations de ces structures dans le complexe de la Baie d'Hudson restent à ce jour très peu connues (Kenchington et al., 2010, 2011). Par ailleurs, les résultats des recherches sur les communautés épibenthiques du complexe restent limités chronologiquement, spatialement et taxonomiquement et aucunes de ces recherches ne font état des relations communautés-environnement (Kenchington et al., 2011; Piepenburg et al., 2011; Jørgensen et al., 2016; Wei et al., 2019). La méconnaissance de la localisation et des caractéristiques des habitats à structures biogéniques dans le complexe de la baie d'Hudson, nous a contraint à choisir des sites dans l'archipel canadien dont nous avions une meilleure connaissance.

Fonctionnement de l'écosystème benthique dans les habitats à structures biogéniques: cas de l'est de l'Arctique canadien

Le détroit de Davis et la baie de Baffin (Figure 9) présentent une forte concentration d'habitats vulnérables composés de structures biogéniques (Figure 10B; Kenchington et al., 2010, 2011; Pizzolato et al., 2016) et sont exposés à d'importantes pêches commerciales de flétan du Groenland et de crevettes nordiques. De par la forte vulnérabilité et la facilité d'accès de ces régions, de nombreuses recherches se sont portées sur la distribution et l'étude des habitats benthiques vulnérables dans cette région pour les inclure comme prioritaires dans la conservation de la biodiversité (par exemple, Wareham et Edinger, 2007; Kenchington et al., 2010, 2012; Neves et al., 2015; Hiltz et al., 2018; Dinn et al., 2019). Cependant, le fonctionnement benthique des habitats vulnérables dans l'Arctique canadien est peu connu alors que celui des sédiments meubles est bien étudié (Welch et al., 1997; Grant et al., 2002; Rysgaard et al., 2004; Renaud et al., 2007b, 2007a; Morata et al., 2011, 2008; Link et al., 2011, 2013b, 2013a; Darnis et al., 2012; Link, 2012; Grebmeier et Cooper, 2014b, 2014a; Bourgeois et al., 2017). Face à une augmentation attendue des prises de pêches dans cette région et une potentielle disparition ou dégradation de ces habitats en raison du passage des chaluts de fond, comprendre le rôle des structures biogéniques sur le fonctionnement de l'écosystème benthique est crucial (Thrush et Dayton, 2002; Rossi, 2013a; Tai et al., 2019)

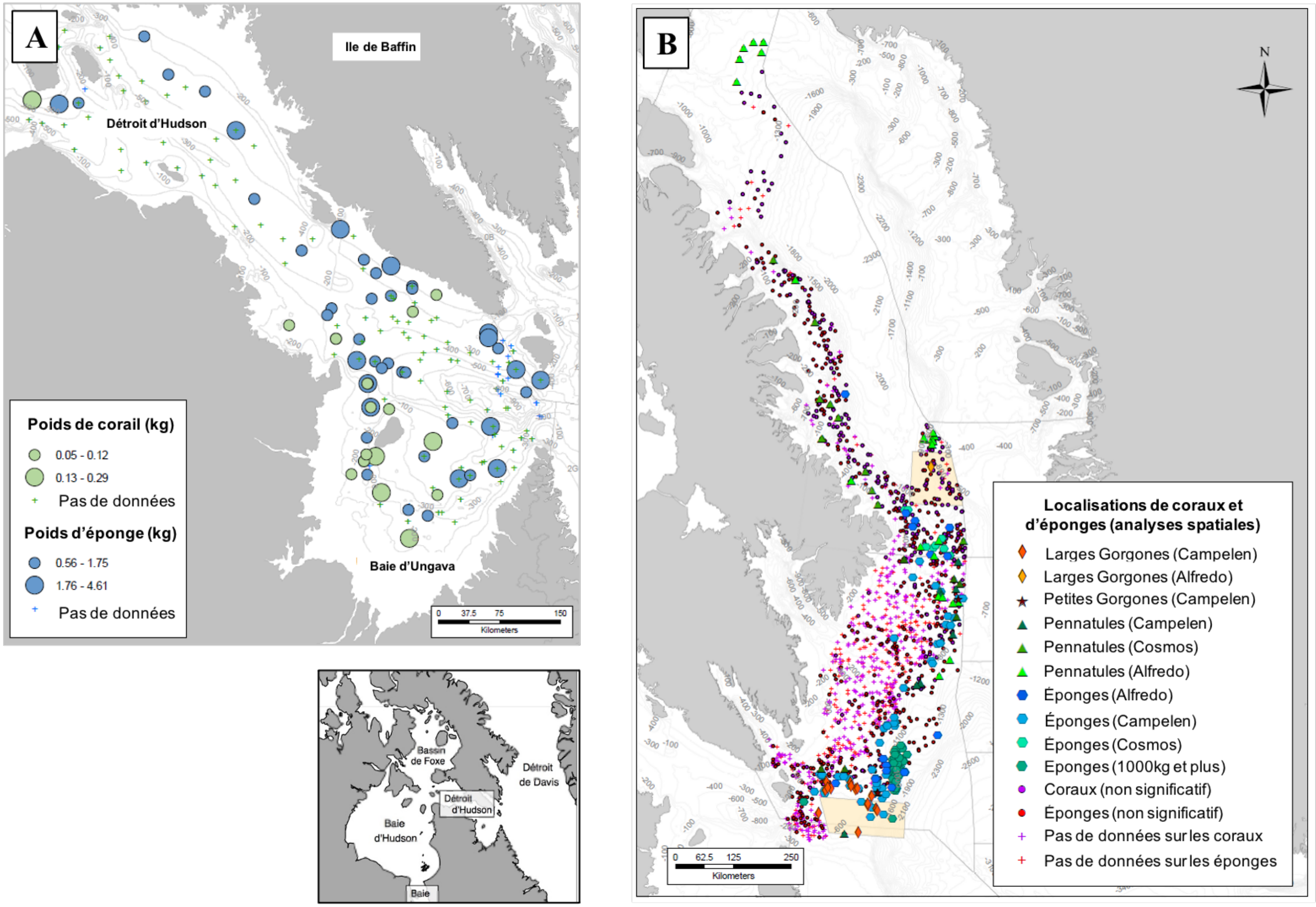

Figure 10. Principales localisations des structures biogéniques dans l'est de l'Arctique canadien. (A) Localisation des éponges et des coraux mous dans le détroit d'Hudson; et (B) Localisations des éponges, coraux et plumes de mer dans le détroit de Davis et la baie de Baffin (Kenchington et al., 2010, 2011).

Organisation de la thèse et objectifs

En 2010, le Canada s'est engagé auprès des Parties à la Convention sur la diversité biologique à conserver, d'ici 2020, 10% des aires marines et côtières importantes pour la biodiversité et pour les services écosystémiques (Aichi Target). Les travaux réalisés au cours de ces dernières années ont permis d'atteindre 13.8% de zones conservées contribuant aux objectifs de conservation marine (https://www.dfo-mpo.gc.ca/oceans/conservation/areas-zones/index-fra.html). Ainsi en 2020, le premier Ministre s'est engagé à collaborer avec le Ministère des Pêches afin de présenter un nouveau plan visant à préserver 25% des océans du Canada (Gouvernement du Canada, 2020). À ce titre, il est notamment nécessaire d'élargir nos connaissances sur les écosystèmes benthiques, et en particulier, de mieux comprendre les facteurs influençant leur diversité et leur fonctionnement. Ainsi, cette thèse a pour objectifs :

(1) d'apporter une description plus complète et actualisée de la diversité et la distribution spatiale des communautés benthiques dans le complexe de la baie d'Hudson en lien avec les variables environnementales ;

(2) de comprendre les effets des changements climatiques sur la biodiversité et le fonctionnement des écosystèmes benthiques ; et

(3) d'enrichir les connaissances des écosystèmes benthiques et d'appuyer la désignation de zones d'intérêt écologique et biologique ainsi que des aires marines protégées.

Pour atteindre les objectifs désirés, cette thèse se divise en trois axes de recherche interconnectés (Figure 11) s'intéressant à différents compartiments benthiques (épifaune et endofaune), à différentes échelles spatiales (régionale et locale) et temporelles (actuelle et future) ainsi qu'à différentes composantes des écosystèmes benthiques (composition et caractérisation des communautés et fonctionnement de l'écosystème)

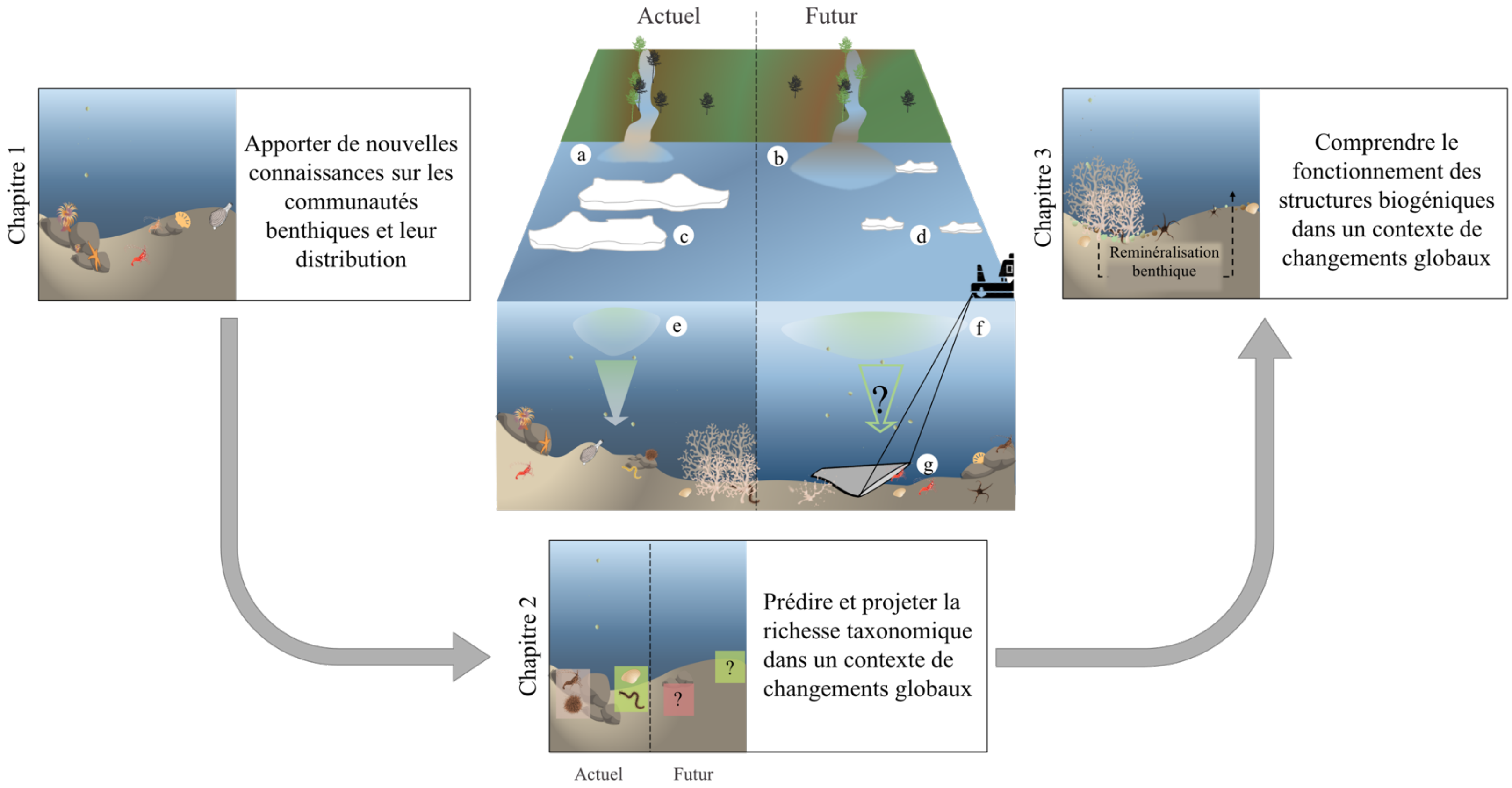

Figure 11. Modèle conceptuel de la structure de la thèse. (a-b) correspondent à une augmentation des débits de rivières avec un apport accru des eaux douces et des particules terrigènes; (c-d) correspondent à une diminution de la glace de mer; (e-f) correspondent à un potentiel changement dans l'étendue et l'intensité de la floraison phytoplanctonique et (g) correspond à la destruction des habitats à structures biogéniques par des filets de pêche.

Le premier chapitre se concentre sur la description de la composition et la distribution des communautés épibenthiques du complexe de la baie d'Hudson. Ce chapitre a pour objectifs spécifiques de i) délimiter et caractériser les communautés benthiques du complexe de la Baie d'Hudson ; et ii) de déterminer les paramètres environnementaux responsables de la distribution spatiale de ces communautés. Ce chapitre constitue la première étude de référence de la composition des communautés de la macrofaune benthique dans le complexe de la baie d'Hudson. Les hypothèses de ce chapitre sont reliées aux paramètres environnementaux influençant les communautés benthiques :

Hypothèse 1.1 : La baie d'Hudson est caractérisée par des communautés benthiques moins diversifiées au niveau des côtes en raison d'une plus forte influence des rivières alors que les régions plus au large comprennent des communautés plus diversifiées.

Hypothèse 1.2 : Les assemblages benthiques sont majoritairement structurées par la profondeur, la salinité, la couverture de glace de mer et l'apport de nourriture.

Le deuxième chapitre a pour objectif principal de décrire la variabilité spatio-temporelle (actuelle et future) de la distribution et de la richesse taxonomique des communautés épibenthiques à l'échelle de ce complexe. Ce chapitre rassemble les données utilisées dans le premier chapitre et les données les plus récentes et disponibles pour le complexe de la Baie d'Hudson. Il a comme objectifs spécifiques de i) développer un modèle prédictif de la richesse taxonomique des communautés benthiques en fonction de paramètres environnementaux sélectionnés ; et de ii) prédire la richesse taxonomique des communautés benthiques sous un scénario de « profils représentatifs d'évolution de concentration » (RCP).

Le troisième chapitre s'inscrit dans l'optique de mieux comprendre le rôle des structures biogéniques dans le fonctionnement de l'écosystème benthique. Ce chapitre a pour objectifs de déterminer l'influence des structures biogéniques sur i) la composition et les caractéristiques des communautés endobenthiques et ii) sur la dynamique des flux benthiques. Les hypothèses de ce chapitre sont :

Hypothèse 3.1 : les organismes endobenthiques sont plus abondants et diversifiés dans les habitats à structures biogéniques que dans les habitats dépourvus de ces structures, indépendamment de la profondeur et de l’espèce constituant les habitats à structures biogéniques.

Hypothèse 3.2 : les sédiments des habitats à structures biogéniques présentent une plus forte demande en oxygène et des flux biogéochimiques plus importants comparés aux sédiments dépourvus de ces structures en raison d’une plus forte sédimentation de matière organique.

Hypothèse 3.3 : les flux biogéochimiques sont majoritairement expliqués par la disponibilité des ressources, la densité des organismes endobenthiques et les activités de bioturbation.

Chapitre 1 - Spatial distribution of epifaunal communities in the Hudson Bay Complex: Patterns and drivers

1.1. Résumé

Dans ce chapitre, nous nous sommes attelés à fournir le recensement le plus récent et le plus complet des espèces épibenthiques peuplant le complexe de la Baie d'Hudson. À partir de 46 stations d'échantillonnage, nous avons pu identifier 71% des taxons présents dans le complexe de la Baie d'Hudson. Trois communautés ont été définies en lien avec le type de substrat, la salinité et la production primaire annuelle. La communauté à substrat grossier, présente le long des côtes et près des embouchures des rivières, se caractérise par une faible densité et une faible diversité. La communauté à substrat meuble, répartie dans les eaux plus profondes, montre une forte densité d'organismes déposivores. Enfin, la communauté à substrat mixte, située dans les zones de polynies, présente de larges organismes épibenthiques diversifiés. Cette étude accroît nos connaissances des communautés benthiques du complexe de la Baie d'Hudson et de leurs relations avec leur environnement.

1.2. Abstract

The seasonal sea ice cover and the massive influx of river runoff into the Hudson Bay System of the Canadian Arctic are critical factors influencing biological production and, ultimately, the dynamics and structure of benthic communities in the region. This study provides the most recent survey of epibenthic communities in the Hudson Bay System and explores their relationships with environmental variables, including mean annual primary production and particulate organic carbon in surface water, bottom oceanographic variables, and substrate type. Epibenthic trawl samples were collected at 46 stations, with a total of 380 epibenthic taxa identified, representing 71% of the estimated taxa within the system. Three communities were defined based on biomass and taxonomic composition. Ordination analyses showed them to be associated primarily with substrate type, salinity and annual primary production.

A first community, associated with coarse substrate, was distributed along the coastlines and near the river mouths. This community was characterized by the lowest density and taxonomic richness and the highest biomass of filter and suspension feeders. A second community, composed mostly of deposit feeders and small abundant epibenthic organisms, was associated with soft substrate and distributed in the deepest waters. A third community, associated with mixed substrate and mostly located near polynyas, was characterized by high diversity and biomass, with no clearly dominant taxon. The overall analysis indicated that bottom salinity and surface-water POC content were the main environmental drivers of these epibenthic community patterns. In the face of climate change, projections of increased river inflow and a longer open water season for the Hudson Bay System could have major impacts on these epibenthic communities, emphasizing a need to continually improve our ability to evaluate and predict shifts in epibenthic richness and distribution.

1.3. Introduction

The spatial distribution of benthic community structure is predominantly related to variables such as water depth, salinity, substrate type and food supply (Piepenburg, 2005; Grebmeier et al., 2006a; Cusson et al., 2007; Witman et al., 2008; Roy et al., 2014). In Arctic waters, sea ice cover is an additional variable that influences primary production and thus the efficiency of pelagic-benthic coupling (Piepenburg, 2005; Renaud et al., 2007; Boetius et al., 2013; Roy et al., 2015; Olivier et al., 2020). Most Arctic marine ecosystems are currently responding to climate-induced changes to environmental and ecological variables, such as changing precipitation, river discharge, sea ice cover and marine biota (Déry et al., 2016; Bring et al., 2017; Osborne et al., 2018; Derksen et al., 2019). In some Arctic regions, such as the northern Bering Sea, the decline of the sea ice cover has resulted in decline of the clam populations (Grebmeier et al., 2006b; Grebmeier, 2012). Despite a growing number of species inventories being collected by various research projects and programs around the Arctic (Piepenburg et al., 2011; Link et al., 2013; Roy et al., 2014, 2015), baseline knowledge of some Arctic regions is still limited, preventing accurate predictions of how species richness and distribution will respond to climate change (Piepenburg et al., 2011).

Because of its unique attributes, the Hudson Bay System (HBS) nested within the Canadian Arctic (Figure 1.1) has been identified as one of the most sensitive regions to climate change (Gagnon and Gough, 2005; Tivy et al., 2011; Derksen et al., 2019). The HBS sea ice season has already grown shorter (Andrews et al., 2018) and is projected to continue to shorten, leading to an extended open water season (Derksen et al., 2019). River inflow is projected to increase up to 50% due to an earlier snowmelt in the surrounding drainage basins and an overall increase in precipitation (Gagnon and Gough, 2005; Bring et al., 2017). These different water inputs lead to variations of nutrient concentrations and salinity within the system that in turn affect biological processes (Déry et al., 2011, 2016). However, little is known about the environmental drivers of benthic communities in the HBS compared to other Arctic regions, such as the Canadian Arctic Archipelago. To date, most of our knowledge on benthic communities comes from relatively old or low spatial resolution diversity data and is based mainly on grab sampling (Atkinson and Wacasey, 1989a, 1989b; Cusson et al., 2007; Kenchington et al., 2011; Piepenburg et al., 2011; Jørgensen et al., 2016; Roy and Gagnon, 2016; Pierrejean et al., 2019; Wei et al., 2019). Most of these studies focused on infaunal organisms, and none related benthic community structure to environmental drivers.

This study aimed to assess the influence of various environmental factors on the structure of epibenthic communities in the study area. The specific objectives of this study were to: i) characterize the epifaunal diversity and density patterns according to environmental variables; ii) delineate epibenthic communities; and iii) determine which abiotic factors may drive spatial distribution of the epibenthic communities in the study area. We hypothesized that benthic assemblages will differ along a coast-to-offshore gradient and that salinity, food supply and sea ice cover will be strong drivers of the epibenthic community structure.

1.4. Materials and methods

1.4.1 Study area

The HBS is composed of four regions: James Bay, Hudson Strait, Hudson Bay and the Foxe Basin (Figure 1.1) occupying an area of 1.3 million km^2. Water masses from the Arctic Ocean enter the HBS from the Canadian Arctic via Fury and Hecla Strait, and from Baffin Bay via

Hudson Strait (Drinkwater, 1986; Prisenberg, 1986). Within Hudson Bay, water is rotated cyclonically around the Bay and eventually exported through Hudson Strait (Saucier et al., 2004). However, the major water input for the HBS is river discharge, with around 900 km^3 discharged per year from 42 rivers (Déry et al., 2011, 2016). Over half of this river discharge enters the southern and eastern portions of Hudson Bay, with the largest contributions from La Grande (84.22 km^3 y^{-1}) and the Nelson River (102.70 km^3 y^{-1}; Déry et al., 2016). Furthermore, the HBS is covered by a dynamic seasonal ice cover for most of the year (Hochheim and Barber, 2014). Freeze-up progresses from northwest to southeast across the HBS, and during recent years has begun in November and formed a complete ice cover by the end of December (Andrews et al., 2018). Within Hudson Bay, sea ice breakup generally starts in the northwestern and eastern parts of the Bay between May and June and progresses towards the southern region where the last ice typically remains until late July (Andrews et al., 2018; Kirillov et al., 2020). Within the dynamic seasonal ice cover of the HBS, offshore winds generate numerous coastal latent heat polynyas, biologically active areas of open water and thin ice in the dead of winter (Barber and Massom, 2007). The largest polynya is in northwestern Hudson Bay, but several smaller polynyas are located close to the Nelson River Estuary, the Belcher Islands, Coats and Mansel Islands and along the coast of Quebec (Barber and Massom, 2007).

1.4.2. Biological data collection

Benthic organisms were sampled at 46 stations in Hudson Bay, Hudson Strait and Ungava Bay (i.e., study area), between May and July in 2010, 2017 and 2018 (Figure 1.1). These samples were taken onboard the Canadian scientific icebreaker CCGS *Amundsen* as part of Arcticnet, the Hudson Bay System study (BaySys) and the Bridging Global Change, Inuit Health and the Transforming Arctic Ocean project (BriGHT). Stations were scattered throughout the HBS in geographically and biologically defined regions with depths ranging from 10 to 322 m (Figure 1.1; Barber and Massom, 2007; Wilkinson et al., 2009; Kenchington et al., 2011). Epifauna samples were collected with an Agassiz trawl (aperture of 1.5 m and net mesh size of 5 mm) with an average trawling time of 3 min and speed of 1.5 knots, respectively. Four coastal stations were sampled with an epibenthic trawl (aperture of

1 m and net mesh size of 3 mm) with an average trawling time and speed of 3 min and 1.3 knots, respectively. Samples were sieved through 2-mm mesh to retain only macrofauna and megafauna, and identifications were made onboard to the lowest possible taxonomic level. Unidentified taxa were fixed with 4% formaldehyde solution and later identified to the lowest possible taxonomic level under a dissecting microscope (Table S1.1). Vertebrates (e.g., Actinopterygii) and planktonic invertebrates (e.g., Chaetognatha and Euphausiacea) collected by the trawl were removed from the analyses. Some taxa were only identified to the phylum level because no complete identification keys exist for Hudson Bay waters (e.g., Nemertea, Nudibranchia and Porifera) and hence taxonomic richness could be underestimated in this study. Taxonomic names were checked and updated using the World Register of Marine Species (WoRMS Editorial Board, 2020).

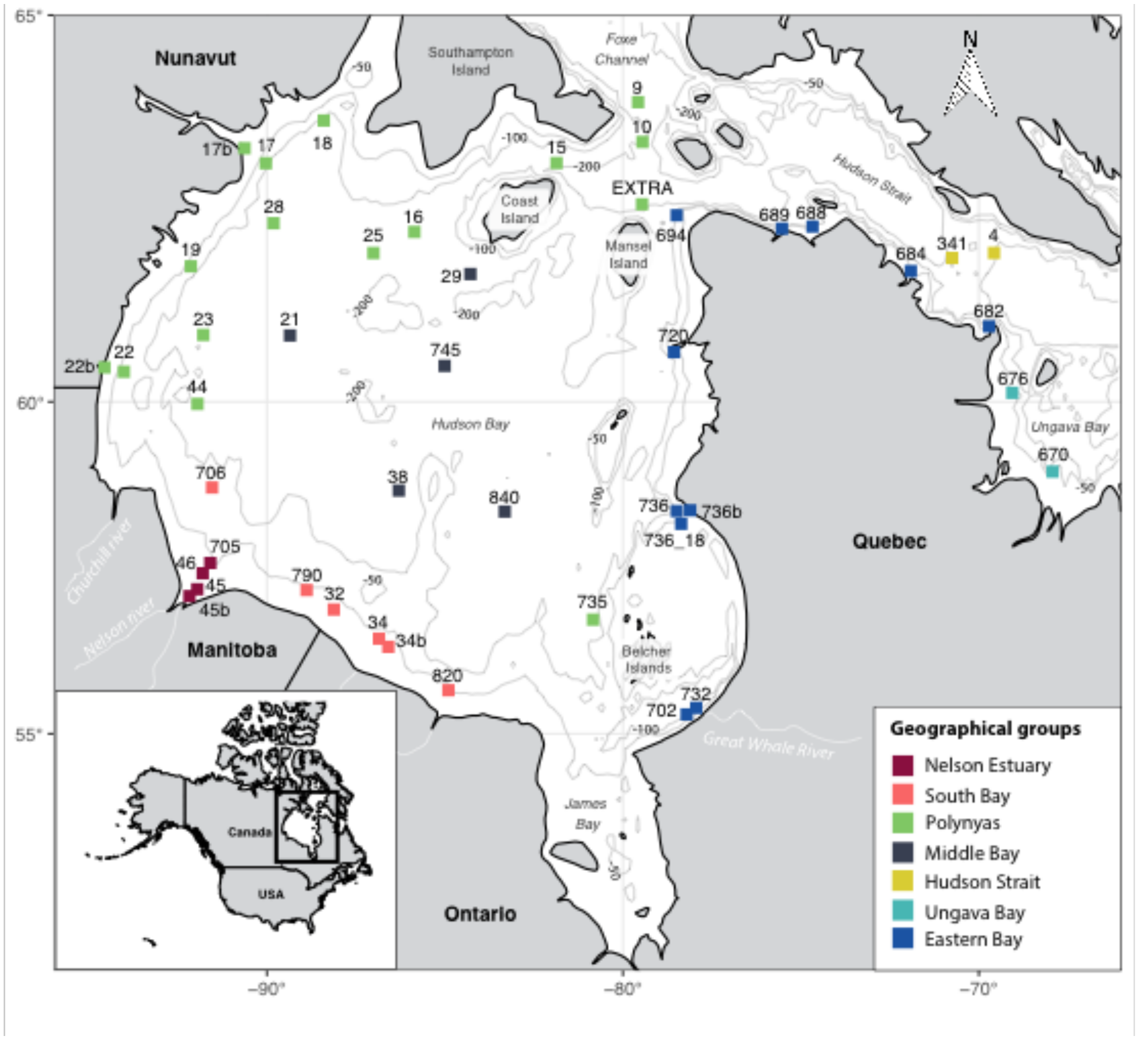

Figure 1. 1. Map of the study area with locations of stations investigated in the Hudson Bay System. Color squares on the enlarged map of the Hudson Bay System indicate sampling stations that are divided into seven geographical groups: purple squares correspond to the Nelson Estuary area; pink squares, to the Southern Bay; green squares, to areas near recurring polynyas; grey squares, to the middle of the Bay; yellow squares, to Hudson Strait; light blue squares, to Ungava Bay; and dark blue squares, to the Québec coasts.

1.4.2. Environment variables

At each sampling station, a conductivity-temperature-depth probe (CTD) recorded bottom temperature (°C), bottom dissolved oxygen (µM) and bottom salinity (Table 1.1). Particulate organic carbon (POC; mg m^{-3}) content measured at the surface of the water column over multiple years (1998–2008) and mean annual surface primary production (PP; mg C m^{-2} y^{-1}) measured over multiple years (2006–2010) were extracted from interpolated environmental data layers generated at the global scale (GMED), as well as in the Eastern Canadian Arctic and Sub-Arctic regions (https://data.mendeley.com/datasets/zmwyjs222s/2) using the package "raster" in R (Table 1.1; Basher et al., 2018; Beazley et al., 2019; Hijmans and van Etten, 2020). The substratum type at each station was classified into three separate qualitative classes based on either visual observation from trawls or substratum data presented by Henderson (1989) and Pelletier (1986). The three classes of the substrate are: 'coarse', referring to stations composed mostly of gravel, sandy gravel and pebbles (grain size > 2 mm); 'mixed', referring to stations containing particles ranging in size from silt to boulders; and 'mud', referring to stations characterized by fine-grained sediment (grain size < 0.06 mm).

The timing of sea ice breakup and freeze-up and, therefore, the duration of the open water (OW) period at each station were extracted from regional ice charts produced weekly by the Canadian Ice Service. Ice charts were produced through expert manual interpretation of remotely sensed imagery, which since 1996 have been based primarily on imagery provided by RADARSAT-1 and -2 (Tivy et al., 2011). In the current study, we defined the sea ice breakup (freeze-up) by the week that the total ice concentration at the study site fell below (surpassed) one-tenth.

Table 1. 1. Environmental variables at the stations investigated in the Hudson Bay System

Stations	**Date**	**Depth (m)**	**B_{O2}[a] (µM)**	**B_T [b] (°C)**	**B_S[c]**	**OW[d] (days)**	**POC[e] (mg m^{-3})**	**PP[f] (mg C m^{-2} y^{-1})**
702	2010	129	255	–1.36	31.78	189	817	ND[g]
705	2010	71	329	–1.32	31.65	161	458	613
706	2010	77	311	–1.40	32.38	161	174	598
735	2010	185	192	–1.23	32.94	191	380	640
745	2010	184	219	–1.49	33.28	168	113	619
790	2010	38	369	–0.64	31.15	147	485	527
820	2010	53	298	–1.47	31.60	140	413	607
840	2010	174	180	–1.42	33.18	172	127	632
EXTRA	2010	316	269	–1.06	32.99	172	152	637
670	2017	117	372	–0.83	31.72	233	264	628
676	2017	98	351	–1.20	31.98	206	221	530
682	2017	95	328	–1.34	32.22	174	207	ND
684	2017	108	330	–1.24	32.33	169	348	ND
688	2017	107	321	–1.29	32.53	170	255	ND
694	2017	103	330	–0.98	32.34	180	214	ND
720	2017	91	293	–1.10	31.25	176	303	ND
732	2017	120	254	–1.18	31.66	192	817	ND
736	2017	91	251	–1.18	31.28	202	653	ND
15	2018	188	307	–1.72	32.67	193	135	671
16	2018	136	266	–1.07	32.71	173	124	683
17	2018	94	296	–1.63	32.89	212	147	670
17b	2018	61	ND[e]	–1.49	32.63	150	774	ND
18	2018	118	312	–1.80	33.41	198	128	710
19	2018	83	341	–1.01	33.02	205	172	613
21	2018	151	232	–1.24	32.98	166	124	675
22	2018	63	345	–0.99	33.16	214	181	613
22b	2018	33	ND	0.19	33.09	181	736	ND
23	2018	109	292	–1.75	33.08	198	108	712
25	2018	144	269	–1.14	32.72	183	121	663
28	2018	160	303	–1.80	33.17	205	115	746
29	2018	180	249	–1.04	32.81	167	128	658
32	2018	31	340	–1.62	31.13	162	410	517
34	2018	37	335	–1.70	31.68	156	322	580
341	2018	308	276	0.89	33.76	198	133	605
34b	2018	46	ND	–1.70	31.55	156	323	584
38	2018	180	191	–1.34	33.10	164	103	738
4	2018	271	278	0.85	33.76	230	153	605
44	2018	104	266	–1.58	32.85	178	140	703
45	2018	18	345	2.08	28.92	188	458	629
45bis	2018	17	335	1.07	29.62	188	458	616
46	2018	44	335	–1.28	31.72	253	441	669
689	2018	127	301	–1.22	32.41	171	316	ND
10	2018	200	282	–0.96	32.67	184	147	600
736_18	2018	88	231	–1.16	31.84	202	653	ND
736b	2018	10	ND	3.15	24.40	202	ND	ND
9	2018	322	303	–1.69	33.10	179	125	610

[a] B_{O2} = bottom dissolved oxygen; [b] B_T = bottom temperature; [c] B_S = bottom salinity; [d] OW = duration of the open water period; [e] POC = particulate organic carbon content measured at the surface of the water column; [f] PP = mean annual surface primary production; [g] ND = no data.

1.4.3. Statistical analyses

1.4.3.1. Epibenthic characteristics of the study area

Epibenthic characteristics determined for each of the 46 stations were wet biomass (g m^{-2}), density (ind m^{-2}), and three biodiversity metrics: taxonomic richness (S, number of taxa), Shannon-Wiener's diversity index (H') and Pielou's evenness index (J'). The indices H' and J' were calculated based on biomass data, including colonial taxa. Bryozoa, Porifera and Cnidaria were excluded from density analysis because whole organisms were not collected by the sampling method. The non-parametric Chao2 index, which represents the expected number of taxa in the study area, was calculated using the "vegan" package (Oksanen et al., 2017). The Chao2 estimator is defined as $Chao2 = S_{obs} + \frac{Q_1^2}{2Q_2}$, where S_{obs} is the total number of observed taxa, Q_1 is the number of taxa found at only one station and Q_2 is the number of taxa found at exactly two stations (Chao, 1987).

Principal component analysis (PCA) was applied to the environmental variables from 32 stations to reduce the dimensionality of the dataset using the "FactoMineR" package (Pages, 2004). Fourteen stations were removed from this analysis due to missing data in primary production and bottom dissolved oxygen (Table 1.1). Environmental variables used in the PCA were depth, bottom salinity, bottom temperature, bottom dissolved oxygen, mean annual surface primary production, surface POC and duration of the open water season. The first resulting components (PC1, PC2 and PC3), representing a set of environmental variables, were used in linear regressions to model the relationships between community characteristics (density, biomass and taxonomic richness) and environmental variables. Homogeneity of variance and normality of residuals had been verified using regression diagnostic plots and the Shapiro-Wilk test on residuals.

1.4.3.2. Epibenthic communities

- Epibenthic community composition

The list of taxa identified at each station were downgraded to the family level (158 taxa) due to an incomplete set of organisms restraining the identification at the species level for analysis of the epibenthic community composition. Bray-Curtis dissimilarity was calculated on the fourth root transformed data for the biomass matrix in order to include colonial taxa. The fourth-root transformation was chosen to balance the effects of high and low biomass taxa (Clarke and Warwick, 2001). To define distinct communities in the study area, the dissimilarity matrix was subjected to a hierarchical cluster analysis using Ward minimum variance method (Ward, 1963). Community clusters were determined by selecting a distance where stations were fused in well-defined clusters. The geographical distribution of these communities in the study area was then mapped using the “ggplot2” package (Wickham, 2016). Similarity percentage analysis (SIMPER) determined which taxa contributed to the dissimilarity between community clusters based on the biomass matrix (cut-off at 70% similarity; Clarke, 1993).

- Epibenthic community characteristics

Epibenthic community characteristics determined at each station were density (ind m^{-2}), wet biomass (g m^{-2}) and the alpha (α) and beta (β) diversities. Alpha diversity (α) is determined as the mean number of taxa at a given station. Beta diversity (β), also called turnover diversity, provides an indication of species replacement between habitats or along an environmental gradient and indirectly indicates the habitat diversity. The latter is calculated as the ratio between gamma (γ, total number of taxa in a given community) and alpha (α) diversities (Whittaker, 1960).

1.4.3.3. Relationships between community composition and the environment

The relationship between epibenthic community composition based on wet biomass and the environmental variables was evaluated for 32 stations using a multivariate method of constrained ordination, canonical correspondence analysis (CCA; ter Braak and Verdonschot, 1995). To down-weight rare species, we used a stepwise method that removes the species with occurrence 1, then the species with occurrence 2 and so on. At each step, we compared eigenvalues and the total inertia of the analysis. When a marked decrease of ca 4% was observed in these values, we preserved the previous analysis (Legendre and Legendre, 2012). Removing rare species reduced the total number of taxa from 158 to 101, but this reduction had no impact on the outcome of the analyses. Environmental variables entered into the model were similar to the multiple regressions. To avoid redundancy in the model we tested linear dependencies among constraints. An ANOVA for CCA was used to assess the significance of variables and axes. We performed these analyses using the “vegan” package (Oksanen et al., 2017) in R (R Core Team, 2020).

1.5. Results

1.5.1. Epibenthic characteristics of the study area

We observed 380 taxa across the 46 stations sampled. The Chao2 index reached a value of 539 taxa, exceeding the number of observed taxa. Epifaunal biomass ranged from 0.02 to 45.2 g m^{-2}, density from 0.11 to 29.5 ind m^{-2}, taxa richness from 5 to 71 taxa per station, diversity index H’ from 0.26 to 2.64, and evenness index J’ from 0.09 to 0.88 (Figure 1.2).

Principal components 1, 2 and 3 accounted for about 47, 18 and 15%, respectively, of the variance in the selected environmental variables, for an approximate combined 80% of the variance (Table 1.2; Figure S1.1). PC1 strongly correlated with depth, bottom salinity, bottom dissolved oxygen, surface-water POC and mean annual primary production (coordinates > 0.6 or < -0.6; Table 1.2). PC1 reflected an environmental gradient, with low PC1 scores related to shallow depths and low bottom salinity, high POC content, high bottom dissolved oxygen and low mean annual primary production, whereas high PC1 scores related to deeper waters, high bottom salinity, low POC content, low bottom dissolved oxygen and high mean primary production. Conversely, PC2 had the strongest correlation with the duration of open water (coordinates > 0.6), while PC3 had the strongest correlation with bottom temperature (Table 1.2).

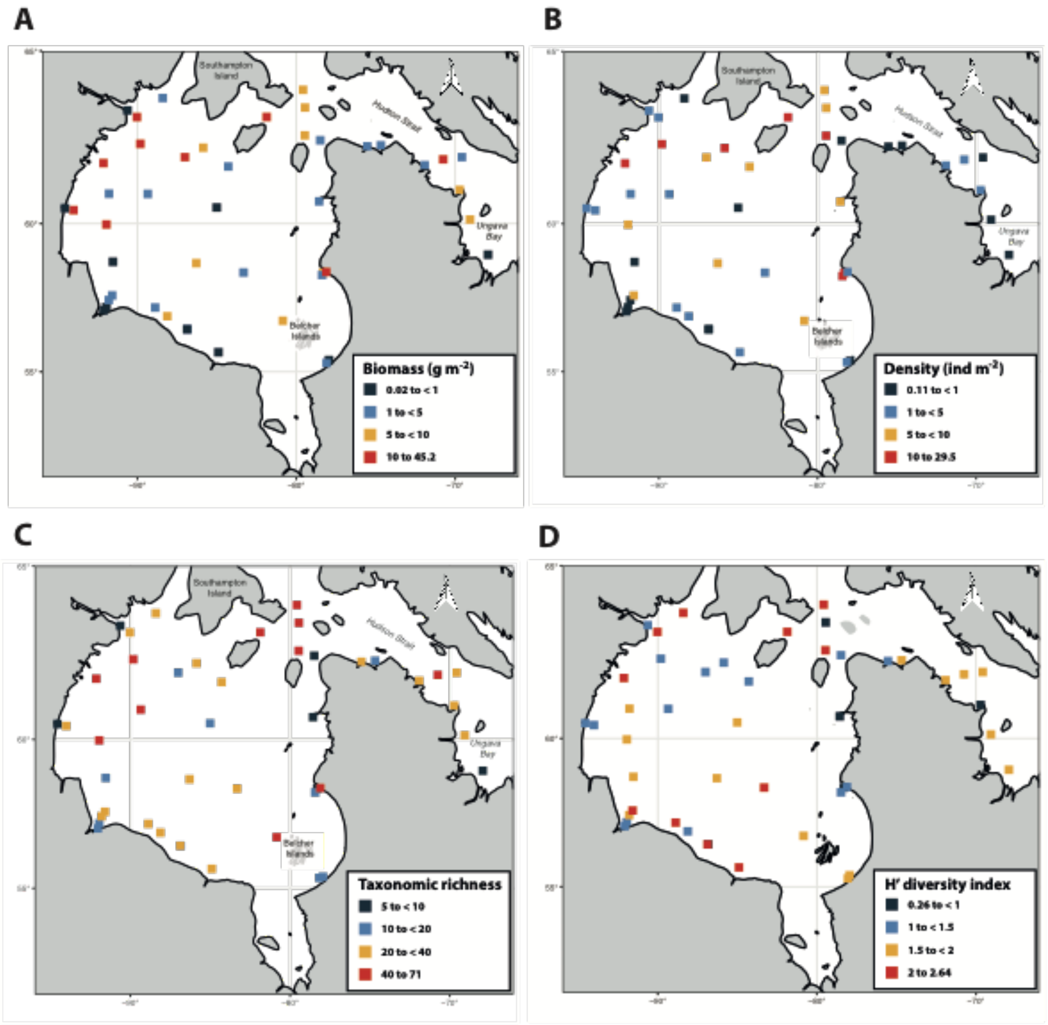

Figure 1. 2. Distributions of epibenthic characteristics at 46 stations in the Hudson Bay System. Characteristics shown are (A) biomass (g m–2), (B) density (individuals m–2), (C) taxonomic richness, and (D) Shannon-Wiener diversity index. Blue dots represent low values and red dots represent high values for these epibenthic characteristics.

Table 1. 2. Correlation-based principal component analysis (PCA) of environmental variables determined in the study area.

Results of PCA	**PC1**	**PC2**	**PC3**
Eigenvalues	3.27	1.27	1.03
Variation explained (%)	46.7	18.2	14.7
Linear coefficients by environmental variable			
Depth	0.75	0.15	0.52
Temperature	–0.43	0.49	0.67
Salinity	0.91	0.05	–0.05
Bottom dissolved oxygen	–0.73	0.31	–0.30
POC content	–0.89	–0.11	0.03
Mean primary production	0.60	0.20	–0.39
Open water duration	0.07	0.93	–0.24

Linear models for epibenthic characteristics showed that variables included in the PC1 were significant (*p*-value < 0.05; Table S1.2). Biomass, density and taxonomic richness increased with PC1 scores (Table S1.2, Figure 1.3), which means with deeper water, high bottom salinity, low POC content, low bottom dissolved oxygen and high mean primary production. The stations located near the Nelson Estuary and in the southern part of Hudson Bay presented the lowest PC1 scores and the lowest values of biomass, density and taxonomic richness (Figures 1.2 and 1.3). The same observation was noted for Ungava Bay (Figures 1.2 and 1.3). Stations located in western HB, northern HB, around the Belcher Islands and in Hudson Strait presented the highest values of PC1 scores and benthic characteristics (Figures 1.2 and 1.3). In contrast, the middle of the Bay was characterized by low values of biomass, density and taxonomic richness (Figures 1.2 and 1.3). Neither PC2 nor PC3 was significant for epibenthic characteristics (Table S1.2).

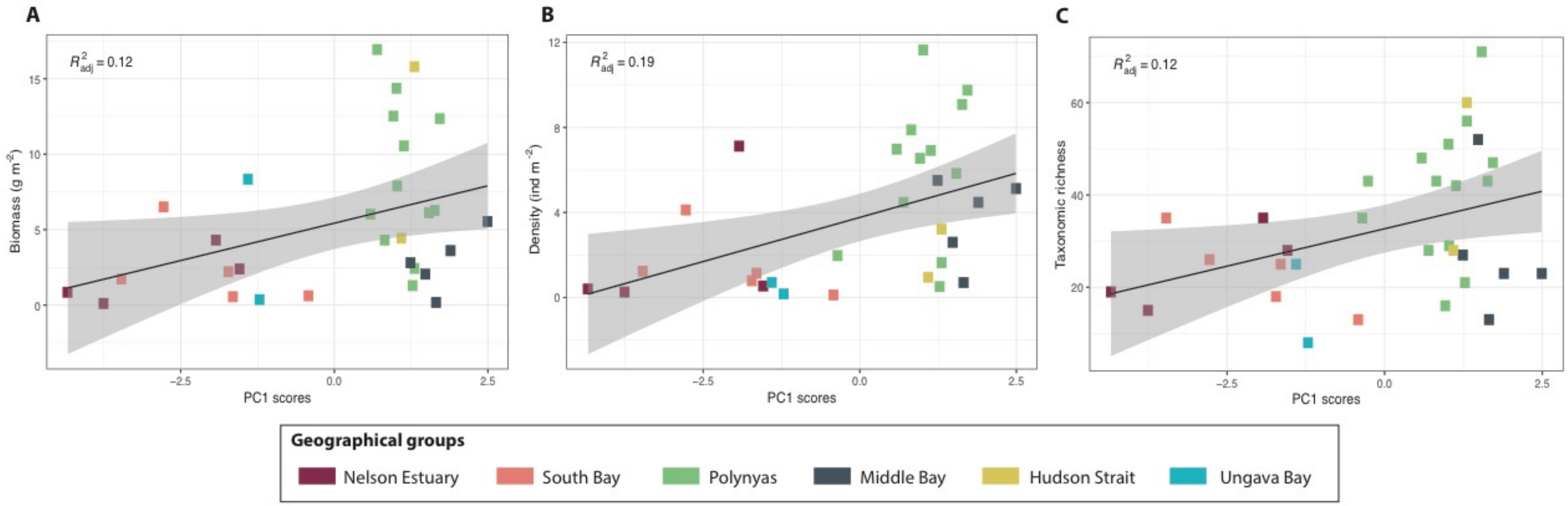

Figure 1. 3 Relationships of epibenthic characteristics with first principal component scores based on environmental variables. Shown are (A) biomass (g m–2), (B) density (individuals m–2), and (C) taxonomic richness, along with coefficients of determination of significant linear regression ($p < 0.05$) in each case. Gray shaded areas indicate the 95% confidence interval.

1.5.2. Identification of epibenthic communities of the study area

- Composition of epibenthic community identified

Cluster analysis of all 46 stations based on Bray-Curtis dissimilarity of biomass data highlights three communities independent of the sampling year and the sampling gear (Figure 1.4A). These communities are distributed along a coastal-to-offshore gradient (Figure 1.4B). Community 1 is located along coastal areas, whereas Community 3 is mainly located in the middle part of the Bay and Community 2 is generally located between the other two (Figure 1.4B).

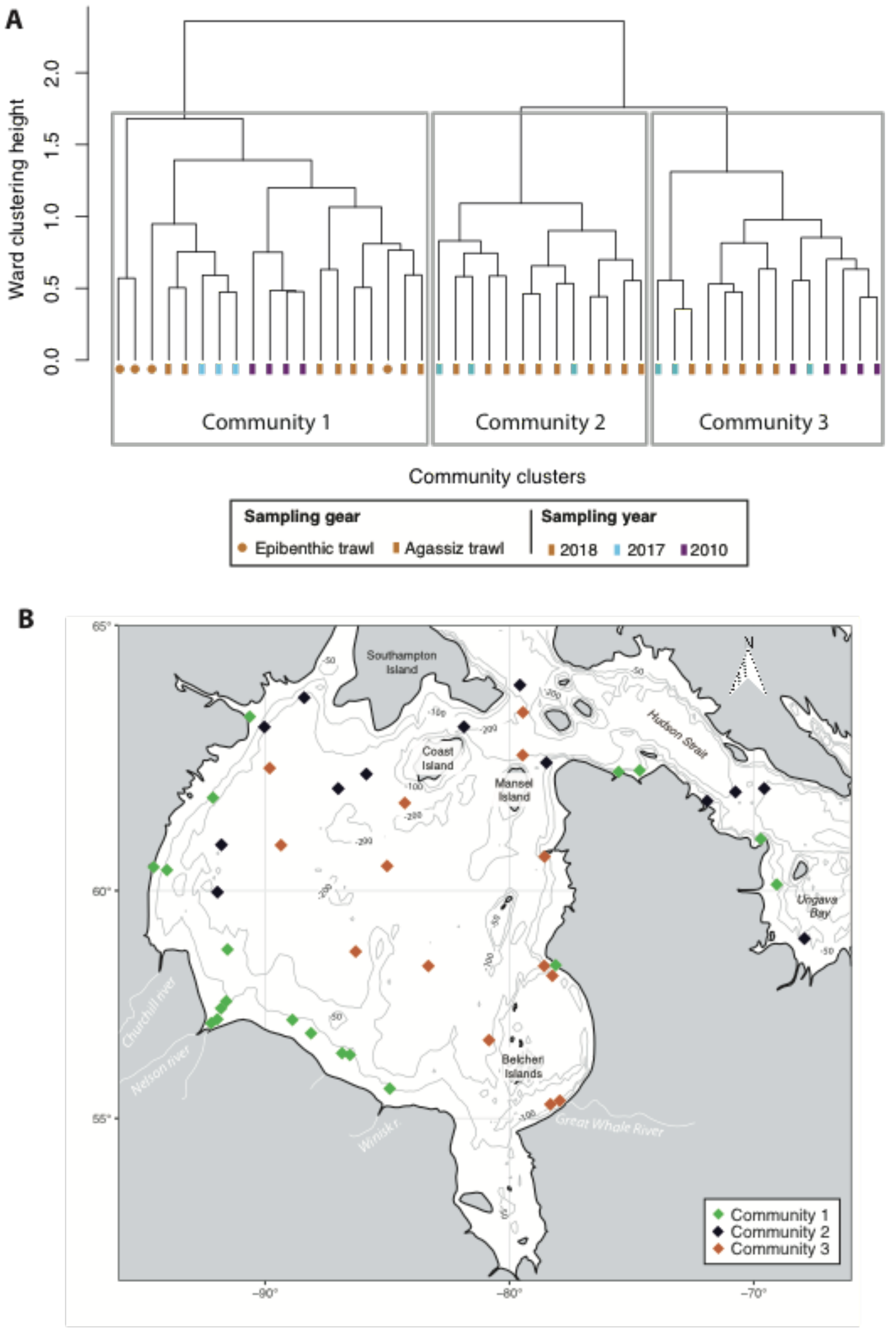

Figure 1. 4. Epibenthic communities in the Hudson Bay System. (A) Cluster tree (Ward distance), based on Bray-Curtis dissimilarity matrix using fourth root transformed species biomass data, showing determination of three epibenthic communities with color-coding for sampling gear and sampling year; and (B) sampling locations color-coded for each of the three communities.

Across all of the communities, Echinodermata was dominant with different proportions of Echinoidea, Ophiuroidea and other Echinodermata (Figure 1.5). A higher proportion of Echinoidea, predominantly sea urchins (e.g., *Strongylocentrotus* sp.), was observed in Community 1 (23%), whereas Ophiuroidea presented the opposite pattern to Echinoidea with a higher proportion in Community 3 (63%). Community 2 presented an intermediate value of Ophiuroidea and similar proportions of Echinoidea and other Echinodermata (34%, 13% and 12%, respectively). Arthropoda decreased from Community 1 to Community 3 (19% and 6%, respectively). Mollusca presented a higher proportion in Communities 1 and 3 (22% and 15%, respectively) than in Community 2 (2%). The latter community presented a higher proportion of Porifera (23%). Other taxa, including tunicates (e.g., Ascidiacea), soft corals (e.g., Nephtheidae) and sea anemones (e.g., Actiniaria), were present in notable quantities in Communities 1 (12%), 2 (4%) and 3 (4%). The proportion of Annelida was low across all communities, which reflects reflecting the nature of sampling by trawl. Thirteen taxa were responsible for the differences among the communities, indicating that a particular set of taxa and their respective biomass are discriminant of community dissimilarity (SIMPER analysis, Table S1.3).

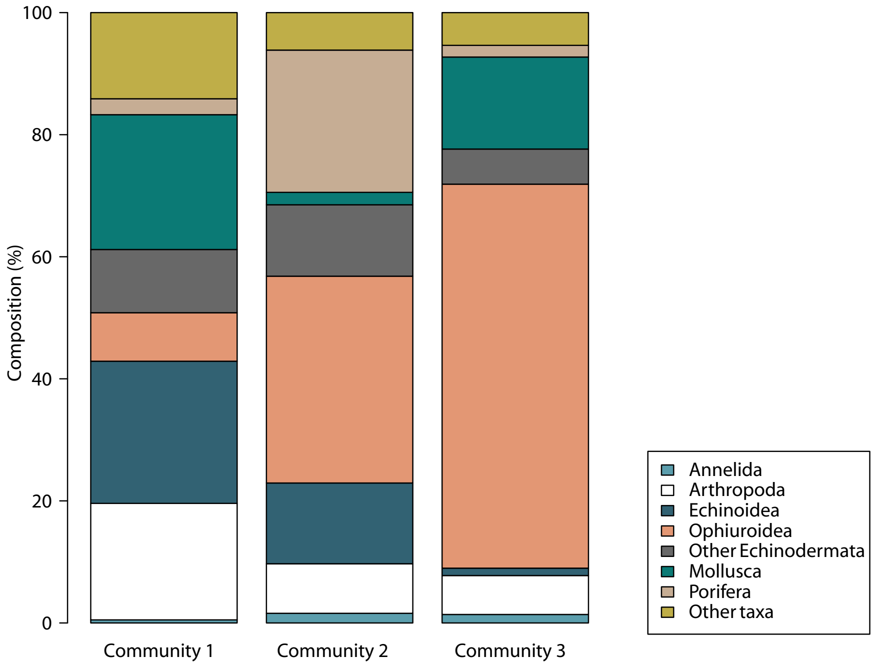

Figure 1. 5. Mean biomass composition (%) for the main phyla or classes in the three community clusters.

- Characteristics of epibenthic community identified

The highest α diversity was observed in Community 2 (28.2 ± 3.3 taxa, n = 11) whereas the lowest value was found in Community 1 (20.5 ± 1.9 taxa, n = 9). The highest value of turnover (β) diversity was found in Community 1 (4.87) compared to the others (3.84 and 4.26 for Communities 2 and 3, respectively). Community 1 was also characterized by a low density and an intermediate biomass (3.07 ± 1.52 ind m^{-2} and 6.81 ± 2.58 g m^{-2}; n = 9). Community 2 had the highest biomass and intermediate density (7.42 ± 1.66 g m^{-2} and 5.29 ± 6.61 ind m^{-2}; n = 11), whereas Community 3 showed the highest density and the lowest biomass (6.65 ± 1.48 ind m^{-2} and 4.22 ± 0.89 g m^{-2}; n = 12).

- Relationships between community composition and the environment

For all data, the first two axes generated by CCA explained approximately 43% of the taxa biomass-environment relationship, with the first axis explaining the highest variation of 26% (Table 1.3). The variables coarse substrate, bottom dissolved oxygen, bottom temperature, POC content and the duration of open water correlated positively with the first axis. Mud substrate, depth and mean primary production were inversely correlated with these factors and with the first axis (Table 1.3; Figure 1.6A). The mixed substrate was located along the second axis (Table 1.3; Figure 1.6A). Among the environmental variables considered, only substrate type, salinity and mean primary production were significantly correlated to the communities (p-value < 0.01; Table 1.3).

Table 1. 3. Results of canonical correspondence analysis using epibenthic biomass and environmental variables.

Results of CCA	**Axis 1**	**Axis 2**	***p*-value**[a]
Eigenvalues	0.66	0.44	***
Variation explained (%)	25.8	17.3	**
Linear coefficients by environmental variable			
Depth	–0.65	0.19	NS
Temperature	0.21	0.03	NS
Salinity	0.002	–0.15	**
Oxygen	0.84	0.04	*
POC content	0.18	–0.07	NS
Mean primary production	–0.57	–0.21	**
Open water	0.58	0.01	*
Coarse sediment	0.93	–0.39	***
Mixed sediment	–0.32	0.79	***
Mud sediment	–0.66	–0.54	***

[a] From permutation ANOVA tests (9999 permutations), where NS indicates not significant ($p > 0.05$); *, $p = 0.05$; **, $p = 0.01$; and ***, $p < 0.01$.

The arrangement of the samples on the CCA biplot showed three primary aggregates driven by the substrate type (Figure 1.6). Stations hosting Community 1 were associated with shallower waters with high values of bottom dissolved oxygen, longer duration of open water and coarse substrate. These stations were more associated to deposit feeders (e.g., Strongylocentrotidae), filter-feeder bivalves and barnacles (e.g., Pectinidae, Balanidae) and opportunist-predator decapods (e.g., Thoridae and Oregoniidae; Figure 1.6B). Stations hosting Community 2 were spread along the second axis indicating a high variability of the environmental variables. These stations were found at different depths and temperatures with mixed substrate (Figure 1.6A). Mixed substrate was linked to filter-feeder sponges, basket stars (e.g., Porifera and Gorgonocephalidae) and soft corals (e.g., Nephtheidae; Figure 1.6B). Conversely, Community 3 was strongly correlated with high values of mean primary production, low dissolved oxygen, longer duration of ice cover and deeper waters with mud substrate (Figure 1.6A). This community was associated with deposit- and filter-suspension feeder bivalves (e.g., Yoldiidae and Astartidae, respectively) and opportunist-predator brittle stars (e.g., Ophiuridae; Figure 1.6B).

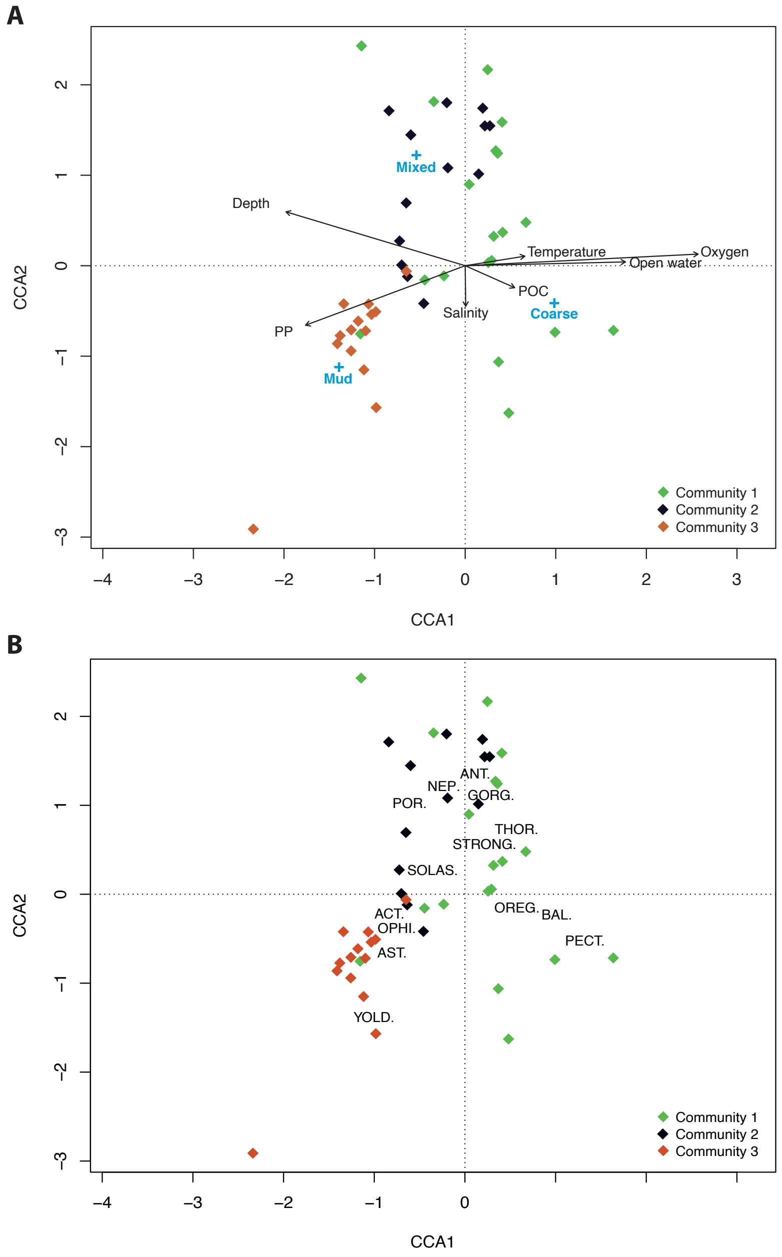

Figure 1. 6. Canonical correspondence analysis (CCA) ordination biplots of epibenthic composition based on biomass. (A) Ordination biplot with environmental variables, where quantitative variables are illustrated by arrows and qualitative variables (type of substrate: coarse, mixed, and mud) by blue cross symbols; and (B) ordination biplot with principal taxa (diamond symbols) from SIMPER analysis: Yoldiidae (YOLD), Asteridae (AST), Ophiuridae (OPHI), Actiniaria (ACT), Solasteridae (SOLAS), Porifera (POR), Nephtheidae (NEP), Gorgonocephalidae (GORG), Strongylocentrotidae (STRONG), Thoridae (THOR), Oregonidae (OREG), Balanidae (BAL), and Pectinidae (PECT). Diamond symbols in both plots are color-coded by community (see Figure 4).

1.6. Discussion

Based on bottom trawl bycatch surveys in the HBS, Jørgensen et al. (2016) estimated a benthic megafauna species richness ranging from 3 to 59 species per station. In our study, the macro-megabenthic taxa richness ranged from 5 to 71 taxa per station. Despite a difference in the gear used to sample river mouths, our results showed no influence of the different types of sampling gear. Moreover, our work increases the observed richness of the macro-megabenthic taxa of the study area (i.e., Hudson Bay, Hudson Strait and Ungava Bay) to 380, which is 71% of the taxa expected in the study area, indicating that about one-third of the expected species pool is still unrecorded. Unlike previous studies, which have concluded that the Hudson Bay was a less productive ecosystem than other Arctic regions, our results demonstrate that present values of epibenthic characteristics (i.e., biomass, density and taxonomic richness) are comparable to other Arctic regions (Grebmeier et al., 2006a; Piepenburg et al., 2011; Roy et al., 2015).

1.6.1. Epibenthic characteristics of the study area

Food supply, salinity gradients and freshwater discharge are generally considered to be significant environmental drivers for both pelagic and benthic organisms (Remane and Schlieper, 1971; Mayer and Piepenburg, 1996; Piepenburg, 2005; Cusson et al., 2007; Palmer et al., 2011). Univariate characteristics related to biodiversity (density, taxonomic richness, biomass and Shannon Index) highlighted differences among the 46 stations sampled across the study area. As shown by the PCA analysis, epibenthic biomass, density and taxonomic richness were driven by the first environmental principal component (PC1), which reflected the following environmental variables: salinity, POC content, depth, dissolved oxygen and mean annual primary production. Salinity and POC content contributed the most to PC1 and can be considered the main drivers of these benthic community characteristics. Thus, an increase of biomass, density and taxonomic richness was linked to an increase in bottom salinity and mean annual primary production as well as a decrease in the POC content.

Previously, Pearson and Rosenberg (1978) found that enrichment of organic material (e.g., POC content) generally reduced the number of species and increased both biomass and abundance. Our study showed that high POC content, which we attribute to strong terrestrial contributions, decreased the number of taxa, as well as biomass and density. Stations located in the Nelson River Estuary and along the south coast of Hudson Bay showed the highest POC content and the lowest values of benthic community characteristics. This area is known to be strongly influenced by river discharge (Prisenberg, 1986; Granskog et al., 2007), which causes a reduction in salinity (to values that range from 28.92 to 32.38) and promotes the deposition of fine riverine particles (Duboc et al., 2017), which alters substrate composition and thus can impact benthic structure significantly (Harrison et al., 2007).

Moreover, the relationships between salinity and primary productivity and benthic biodiversity have already been observed in the Estuary and Gulf of the St. Lawrence River and in the Arctic, especially in the Beaufort Sea (Witman et al., 2008). A drop in salinity is assumed to be responsible for the reduction in benthic richness observed in the Nelson River Estuary and along the south coast of Hudson Bay. Similarly, stations located in eastern Hudson Bay showed mainly low values of benthic characteristics. Despite the occurrence of polynyas in the area, increased freshwater runoff and a longer ice season (i.e., late breakup; Kirillov et al., 2020) limit food supply in the area (Granskog et al., 2007; Lapoussière et al., 2009; Ferland et al., 2011; Sibert et al., 2011). Highly biologically productive areas, such as polynyas, generally promote benthic systems in terms of taxa richness, biomass and secondary production (Ambrose and Renaud, 1995; Link et al., 2011). Despite relatively lower POC content compared to the other geographical areas, stations located near polynyas showed higher diversity, biomass and density (Figures 1.2 and 1.3), hence reflecting strong pelagic-benthic coupling in these areas (Lapoussière et al., 2009; Hochheim et al., 2010).

Central Hudson Bay is deeper and less productive than both western and eastern Hudson Bay due to, among other factors, local hydrodynamics (e.g., strong haline stratification in summer) and a longer ice season (Ferland et al., 2011; Kenchington et al., 2011; Sibert et al., 2011). In central HB, stations were associated with lower values of biomass, density and taxonomic richness. Previous studies have shown that Hudson Strait was more productive than Hudson Bay during summer and fall (Lapoussière et al., 2009; Ferland et al., 2011). However, our results suggest that Hudson Bay could be as productive as Hudson Strait in spring because of higher stratification in Hudson Strait confining phytoplankton to the euphotic zone and thus limiting carbon export towards benthic organisms (L Matthes, personal communication). Despite a limited number of stations sampled in Hudson Strait, we observed diversity and biomass similar to Hudson Bay. Remarkably, stations located in Ungava Bay showed low values of epibenthic characteristics that were similar to those observed near the Nelson River Estuary and southern part of Hudson Bay. This pattern could be because Ungava Bay is subject to a higher stratification due to large freshwater inputs and intense tidal mixing (up to 17 m) that ultimately reduce food supply by flushing out local production (Markham, 1986; Drinkwater and Jones, 1987).

Our results highlight that epibenthic characteristics are spatially segregated by salinity and food supply (i.e., surface-water POC content and mean annual primary production). Thus, we have shown that epibenthic biomass, density and diversity increase further off the coast as salinity increases and POC content decreases, until the waters become too deep and these epibenthic variables decline again in central Hudson Bay.

1.6.2. Relationships between community composition and the environment

Salinity, food supply, depth, temperature and substrate type are known as critical environmental factors that explain the distribution and composition of benthic macrofauna (Mayer and Piepenburg, 1996; Cusson et al., 2007; Bluhm et al., 2009; Palmer et al., 2011; Roy et al., 2014). Data on substrate type are relatively scarce, rather dated and at low spatial resolution in the Hudson Bay System (e.g., Pelletier, 1986; Henderson, 1989; Misiuk et al. 2020). Despite the difficulty in obtaining recent information on substrate type in the study area, the CCA revealed noticeable changes in diversity and composition of benthic macro-megafauna along an environmental gradient mostly driven by the substrate type, thus also reflecting different feeding types. Epibenthic community structure was divided into three communities based on the substrate (coarse to soft) that characterizes their habitat. Soft substrate mainly characterized the deeper and more productive stations of the study area and the middle of the Bay with low POC content, whereas coarse substrate mainly characterized the shallower and oxygenated stations along the coasts with high POC content.

- **Coarse substrate community**

Community 1 was associated with coarse substrate and dominated by deposit feeders such as echinoderms (e.g., Echinoidea and Strongylocentrotidae) and filter feeders such as bivalves (e.g., Pectinoidae), arthropods (e.g., Balanidae) and ascidians (Ascidiacea). Generally, coarse substrate occurs in areas with strong currents that re-suspend sediments and therefore provide food for filter and suspension feeders (Bluhm et al., 2009). This type of benthic community (Community 1), typically attached to rocks and cobbles, was found in coastal areas where river discharge maintained high POC content and high dissolved oxygen, along with strong currents and a longer open water season. Moreover, this community had the lowest density and α diversity values, but the highest value for β diversity. Turnover diversity (β) provides an indication of species replacement and, indirectly, of habitat diversity (Whittaker, 1960; Cusson et al., 2007). A high β value indicates a large difference in community composition among the stations in this community. We attribute this difference to the environmental heterogeneity found in this coastal community. These coastal stations encompass a wide range of depths (from 10 to 127 m), salinity (from 24.4 to 33), dissolved oxygen (from 298 to 369 μM) and POC content (from 171 to 774 mg m^{-3}), reflecting the specific characteristics of each river in the HBS. The strong influence of rivers causes salinity to vary between stations, leading to low values of α diversity (24.2 ± 2.4 species, n = 9) and density (3.07 ± 1.52 ind m^{-2}, n = 9).

- **Soft substrate community**

Community 3 was associated with soft substrate (i.e., clay and mud) and dominated by deposit and suspension feeders such as bivalves (e.g., Yoldiidae, Astartidae and Arcidae), deposit feeders such as holothurians (e.g., Myriotrochus rinkii and Eupyrgus scaber) and brittle stars (e.g., Ophiuridae). Ophiuroids are common in Arctic shelf and slope habitats compared to coastal habitats (Piepenburg, 2000, 2005; Piepenburg et al., 2011). Not surprisingly, brittle stars dominated deeper communities in this study. Moreover, stations characterized by Community 3 were strongly influenced by mean primary production and presented high epifaunal density. However, the prolonged ice cover observed in this area indicates a dominant sympagic system and delayed pelagic primary production (Sibert et al., 2011), suggesting a pulsed food supply. Holothurians are known to exploit fresh phytodetrital pulses on soft sediment (Bluhm et al., 2009; Boetius et al., 2013; Kirillov et al., 2020). Their presence and the presence of deposit and suspension feeders as well as the low biomass observed (4.22 ± 0.89 g m–2, n = 12) are consistent with a discontinuous food supply in this area. Furthermore, this community was found on average in deeper waters than the coarse substrate community (i.e., Community 1) and presented a high α diversity. As the number of taxa generally increases at depths between 0 and 1000 m (Levin et al., 2001), the difference in mean depth between Communities 1 and 3 (58 ± 8 m, n = 9, and 160 ± 16 m, n = 12, respectively) could explain the difference in α diversity.

- **Mixed substrate community**

Community 2 was associated with mixed substrate (i.e., particles ranging from coarse to soft sediment) and combined taxa from the other two communities without exhibiting a specific dominant group or class. For example, filters and suspension feeders, such as sponges and soft corals (i.e., Porifera and Nephtheidae), have been associated with poorly sorted sediment (coarse to soft substratum; Hogg et al., 2010). As a consequence, substrate heterogeneity that includes pebbles, cobbles and/or boulders likely explains why sponges and soft corals were more present in Community 2 than the other communities. Deposit feeders, however, such as Echinoidea (i.e., Strongylocentrotidae) and Ophiuroidea (e.g., Ophiuridae and Gorgonocephalidae), presented intermediate values of biomass. Moreover, stations supporting these communities were mostly located in deep waters (163 ± 23 m, n = 11) and near recurrent polynyas, such as the large polynya in northwestern Hudson Bay (Barber and Massom, 2007; Landy et al., 2017). These areas are generally characterized by high food supply and strong pelagic-benthic coupling (Kenchington et al., 2011). Unfortunately, due to the substrate type and sampling method, quantifying sediment pigment concentrations in this study was not possible. Nevertheless, this community showed high α diversity, density and biomass, highlighting niche diversification (coarse to soft substratum) and an important food supply to this benthic community.

1.7. Conclusion

This study presents results from the most recent survey of epibenthic organisms in part of the Hudson Bay System. We identified 380 epibenthic taxa, representing 71% of the total taxa that are estimated to be present within the study area (i.e., Hudson Bay, Hudson Strait, Ungava Bay). The overall analysis of epibenthic characteristics showed that bottom salinity and surface-water POC content were the main environmental drivers. We showed that coastal waters, directly influenced by rivers, harbored the lowest epibenthic density, biomass and taxonomic richness. These low values were located in shallower depths with low salinity and high POC content. In accordance with previous studies, we also showed that central Hudson Bay was less productive than the other regions of Hudson Bay given the low values of epibenthic characteristics. In contrast, polynya areas, where high primary production occurs, were associated with abundant and diverse epibenthic communities. Additionally, while Hudson Bay was historically thought to be less productive than Hudson Strait, we showed that some areas of Hudson Bay can be as productive as Hudson Strait (i.e., high density, biomass and taxonomic richness). Further benthic sampling between these two regions would be necessary to confirm this result conclusively.

Based on biomass data, three epibenthic community clusters have been identified and broadly related to the substrate type reflecting food supply proxies (i.e., mean annual primary production and surface-water POC content). More specifically, coarse substrate along the coastlines hosted a higher biomass of filter and suspension feeders, whereas soft substrate in deeper water was mostly associated with deposit and suspension feeders. We showed that the low density and taxonomic richness occurring in the coarse substrate community could be attributed to high POC content and freshwater discharge from rivers. In contrast, the soft substrate community likely received a pulsed food supply because of the longer duration of ice cover and dominant sympagic system. The mixed substrate type did not show dominant taxa or classes and was characterized by large and diverse epibenthic organisms. This last community showed the highest biomass and diversity, which was attributed to a high food supply and strong pelagic-benthic coupling near polynyas.

Benthic organisms respond to natural and anthropogenic changes occurring in their environment, leading to changes in their distribution. Given our results, high POC content of overlying surface water and low salinity bottom water lead to a decrease of biodiversity and change in epibenthic community composition in the study area. Projections towards a longer open water season and increased river discharge as a result of climate change may have a major impact on these epibenthic communities due, in particular, to increases in open-water primary production, freshwater inflow, and inputs of terrestrial organic matter from permafrost thaw and forest growth upstream of the HBS.

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Data accessibility statement

All data are accessible at the Polar Data Catalogue (https://www.polardata.ca/pdcinput/) and will be made public prior to publication.

Chapitre 2 - Modelling benthic communities in the Hudson Bay under current and future environmental conditions

2.1. Résumé

En réponse à l'augmentation de la température causée par le changement climatique, la Baie d'Hudson est sujette à une diminution de son couvert de glace et de sa salinité. À partir d'une modélisation hiérarchique des communautés d'espèces appliquée à 115 familles d'invertébrés benthiques, la diversité a été prédite à l'échelle de la Baie d'Hudson sous des conditions environnementales actuelles et futures. Nos prédictions ont mis en évidence des points chauds de diversité dans la polynie de Roes Welcome Sound, l'est de l'île Southampton, le cap Churchill, l'estuaire de la rivière Nelson et enfin dans le centre de la Baie d'Hudson. Nos projections prévoient également un déclin de diversité dans le centre de la Baie tandis que les côtes semblent constituer de nouveaux points chauds de diversité. Le modèle utilisé dans cette étude pourrait représenter un nouvel outil dans la prise de décisions de gestion et de surveillance des communautés benthiques.

2.2. Abstract

Hudson Bay Complex is prone to sea ice cover and salinity variations due to the consequences of climate change and freshwater discharge from many rivers. These variations can control species richness and thus could have consequences on benthic communities. In this study, we projected taxa richness under current environmental conditions and future climate change scenarios for a set of 115 families in the Hudson Bay. Epibenthic taxa richness was performed at the community-level, using Hierarchical Modelling Species Communities based on occurrence and environmental parameters. Results showed taxa richness was higher in the Roes Welcome Sound Polynya, East of Southampton Island, Cape Churchill, Nelson River Estuary and finally in the Central Hudson Bay that under current environmental conditions. Our results predicted a high decline of taxa richness in the Central

Hudson Bay under a future climate change scenario, where a sharp sea ice shrinking will occur. On the contrary, our study predicted coastal areas as new hotspots of taxa richness despite a rise in bottom temperature and a decrease in bottom salinity. Coastal taxa in the Hudson Bay are exposed to high salinity and temperature variation linked with river runoff during the year. Hence, these taxa would be adapted to a wide range of temperature and salinity. This model could help in current and future management and monitoring decisions and, finally, could be considered as a first approximation of the potential impact of climate change on epibenthic communities in the Hudson Bay.

2.3. Introduction

Knowledge of benthic species distributions is an essential step in assessing ecosystem functioning and establishing management and monitoring planning. In regions with limited access and sparse data, modelling constitute an alternative to gather a deeper understanding and to predict species distributions (Elith and Leathwick, 2009). Species distribution models (SDMs), which predict the distribution of species by linking their occurrence to environmental predictors, are widely used across freshwater, terrestrial and marine ecosystems (Elith and Leathwick, 2009; Reiss et al., 2011; Guijarro et al., 2016; Goldsmit et al., 2017, 2020). Over the last decade, joint species distribution models (JSDMs), an extension of SDMs, have generated a growing interest in the field of community ecology (Latimer et al., 2009; Ovaskainen et al., 2016, 2017). JSDMs estimate distributions of multiple species simultaneously (*i.e.*, community level) by assuming that the species respond jointly to the environment and each other in space (Ovaskainen and Soininen, 2011; Clark et al., 2014; Ovaskainen et al., 2017). JSDMs are very efficient in predicting changes in species distribution in response to environmental conditions (Norberg et al., 2019). As such, these tools are helpful for management, monitoring and conservation scenarios by identifying ecologically and biologically significant areas (EBSAs; Dunn et al., 2014). Identification of areas of interest is based on seven site criteria: uniqueness or rarity; special importance for life history of species; importance for threatened, endangered or declining species and/or habitats; vulnerability, fragility, sensitivity, slow recovery; biological productivity; biological diversity and naturalness (Dunn et al., 2014).

In the Hudson Bay Complex (HBC; *i.e.*, Hudson Bay, Hudson Strait, Ungava Bay, Foxe Basin and James Bay), some regions have been designated as EBSAs concerning benthic production based on physical oceanographic properties (*e.g.*, polynya), megabenthic (*e.g.*, density of corals and sponge beds in Hudson Strait) and endobenthic diversities (Kenchington et al., 2011). However, too few surveys have been carried out in the HBC despite predictions of a large future shift in sea ice cover and freshwater input projected from climate change impacts (Gagnon and Gough, 2005; Tivy et al., 2011; Derksen et al., 2019). As a result of climate change, the seasonal sea ice is subject to an earlier melt and a later sea ice freeze-up (*i.e.*, shorter sea-ice season), and potentially drive shifts in the timing and the extent of primary production (Onarheim et al., 2018; Niemi et al., 2019). The HB complex includes some of the largest Canadian rivers by annual discharge to the coastal ocean (*e.g.*, La Grande Rivière and Nelson and Churchill rivers) and receives around 900 km^3 of freshwater per year (Déry et al., 2011, 2016, 2018). Large deviations in river discharge levels have occurred in recent decades, reflecting precipitations anomalies and strong seasonality in river runoff due to hydroelectric dams regulation (Shein, 2006; Déry et al., 2011, 2016). These deviations are expected to strengthen by 2090 with a rise of river discharge leading to a salinity decrease in coastal regions into the HB Complex (Bring et al., 2017).

Seasonal sea ice and riverine freshwater supply are known to influence biological processes and components spatially (*e.g.,* primary production, chlorophyll *a* biomass and particulate organic material) (Granskog et al., 2007; Lapoussière et al., 2009; Ferland et al., 2011; Sibert et al., 2011). Changes in sea ice cover and salinity gradients impact the efficiency of the pelagic-benthic coupling and benthic species distribution and diversity (*e.g.*, Cusson et al., 2007; Witman et al., 2008; Grebmeier et al., 2010; Grebmeier, 2012; Roy et al., 2014). Historical surveys in the HB Complex were primarily carried out on grab sampling and targeted infaunal community (Atkinson and Wacasey, 1989b, 1989a; Cusson et al., 2007). Since 2005, epibenthic surveys in the Hudson Strait and Ungava Bay have been carried out by annual monitoring of shrimp (*e.g.*, *Pandalus borealis*; Siferd, 2015) by-catch and many samples have been identified at the phylum level. Comparatively, surveys in the Hudson Bay (HB) are quite recent (MERs Intérieures du Canada, ArcticNet (2010), the Hudson Bay System study (BaySys 2017-2018), the Bridging Global Change, Inuit Health and the Transforming Arctic Ocean project (BriGHT 2018), *R/V William Kennedy* expedition 2019) and have provided higher taxonomic resolution (down to species or lowest taxonomic level possible). Despite this sampling effort, we do not know all of the benthic communities in the HB due to sparse point data and presence-absence data for the most benthic species. Therefore, modelling approaches such as JSDMs could provide a better estimate of species distributions and highlight hotspot areas of taxa richness (*i.e.*, high taxa richness). It is within this changing environment that this study aimed at forecasting the epibenthic community (*i.e.*, taxa richness) within the HB under current environmental conditions and projected future environmental conditions. Moreover, this study compared EBSAs, previously designated by Kenchington et al. (2011), and predicted hotspots of taxa richness.

2.4. Methods

2.4.1. Study site

Hudson Bay is a large (~ 840 000 km^2) estuarine system with a mean depth of 150 m. Water masses from the Arctic Ocean enter HB through the Foxe Basin at its northwest part and, a portion joins the cyclonic circulation around the Bay (Saucier et al., 2004). In the northeast, inflow and outflow waters occur through the Hudson Strait (Drinkwater, 1986; Prisenberg, 1986). Hudson Bay receives a large freshwater input from terrestrial rivers representing ~760 km^3 year^{-1} (Macdonald and Kuzyk, 2011) and is characterized by numerous polynyas with the largest located in the northwestern part of Hudson Bay (Barber and Massom, 2007). Smaller polynyas are located close to the Nelson River Estuary, the Belcher Islands, the northern part of HB and along the coast of Quebec (Figure 2.1; Barber and Massom, 2007). Sea ice breakup generally starts in the Eastern and Northwestern parts of the Bay between May and June and progresses towards the southern regions (Andrews et al., 2018). In recent years, freeze-up began in the Northwestern part in November and ended in December in the Eastern part of the Bay (Andrews et al., 2018).

2.4.2. Epibenthic data compilation

Species occurrence data were compiled from five datasets: Cusson et al. (2007), ArcticNet (2010), the Hudson Bay System Study (BaySys, Pierrejean et al. *in press*), the Bridging

Global Change, Inuit Health and the Transforming Arctic Ocean project (BriGHT) and the global database Ocean Biogeographic Information system OBIS (OBIS, 2020). This dataset encompassed 48 stations within the HB (Figure 2.1), with sampling stations depths ranging from 3.2 to 429 m. Samples were collected with epibenthic and shrimp trawls and dredges. Vertebrates (*e.g.*, Actinopterygii), planktonic invertebrates (*e.g.*, Chaetognatha and Euphausiacea) and Annelida were removed from the analyses. Annelids were removed from our analyses due to low representation in epifauna trawl samples, and because most of them are not epibenthic species. Taxa were pooled to the family level and the phylum level (*e.g.*, Nemertea, Nudibranchia, Porifera and Bryozoa) because of identification problems, which would have caused unreliable estimations of species richness (Table S2.1). Taxonomic names from each dataset were validated using World Register of Marine Species (WoRMS Editorial Board, 2018).

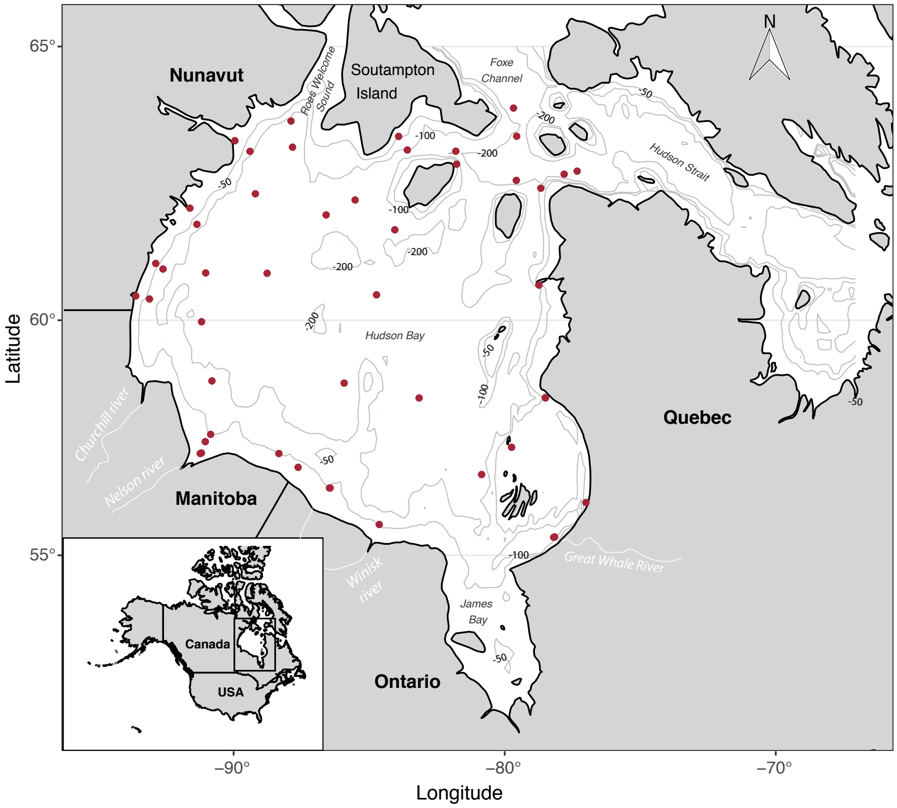

Figure 2. 1. Positions of trawl stations in the Hudson Bay.

2.4.3. Environmental data compilation

Five environmental variables were selected *a priori* according to their importance as drivers for epibenthic species: depth, mean bottom salinity and temperature, substratum type (three levels: coarse, mud ad mixed substrate) and mean ice thickness (Table 2.1). Mean bottom temperature and salinity were obtained from the World Ocean Atlas 2018 compiled at the National Oceanic and Atmospheric Administration's (NOAA) National Oceanographic Data Center (NODC; Locarnini et al., 2019; Zweng et al., 2019). To extract mean values for sampling stations, we built a 0.4 degrees decimal buffer zone using the package "sf" in R under EPSG:4326 projection (Pebesma, 2018). Mean ice thickness (m) was extracted from interpolated environmental data layers generated at the global scale from Bio-ORACLE v2 (Tyberghein et al., 2012). The substratum type at each station was extracted from a raster created from the substratum data presented by Henderson (1989) and Pelletier (1986) in ArcMap V10.2.2. There were three classes of substrate: 'coarse' referred to stations mostly composed of gravel, sandy gravel and cobbles; 'mixed' referred to stations composed of a mix between silt and gravel; and 'mud' referred to stations characterized by fine-grained sediment. We used the "raster" package (Hijmans and van Etten, 2020) in R (R Core Team, 2020) to extract the environmental variables from sampling stations.

Table 2. 1. Variables used to build the community model.

Variables	**Units**	**Range**	**Source**
Mean bottom temperature	°C	-1.72 – 3.46	NODC
Mean bottom salinity	-	29.20 – 33.47	NODC
Depth	m	3.2 – 429	Pierrejean et al., *in press*; Cusson et al., 2007; *R/V William Kennedy* expedition 2019
Substratum type	-	Coarse – Mud – Mixed	Modified from Henderson (1989) and Pelletier (1986)
Mean ice thickness	m	0.29 – 0.51	Bio-ORACLE v2

2.4.4. Hierarchical Modelling of Species Community

Hierarchical Modelling of Species Community (HMSC) is a general and adaptable framework for fitting JSDMs (Ovaskainen et al., 2017). HMSC was used to model taxa richness in the Hudson Bay because of its efficiency to make prediction f communities evolution in response to environmental changes (Norberg et al., 2019). The HMSC approach was used to determine the distribution of taxa presence-absence with scaled environmental variables (*i.e.*, to remove the effects of units) and a community-level random effect that accounted for variation unexplained by the environment to predict community assemblage. By including "site" as a random effect, we partitioned the model's explained variance between fixed and random effects. Specifically, a probit link was used to construct the model. The HMSC approach relies on a Bayesian approach and uses Markov chain Monte Carlo (MCMC) for parameter estimation. Convergence of the MCMC was evaluated using a Geweke convergence diagnostic (Geweke, 1991) for all estimated parameters. The MCMC converged after 135 000 iterations, the first 50 000 of which were discarded (burn-in). Model explanatory power was evaluated using the Tjur (2009) coefficient of determination calculated as follows: $R^2_{Tjur} = mean\left(y\_1^{prediction}\right) - mean(y_0{}^{prediction})$; where $y\_1^{prediction}$ represents observations where there is a predicted presence and $y_0{}^{prediction}$ represents observations where there is a predicted absence. Variance partitioning was investigated to describe which components of the model accounted for the explained variance. We performed these analyses using the "HMSC" version 0.22 (Blanchet et al., 2019) in R (R Core Team, 2020) and environmental layers downloaded from Bio-ORACLE v2 with a spatial resolution of 5 arcmin. These layers were produced with monthly averages of climate data for the period from 1998 to 2014. Taxa richness was obtained by summing the predicted probabilities of each taxa, output of the HMSC model, across all estimated grid cell of the entire prediction area to construct the prediction map.

2.4.5. Projection modelling under climate change scenario

Taxa richness was predicted using future projected environmental layers used to build the model under current conditions. Maximum bottom temperature, minimum bottom salinity and sea ice thickness were available for projected future scenarios at 5 arcmin resolution (Table S2.2). Future environmental layers were obtained from Bio-ORACLE v2 for RCP4.5 emission scenario for 2100 (see Assis et al., 2017 for more information). In this study, the RCP4.5 scenario was chosen since it represents an intermediate greenhouse emission (temperature anomaly of 2.4 °C by 2100) and a stabilization scenario of CO_2 concentration

(Clarke et al., 2007; Moss et al., 2010). Depth and substrate types were assumed to remain constant over time. Difference in taxa richness was obtained by the subtraction between projected taxa richness and predicted taxa richness. Taxa richness changes between the present and future climate scenarios were analyzed spatially to identify regions with loss, gain or no change over time.

2.5. Results

2.5.1. Model convergence

The Z-scores resulting from Geweke diagnostics showed that only a few values exceeded 2 standard deviations (Figure S2.1). After investigation, we found that these extreme values did not affect the convergence of the MCMC chains to the posterior distribution (Figure S2.2).

2.5.2. Hierarchical Modelling of Species Community

In total, the distribution of 115 epibenthic taxa were modelled for the Hudson Bay. The community-level Tjur R^2 was 0.17 for the analysis. At the taxa-level, Tjur R^2 varied between 0.01 and 0.61 with a minimum value for the family Dendronotidae and a maximum value for the bivalves Yoldiidae (Figure 2.2). A variance partitioning among effects revealed that substrate type, site location and salinity explained, across all taxa, on average, ~47, 14 and 12%, respectively, of the community composition's total variation data. More specifically, taxa differed substantially in their responses (Figure 2.2). The substrate type appeared to be a relevant environmental parameter for ophiuroids (e.g., Ophiacanthidae and Ophiuridae) or crinoids (i.e., Antedonidae), while salinity appeared to be another relevant environmental parameter for pycnogonids (i.e., Nymphonidae).

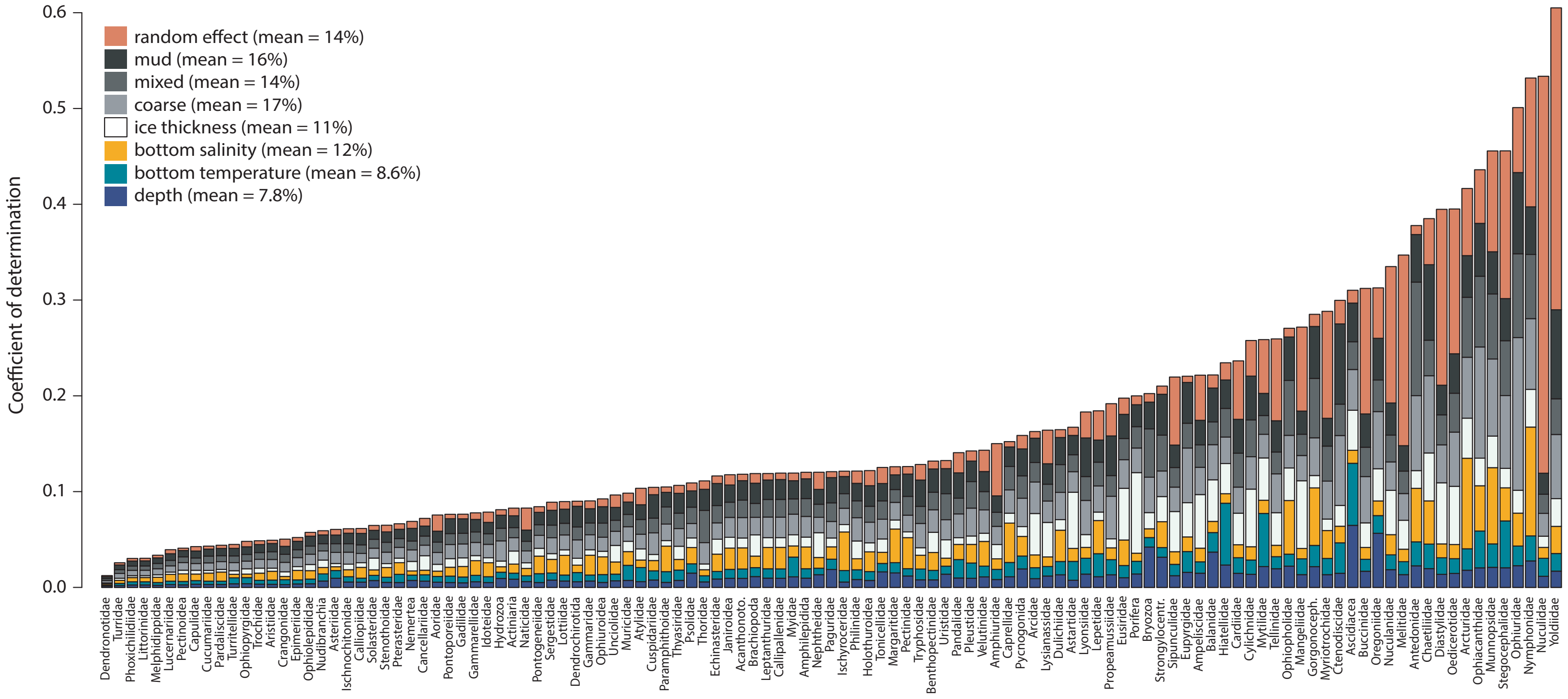

Figure 2. 2. Variance partitioning in epibenthic composition among random and fixed effects in the Hudson Bay. Each bar corresponded to one taxon and is ordered according to the taxa-level coefficient of determination (R^2), in increasing order. The legend shows mean values over the epibenthic community composition, multiplied by the proportion of explained variance.

Figure 2.3 showed taxa richness under current environmental conditions as predicted by HMSC. The map highlighted the areas of epibenthic taxa richness hotspots and coldspots within the Hudson Bay. Along the coasts, predicted taxa richness showed the lowest values ranging from 4.98 to 15 taxa. The western half of the central Bay and the northern part of the study area around Southampton and Coats islands exhibited high taxa number values, ranging from ~20 to 33 taxa. This increase also occurred in the offshore areas in the south, near Churchill and Nelson areas, and towards James Bay. One distinct region was highlighted in the middle of the Bay by a taxa richness exceeding 30.

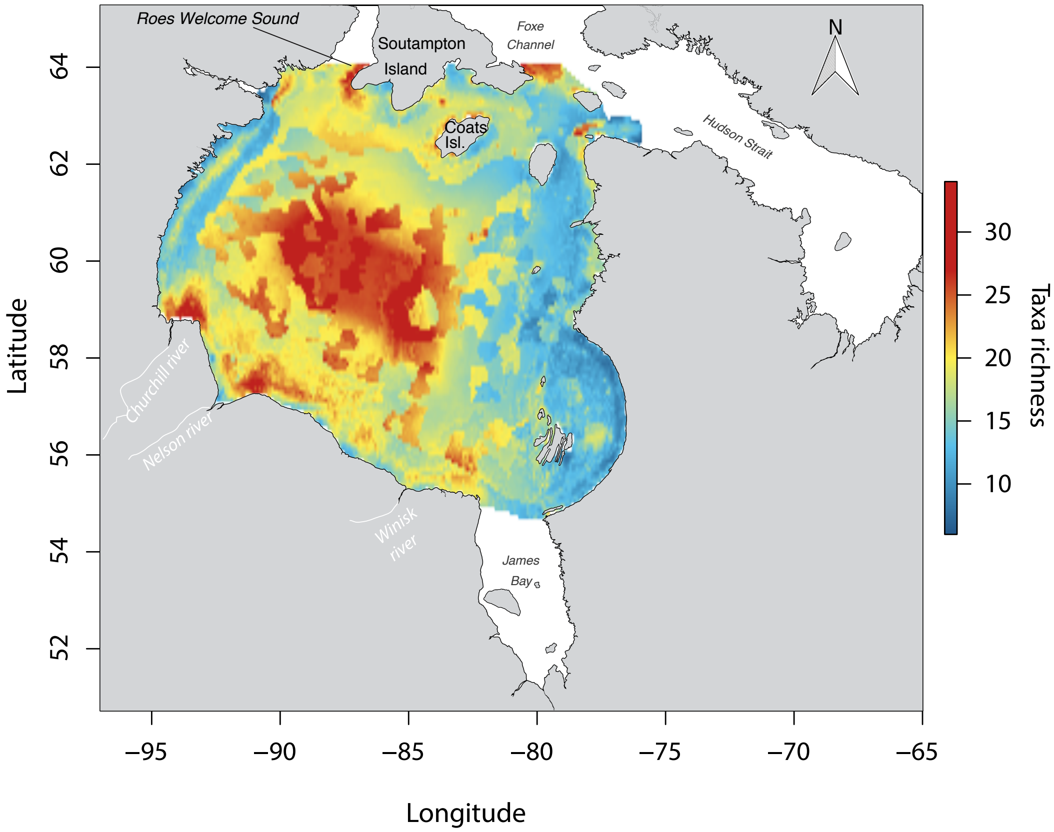

Figure 2. 3. Epibenthic taxa richness predicted for Hudson Bay under current environmental conditions.

2.5.3. Distribution change

Taxa richness was projected from the HMSC under the RCP4.5 scenario (Figure 2.4A). The model predicted high taxa richness along the coast and in the Roes Welcome Sound Polynya. More specifically, the polynya presented taxa richness ranged from 20 to 40. The southern parts, especially in the Nelson River Estuary and Winisk River, presented taxa richness above 40. The eastern and western parts presented taxa richness reached up to 30. On the contrary, the middle of the Bay exhibited taxa richness lower than 20. Figure 2.4B showed the difference in taxa richness between current conditions and under RCP4.5 scenario as predicted by the HMSC. The taxa gain between the present and the future model was highest in the northwestern, the southern and the eastern part with an increase between 5 and 40 taxa. The highest increase of taxa (> 30) was especially predicted in the estuaries of the Nelson and Winisk rivers. On the contrary, the middle of the Bay was characterized by a significant loss in taxa richness (Figure 2.4B).

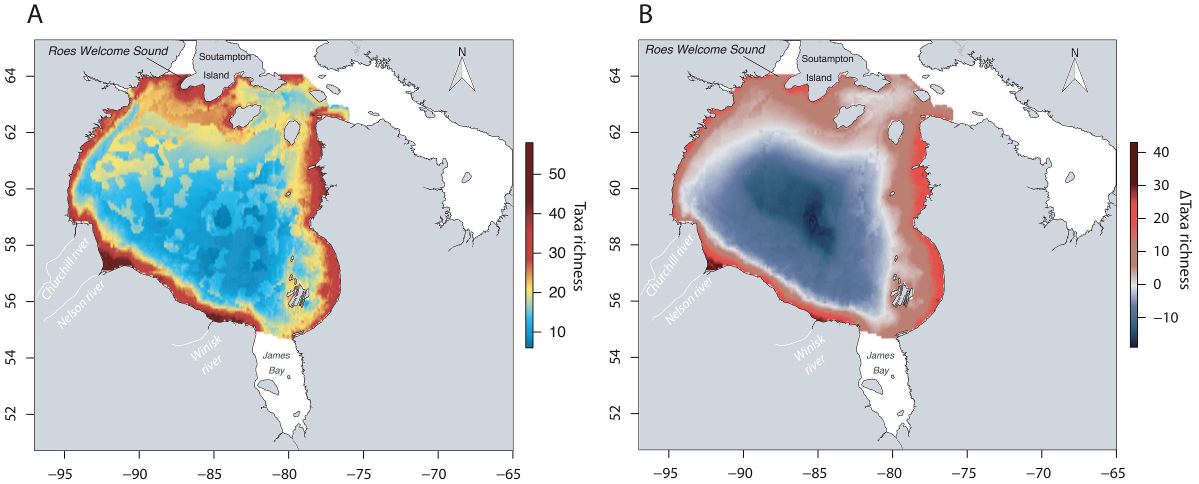

Figure 2. 4. Epibenthic taxa richness projected for the Hudson Bay under RCP4.5 emission scenario: (A) and difference in taxa richness projected in 2100 with current richness predicted.

2.6. Discussion

In the Arctic marine environment, pelagic primary production is tightly coupled to the physico-chemical forcing such as sea ice thickness, temperature and salinity implemented in our model (Witman et al., 2008; Boetius et al., 2013). Benthic communities depend on food supply deriving from sympagic and pelagic primary production, supplemented by macroalgal detritus originating from shallow waters (Wassmann and Reigstad, 2011; Boetius et al., 2013; Gaillard et al., 2017; Filbee-Dexter et al., 2018; Olivier et al., 2020). The latter are strongly influenced by the bathymetry as well as the presence/absence of sea ice, its thickness and its snow cover. However, chlorophyll *a* and primary productivity layers were not implemented in the model due to the lack of available future estimates of these forcing variables in this region and the relatively weak explanatory power of these variables on benthic species distribution (Belanger et al., 2012; Bosch et al., 2018). In contrary, the strong explanatory power of physical variables employed in our model (*e.g.*, sea ice thickness and bathymetry) could come, in part, from their strong functional link to some biological variables (*e.g.*, sea ice thickness and cover define the sympagic productivity and thus chlorophyll *a*). Since some parameters such as invasive species, biotic interactions, sampling of coastal species, turbidity and food supply were not implemented in the present study, results of our model should be treated cautiously. However, to the best of our knowledge, our model was built with the most complete and the best data set of current and projected environmental variables available to predict epibenthic communities in the HB. As such, our model could be seen as a first approximation of the current distribution of the HB epibenthic communities and their response to potential impact of climate change.

2.6.1. Current taxa richness

In spring, sea ice melts rapidly in the HB's western part and moves towards the eastern part, pushed by the dominant winds (Landy et al., 2017; Kirillov et al., 2020). Following the retreating sea ice cover, these open-water areas are generally characterized by a short and intense phytoplankton bloom during spring (Wassmann et al., 2006; Arrigo et al., 2012). These areas, designed as the marginal ice zone, contribute a large food supply to benthic communities in Southampton Island Polynya (Schewe and Soltwedel, 2003). Southampton Island area has been identified as an EBSA (Kenchington et al., 2011) based on the presence of a recurring coastal polynya in the Roes Welcome Sound (Barber and Lukovich, 2011; Hochheim and Barber, 2014), and the confluence of currents from Foxe Channel and the inflow of Hudson Strait (Saucier et al., 2004). However, no benthic data have been considered to designate this area as an EBSA (Kenchington et al., 2011). Predictive mapping showed high epibenthic diversity in these areas reflecting their unique physical parameters. Indeed, because of the the confluence of currents and the marginal ice zone, these areas are predicted to sustain a nutrient-rich upwelling and therefore generate high productivity (Sibert et al., 2011; Tremblay et al., 2019).

Smaller latent heat polynyas also occurred along Cape Churchill, near the Nelson River Estuary and off the west coast of Quebec (Hochheim et al., 2010). Furthermore, Matthes et al. (*in prep.*) pointed out some evidence of an under-ice bloom in the southern central HB that forms beneath the mobile ice cover in spring. These areas have been defined as EBSAs owing their high food supply for the benthos (*i.e.*, sedimentary pigment and organic carbon contents) and on potentially rich benthic communities (Kenchington et al., 2011). Our results corroborated evidence for rich epibenthic communities, except on the west coast of Quebec. This coast is characterized by strong freshwater inflows and accumulation of drifting sea ice (Déry et al., 2005; Granskog et al., 2007; Landy et al., 2017; Kirillov et al., 2020). Salinity gradients and freshwater discharge are important factors controlling primary productivity and benthic species richness (Remane and Schlieper, 1971; Cusson et al., 2007; Witman et al., 2008). As such, freshwater discharge and the thicker sea ice could limit food supply and are assumed to be responsible for the lowest benthic richness observed in the EBSA of the west coast of Quebec (Granskog et al., 2007; Lapoussière et al., 2009; Ferland et al., 2011).

Several studies have reported a low summer primary production in the deeper part of the HB and described it as an oligotrophic area in summer and fall (Ferland et al., 2011). Due to the low export of biomass during summer, spring sea ice production must play a significant role for the benthos in the central HB as previously shown in the Arctic by Yunda-Guarin et al. (2020). Despite the fact that no observations have been made during the ice algae blooming period between March and May, high biomasses of the sub-ice diatom, *Melosira arctica*, have been observed in June in the central HB (Matthes et al., *in prep.*). These sub-ice algae grow in long strands anchored to the ice bottom and are known to substantially contribute to the carbon export to the deepest Arctic seafloor (Boetius et al., 2013; Vedenin et al., 2018). The food supply provided by sea-ice-associated algae, such as *Melosira arctica*, could be an important source for HB's epibenthic communities and could in part explain the high predicted taxa richness observed in this deeper part. Poorly sampled so far, the central HB was not designated as an EBSA by Kenchington et al. (2011). However, our results highlighted the highest taxa richness in this area. Further studies should be undertaken in this area to strenghten the knowledge of benthic communities and their potential role in the ecosystem functioning in order to update the identification of EBSAs.

In coastal waters, macrophytes, including macroalgae and seagrasses grow to a depth receiving about 1% of incident solar radiation (Gattuso et al., 2006). Kelps occur on rocky coasts of the western part of the HB and around the Southampton Island (DFO, 2011; Loewen et al., 2020). Many kelp create habitats for numerous invertebrates and produce large amounts of particulate detritus providing food to these benthic organisms (Filbee-Dexter et al., 2018). The south of Southampton Island and the western part of the HB have been identified as an EBSA based on macrophytes' presence (DFO, 2011; Loewen et al., 2020). In the shallower part of these regions, our model highlighted a high taxa richness which could reflect the presence of these macrophytes.

Our model, based on physico-chemical variables corroborates the EBSAs previously defined by Fisheries and Oceans Canada (DFO, 2011; Kenchington et al., 2011) as hotspots of epibenthic diversity. However, it also highlights the central HB, an area not previously defined as an EBSA, as one of the most important hotspots of epibenthic diversity due to its unique physical properties (bathymetry and ice thickness) reflecting a strong sympagic-benthic coupling.

2.6.2. Changes under climate change scenario

As models suggest, climate change will be most pronounced in the Arctic with warming two to four times faster than the global average (Seneviratne et al., 2018). Arctic ecosystems will experience an increase in sea surface temperature, in freshwater input and a decline in sea ice thickness, extent and duration (Wassmann and Reigstad, 2011; Derksen et al., 2019). Increasing seawater temperature and declining salinity can lead to changes in species distributions, particularly to those close to their tolerance limits. Interestingly, our model projected higher taxa richness along the coast under RCP4.5 scenario. Some taxa observed in the Hudson Bay (Table S2.1), such as Mytilidae (*e.g.*, *Musculus discors*) or Hiatellidae (*e.g.*, *Hiatella arctica*), are also located at lower latitudes (OBIS, 2020). Increases in seawater temperature could benefit coastal epibenthic taxa since these taxa are often adapted to a wide range of temperature (Wesławski et al., 2011). Hence, climate change will favor taxa with broad thermal windows (Pörtner and Farrell, 2008). Moreover, some species have a high tolerance to low salinity levels due to their acclimatization to large variations in river runoff throughout the year (Déry et al., 2018). For example, some pycnogonids, observed in the HB (*e.g.*, *Nymphon brevirostre;* Table S2.1) have been already observed in estuaries where the salinity was below 20 (Arnaud and Bamber, 1988). The bivalve *Portlandia arctica* (Yoldiidae), as well as the echinoderm *Myriotrochus rinkii* (Myriotrochidae) and the isopod *Saduria sibirica* (Chaetiliidae), occur in polyhaline-Arctic water (bottom salinity ranged from 18 to 30) (Kassens et al., 1999). This is consistent with the present study results, where temperature and salinity were relevant environmental parameters on some taxa such as Hiatellidae, Chaetiliidae and Nymphonidae, respectively. Thus, climate change might induce a higher probability of occurrence of these tolerant species in shallower regions.

Increasing seawater temperature will also lead to an earlier melt in spring and a later freeze-up in fall increasing the duration and extend of open-water areas. Reduced ice extent and thickness should result in a shorter bloom period for sympagic production at the benefit of the pelagic production (Arrigo et al., 2008; Pabi et al., 2008). While sea ice algae currently dominate primary production in the central HB (Matthes et al., *in prep.*), a decrease can be expected in the export of high quality organic matter to the seafloor in the future, due to the gradual decrease in ice thickness. Under RCP 4.5 scenario, our model highlighted the reduction of ice thickness associated with a predicted loss of taxa richness in the central HB.

In coastal waters (*i.e.*, shallower waters), the reduced sea ice thickness will also increase the solar radiation with a potential extension of macrophytes (Krause-Jensen and Duarte, 2014; Khan et al., 2018). Several studies highlighted the link between poleward range extension and increasing temperature (Krause-Jensen and Duarte, 2014; Khan et al., 2018; Filbee-Dexter et al., 2019). Thus, the temperature increase in our model might reflect a potential extension of macrophytes, which might lead to an increase in diversity along the coast, as previously suggested by Kortsch et al. (2012). Nevertheless, a decrease of salinity can negatively impact the recruitment of macrophytes (*e.g.*, kelp) which might counterbalance the positive effect of higher temperatures and more extended ice-free periods (Filbee-Dexter et al., 2019). However, despite predicting an average decrease in salinity from approximately 0.5 (Assis et al., 2017), our model highlighted a hotspot of benthic diversity in shallower waters.

2.7. Conclusion

Based on physico-chemical variables, our model provided a first approximation of the epibenthic communities' distribution across the HB. Our study has highlighted epibenthic diversity hotspot corresponding to EBSAs previously defined by Kenchington et al. (2011) as well as another epibenthic diversity hotspots in the central HB. This latter is likely the result of the large pelago-benthic coupling prevailing in this region and which mainly comes from the sea ice primary production. Furthermore, projections allowed identifying this area as the most vulnerable in terms of taxa richness. Indeed, the projected high loss of taxa in the central HB is likely linked to a decrease in sea ice thickness, resulting decrease in the quality and quantity of the food supply. On the contrary, coastal areas, previously defined as EBSAs by Kenchington et al. (2011), appear to gain taxa despite increasing temperature and decreasing salinity. It was attributed to the large plasticity of organisms inhabiting coasts and to the potential extension of macrophytes in shallower waters. However, our study should be treated with caution due to the lack of data on biotic interactions, resource availability, sampling of coastal species, invasive species in our study area. Given our results, our study may represent a new management tool in decision-making and conservation of HB ecosystems. In addition, it seems relevant to further studies on the distribution of epibenthic communities in the HB and particularly in the central part to update the knowledge of benthic communities and their potential role in the ecosystem functioning in order to update the identification of EBSAs.

Chapitre 3 - Influence of deep-water corals and sponge gardens on infaunal community composition and ecosystem functioning in the Eastern Canadian Arctic

3.1. Résumé

La reminéralisation de la matière organique dans les sédiments est considérée comme un processus écosystémique important conduisant à la régénération des nutriments dans la colonne d'eau. De nombreuses études se sont intéressées à cette fonction dans les sédiments meubles de l'Arctique mais aucune n'a documenté l'effet des structures biogéniques sur le fonctionnement de l'écosystème benthique. La présente étude vise à accroître nos connaissances sur le fonctionnement de ces écosystèmes vulnérables dans l'Est de l'Arctique Canadien. La présence de coraux bambous améliorait considérablement la densité, la structure et la libération d'éléments nutritifs de ses sédiments. En revanche, l'effet des lits d'éponges n'était pas aussi évident que pour les coraux, probablement en raison de la forte hétérogénéité de leur habitat adjacent servant de point de comparaison. Ainsi, nous avons confirmé l'importance des coraux bambous sur le fonctionnement de l'écosystème profond, tandis que celle des lits d'éponges, dans l'écosystème peu profond, reste incertaine.

3.2. Abstract

The relationships between infaunal diversity and ecosystem function of biogenic structures in the Eastern Canadian Arctic remain poorly documented. Our study investigated the influence of sponge gardens at the Frobisher Bay site (138 m) and bamboo corals at the Baffin Bay site (1007 m) on the infaunal community structure and benthic ecosystem functioning. The occurrence of both types of biogenic structure type enhanced particular taxa and/or feeding guilds. A large density of suspension filter feeders was observed in bamboo coral sediment, whereas bare sediment exhibited a large proportion of nematodes and deposit-detritus feeders. Sponge gardens' sediment showed a high proportion of isopods, Paraonidae polychaetes and up/down conveyors whereas bare sediment exhibited a large density of filter feeders. Through incubation cores, we measured *ex-situ* benthic nutrient and oxygen fluxes at the sediment-water interface in each habitat and site. Biogeochemical fluxes varied significantly between habitats in the Baffin Bay site with a significant impact of bamboo coral habitat on nutrient fluxes (nitrate, ammonium and silicate). Surprisingly, the sediment hosting bamboo corals acted as a source of nitrate and ammonium reaching values similar or higher to the Frobisher site despite the difference in water depth, and thus food supply between the two sites. These significant releases could derive from (i) a high organic matter deposition in bamboo coral habitat, allowed by their erected structure, (ii) a high efficiency of bioturbators (surficial modifiers and burrowers) mixing the surface layer of the sediment and (iii) the difference in sediment type. Our study highlighted that, compared to its adjacent habitat, the presence of bamboo corals appeared to enhance the infaunal density and nutrient release of its sediment. In contrast, the impact of sponge gardens was not as clear as for bamboo coral habitat, likely due to the relatively significant presence of megabiota in the sponge garden adjacent habitat. Thus, our results based on a relatively small sample size, indicate that the bamboo coral habitat seems to increase the efficiency of deep-benthic ecosystem functioning, while that of sponge garden on the shallow ecosystem functioning remains uncertain.

3.3. Introduction

Three-dimensional biogenic structures, designated as marine animal forests, are composed primarily of ecosystem engineering species such as sponges, cnidarians, bryozoans, ascidians and other sessile benthic organisms (Gili and Coma, 1998; Rossi et al., 2012). Ecosystem engineering species shape their habitat and the resources therein, which directly or indirectly benefits the entire ecosystem (Jones et al., 1994). Habitat heterogeneity resulting from these structures represents one of the main factors that influences the distribution of biodiversity at both local and regional spatial scales (Levin et al., 2001; Buhl-Mortensen et al., 2010). Biogenic structures provide microhabitats and shelters for a large assembly of fish species, mobile crustaceans and mollusks (Fosså et al., 2002; Cerrano et al., 2010; Baillon et al., 2012; Buhl-Mortensen and Buhl-Mortensen, 2014), and usually harbor more biodiversity than bare sediment (*i.e.,* habitat without biogenic structures; Cerrano et al., 2010) at comparable depths. The main factor driving this biodiversity gain in biogenic habitats is derived, in part, from their erected structure. Indeed, by decreasing the current flow velocity, biogenic structures stabilize soft substrates and increase organic matter sedimentation (Bruno and Kennedy, 2000; Cerrano et al., 2010). Previous studies have shown that hotspots of organic matter processing formed by scleractinian cold-water corals contribute to an enhancement of the microbial activity altering nutrient cycling (*e.g.,* nitrogen), and thus inducing a higher oxygen consumption and nutrient releases (Khripounoff et al., 2014; Cathalot et al., 2015). Similarly to biogenic structures, sponges help to consolidate and stabilize the sediment (Bell, 2008). Sponges may also influence the water column by consuming dissolved oxygen by respiration (Bell, 2008), filtering and catching particles for food supply (*e.g.,* dissolved organic carbon; Yahel et al., 2003) and altering nutrient cycling (*i.e.*, silicate and nitrogen; Bell, 2008).

Resource availability, water depth, biodiversity, and climate change strongly influence ecosystem functioning (Bourgeois et al., 2017). The remineralization of sediment organic matter is considered to be an important ecosystem process and is measured as oxygen consumption and benthic nutrient fluxes (*e.g.,* ammonium, nitrate, nitrite, phosphate and silicate). The quantity and the quality of food supply (*i.e.,* organic matter and pigments) reaching the seafloor are generally related to the mineralizing activity of bacteria in the water column. Consequently, a decrease in organic matter availability and quality is often observed with increasing water depth. Water depth and resource availability (*i.e.,* quality and quantity) have a great influence on sediment oxygen demand (SOD) (Mouret et al., 2010; Bourgeois et al., 2017). Functional diversity has profound implications for ecosystems and their functioning (Mermillod-Blondin et al., 2004; Michaud et al., 2006, 2009; Link et al., 2013; Snelgrove et al., 2014) and seems to be more important than the diversity *per se* (Bolam et al., 2002; Belley et al., 2016; Belley and Snelgrove, 2017). As a result of their bioturbation activities (*e.g.,* reworking sediment and bio-irrigation) and their behavior (*e.g.,* feeding, mobility), which generate different levels of disturbance (Biles et al., 2002), infaunal organisms may cyclically enhance oxygen penetration within the sediment, increase oxic respiration, stimulate organic matter degradation and change inorganic nutrient fluxes at the sediment-water interface (Vopel et al., 2003; Belley and Snelgrove, 2016). By transporting fresh organic matter into the deeper sediment layers, gallery diffuser organisms (*i.e.,* digging galleries in the sediment) stimulate microbial processes inducing an influx of oxygen and nitrate from the water into the anoxic parts of the sediment and a release of ammonium and phosphate (Aller, 1988; Michaud et al., 2006; Piot et al., 2013; Belley and Snelgrove, 2017).

Climate change is also an important factor in driving the Arctic ecosystem functioning (Hoegh-Guldberg et al., 2018). With global warming, a significant decrease in the extent and duration of ice cover is already observed (Hoegh-Guldberg and Bruno, 2010; Barnhart et al., 2016). These changes will (i) affect the duration and magnitude of phytoplankton blooms (Wassmann and Reigstad, 2011) and consequently the resources availability for benthic communities as well as (ii) open more shipping routes in the Arctic. The latter would intensify maritime activities such as fishing and transport (Melia et al., 2016) and increase the risk of introducing invasive species (Goldsmit et al., 2019). Although biogenic structures may adapt to naturally changing environmental variables (*e.g.*, water mass temperature anomaly; Rossi et al., 2011), direct disturbances such as bottom trawling, overfishing, the introduction of invasive species and oil drilling represent a significant threat to habitat heterogeneity, food availability, biodiversity, sediment dynamics and ecosystem functioning (Thrush and Dayton, 2002; Rossi, 2013; Pusceddu et al., 2014). Biogenic structures have been defined as vulnerable marine ecosystems due to their scarcity, fragility, and the high density and diversity of organisms associated with them (FAO, 2009). In order to provide for the consequences of increased human activity (*e.g.,* bottom trawling, oil drilling), baselines must be established with respect to biodiversity within vulnerable marine ecosystems, interspecies relationships and their impact on ecosystem functioning. In 2010, a strategic plan for biodiversity (Aichi Biodiversity Targets) was adopted to increase, inter alia, the conservation areas of particular importance for biodiversity and ecosystem services (Target 11, Strategic Goal C) (Secretariat of the Convention on Biological Diversity, 2014). In Eastern Canadian Arctic areas of high coral and sponge density have been identified using scientific trawl surveys data (Kenchington et al., 2010). More recently, remotely operated vehicle (ROV) video surveys in this region led to the identification of two areas holding high concentrations of biogenic structures. Neves et al. (2015) reported dense aggregations of bamboo coral colonies (*Keratoisis* sp.) living on a soft substrate in the Southeast of Baffin Bay (873 m). Furthermore, Dinn et al. (2019) reported the presence of dense aggregations of sponges (*Iophon koltuni*) on soft substrate in Frobisher Bay (137 m).

Our study aimed at assessing the influence of biogenic structures (*i.e.,* bamboo corals and sponges) on the infaunal community structure and ecosystem functioning. We addressed our objectives by exploring the following research questions: i) are the taxonomic and functional diversities of infaunal communities similar in bare sediment and biogenic structure sediment?; ii) do biogeochemical fluxes at the sediment-water interface vary spatially according to the nature of the habitat (biogenic structures vs. bare sediment)?; iii) which environmental and biological variables explain biogeochemical fluxes in these habitats?

We formulated the following hypotheses: i) infauna are more abundant and diverse in biogenic structures compared to bare sediment regardless of water depth and the nature of the biogenic structure; ii) sediment in biogenic structures exhibits a higher oxygen demand relative to bare sediment due to the higher levels of organic matter deposition and larger biogeochemical fluxes and; iii) resource availability (*i.e.,* sedimentary organic matter content and chlorophyll *a* concentration), infauna density and bioturbation activities are the main variables explaining biogeochemical fluxes.

3.4. Methods

3.4.1. Study area and field sampling

Samples were collected at two sites in the Eastern Canadian Arctic (Figure 3.1) aboard the scientific icebreaker CCGS *Amundsen* during the summer of 2017 (July 15–27). In Frobisher Bay (FB), the sampled sites are in the shallowest enclosed portion of the Bay at depths of 135–138 m within an area of submarine slope failures < 1 km from Hill Island (Figure 3.1; Deering et al. 2018). Although the sampled locations were in areas mainly composed of soft substrate, a Super Mohawk ROV (Amundsen Science) video survey revealed the presence of bedrock walls near the targeted stations. In Baffin Bay (BB), the sampled site is located offshore in the Southeast portion of the Bay, at ~140 km from Baffin Island, Canada (Figure 3.1). Multibeam bathymetry of the area indicated an overall flat slope, and ROV video surveys did not indicate the presence of rocky environments near the study area. BB samples were collected at depths of 874–1007 m.

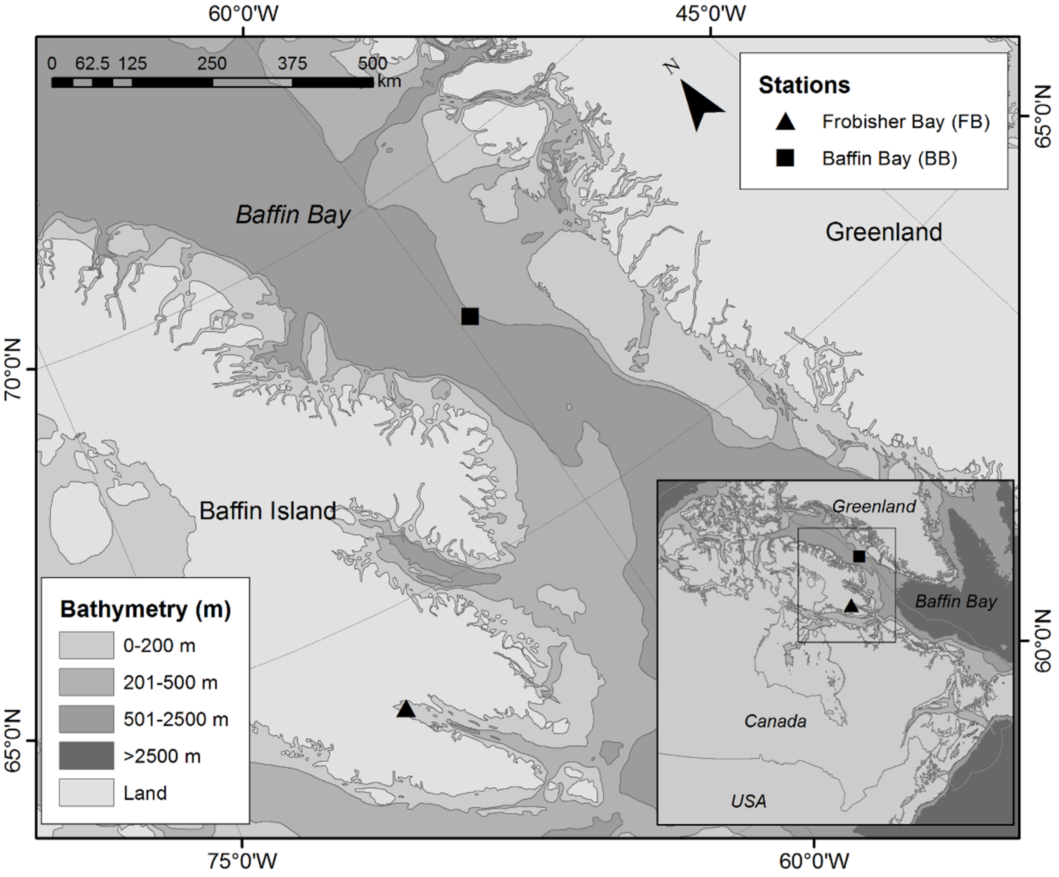

Figure 3. 1. Sampling sites in Frobisher Bay (FB, 135m depth) and in Baffin Bay (BB, 1007m depth) in July 2017.

The sites were characterized by areas of bare sediment and biogenic habitats comprised of sponge gardens *Iophon koltuni* (Dinn et al., 2019) and bamboo corals *Keratoisis* sp. (Neves et al., 2015) in FB and BB respectively. *I. koltuni* was the most abundant and dominant sponges in FB (Figure 3.2a); unfortunately, it was not possible to count individuals or estimate the covering percentage from the ROV videos because the camera was positioned in a forward-looking angle, rather than downward. Colonies of *Keratoisis* sp. were found in very high densities in this region (*e.g.*, a 2000 kg trawl bycatch has been reported for this location; Kenchington et al., 2010) and grew from "root-like" branches, instead of from a single point of attachment (Figure 3.2c; Neves et al., 2015). Colonies could not be distinguished from one another based on our video data, and therefore the estimation of colony density was not possible. However, colonies are estimated to measure <1 m in height.

The sampling positions at biogenic and non-biogenic habitats were defined during ROV video surveys at the two sites (Figure 3.2a-d). Positions were carefully selected to avoid overlap between the two types of habitats (*i.e.*, when most of the camera's field of view was dominated by a single habitat over the course of approximatively 5 meters). At each site, we deployed two box cores (0.5 × 0.5 m) per habitat (*i.e.*, inside the biogenic structures and in the bare sediment; Figure 3.2e) approximately 200 m apart in FB site and 500 m apart in BB site. From each box core, we collected three sediment cores (i.d = 9.8 cm, H = 30 cm) for a total of six cores per habitat and 12 cores per site. Sediment cores sampled in biogenic structures habitats were visually exempted from biogenic structures. Bottom (10 m above the seafloor) temperature, salinity and oxygen saturation at each site were recorded with a conductivity-temperature-depth (CTD) probe. Sediment samples for chlorophyll *a*, phaeopigments and sediment properties were also collected from each box core (*Section 3.4.6*).

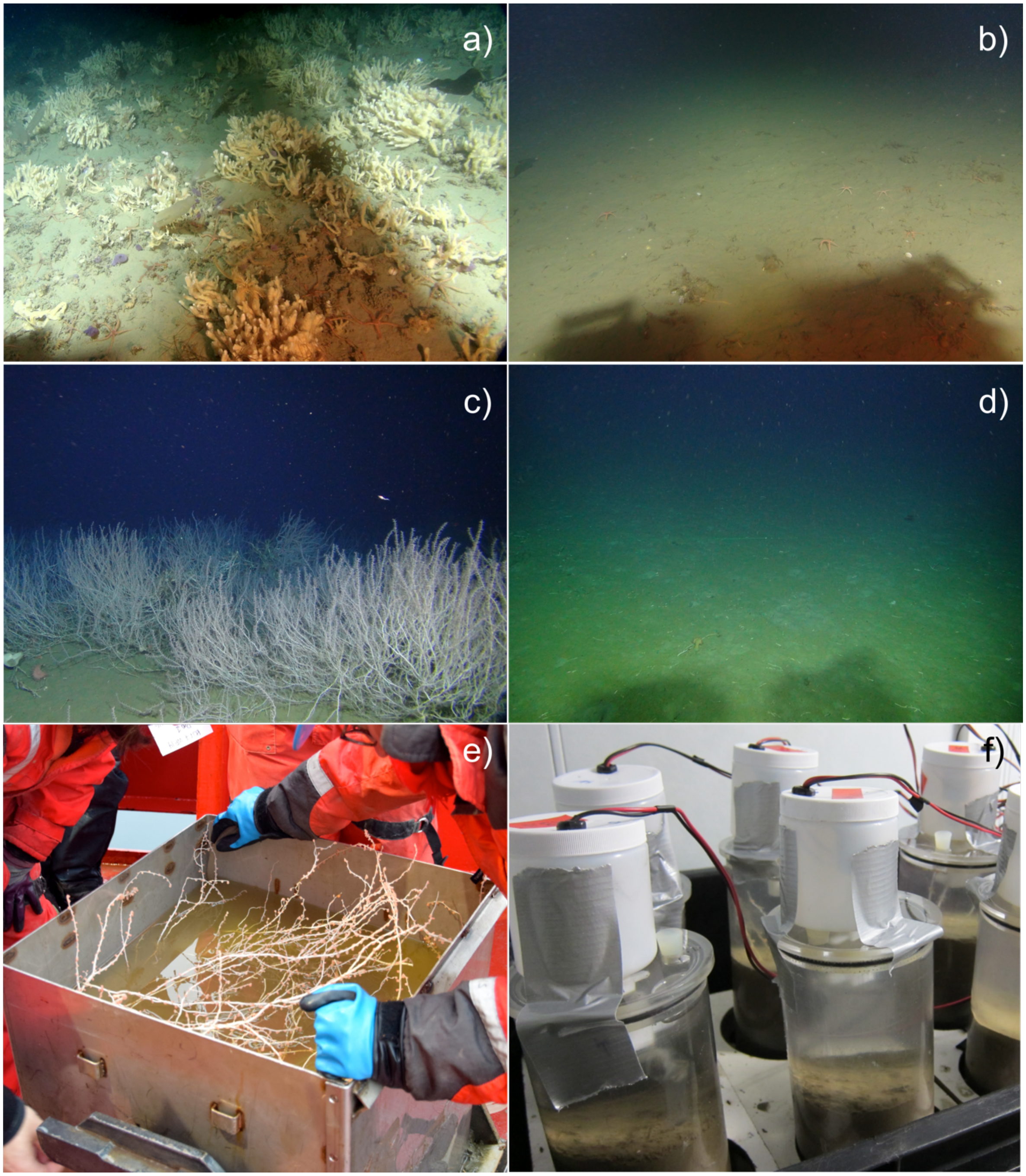

Figure 3. 2. Photo-plate of the sampling sites and incubations experiments: a) Sponge gardens (*Iophon koltuni*) in the FB site, b) Bare sediment in the FB site, c) Bamboo coral habitat (*Keratoisis* sp.) in the BB site, d) Bare sediment in the BB site, e) sample of the box-core deployed in bamboo corals, f) Incubations experiments of the sediment cores. Credits a-d): ArcticNet-CSSF-DFO.

3.4.2. Incubations

Incubation cores, enclosing a 10 cm water layer on top of the 20 cm sediment layer, were carried out using bottom water collected from the same depth (Figure 3.2f). Sediment cores were acclimated for 6h to allow suspended sediment particles to settle to the sediment surface. During this acclimation period, the water supernatant in cores was supplied with air using aquarium air pumps to avoid sub-oxic conditions during incubations. The cores were kept in the dark. After the acclimation period, each sediment core was sealed with a lid equipped with a magnetic stirrer and a hole open only for water sampling. Sediment cores were incubated in the dark at a temperature-controlled room (2-4°C) until a maximum of 20% of available oxygen was consumed. This procedure was carried out to avoid suboxic conditions and biogeochemical transformations (Renaud et al., 2007; Link et al., 2011). The duration of the incubation periods was 28 h and 48 h for FB and BB sites, respectively. Three supplementary cores, incubated with bottom water only, served as controls, to measure oxygen consumption and nutrient concentrations in the water layer.

3.4.3. Benthic fluxes measurements

The sediment (community) oxygen demand was measured periodically (at 3h intervals) by introducing an oxygen dipping probe through a hole in the lid (Fibox, PreSens, Regensburg, Germany). To determine the nutrient concentrations (NH_4^+, NO_3^-, NO_2^-, $Si(OH)_4$, PO_4^{3-}), water samples were collected at the sediment-water interface at the beginning, midpoint and end of incubations (Renaud et al., 2007; Link et al., 2011). The sampled water was immediately replaced by an equivalent volume of bottom water, with a known solute concentration. To prevent spurious measures, the volume of water withdrawn and replaced during each sampling never exceeded 10% of the total volume of the core. Water samples were filtered through GF/F filters (nominal porosity 0.7 µm) using acid-rinsed plastic syringes. Each sample was stored at -20°C until analysis. Measurements of nitrate, nitrite, phosphate and silicate were performed using a Bran and Luebbe Autoanalyzer 3 applying colorimetric methods adapted from Grasshoff et al. (1999). For ammonium measurements, water samples were analyzed using a Turner Design fluorimeter following the method proposed by Holmes et al. (1999). The detection limit was 0.100 $\mu mol\ L^{-1}$ for ammonium, 0.010 µmol L^{-1} for nitrate and nitrite, 0.020 µmol L^{-1} for phosphate and 0.016 µmol L^{-1} for silicate.

Oxygen and nutrient fluxes were assessed from the slope of the linear regression of oxygen and nutrient concentration versus time of incubation and corrected for solute concentration in the replacement water measured at each filling. Median flux determined in the control cores was subtracted from each sediment core measurement. A positive nutrient flux indicates a release of nutrients from the sediment into the water column, while a negative flux signifies an uptake of nutrients from the water column into the sediment.

3.4.4. Infauna identification and taxonomic diversity

Following incubation, sediment cores were sieved through a 500 µm mesh sieve to collect infauna. Organisms were fixed with 4% formaldehyde solution. They were sorted under a dissecting microscope in the laboratory and identified to the lowest possible taxonomic level. We determined density (N; mean ± SE individuals m^{-2}) for each taxon, wet biomass (mean ± SE g m^{-2}) and taxonomic richness as the number of taxa present in each sediment core (mean ± SE). We also calculated the Shannon-Wiener (H') and Pielou's evenness (J') diversity indices for each sediment core using the "vegan" R package (R Core Team, 2020).

3.4.5. Biological traits and functional diversity

We selected four biological trait categories, and 15 modalities based on availability for all taxa (Table 3.1) to reflect ecosystem functioning in terms of sediment oxygen consumption and nutrient cycling (Macdonald et al., 2010; Link et al., 2013; Queirós et al., 2013; Degen et al., 2018; WoRMS Editorial Board, 2018). When a biological trait was not available for a specific taxon, we obtained information from one higher taxonomic level (Table S3.1). We assigned a code, from 0 to 1 to each taxon for each modality. Hence, a value of 0 means complete absence of the modality and a value of 1 means complete dominance of the modality. For example, the Sedentaria Annelida *Aricidea suecica* can adjust its feeding type according to the environmental conditions, between filter/suspension feeder and deposit feeder, so we assigned 0.5 for its feeding type modality. Functional and taxa abundance matrices were used to measure multidimensional functional diversity indices (see below) using the "FD" package (Laliberté et al., 2014) in R (R Core Team, 2020): functional richness

(FRic), functional evenness (FEve) (Villéger et al., 2008) and a single-trait-based index (*i.e.,* the community-level weighted means of trait values (CWM)). CWM is weighted by the relative abundance of organisms identified by the trait's modality and represents functional composition (Lavorel et al., 2008; Laliberté and Legendre, 2010).

Table 3. 1. Biological traits used in the functional diversity analysis according the categories and the modalities.

Category	Modality
Mobility	Sessile (S) Mobile (M) Limited mobility (L)
Feeding type	Detritus feeder (Dt) Carnivore/Predator (C) Filter/Suspension feeder (F) Scavenger (Sc) Deposit feeder (D)
Sediment reworking	Biodiffusor (B) Up/Down conveyor (UCDC) Epifauna (E) Surficial modifier (S)
Body size	Small (S < 3mm) Medium (3 mm < M < 10 mm Large (L > 10 mm)

3.4.6. Environmental variables

Three sub-cores of 2.4 cm in diameter were sampled within each box-core, for a total of six replicates per habitat, to characterize sediment surface properties: chlorophyll *a* (Chl *a*) and phaeopigment (phaeo) concentrations (mg m^{-2}), organic matter content (% of dry sediment), porosity (%) and grain size (%).

Chlorophyll *a* and phaeopigment concentrations were quantified using a modified protocol of Riaux-Gobin and Klein (1993) and Link et al. (2011). We placed 2 g of wet sediment (the top centimeter of the sediment) in 10 mL of 90% acetone (v/v) for 24 hours at 4°C and then analyzed the supernatant before and after acidification (HCL 5%) using a TURNER Design 10AU fluorometer. Then, the sediment was dried and weighed to standardize pigment concentrations per gram of dry sediment. We sampled the top centimeter of the sediment sub-cores to quantify organic matter (OM) content by loss of ignition (500°C). The water content was determined by comparing the mass of wet and dried sediment. Porosity was then calculated using a dry sediment density of 2.65 g cm^{-3} (Berner, 1980). We sampled the first five centimeters of sediment to determine grain size with a Laser Diffraction Particle Size Analyzer LA-950 HORIBA. Sediment type classes were based on Wentworth (1922) and Folk and Ward (1957): mud (< 3.9 µm), silt (3.9 µm < X < 62.5 µm), sand (62.5 µm < X < 2 mm) and gravel (> 2 mm). No sieving was performed prior to analysis because no large particles (> 2 mm) occurred in our sediment samples. Sediment properties are presented in Table 3.2.

3.4.7 Statistical analyses

3.4.7.1 Spatial variation of environmental parameters

Principal Component Analysis (PCA; Hotelling, 1933), performed on a correlation matrix, was used to identify the combinations of environmental parameters that best explain habitat variability. Variables with a high Pearson's correlation among themselves (> 0.85) were excluded from the analysis. Chl *a* and phaeopigment concentrations were combined into a Chl *a*:phaeopigment ratio and only sand content was retained due to the negative correlation with mud. We carried out the PCA in R (R Core Team, 2020) using the "FactoMineR" package (Husson et al., 2019).

3.4.7.2 Spatial variation of benthic communities and benthic fluxes

Frobisher Bay and Baffin Bay sites were analyzed separately. Density, univariate measures of biodiversity as well as benthic fluxes were analyzed using Student *t*-test with habitats (two levels: biogenic structures versus bare sediment) as factors and individual cores as replicates. All data were tested for normality and heteroscedasticity using Shapiro-Wilk and Bartlett's test, respectively. When conditions were not satisfied, a non-parametric Mann-Whitney-Wilcoxon test was used instead. We carried out these analyses in R (R Core Team, 2020).

Table 3. 2. Environmental conditions (mean ± SE) corresponding to the site (Frobisher Bay FB; and Baffin Bay BB) and the habitat.

Site	Habitat	Water depth (m)	Bottom temperature (°C)	Sand content (%)	OM content (%)	Porosity (%)	Chlorophyll *a* (mg m^{-2})	Phaeopigment (mg m^{-2})	Chl*a*:phaeo ratio
FB	Bare sediment	137	-1.2	24.52 ± 1.60	4 ± 0.7	68.17 ± 0.90	16.80 ± 1.08	80.73 ± 4.88	0.21 ± 0.01
	Sponge gardens	135	-1.2	22.10 ± 1.61	5 ± 0.2	74.51 ± 0.91	14.04 ± 1.14	66.27 ± 4.95	0.21 ± 0.02
BB	Bare sediment	1007	0.7	38.15 ± 1.81	4 ± 0.2	66.40 ± 1.69	1.79 ± 0.08	14.96 ± 1.41	0.13 ± 0.01
	Bamboo corals	874	0.7	18.13 ± 5.15	6 ± 0.6	79.50 ± 2.51	1.81± 0.26	21.72 ± 3.57	0.10 ± 0.01

3.4.7.3 Benthic biogeochemical flux drivers

Redundancy analysis (RDA; Rao, 1964) was used to identify the functional and taxonomic diversity indices as well as the environmental variables (explanatory variables) influencing biogeochemical flux variation (response variables) in biogenic structures and bare sediment. Predictor variables with a high Pearson's correlation among themselves (> 0.85) were excluded from the analyses (Shannon-Wiener index, bottom water dissolved oxygen, total pigments, Chl *a*, phaeo, mud content, and temperature). To obtain the model with the most parsimonious set of variables, a forward stepwise model selection was performed on the environmental variables (Chl *a*:phaeo ratio, organic matter content, porosity, sandy composition, water depth) and the diversity variables (taxa richness, density, Pielou's evenness index, functional richness, functional evenness, CWM_*modalities* (Table 3.1); Blanchet et al., 2008). A permutation-based ANOVA was used to test the significance of axes and the term selected by the model. We performed the RDA using the "vegan" package (Oksanen et al., 2017) in R (R Core Team, 2020).

3.5. Results

3.5.1. Sediment properties

Near-bottom water temperature at the study sites varied between -1.2 and 0.7°C, in the FB and BB sites, respectively (Table 3.2). Chl *a* concentration in the surficial seafloor sediments varied between 14.04 and 16.80 mg m^{-2} in the shallowest site FB and between 1.79 and 1.81 mg m^{-2} in the deeper site BB (Table 2). Phaeopigment concentrations in the surficial seafloor sediments ranged from 66.27 to 80.73 mg m^{-2} in the FB site and from 14.96 to 21.72 mg m^{-2} in the BB site (Table 2). The sediment had a sand content varying between 22.10 and 24.52 % in the FB site and between 18.13 and 38.15 % in the BB site (Table 2). The organic matter content ranged from 4 to 5 % in the FB site and from 4 to 6 % in the deeper site BB (Table 2).

The first and second principal components (PC1 and PC2, Figure 3.3) explained 62.3 % and 24.8 % of the variation within the data set, respectively. The sand content was negatively related to the OM content and porosity along PC1 (Figure 3.3). FB sites were separated from BB sites along the PC1 axis. Chlorophyll *a* to phaeopigment ratio was correlated positively along PC2. This shows that FB sites were correlated with a high Chl *a*:phaeo ratio, indicating a high concentration of Chl *a* and a low concentration of phaeopigment in the sediment (Table 3.2; Figure 3.3). BB sites presented a lower concentration of those. Biogenic structure and bare sediment habitats in BB site were strongly separated across the PC2 axis. The sediment amongst biogenic structures at the BB site was muddy with high porosity and presented a high OM content. By contrast, bare sediment presented coarser sediment with low porosity and a lower OM content (Table 3.2; Figure 3.3).

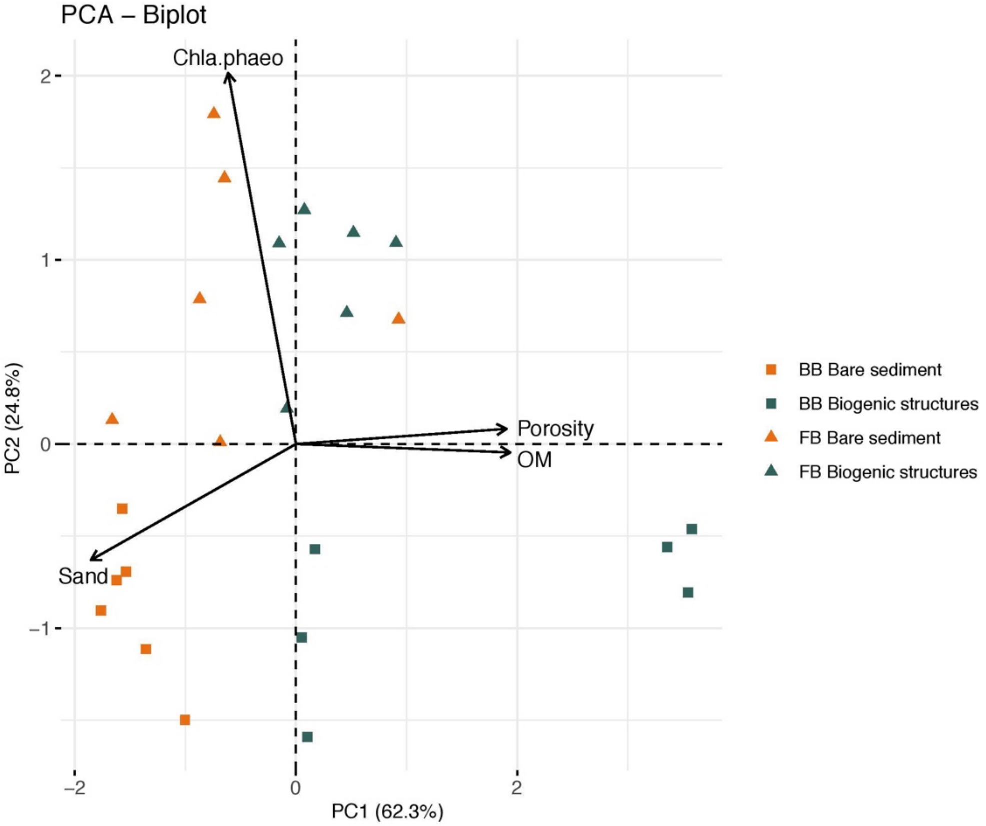

Figure 3. 3. Principal component analysis (PCA) plot of environmental variables. Vectors indicate the direction and strength of each variables' contribution to the overall distribution. Triangle and square labels define Frobisher Bay and Baffin Bay respectively while their colors (green and orange) represent the habitat: biogenic structures and bare sediment respectively. The explicative variables are designated by Chla.phaeo (chlorophyll *a*:phaeopigment ratio), OM (% organic matter content), Sand (% sand content) and Porosity (%).

3.5.2. Infaunal community composition

A total of 115 taxa from 11 phyla were identified in this study. Fifty-three taxa were present in biogenic structure sediment and 60 taxa in bare sediment at the FB site. At the BB site, 39 taxa were present in biogenic structure sediment and 28 taxa in bare sediment.

At FB site, all polychaete families had similar proportions in each habitat, except for Paraonidae with a slightly higher proportion in biogenic structure than bare sediment (9 and 4 % respectively), and Maldanidae with a lower proportion biogenic structure than bare sediment (4 and 8 % respectively; Figure 3.4A). Biogenic structure sediment and bare sediment had similar proportions of amphipods (4 % and 6 %, respectively) and cumaceans (7 %). In contrast, biogenic structures had higher proportion of isopods (9 %) dominated by *Desmosoma lineare*. Bare sediment had higher proportion of bivalves (7 %) dominated by *Ennucula tenuis* and *Macoma calcarea.* Bioturbation type composition differed between habitats with higher proportion of surficial modifiers in biogenic structure sediment (*e.g.*, *Ennucula tenuis* and *Leucon nasicoides*; 71%; Figure 3.4B). In contrast, bare sediment was distinguished from the biogenic structure sediment by higher proportion of up/down conveyors (*e.g.*, Maldanidae; 23%). Deposit feeders showed similar densities in each habitat (Figure 3.4C). Feeding type composition differed between habitats with higher densities of filter feeders in bare sediment (*e.g.*, *Macoma calcarea*; 14%; Figure 3.4C).

At BB site, nematodes were the most abundant group (47 %) which had a slightly higher proportion in bare sediment (51 %) than in biogenic structures (44 %; Figure 3.4A). Polychaetes had similar proportions in both habitats. However, some taxa were only found in biogenic structure sediment such as Syllidae (e.g., *Ancistrosyllis groenlandica*), Paraonidae and Maldanidae. Moreover, bare sediment had the highest proportion of arthropods dominated by isopods (10 %) and cumaceans (3 %). In contrast, biogenic structure sediment showed a higher proportion of bivalves (7 %) dominated by *Thyasira* sp. and *Astarte* sp. Biogenic structure sediment also had the highest proportion of “Other taxa” (2 %) dominated by the hydrozoan *Corymorpha* sp. and the brachiopod Terebellinae. Surficial modifiers were the most abundant bioturbation group and showed similar proportions in each habitat (~73%; Figure 3.4B). Bare sediment was distinguished from biogenic structure sediment by having slightly higher proportion of biodiffusors (*e.g.*, Paraonidae; 22%), while biogenic structure sediment had a slightly higher proportion of epifauna (Figure 3.4B). Feeding type composition differed between habitats with higher proportion of filter feeders in biogenic structures (*e.g.*, Thyasiridae; 11%) and higher densities of detritus/deposit feeders in bare sediment (*e.g.*, Nematoda; 75%; Figure 3.4C).

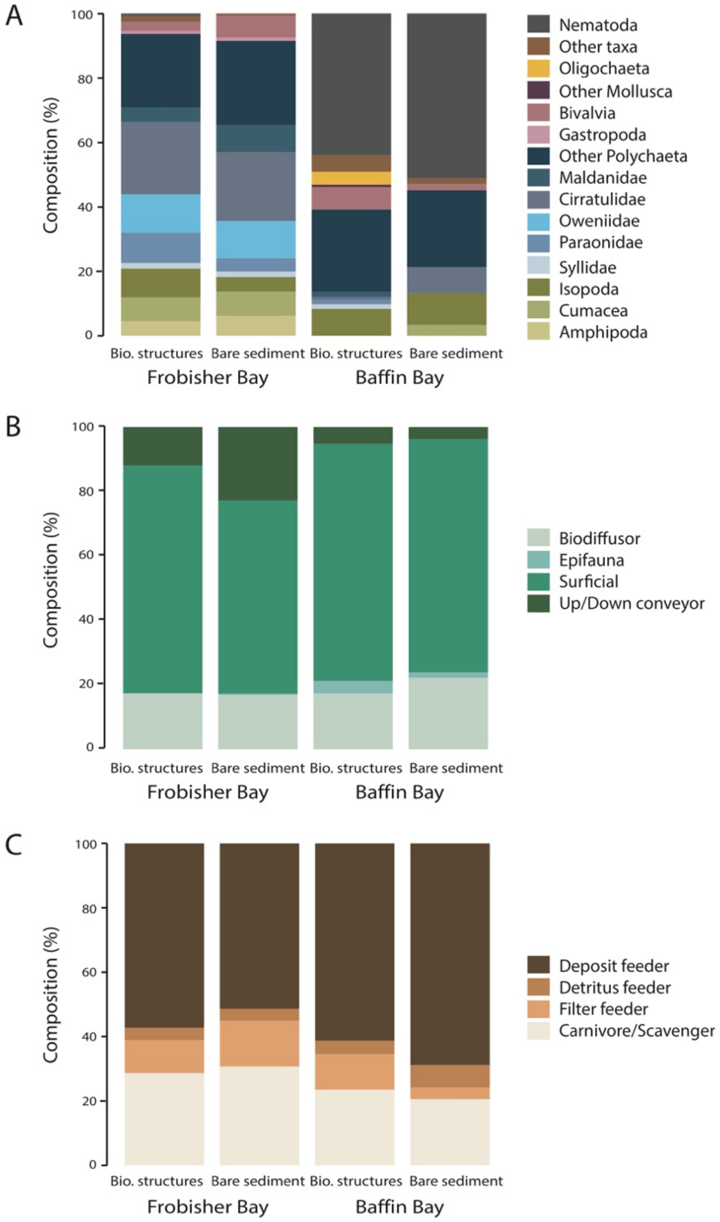

Figure 3. 4. Taxonomic and functional trait composition in biogenic structure and its adjacent bare sediment habitat as a function of site (Baffin Bay and Frobisher Bay). (A) Taxonomic composition of dominant infauna. Other taxa include Cnidaria, Chordata, Echinodermata, Sipuncula and Brachiopoda. (B) Bioturbation type and (C) Feeding type.

3.5.3. Variation in diversity and functional indices

At FB site, a higher average infaunal density trend was observed in bare sediment (1061 ± 69 ind m^{-2}) compared to biogenic structure sediment (875 ± 67 ind m^{-2}) but the difference was not statistically significant ($p = 0.08$; Table 3.3; Figure 3.5A). Taxa richness presented similar values in biogenic structure sediment and bare sediment (19 ± 2 and 21 ± 1 taxa, respectively; Table 3.3; Figure 3.5B). The same pattern was observed for biomass, which ranged from 24.3 ± 9.7 to 27.1 ± 9.9 g m^{-2} in biogenic structure sediment and bare sediment, respectively ($p > 0.05$; Table 3.3; Figure 3.5C). Diversity indices (Shannon index and Pielou's evenness) and functional indices (functional richness and functional evenness) did not differ between habitats ($p > 0.05$, Table 3.3).

At BB site, infaunal density differed between habitats with a higher value in biogenic structure sediment (430 ± 78 ind m^{-2}) compared to bare sediment (242 ± 29 ind m^{-2}; $p < 0.05$; Figure 3.5A). Biogenic structure sediment showed a slightly higher number of taxa (10 ± 1 taxa) compared to bare sediment (7 ± 1 taxa; $p = 0.06$; Table 3.3; Figure 3.5B). Biomass presented similar values in biogenic structure sediment and bare sediment (1.1 ± 0.6 and 0.3 ± 0.1 g m^{-2}, respectively; $p > 0.05$; Figure 3.5D-F). Diversity indices (Shannon index and Pielou's evenness) and functional richness did not differ between habitats ($p > 0.05$; Table 3.3). In contrast, functional evenness differed between habitats, with a higher evenness observed in bare sediment ($p < 0.05$; Figure 3.5G).

Table 3. 3. Student's t-test and Mann-Whitney-Wilcoxon (W) test results for density, diversity and functional indices to test the effect of habitat (biogenic structures and bare sediment) in Frobisher Bay and Baffin Bay sites.

	Frobisher Bay site		Baffin Bay site	
Source of variation	t or W	p	t or W	p
Taxa richness				
Habitat	0.86 (t)	0.41	-2.06 (t)	0.06
Density				
Habitat	1.93 (t)	0.08	2 (W)	0.01
Biomass				
Habitat	21 (W)	0.70	7.5 (W)	0.11
Functional richness				
Habitat	22 (W)	0.59	-1.39 (t)	0.20
Functional evenness				
Habitat	0.12 (t)	0.91	36 (W)	<0.01
Shannon				
Habitat	0.43 (t)	0.68	-0.86 (t)	0.41
Pielou's evenness				
Habitat	-0.25 (t)	0.80	-0.22 (t)	0.83

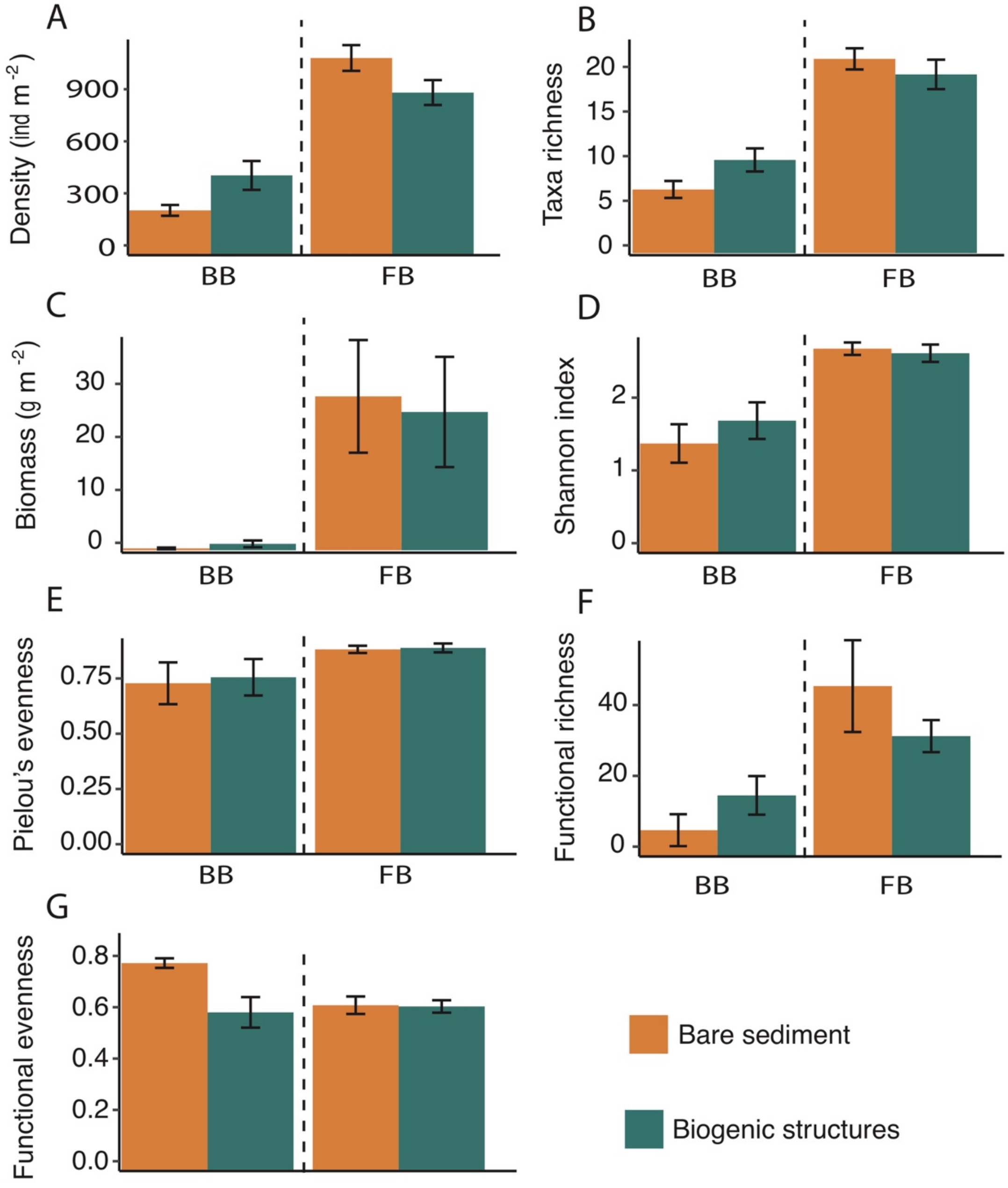

Figure 3. 5. Mean functional and taxonomic diversity indices (± SE) in Baffin Bay (BB) and in Frobisher Bay (FB) within biogenic structures and bare sediment: (A) the density of benthic organisms (individuals m^{-2}), (B) taxa richness (number of taxa), (C) wet biomass (g m^{-2}), (D) Shannon index, (E) Pielou's evenness index, (F) functional richness and (G) functional evenness. Dash lines separate the site Baffin Bay and Frobisher Bay sites.

3.5.4. Variation in benthic biogeochemical fluxes

At FB site, sediment oxygen uptake varied between 3242 ± 1014 µmol O_2 m^{-2} d^{-1} in the biogenic structure sediment and 4291 ± 478 µmol O_2 m^{-2} d^{-1} in the bare sediment (Figure 3.6A). The uptake of nitrite ranged from -2.7 ± 1 to -0.9 ± 1.4 µmol NO_2^- m^{-2} d^{-1} in bare sediment and biogenic structure sediment, respectively (Figure 3.6E). Nitrate was released from the sediment with values varying between 73 ± 19 and 90 ± 20 µmol NO_3^- m^{-2} d^{-1} in biogenic structure sediment and bare sediment, respectively (Figure 3.6F). The pattern for ammonium fluxes was more variable within the two habitats, with release values varying between 1.5 ± 35 and 36 ± 35 µmol NH_4^+ m^{-2} d^{-1} in biogenic structure sediment and bare sediment, respectively (Figure 3.6D). The release of silicic acid ranged from 1522 ± 178 to 2145 ± 242 µmol $Si(OH)_4$ m^{-2} d^{-1} in biogenic structure sediment and bare sediment, respectively (Figure 3.6B). Phosphate was also released from the sediment with values ranging from 15 ± 5 to 29 ± 18 µmol PO_4^{3-} m^{-2} d^{-1} (Figure 3.6C). Benthic nutrient fluxes did not differ between habitats ($p > 0.10$), except for a trend of higher silicate release in bare sediment ($p = 0.06$; Table 3.4; Figure 3.6).

At BB site, sediment oxygen uptake was significantly ($p < 0.01$; Table 3.4) higher in biogenic structure sediment (1657 ± 186 µmol O_2 m^{-2} d^{-1}) than in bare sediment (659 ± 100 µmol O_2 m^{-2} d^{-1}; Figure 3.6A). Nitrite uptake did not differ between habitats ($p = 0.13$; Table 3.4), with values ranged from -5.4 ± 0.9 to -3.4 ± 0.4 µmol NO_2^- m^{-2} d^{-1} in bare sediment and biogenic structure sediment, respectively (Figure 3.6E). Nitrate was significantly ($p < 0.01$) higher in biogenic structure sediment (193 ± 40 µmol NO_3^- m^{-2} d^{-1}) than in bare sediment (55 ± 11 µmol NO_3^- m^{-2} d^{-1}; Figure 3.6F). The pattern for ammonium fluxes differed significantly between habitats ($p < 0.01$) with a release in biogenic structure sediment (34 ± 25 µmol NH_4^+ m^{-2} d^{-1}) and an uptake in bare sediment (-66 ± 9 µmol NH_4^+ m^{-2} d^{-1}; Figure 3.6D). The release of silicic acid was significantly higher ($p < 0.01$) in biogenic structure sediment (745 ± 59 µmol $Si(OH)_4$ m^{-2} d^{-1}) than in bare sediment (427 ± 27 µmol $Si(OH)_4$ m^{-2} d^{-1}; Figure 3.6B). Phosphate fluxes did not differ between habitats ($p =0.40$; Table 3.4), with a trend of release (6 ± 8 µmol PO_4^{3-} m^{-2} d^{-1}) within the biogenic structure sediment, and a clear uptake in bare sediment (-3 ± 0.6 µmol PO_4^{3-} m^{-2} d^{-1}; Figure 3.6C).

Table 3. 4. Student's t-test and Mann-Whitney-Wilcoxon (W) test results for individual biogeochemical fluxes to test the effect of habitat (biogenic structures and bare sediment) in Frobisher Bay and Baffin Bay sites.

	Frobisher Bay site		Baffin Bay site	
Source of variation	t or W	p	t or W	p
Sediment oxygen demand				
Habitat	0.94 (t)	0.38	-4.73 (t)	<0.01
Ammonium				
Habitat	0.71 (t)	0.50	1 (W)	<0.01
Nitrate				
Habitat	0.62 (t)	0.55	2 (W)	<0.01
Nitrite				
Habitat	-1.05 (t)	0.32	8 (W)	0.13
Silicate				
Habitat	2.07 (t)	0.06	-4.91 (t)	<0.01
Phosphate				
Habitat	19 (W)	0.87	12 (W)	0.40

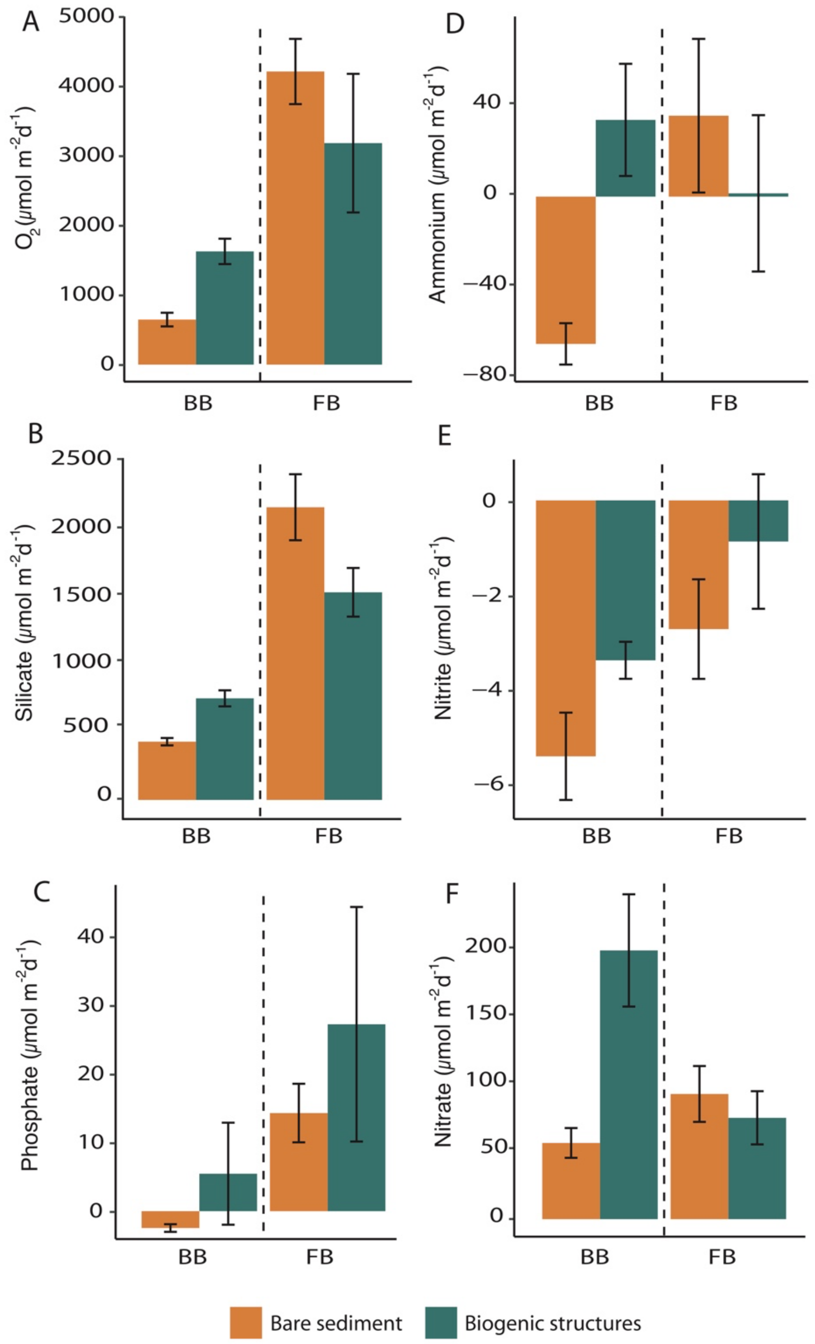

Figure 3. 6. Mean biogeochemical flux (± SE) of (A) sediment oxygen demand, (B) silicate, (C) phosphate, (D) ammonium, (E) nitrite and (F) nitrate measured within biogenic structures and bare sediment at each site (BB = Baffin Bay, FB = Frobisher Bay). Units are in µmol m^{-2} d^{-1}. Green bars represent fluxes measured in biogenic structures and orange bars represent fluxes measured in bare sediment. Dash lines separate the site Baffin Bay and Frobisher Bay sites.

3.5.5. Benthic biogeochemical flux drivers

3.5.5.1. Environmental variables

From the five tested environmental parameters (*i.e.*, Chl *a*:phaeo ratio, OM content, porosity, sandy composition and water depth), the stepwise model selected only water depth and sand content as the drivers of benthic fluxes. The model explained 38% (R^2= 0.43) of the total multivariate benthic flux variation. Permutational ANOVA test showed a significance of constraints of axes (p-value < 0.05). The first and the second axis account for 28 % and 15 % of the total flux variation respectively (Table S3.2; Figure 3.7). Depth was positively correlated to the first axis, explaining 66 % of the fitted flux variation (Table S3.2; Figure 3.7). The sand content was inversely correlated to the second axis, explaining 34 % of the fitted flux variation.

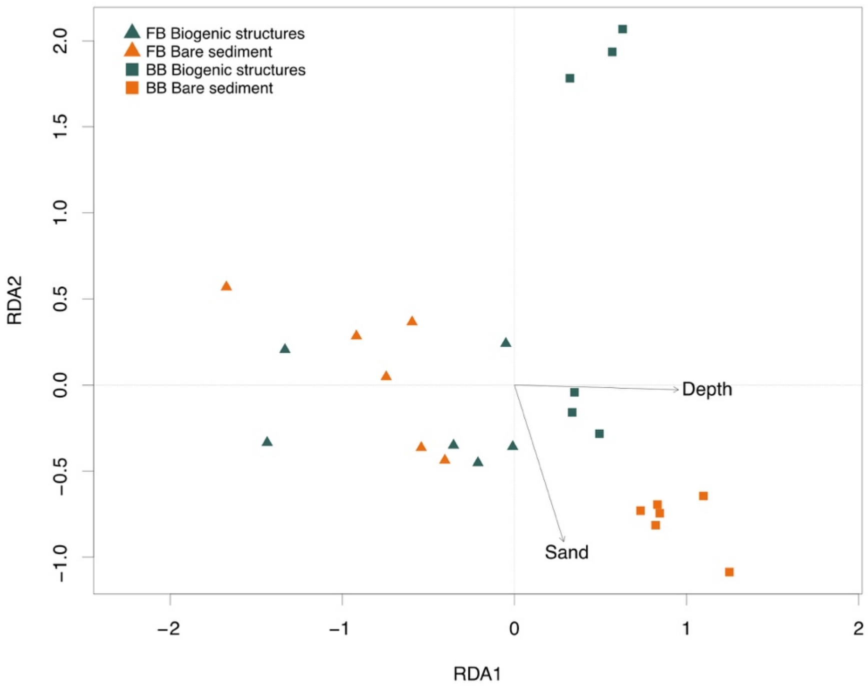

Figure 3. 7. Plot of the redundancy analysis (RDA) models of environmental variables best explaining variation in Baffin Bay (BB) and Frobisher Bay (FB) biogenic structure sediment and bare sediment. Triangle and square labels define Frobisher Bay and Baffin Bay respectively while their colors (green and orange) represent the habitat: biogenic structures and bare sediment respectively.

3.5.5.2. Diversity indices

Of the 22 tested diversity indices (listed in *section 2.7.3*), the stepwise model selected only six variables: community weighted means of surficial modifiers (CWM.Surficial), up and down conveyors (CWM.UCDC), mobile organisms (CWM.Mobile), sessile organisms (CWM.Sessile), taxa richness (S) and functional evenness (FEve) as the drivers of benthic fluxes. The model explained 48% (R^2= 0.61) of the total multivariate benthic flux variation. The first and second axis of the RDA model accounted for 36 % and 15 % of total biogeochemical flux variation, respectively (Table S3.3; Figure 3.8). The community weighted means of up and down conveyors (CWM.UCDC), sessile (CWM.Sessile) and taxa richness (S) contributed to the first axis explaining 58% of the fitted flux variation (Table S3.3; Figure 3.8). The second axis was correlated to functional evenness (Feve), explaining 25 % of the fitted flux variation (Table S3.3; Figure 3.8). Benthic fluxes at the FB site were driven by high values of community weighted means of up and down conveyors and sessile organisms (CWM.UCDC and CWM.Sessile, *e.g.,* Maldanidae) and higher taxa richness. Whereas, benthic fluxes at the BB site were primarily driven by high values of community weighted means of surficial modifiers (CWM.Surficial), mobile organisms (CWM.Mobile) and a high functional evenness (FEve).

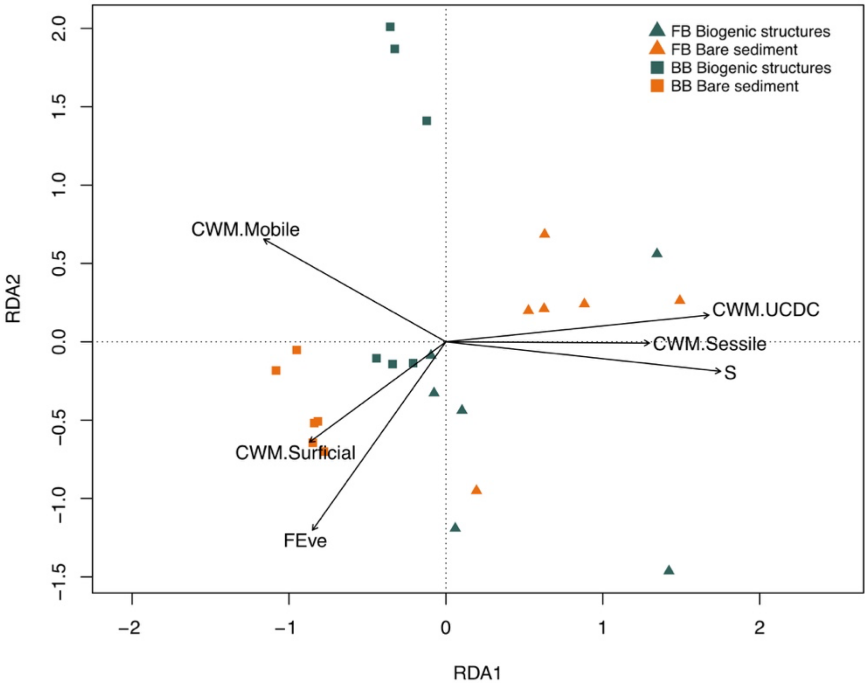

Figure 3. 8. Plot of the redundancy analysis (RDA) models of functional and diversity indices best explaining variation in Baffin Bay (BB) and Frobisher (FB) Bay biogenic structure sediment and bare sediment. Triangle and square labels define Frobisher and Baffin Bay respectively while their colors (green and orange) represent the habitat: biogenic structures and bare sediment respectively.

3.6. Discussion

3.6.1 Infaunal communities

Habitat heterogeneity (grain size, substrate variability, and food supply) decreases with increasing water depth (Freiwald et al., 2004), inducing most generally a homogeneity in deep environments. At local scales, the occurrence of biogenic structures in a homogeneous habitat enhances its complexity by modifying the sedimentation of the particles and increasing the surface area available for settlement, shelter and niche space (Thrush and Dayton, 2002; Costello et al., 2005; Beazley et al., 2015). Effects of deep-water sponge gardens on infaunal assemblages have been shown previously in water depths above 245 m (Bett and Rice, 1992; Barrio Frojan et al., 2012; Beazley et al., 2015). In the current study, we highlighted some differences in the infaunal composition at a shallower depth (137 m; FB site). Sponge gardens provide a suitable habitat for reproduction, shelters, nurseries and constant food supply (Przeslawski et al., 2013; Kersken et al., 2014). Some infaunal organisms have been reported to live in association with sponge gardens (*e.g.,* amphipods and polychaetes). For instance, we observed a higher proportion of isopods and the polychaete family Paraonidae in the FB sponge garden habitat where they could find shelters. On the contrary filter feeders like bivalves had a lower proportion in sponge garden habitat compared to bare sediment. Although biogenic structures generally increase organic particle sedimentation (Bruno and Kennedy, 2000; Cerrano et al., 2010), sponges are known to filter large volumes of water, reducing the detrital input to the surrounding seafloor due to their considerable filtration capacity (Vogel, 1977). Limiting the deposition of organic matter on the seafloor, sponge gardens at the FB site seem to result in a lower proportion of filter feeders and a lower infaunal density compared to its adjacent habitat. However, large ascidians, crinoids (*Heliometra glacialis*), sea anemones, drift/detrital kelp and other less represented sponges were abundant around sponge gardens, as previously reported by Dinn et al. (2019). Their patchy distributions in bare sediment might also contribute to infaunal density, inducing its higher heterogeneity in comparison to bare sediment found in the deep-sea. Therefore, in shallow habitats like FB (< 245 m), we suggest that the effect of sponges on infauna might be virtually nonexistent or harder to detect due to the apparent high heterogeneity of megabiota in its adjacent habitat and the high heterogeneity in the sponge gardens.

Contrary to sponges-associated infaunal communities, coral-associated infaunal communities exhibited differences from its adjacent bare sediment habitat. Cold-water corals have been reported to enhance biodiversity regardless of the coral taxa, although different levels of infaunal abundance or species richness have been noted (Demopoulos et al., 2014; Bourque and Demopoulos, 2018). Cold-water corals are frequently reported along continental margins with locally accelerated currents (Roberts and Cairns, 2014), and their occurrence directly modulates the availability of resources to their surrounding environment by enhancing the trapping of organic matter (Jones et al., 1994; Mienis et al., 2009; Van Oevelen et al., 2009; Cathalot et al., 2015). The high proportion of filter/suspension and deposit feeders, such as bivalves (*e.g., Thyasira* sp. and *Astarte* sp.), oligochaetes and "Other taxa" (*e.g.,* Brachiopoda and Ascidiacea) in the bamboo coral habitat reflected its enrichment in suspended and particulate organic matter. Consistent with this finding, the high percentage of organic matter in bamboo coral sediment compared to its adjacent sediment (6 ± 0.6 % and 4 ± 0.2%, respectively) attested to their positive effect on the trapping of organic matter. By improving food availability, bamboo coral habitat enhanced infaunal density. The distinction between BB habitats was also apparent in the functional trait analysis. The bare sediment habitat presented the highest functional evenness denoting less diverse functional traits. Thus, bamboo coral sediment appeared to be a more complex ecosystem compared to bare sediment habitat in the deep-sea.

Our results highlight the importance of octocorals as key ecosystem engineers in the deep-sea, which are critical to increase infauna density. For sponge gardens, the effect of this habitat seems to be more complex and some uncertainties could be underlined due to the heterogeneity of shallower site (FB).

3.6.2 Benthic biogeochemical flux drivers

Sediment oxygen demand (*i.e.*, SOD), measured in this study, exhibited comparable values to those reported in previous Arctic and Antarctic studies regarding continental shelves (10 460 ± 7 940 µmol O_2 m^{-2} d^{-1}) and slope/rise (2 230 ± 2 370 µmol O_2 m^{-2} d^{-1}; Piepenburg et al., 1995; Clough et al., 2005; Renaud et al., 2007; Hartnett et al., 2008; Link et al., 2011, 2013a, 2013b; Kim et al., 2016; Bourgeois et al., 2017). A high quantity of food supply reaching the sediment increases benthic mineralization processes and, therefore, oxygen consumption (Bianucci et al., 2012; Bourgeois et al., 2017). As previously mentioned, biogenic structures at the BB site showed a positive effect in the trapping of organic matter. Consistent with this observation, the highest SOD observed in biogenic structures at the BB site reflected its higher food supply to the benthos.

Regarding benthic nutrient fluxes (phosphate, silicate, nitrate, nitrite and ammonium), there are only a few reports for the Canadian Arctic sediment and data were mostly obtained from the Western Arctic and Northern Baffin Bay (Rysgaard et al., 2004; Kenchington et al., 2011; Link et al., 2011, 2013a, 2013b). Values in our study were in the range found in other regions of Arctic and Antarctic (Link et al., 2011, 2013a, 2013b; Kim et al., 2016; Bourgeois et al., 2017).

Bioturbation affects ecosystems and biogeochemical processes at the water-sediment interface at a varying degree depending on the community composition and the functional composition (Clough et al., 1997; Mermillod-Blondin et al., 2004; Michaud et al., 2006; Link et al., 2011, 2013b; Belley and Snelgrove, 2017). Bare sediment in the FB site presented a higher proportion of upward conveyors (*e.g.,* polychaetes Maldanidae), feeding head-down at depth in the sediment. Thus, they could excrete components produced at depth to the surface (*e.g.,* silicate, ammonium and nitrate; Kristensen et al., 2012) and explained the higher release of silicate in bare sediment habitat.

Low phosphate release was observed from the two habitats within the two sites. Since phosphate cannot be used as an electron acceptor (Hensen et al., 2006), its release to overlying water column was mostly explained by the aerobic organic matter mineralization and/or from the loss of phosphate adsorption capacity from the sediment (Sundby et al., 1992; Jensen et al., 1995; Anschutz et al., 2007). The phosphate release observed in the FB site was certainly due to an intensified oxic degradation of organic matter reflected by a higher SOD.

Fluxes involved in the nitrogen cycle (*e.g.,* nitrate and ammonium) presented a complex pattern disturbed by (i) the water depth, (ii) the presence of bioturbators and (iii) the sediment grain size. Shallow sediments (< 500 m) usually present a high release of nitrate (~100 µmol NO_3^- m^{-2} d^{-1}) whereas at deep depth (> 790 m), they present a low release of nitrate (< 100 µmol NO_3^- m^{-2} d^{-1}; Link et al., 2013b). Generally, highest nitrite uptake is linked to sediment with a low nitrate release and therefore indirectly correlated with water depth (Link et al., 2013a). Consistent with these findings, nitrate fluxes had values around 100 µmol NO_3^- m^{-2} d^{-1} and a low nitrite uptake in both habitats at the shallower site FB. As expected, we also observed a nitrate release below 100 µmol NO_3^- m^{-2} d^{-1} associated to a slightly higher nitrite uptake in bare sediment at the deeper BB site. Interestingly, we observed the highest value of nitrate release (192 ± 40 µmol NO_3^- m^{-2} d^{-1}) in biogenic structure habitat at the deeper BB site. Likewise, BB biogenic structure sediment acted as a source of ammonium. This latter may suggest that much ammonium was produced, which could not wholly be turned over by nitrification to nitrate. These releases highlighted that the presence of cold-water corals stimulates ammonium release and nitrification rates of the underlying sediment (de Froe et al., 2019).

Burrower organisms, such as the bivalve *Astarte* sp. and the polychaete *Ancistrosyllis groenlandica* and *Prionospio* sp., ventilate their burrows which favors introducing fresh oxygenated water into the sediment. This input of oxygenated water in the nitrification zone (0 to 4 cm; Michaud et al., 2006) may stimulate nitrification reactions (Aller, 2001) and explain the release of nitrate and ammonium in biogenic structures sediment observed at the BB site. Moreover, bamboo coral sediment presented a high abundance of bivalves (*e.g., Astarte* sp.), mobile polychaetes (*e.g., Pholoe* sp., *Ancistrosyllis groenlandica*) and nematodes. All of these taxa, defined as surficial modifiers, mix the surface of the sediment (*i.e.,* oxic layer where nitrate is produced) and despite their relatively low impact on bioturbation (Queirós et al., 2013), their high abundance positively affected nitrate and silicate fluxes (Aller, 1994; Soetaert et al., 1997; Ingels et al., 2009; Piot et al., 2013; Belley and Snelgrove, 2016). In our study, their presence might have stimulated organic matter degradation and hence the release of nutrients (*e.g.,* nitrate and silicate).

On the contrary, bare sediment at the BB site acted as a sink of ammonium. This ammonium uptake could be related to (i) a sandier sediment and/or (ii) to a higher functional evenness. The permeable substrate supports the transport of solute advection that can affect sediment biogeochemistry and benthic exchange fluxes (Janssen et al., 2005; Rao et al., 2012; Huettel et al., 2014). For example, enhanced O_2 supply can promote the reoxidation of reduced inorganic species produced under anaerobic conditions. This process would transport oxygen deeper in BB bare sediment, decreasing the SOD and deepening the different diagenetic redox fronts. The low phosphate uptake measured in BB bare sediment is in agreement with a deeper Fe-oxide rich horizon as discussed above. These conditions would favor the production of nitrate from ammonia and nitrite, by nitrification and chemioxidation (via metal-oxides oxidation). The exact mechanisms to form nitrate need further investigations and the net fluxes measured here do not allow to discriminate the diagenetic pathways involved. However, BB sediments are a source of benthic nitrate and its production requires the input of both ammonia and nitrite from the water column. Similarly to Belley and Snelgrove (2017), we highlighted that a higher functional evenness was associated with lower benthic fluxes in bare sediment, despite a similar functional richness to biogenic structure's sediment at the BB site. The difference in the density of some bioturbators (*i.e.*, functional evenness) might be responsible for the differences in fluxes. For instance, the presence of micro-burrowers, built by nematodes at small-scale, is known to enhance sediment porosity which may facilitate fluid advection (Aller and Aller, 1992; Pike et al., 2001; Piot et al., 2013). The sandier sediment in bare sediment at the BB site (38.15 ± 1.81 %) and the density of bioturbators (*e.g.*, nematodes, biodiffusors) might affect the porosity (66.40 ± 1.69 % and 79.5 ± 2.51 % in bare sediment and biogenic structures sediment, respectively), the solutes transport processes and then the benthic fluxes. The latter might lead to an ammonium uptake and nitrate release in bare sediment habitat.

The benthic remineralization efficiency between the two sampling habitats at the BB site pointed to the importance of food supply and infaunal community bioturbators (*e.g.*, up/down conveyors and surficial modifiers). Despite the lower infaunal density, taxonomic and functional diversity at the BB deep site, bamboo coral habitat seems to strongly influence deep-benthic ecosystem functioning by increasing its efficiency in the deep-sea and more particularly nitrate efflux, an element limiting for primary production in the Arctic sea (Tremblay et al., 2015).

3.7 Conclusion and perspectives

Our study is the first to document and compare biodiversity and benthic fluxes within biogenic structures and bare sediment in the Canadian Arctic. Although the effects of sponge gardens on benthic biogeochemical fluxes and infaunal biodiversity have been previously highlighted in other studies, we could not demonstrate their effects, which might be related to the high heterogeneity of this shallower site. On the other hand, bamboo corals appeared to enhance the infaunal density and ecosystem functioning, despite their deep-water location, where food quality and supply are more limited. Nitrate efflux was the highest in this habitat, leading to a strong nutrient export towards surrounding waters. The latter was mostly derived from the impact of the physical structure of bamboo corals on particles deposition, associated to a high abundance of infaunal bioturbators (surficial modifiers). Our sample size was small due to the constraints of working in the Arctic and deep-water environments; therefore, our results should be interpreted in light of this limitation.

Bamboo corals, such as the ones found at the BB site, are vulnerable marine ecosystem indicators, and the surveyed area is part of a marine refuge (Disko Fan Conservation Area) where bottom-contact fishing activities are currently partly prohibited (Hiltz et al., 2018). A better understanding of their spatial distribution both inside and outside of the refuge boundaries, as well as of their capacity in the trapping of organic matter, and their role as habitat for epifauna is warranted. Arctic sponge gardens at the FB site, have only recently been discovered. However, although we were less successful at identifying a clear ecosystem functional role of these sponges in terms of their influence on infauna and biogeochemical fluxes, a better comprehension of sponge gardens distribution and ecological roles is still essential before they become exposed to physical damage from anthropogenic activities. In view of a seafloor homogenization due to the anticipated increase in fisheries in the Arctic, it seems necessary to extend studies on biogenic structures to better understand their role in the Arctic ecosystem functioning.

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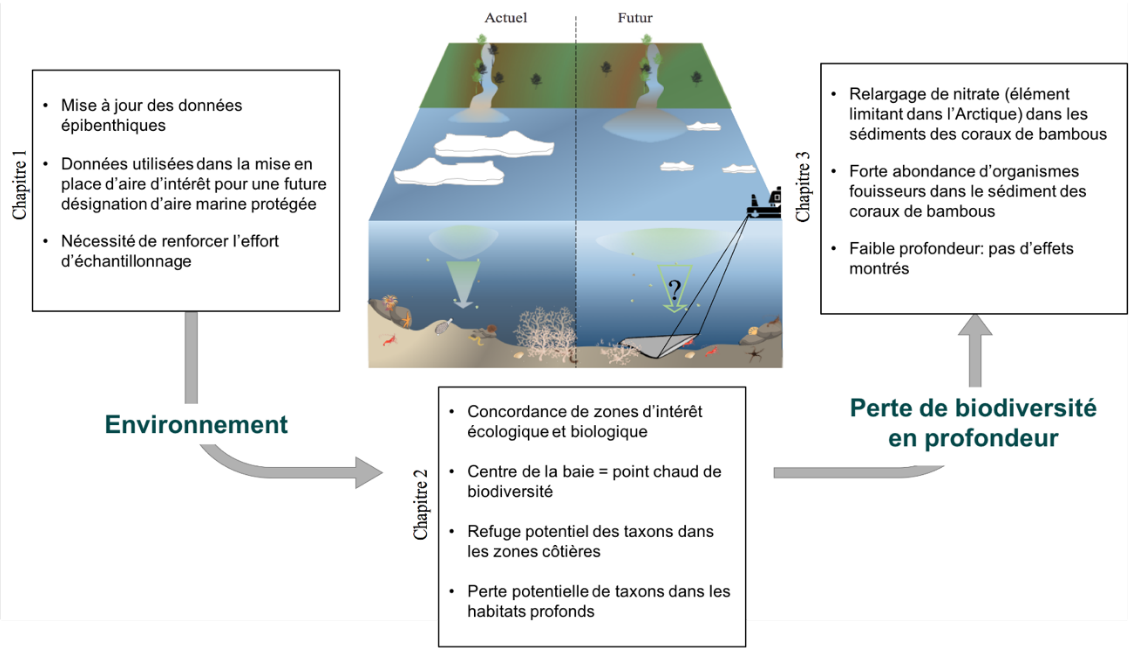
Conclusion

Cette thèse avait pour objectifs : (1) d'apporter une description la plus complète et la plus actualisée de la diversité et la distribution spatiale des communautés benthiques dans le complexe de la Baie d'Hudson; (2) de comprendre indirectement les effets des changements climatiques sur la biodiversité et le fonctionnement des écosystèmes benthiques et (3) d'enrichir nos connaissances des écosystèmes benthiques et d'appuyer la désignation de zones d'intérêt écologique et biologique (ZIEB) ainsi que des aires marines protégées. La figure 12 montre les principaux résultats et les contributions générales de l'ensemble de la thèse ci-dessous.



Chapitre 1

- Mise à jour des données épibenthiques
- Données utilisées dans la mise en place d'aire d'intérêt pour une future désignation d'aire marine protégée
- Nécessité de renforcer l'effort d'échantillonnage

Chapitre 2

- Concordance de zones d'intérêt écologique et biologique
- Centre de la baie = point chaud de biodiversité
- Refuge potentiel des taxons dans les zones côtières
- Perte potentielle de taxons dans les habitats profonds

Chapitre 3

- Relargage de nitrate (élément limitant dans l'Arctique) dans les sédiments des coraux de bambous
- Forte abondance d'organismes fouisseurs dans le sédiment des coraux de bambous
- Faible profondeur: pas d'effets montrés

Figure 12. Synthèse des principaux résultats obtenus pour répondre aux objectifs de la thèse qui étaient d'enrichir les connaissances sur les communautés benthiques du complexe de la baie d'Hudson et de comprendre les effets des changements climatiques sur les écosystèmes benthiques arctiques.

Recensement de la diversité épibenthique à l'échelle du complexe de la baie d'Hudson

Le dernier recensement des espèces épibenthiques dans le complexe de la baie d'Hudson reposait sur des données récoltées à la fin des années 80 (Atkinson et Wacasey, 1989a, 1989b). Sur la base de ces données et à l'aide d'analyses portant sur trois phyla (mollusques, arthropodes et échinodermes), Piepenburg et al. (2011) ont pu établir une diversité de 290 taxa. Sur la base de prises accessoires des chaluts de fonds, Jørgensen et al. (2016) ont estimé une richesse en espèces de la mégafaune benthique allant de 3 à 59 espèces par station. Dans le cadre du premier chapitre de cette thèse, nous nous sommes attelés à fournir le plus récent et le plus complet recensement d'espèces épibenthiques à l'échelle du complexe de la baie d'Hudson. En nous basant sur un échantillonnage de 46 stations, nous avons mesuré une richesse taxonomique macro-mégabenthique allant de 5 à 71 taxons par station. De plus, nous avons estimé la diversité épibenthique à 380 taxa, identifiés au plus bas niveau taxonomique, dont 265 au niveau de l'espèce. Malgré une faible couverture spatiale à l'échelle du complexe, nous avons été en mesure d'estimer qu'environ 71 % des taxons du complexe de la baie d'Hudson ont été recensés et que 29 % restés à découvrir. Influencée par les eaux du Labrador et arctiques, cette région s'avère intéressante d'un point de vue écologique car c'est une région de transition pour les espèces benthiques entre les écosystèmes subarctiques et arctiques. Cependant, un plus faible effort d'échantillonnage a été mené à bien dans la Baie d'Hudson par rapport aux autres régions de l'archipel, en raison d'une part de la présence de glace d'eau douce complexifiant la navigation et d'autre part de l'attrait grandissant des autres régions pour la communauté scientifique. Les données présentées dans ce chapitre témoignent d'une grande richesse des fonds marins du complexe de la baie d'Hudson mais également que toutes les données d'échantillonnage sont primordiales pour augmenter les connaissances sur la diversité benthique.

Mise en évidence de points chauds de diversité dans le complexe de la baie d'Hudson

Aux chapitres 1 et 2, nous avons démontré que les caractéristiques (biomasse, densité et diversité) et la distribution spatiale des communautés épibenthiques étaient fortement influencées par le substrat, la salinité, les ressources alimentaires et la couverture de glace.

Directement influencées par les rivières, les eaux côtières abritent des communautés moins diversifiées et dominées en termes de biomasse par des filtreurs et des suspensivores. En effet, en raison des courants importants ainsi que du substrat grossier qui caractérisent ces eaux, la remise en suspension des particules sédimentaires y est un phénomène important, permettant le développement des organismes filtreurs (Bluhm et al., 2009). De précédentes études ont montré que les gradients de salinité avaient des effets notoires et directs sur les communautés benthiques *via* l'impact de cette propriété chimique sur la physiologie et le métabolisme des organismes, mais également indirects à travers l'altération de la productivité primaire de surface (Attrill, 2002; Witman et al., 2008). Nous avons pu montrer que les importants volumes d'eaux douces étaient responsables des faibles niveaux de biomasse, d'abondance et de diversité d'espèces épibenthiques observées le long des côtes. En effet, malgré la présence de polynies dans l'est de la Baie d'Hudson, cette région, sous l'influence de nombreux rejets d'eaux douces (Déry et al., 2005; Granskog et al., 2007), arbore des organismes épibenthiques moins diversifiés et moins abondants en termes de biomasse et de densité. À l'inverse, les données récoltées dans les polynies situées plus au large, comme la polynie de Roes Welcome Sound, montrent un fort couplage pélago-benthique se traduisant par une forte productivité en termes de biomasse, de densité et richesse benthique. Le second chapitre de cette thèse a de plus permis de démontrer l'importance de la présence de glace sur la diversité épibenthique occupant le centre de la baie. Couvert de glace durant 5 à 10 mois dans l'année (Hochheim et Barber, 2014), le centre de la baie est caractérisé par une production primaire d'origine principalement sympagique (Matthes et al., *in prep.*). Cette région est ainsi façonnée par des apports nutritifs ponctuels (relargage des algues sympagiques) permettant la dominance des déposivores et des suspensivores au sein de la communauté épibenthique. Enfin, les algues sympagiques contribuent de manière plus significative que le phytoplancton aux apports de matière organique de bonne qualité nutritive sur le fond marin. Ainsi, de par son importante production sympagique, le centre de la baie se caractérise par une grande diversité des organismes épibenthiques.

Changement potentiel important des communautés épibenthiques face aux changements climatiques prédits

Les organismes benthiques réagissent aux changements naturels et anthropiques de leur environnement influençant notamment leur distribution en raison de leur grande sensibilité à la disponibilité des ressources alimentaires et à nombreux paramètres physico-chimiques (Remane et Schlieper, 1971; Cusson et al., 2007). Dans les deux premiers chapitres de cette thèse, nous avons pu montrer une forte influence des rivières (faible salinité associée à une teneur élevée en carbone organique particulaire) sur la biodiversité épibenthique. À l'aide du modèle hiérarchique de communautés d'espèces (HMSC), la distribution des communautés d'espèces épibenthiques a pu être décrite puis projetée à l'échelle de la baie d'Hudson suivant un scénario climatique RCP4.5. Il est à noter que l'application de ce modèle au milieu marin représente une première (Chapitre 2). Sous le scénario RCP4.5, la projection a montré une forte diminution de la diversité des taxons dans le centre de la baie contrastant avec une augmentation le long des côtes. Ainsi, si actuellement les producteurs sympagiques dominent la production primaire dans le centre de la baie où ils rencontrent des conditions propices à leur développement (Matthes et al., *in prep.*), on peut s'attendre dans le futur à une baisse de l'export de matière organique de grande qualité vers les fonds marins en raison de la diminution graduelle de l'épaisseur de glace. Une diminution de la richesse épibenthique dans le centre de la baie est ainsi à prévoir dans les prochaines années. Étonnamment, sous des conditions RCP4.5, les régions côtières arborent un gain en termes de diversité taxonomique malgré une augmentation de la température (+2°C) et une diminution moyenne de la salinité (-0.5) (Assis et al., 2017). De nombreux taxons tels que Mytilidae (par exemple, *Musculus discors*) ou Hiatellidae (par exemple, *Hiatella arctica*) ou encore certains Nymphonidae (par exemple, *Nymphon brevirostre*) sont présents à des latitudes relativement basses (OBIS, 2020) et dans des estuaires où la salinité peut-être inférieure à 20 (Arnaud et Bamber, 1988). Ainsi, ces taxons principalement côtiers sont souvent adaptés à une large gamme de température et de salinité à cause de la faible profondeur des eaux et de l'influence saisonnière des débits de rivières (Węslawski et al., 2009; Déry et al., 2018). Par conséquent, le changement climatique favorisera ces taxons dotés de larges tolérances thermiques et salines (Pörtner et Farrell, 2008). De plus, l'augmentation des températures des eaux côtières peut être favorable au développement des macrophytes, engendrant alors une augmentation de la diversité épibenthique. Toutefois, notre étude doit être traitée avec prudence en raison du manque de données sur les interactions biotiques, la disponibilité des ressources, l'échantillonnage des espèces côtières et l'arrivée des espèces envahissantes dans notre zone d'étude pouvant contribuer à la perte ou au gain de taxons.

Influence des habitats à structures biogéniques sur le fonctionnement de l'écosystème benthique dans l'Arctique canadien

Notre étude est la première à documenter et à comparer la biodiversité et les flux benthiques au sein de sédiments à structures biogéniques et de sédiments adjacents dépourvus de ces structures dans l'est de l'Arctique canadien (Chapitre 3). Dans de nombreuses études (par exemple, Van Oevelen et al., 2009; Cathalot et al., 2015), incluant la nôtre, il a été montré que la présence de coraux bambous permet un piégeage efficace des particules et de la matière organique qui sont normalement en faibles concentrations dans les habitats profonds. Associés à cet enrichissement de la disponibilité des ressources, les habitats à coraux bambous influencent les organismes benthiques en augmentant leur densité et en favorisant la présence de filtreurs (le bivalve *Thyasira* sp.) et de dépositivores (les oligochètes).

Outre l'influence sur la biodiversité des organismes endobenthiques, les résultats du chapitre 3 mettent en avant une plus forte reminéralisation de la matière organique dans les habitats à coraux bambous. En effet, nous avons pu montrer que les sédiments présentant ces structures agissaient comme sources d'ammonium et de nitrates ; ces derniers étant l'élément limitant pour la production primaire en Arctique (Tremblay et al., 2015). Nous avons pu confirmer que les organismes bioturbateurs sont une composante importante contrôlant la reminéralisation benthique. Les modificateurs de surface et les fouisseurs étaient suffisamment abondants pour être retenus comme variables prédictives des flux benthiques. Le rôle des organismes endobenthiques dans la modification des conditions de reminéralisation bactérienne benthique est mis en évidence par ces résultats. En effet, en aérant leurs terriers et en remaniant les sédiments de surface, ces organismes favorisent le renouvellement d'eau oxygénée dans le sédiment et donc les réactions de nitrification (Aller, 2001; Michaud et al., 2006; Belley et Snelgrove, 2016) et l'expulsion de nutriments dans l'eau sus-jacente. Dans l'ensemble, notre étude corrobore les travaux de de Froe et al. (2019)

suggérant que la présence de coraux d'eaux froides stimule les taux de libération d'ammonium et de nitrates dans les sédiments sous-jacents.

Bien que les effets des jardins d'éponges sur les flux biogéochimiques benthiques et la biodiversité endobenthique aient été mis en évidence dans d'autres études (Bett et Rice, 1992; Barrio Frojan et al., 2012; Beazley et al., 2015), nos travaux n'ont pu démontrer ces effets. Les éponges sont capables de filtrer de grandes quantités d'eau réduisant ainsi le dépôt des particules disponibles dans leur environnement pour les organismes endobenthiques. Outre la limitation du dépôt des ressources, le site de la baie de Frobisher (137 m de profondeur) présentait une forte densité de mégafaune comme des ascidies et des crinoïdes. La présence de ces derniers dans les sédiments adjacents et supposés « nus » a pu potentiellement masquer l'impact des éponges sur leur environnement.

Appui à la désignation de zones d'intérêt écologique et biologique ainsi que des aires marines protégées

D'un point de vue écologique et de gestion, il est important de désigner des zones essentielles au maintien du fonctionnement global de l'écosystème. En 2011, Pêches et Océans Canada a mis en place des zones d'importance écologique et biologique (ZIEB) mégabenthiques et macrobenthiques dans l'Arctique canadien (Kenchington et al., 2011). Les données concernant les ZIEB du complexe de la baie d'Hudson sont limitées aux organismes endobenthiques, aux données sédimentaires et à la biomasse des coraux et éponges dans le détroit d'Hudson. Cependant, ces désignations pouvaient être considérées comme partielles en raison du manque d'identification taxonomique des organismes épibenthiques, réduisant notre compréhension du fonctionnement de l'écosystème benthique.

Les données présentées dans les chapitres 1 et 2 de cette thèse peuvent ainsi servir de données de référence sur les caractéristiques des communautés épibenthiques peuplant la baie d'Hudson et de ce fait, contribuer aux désignations de futures zones essentielles. Ces données ont d'ailleurs été utilisées lors d'un travail collaboratif avec Pêches et Océans Canada afin d'estimer le potentiel écologique de la région de l'île de Southampton, désignée auparavant de ZIEB en 2011 (Kenchington et al., 2011), comme une aire marine protégée (Loewen et al., 2020). De plus, les résultats du chapitre 2 sont une première étape pour estimer les influences potentielles du changement climatique sur les communautés épibenthiques de la baie d'Hudson. De ce fait, cette étude devrait permettre de conseiller objectivement les prochaines désignations de ZIEB ou d'aires marines protégées.

La méconnaissance de la concentration et de la localisation des habitats à structures biogéniques dans le complexe de la baie d'Hudson, nous a obligés à nous tourner vers des sites dont nous avions une meilleure connaissance et qui présentaient eux aussi une potentielle vulnérabilité aux répercussions du changement climatique. Une meilleure compréhension de l'influence de ces structures sur les organismes endobenthiques et sur la reminéralisation benthique est essentielle compte tenu de l'importance qu'elles représentent dans la désignation des ZIEB. Les résultats du chapitre 3 peuvent ainsi aider les institutions gouvernementales décisionnaires dans la conservation des structures biogéniques. De telles décisions sont très attendues, notamment en raison de l'homogénéisation des fonds marins qu'engendrera l'augmentation appréhendée des pêcheries, notamment par chalutage, en Arctique (Tai et al. 2019).

Perspectives

Amélioration des modèles de projections

La baie d'Hudson est sujette à de grandes fluctuations saisonnières du débit de ses rivières en raison de la présence de nombreux barrages hydroélectriques (47 % des rivières sont régulées ; Déry et al., 2018). Ces derniers entraînent généralement une rétention d'eau durant le printemps associée à des évacuations ponctuelles et très importantes durant l'hiver. Or, ces larges afflux d'eau ont des répercussions importantes sur les propriétés physico-chimiques et biologiques des eaux estuariennes et côtières. Dans cette thèse, nous nous sommes intéressés à l'influence des paramètres physico-chimiques (observés et donc issus de régulation par les barrages) sur les communautés épibenthiques. Afin de distinguer les impacts du changement climatique (précipitation et fonte de la glace de mer) des effets de la régulation des rivières (rétention, évacuation) sur les communautés épibenthiques, il serait intéressant de tourner le modèle présentement utilisé dans le Chapitre 2, avec des données physico-chimiques obtenues à partir de scénarios avec ou sans régulation des rivières. Ces données pourront être obtenues grâce au travail de l'équipe du projet BaySys qui utilise le modèle NEMO 3.6 couplé au modèle de glace LIM2 afin d'obtenir les paramètres physico-chimiques et biologiques (production primaire et concentration de chlorophylle *a*) sous des scénarios futurs (RCP) (Ridenour et al., 2019). De même, le chapitre 1 a montré une forte influence de la concentration du carbone organique particulaire (COP) sur les caractéristiques des organismes épibenthiques. Les données de COP, issus du modèle BiGCIIM (BioGeoChemical Ice Incorporated Model), pourraient également être ajoutées afin d'améliorer notre modèle et obtenir une représentation plus réaliste de la diversité des communautés de la baie d'Hudson.

Le substrat, un facteur clé structurant les communautés benthiques

Dans de nombreuses études, incluant cette thèse (Chapitre 1), le type de substrat s'est avéré être un facteur structurant les communautés benthiques. Néanmoins, les données granulométriques (taille des grains de substrat) et du type de substrat (meuble, mixte ou dur) sont relativement manquantes et/ou déterminées à une faible résolution spatiale dans le complexe de la baie d'Hudson et dans l'Arctique en général. Ces données sont néanmoins cruciales et permettraient d'obtenir une meilleure représentation de la distribution des espèces. Traditionnellement les données granulométriques sont obtenues à l'aide d'échantillons de sédiments provenant de carottier à boîte. L'utilisation de cet instrument est limitée dans le complexe de la baie d'Hudson en raison du grand nombre de stations présentant un substrat « grossier », empêchant son utilisation. Afin de cartographier les fonds marins, l'utilisation d'un sonar à multi-faisceau combinée à un échantillonnage *in situ* (carottier à boite, benne) représente une approche prometteuse. À l'échelle du complexe de la baie d'Hudson, cette dernière permettrait de valider et d'augmenter la résolution spatiale des données granulométriques établies par Pelletier (1986) et Henderson (1989).

L'endofaune, une fraction de la communauté benthique encore peu explorée

Dans le cadre de cette thèse et en raison du nombre limité de stations échantillonnées par carottier à boîte (déploiement impossible lorsque le substrat est grossier), les communautés endobenthiques du complexe de la baie d'Hudson n'ont pu être étudiées en détail. Néanmoins, à partir des 22 stations échantillonnées, nous avons pu découvrir de nombreuses espèces qui se sont révélées intéressantes d'un point de vue écologique et taxonomique. Par exemple, nous avons recensé l'amphipode *Melita acutigena* (Brunel et al., 1998) dans une station du nord de la baie. Cette espèce n'avait été jusque-là, répertoriée qu'une seule fois dans le golfe du Saint Laurent en tant que *Melita* n.sp.A puis en tant que *Melita acutigena* (Brunel et al., 1998). À ma connaissance, cette espèce n'est pas réapparue dans la littérature depuis les travaux de Brunel et aucune description taxonomique n'a été faite jusqu'à présent. De même, à partir d'échantillons de 1955-1977 récoltés à l'échelle du complexe de la baie d'Hudson, Cusson et al. (2007) ont pu recenser le cumacé *Eudorellopsis biplicata* à l'entrée du détroit d'Hudson seulement. Nos travaux préliminaires ont permis de recenser cette espèce dans l'ouest de la baie d'Hudson, ce qui représente une première. À la différence de l'acquisition des données d'épifaune notamment par relevés annuels des prises accessoires de crevettes (Siferd, 2015), les données d'endofaune sont généralement rares en raison des limites (substrat) et de la spécificité de l'instrumentation nécessaire (carottier à boite). En raison des nombreuses conséquences potentielles du changement climatique (augmentation de la température et diminution de la salinité) dans le complexe de la baie d'Hudson, ce dernier a été identifié comme un potentiel point chaud pour l'établissement d'espèces envahissantes (Goldsmit et al., 2017, 2019, 2020). Selon les derniers modèles de projection, la mye commune (*Mya arenaria*) trouverait notamment un habitat convenable dans le sud de la baie d'Hudson (Goldsmit et al., 2017, 2019). Au vu de ces résultats, il apparait évident que la recherche doit s'intensifier dans le complexe de la baie d'Hudson pour établir des suivis des organismes benthiques (endofaune et épifaune).

Origine du carbone alimentant le compartiment benthique

Les résultats de cette thèse (Chapitre 1 et 2) ont mis en avant l'influence des apports des rivières dans les zones côtières, des polynies et du couvert de glace sur les communautés épibenthiques du complexe de la baie d'Hudson. Il a été suggéré qu'une réduction de glace de mer aurait probablement un fort impact sur la distribution du carbone dans l'Arctique en raison d'un accroissement du couplage phytoplancton-zooplancton au détriment du couplage pélago-benthique (Piepenburg, 2005; Arrigo et al., 2008; Wassmann et Reigstad, 2011). Il est ainsi nécessaire de déterminer la contribution relative des producteurs primaires (en particulier pélagiques et sympagiques) au carbone alimentant les communautés benthiques. Aucune démonstration de l'assimilation des algues de glace par les organismes benthiques n'a été investiguée dans cette thèse et dans le complexe de la baie d'Hudson à ce jour. L'utilisation de traceurs tels que les isotopes stables du carbone (^{13}C) et de l'azote (^{15}N), permettrait de nous éclairer sur l'origine du carbone (pélagique, sympagique, terrigène, macroalgal) qui alimente la faune benthique (Tamelander et al., 2006). Une seconde approche (pouvant être complémentaire) réside en l'utilisation de biomarqueurs lipidiques (isoprénoïdes hautement ramifiés (HBI) : IP_{25} et HBI III). En effet, l'IP_{25} est un biomarqueur des algues sympagiques tandis que les HBI III sont associés à une production pélagique (Brown et Belt, 2012; Brown et al., 2014). Récemment, le développement d'un nouvel outil, intitulé 'H-Print' et basé sur l'utilisation conjointe de l'IP_{25} et du HBI III, a permis d'estimer l'origine du carbone (sympagique ou pélagique) dans de nombreuses espèces marines arctiques, incluant des espèces benthiques (Brown et Belt, 2017; Brown, 2018; Kohlbach et al., 2019). L'utilisation de ces outils dans le complexe de la baie d'Hudson nous permettrait de mieux définir l'importance des algues de glace dans le fonctionnement de l'écosystème benthique afin de mieux appréhender la réponse de ce dernier dans un contexte de réchauffement climatique.

Les structures érigées : des points chauds de diversité à mieux définir

Le chapitre 3 a souligné l'importance des coraux de mers profondes dans l'amélioration du fonctionnement de l'écosystème benthique. Le site Disko Fan, hébergeant les coraux bambous, fait partie d'un refuge marin où les activités de pêche par contact avec le fond sont dorénavant interdites (Hiltz et al., 2018). Ouvert auparavant aux activités de pêche, il a été possible d'observer, durant la plongée du véhicule sous-marin téléguidé, des fragments de coraux bambous gisant sur le fond marin. Des études ont montré que les débris de coraux augmentaient la densité de la méiofaune comparée aux sédiments meubles adjacents et qu'ils étaient également responsables d'un plus grand taux de respiration (Bongiorni et al., 2010; Cathalot et al., 2015). Il serait ainsi intéressant de comparer le fonctionnement de l'écosystème benthique dans des sites présentant des coraux bambous intacts, abimés par des activités de pêche et des sédiments dépourvus de ces structures.

Au même titre, il est possible de se demander si l'effet observé sur le fonctionnement de l'écosystème benthique est attribué à la présence du corail en lui-même (vivant ou mort) ou bien à sa structure érigée. Les milieux profonds sont généralement constitués de sédiments meubles uniformes présentant peu de structure. La présence d'une structure érigée, telle que des structures artificielles, pourrait potentiellement engendrer des modifications dans l'hydrodynamisme influençant alors les flux verticaux et horizontaux des particules de la colonne d'eau près du fond. Par conséquent, l'ajout de ces structures artificielles pourrait faire prospérer les organismes de l'endofaune et accroitre le fonctionnement de l'écosystème benthique. Par ailleurs, ces structures pourraient aussi représenter une surface d'attache pour les organismes constituant l'épifaune. L'apport de telles structures dans des milieux profonds homogènes pourrait ainsi modifier considérablement la diversité et le fonctionnement de l'écosystème benthique.

Les résultats du chapitre 3 n'ont pas permis de comparer l'effet de la nature des structures biogéniques (éponges contre coraux) en raison des profondeurs très différentes à laquelle nos deux types de structures ont été échantillonnés (137 et 1000 m). Pour répondre à cette problématique, des études comparatives entre les types de structures biogéniques à profondeur semblable pourraient être envisagées. Il serait par ailleurs intéressant de déterminer s'il existe une profondeur seuil, à partir de laquelle les structures biogéniques entrainent une amélioration notable du fonctionnement de l'écosystème benthique. Les éponges et les coraux bambous ne sont pas les seules structures biogéniques présentes dans l'archipel canadien. Un site hébergeant des lits d'anémones de mer a notamment été découvert dans la baie de Baffin à environ 700 m de profondeur. Ainsi, il est important de poursuivre l'effort de recherche dans (i) la détermination des différents types de structures biogéniques peuplant l'Arctique, (ii) leur répartition, ainsi que (iii) leur rôle dans le fonctionnement de l'écosystème benthique. Le déploiement conjoint de projets de recherche tels que développés dans le chapitre 3 associés à l'utilisation de véhicule sous-marin téléguidé (notamment dans les régions présentant de forts régimes de courant), devrait permettre de répondre à ces problématiques.

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Annexes A - Chapitre 1

Table S1. 1. The table presents all taxa identified during this study in the Hudson Bay Complex.

Phylum	Class	Family	Scientific name
An**nelida**	**Clitellata**	Hirudinea	-
		Oligochaeta	-
	Polychaeta	Ampharetidae	*Ampharete* sp *Ampharete finmarchica* Ampharetidae *Amphicteis ninonae* *Melinna cristata*
		Aphroditidae	*Aphrodita aculeata*
		Capitellidae	-
		Cirratulidae	-
		Flabelligeridae	*Brada inhabilis* *Brada villosa* *Bradabyssa villosa* *Pherusa plumosa*
		Glyceridae	*Glycera capitata*
		Lumbrineridae	Lumbrineridae *Scoletoma fragilis*
		Maldanidae	Maldanidae *Notoproctus* sp
		Nephtyidae	*Micronephthys minuta* Nephtyidae *Nephtys cf.pente* *Nephtys longosetosa*
		Nereididae	*Ceratocephale loveni* Nereididae *Nereis* sp *Nereis pelagica* *Nereis zonata*
		Onuphidae	*Nothria conchylega* *Nothria hyperborea* Onuphidae
		Opheliidae	*Ophelia limacina*

		Orbiniidae	-
		Pectinariidae	*Cistenides* sp *Cistenides granulata* *Cistenides hyperborea*
		Phyllodocidae	-
		Polynoidae	*Bylgides* sp *Bylgides groenlandicus* *Bylgides promamme* *Bylgides sarsi* *Eunoe nodosa* *Eunoe oerstedi* *Gattyana* sp *Gattyana amondseni* *Gattyana cirrhosa* *Harmothoe* sp *Harmothoe extenuata* *Harmothoe imbricata* Polynoidae
		Sabellidae	*Branchiomma arcticum* *Chone* sp *Jasmineira* sp *Laonome* sp Sabellidae
		Sphaerodoridae	Sphaerodoridae
		Spionidae	Polydora_Dipolydora Spionidae
		Terebellidae	*Axionice flexuosa* *Neoamphitrite affinis* *Nicolea venustula* *Nicolea zostericola* *Pista cristata* *Pista maculata* Terebellidae
		Trichobranchidae	*Terebellides stroemii*
Arthropoda	**Hexanauplia**	Balanidae	*Balanus* sp
	Malacostraca	Acanthonotozomatidae	*Acanthonotozoma cristatum* *Acanthonotozoma inflatum*
		Ampeliscidae	*Ampelisca* sp *Ampelisca eschrichtii* *Ampelisca macrocephala*

			Ampeliscidae *Byblis* sp *Byblis gaimardii* *Haploops* sp *Haploops laevis* *Haploops robusta* *Haploops tubicola*
		Aoridae	-
		Arcturidae	*Arcturus baffini*
		Atylidae	*Atylus carinatus* *Nototropis smitti*
		Calliopiidae	*Calliopius laeviusculus* *Cleippides tricuspis* *Halirages fulvocinctus* *Halirages nilssoni* *Halirages qvadridentatus*
		Caprellidae	*Aeginina longicornis* *Caprella dubia* *Caprella septentrionalis* *Metacaprella horrida*
		Chaetiliidae	*Saduria sabini* *Saduria sibirica*
		Crangonidae	*Argis* sp *Argis dentata* *Argis lar* Crangonidae *Sabinea sarsii* *Sabinea septemcarinata* *Sclerocrangon boreas* *Sclerocrangon ferox*
		Diastylidae	Diastylidae *Diastylis cornuta* *Diastylis goodsiri* *Diastylis rathkei* *Diastylis spinulosa*
		Dulichiidae	*Dyopedos* sp
		Epimeriidae	*Epimeria (Epimeria) loricata*
		Eusiridae	Eusiridae *Eusirus cuspidatus*

			Rhachotropis aculeata *Rhachotropis oculata*
		Gammarellidae	*Gammarellus homari*
		Gammaridae	*Gammarus oceanicus*
		Idoteidae	*Synidotea bicuspida*
		Ischyroceridae	*Ericthonius megalops* *Ericthonius tolli* *Ischyrocerus anguipes*
		Janiroidea incertae sedis	*Tole* sp *Tole laciniata* *Tole spinosa*
		Leptanthuridae	*Calathura brachiata*
		Lysianassidae	Lysianassidae
		Melitidae	*Megamoera dentata* Melitidae *Quasimelita formosa*
		Munnopsidae	*Munnopsis typica* *Munnopsurus giganteus*
		Oedicerotidae	*Acanthostepheia malmgreni* *Arrhis phyllonyx* *Oediceros saginatus* Oedicerotidae *Paroediceros lynceus* *Paroediceros propinquus*
		Oregoniidae	*Hyas coarctatus*
		Paguridae	*Pagurus pubescens*
		Pandalidae	*Pandalus borealis* *Pandalus montagui*
		Paramphithoidae	*Paramphithoe buchholzi* *Paramphithoe hystrix*
		Pardaliscidae	*Pardalisca cuspidata*
		Pleustidae	*Neopleustes pulchellus* *Pleustes (Pleustes) panoplus* Pleustidae
		Pontogeneiidae	*Pontogeneia inermis* *Rozinante fragilis*
		Pontoporeiidae	*Pontoporeia femorata*
		Sergestidae	*Eusergestes arcticus*
		Stegocephalidae	*Stegocephalus* sp

			Stegocephalus inflatus
		Thoridae	*Eualus* sp *Eualus belcheri* *Eualus fabricii* *Eualus gaimardii* *Eualus macilentus* *Lebbeus* sp *Lebbeus groenlandicus* *Lebbeus polaris* *Spirontocaris spinus* *Spirontocaris arcuata* *Spirontocaris cf. intermedia* *Spirontocaris intermedia* *Spirontocaris spinus*
		Tryphosidae	*Lepidepecreum serraculum* *Lepidepecreum umbo* *Paratryphosites abyssi*
		Unciolidae	*Neohela monstrosa* *Unciola leucopis*
		Uristidae	*Anonyx* sp *Anonyx laticoxae* *Anonyx lilljeborgi* *Anonyx nugax* *Anonyx sarsi* *Onisimus* sp *Onisimus littoralis* *Onisimus plautus* *Onisimus sextonae gr.* *Tmetonyx cicada* *Tmetonyx similis*
	Pycnogonida	Callipallenidae	*Pseudopalene brevicollis*
		Nymphonidae	*Boreonymphon* sp *Boreonymphon abyssorum* *Boreonymphon robustum* *Nymphon brevirostre* *Nymphon elegans* *Nymphon helleri* *Nymphon hirtipes* *Nymphon hirtum* *Nymphon longimanum*

			Nymphon longitarse *Nymphon schimkewitschi* *Nymphon sluiteri* Nymphonidae
Brachiopoda	**Rhynchonellata**	Cancellothyrididae	*Terebratulina retusa*
		Hemithirididae	*Hemithiris psittacea*
		Laqueidae	*Glaciarcula spitzbergensis*
Bryozoa	**Gymnolaemata**	Alcyonidiidae	*Alcyonidium* sp *Alcyonidium disciforme* *Alcyonidium gelatinosum* *Alcyonidium pseudosciforme*
		Bryocryptellidae	*Cystisella saccata* *Porella compressa*
		Bugulidae	-
		Candidae	*Notoplites* sp *Scrupocellaria* sp
		Celleporidae	*Celleporina* sp
		Eucrateidae	*Eucratea loricata*
		Flustridae	*Sarsiflustra* sp *Securiflustra securifrons*
		Myriaporidae	*Leieschara* sp *Myriapora* sp
		Smittinidae	*Pseudoflustra solida* *Smittina* sp
		Umbonulidae	*Rhamphostomella* sp Umbonulidae
	Stenolaemata	Tubuliporidae	*Exidmonea* sp
Chordata	**Ascidiacea**	Ascidiacea	-
		Ascidiidae	*Ascidia* sp *Ascidia callosa* *Ascidia obliqua*
		Molgulidae	*Molgula griffithsii*
		Pyuridae	*Boltenia echinata* *Boltenia ovifera* *Halocynthia pyriformis*
		Styelidae	*Kukenthalia borealis* *Styela gelatinosa* *Styela rustica*
Cnidaria	**Anthozoa**	Actiniaria	Actiniaria

			Metridioidea
		Actiniidae	*Bolocera tuediae* *Urticina felina*
		Actinostolidae	*Stomphia coccinea*
		Amphianthidae	*Stephanauge* sp
		Metridioidea	-
		Nephtheidae	*Duva florida* *Gersemia* sp Nephtheidae
	Hydrozoa	Campanulariidae	*Campanularia* sp *Rhizocaulus verticillatus*
		Haleciidae	*Halecium sp*
		Hydrozoa	-
		Sertularellidae	-
		Sertulariidae	-
	Staurozoa	Lucernariidae	*Lucernaria* sp
Echinodermata	**Asteroidea**	Asteriidae	Asteriidae *Icasterias panopla* *Leptasterias* sp *Leptasterias (Hexasterias) polaris*
		Benthopectinidae	*Pontaster tenuispinus*
		Ctenodiscidae	*Ctenodiscus crispatus*
		Echinasteridae	*Henricia* sp
		Pterasteridae	*Pteraster* sp *Pteraster pulvillus*
		Solasteridae	*Crossaster* sp *Crossaster papposus* *Crossaster squamatus* *Solaster endeca*
	Crinoidea	Antedonidae	*Heliometra glacialis*
	Echinoidea	Strongylocentrotidae	*Strongylocentrotus* sp
	Holothuroidea	Cucumariidae	*Cucumaria frondosa*
		Dendrochirotida	-
		Eupyrgidae	*Eupyrgus scaber*
		Holothuroidea	-
		Myriotrochidae	*Myriotrochus rinkii*
		Psolidae	*Psolus fabricii*
	Ophiuroidea	Amphilepidida incertae sedis	*Ophiopus arcticus*
		Amphiuridae	*Amphiura* sp

			Amphiura sundevalli
		Gorgonocephalidae	*Gorgonocephalus sp* *Gorgonocephalus arcticus* *Gorgonocephalus eucnemis*
		Ophiacanthidae	*Ophiacantha bidentata*
		Ophiolepididae	Ophiolepididae
		Ophiopholidae	*Ophiopholis aculeata*
		Ophiopyrgidae	*Stegophiura nodosa* *Stegophiura stuwitzii*
		Ophiuridae	*Ophiocten sericeum* *Ophiura robusta* *Ophiura sarsii* Ophiuridae
		Ophiuroidea	-
Mollusca	**Bivalvia**	Arcidae	*Bathyarca glacialis*
		Astartidae	*Astarte* sp
		Cardiidae	*Ciliatocardium ciliatum* *Parvicardium pinnulatum* *Serripes groenlandicus*
		Cuspidariidae	*Cuspidaria glacialis*
		Hiatellidae	*Hiatella arctica*
		Lyonsiidae	*Lyonsia arenosa* *Lyonsia hyalina*
		Myidae	*Mya truncata*
		Mytilidae	*Crenella faba* *Dacrydium* sp *Musculus* sp *Musculus discors* *Musculus glacialis* *Musculus niger* *Mytilus* sp
		Nuculanidae	*Nuculana* sp *Nuculana minuta* *Nuculana pernula*
		Nuculidae	*Ennucula tenuis*
		Pandoridae	*Pandora glacialis*
		Pectinidae	*Chlamys islandica*
		Pectinoidea	-
		Propeamussiidae	*Similipecten greenlandicus*

		Tellinidae	*Limecola balthica*
			Macoma sp
			Macoma calcarea
			Macoma moesta
		Thyasiridae	*Genaxinus eumyarius*
			Thyasiridae
		Yoldiidae	*Portlandia arctica*
			Yoldia sp
			Yoldia amygdalea
			Yoldia hyperborea
			Yoldiella sp
			Yoldiella intermedia
			Yoldiella lenticula
			Yoldiella lucida
			Yoldiidae
	Gastropoda	Aporrhaidae	*Arrhoges occidentalis*
		Buccinidae	Buccinidae
			Buccinum sp
			Buccinum belcheri
			Buccinum finmarkianum
			Buccinum glaciale
			Buccinum hydrophanum
			Buccinum micropoma
			Buccinum scalariforme
			Colus sp
			Colus holboelli
			Colus pubescens
			Colus sabini
			Neptunea despecta
		Cancellariidae	*Admete viridula*
		Capulidae	*Ariadnaria borealis*
		Cylichnidae	*Cylichna alba*
			Cylichnoides occultus
		Dendronotidae	*Dendronotus* sp
		Lepetidae	*Lepeta caeca*
		Lottiidae	*Testudinalia testudinalis*
		Mangeliidae	*Curtitoma* sp
			Curtitoma decussata
			Curtitoma incisula
			Oenopota sp

			Oenopota elegans *Oenopota pyramidalis* *Propebela* sp *Propebela nobilis* *Propebela turricula*
		Margaritidae	*Margarites costalis* *Margarites groenlandicus* *Margarites helicinus* *Margarites olivaceus* *Margarites sordidus*
		Muricidae	*Boreotrophon clathratus* *Scabrotrophon fabricii*
		Naticidae	*Euspira pallida*
		Nudibranchia	-
		Philinidae	*Philine* sp
		Pyramidellidae	-
		Solariellidae	*Solariella* sp
		Trochidae	-
		Turridae	-
		Turritellidae	*Tachyrhynchus erosus* *Tachyrhynchus reticulatus*
		Velutinidae	*Piliscus commodus*
	Polyplacophora	Ischnochitonidae	*Stenosemus albus*
		Tonicellidae	*Tonicella marmorea*
	Scaphopoda	Gadilidae	*Siphonodentalium lobatum*
Nemertea	**Nemertea**	Nemertea	-
Porifera	**Demospongiae**	Cladorhizidae	*Cladorhiza* sp
		Mycalidae	*Mycale* sp
		Polymastiidae	*Polymastia* sp *Polymastia hemisphaerica* *Tentorium semisuberites*
Sipuncula	**Sipunculidea**	Phascolionidae	-

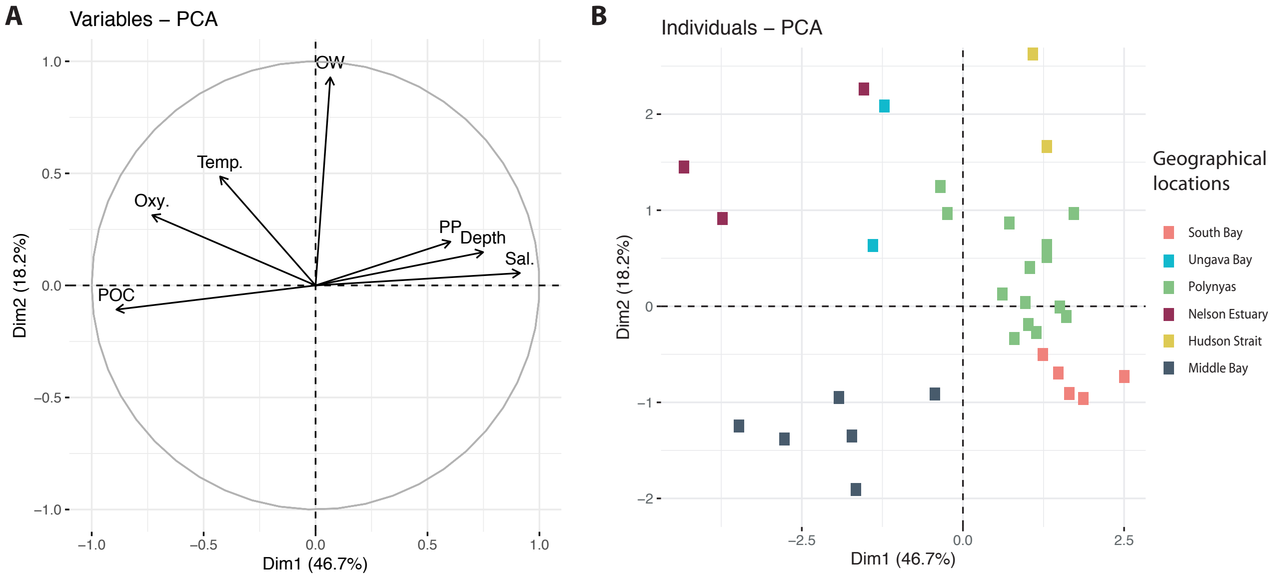

Figure S1. 1. Principal component analysis (PCA) plots among 32 stations. (A) Principal component analysis in terms of environmental variables, and (B) principal component analysis in terms of individual stations. OW indicates duration of open water, and PP indicates primary production based on interpolation from satellite data.

Table S1. 2. Results of linear regression tests of density, biomass and taxonomic richness related to principal component analysis (PCA) axes.

Variables	Estimate	t	p-value
Biomass ($R^2_{adj} = 0.13$)			
Intercept	5.50	6.46	< 0.01
PC1	0.98	2.16	< 0.05
PC2	0.89	1.19	0.25
PC3	–0.22	–0.26	0.80
Density ($R^2_{adj} = 0.19$)			
Intercept	3.76	6.76	< 0.01
PC1	0.83	2.78	< 0.05
PC2	–0.47	–0.98	0.34
PC3	–0.01	–0.02	0.99
Taxonomic richness ($R^2_{adj} = 0.12$)			
Intercept	34.32	13.62	< 0.01
PC1	3.12	2.24	< 0.05
PC2	0.13	0.06	0.95
PC3	2.21	0.89	0.38

Table S1. 3. Results of similarity of percentage (SIMPER) analysis of the taxa contributing to 70% of the dissimilarity in epibenthic composition based on biomass (g m^{-2}) of the three identified communities.

Taxa	Mean biomass		Contribution (%)
Communities 1 and 2			
	Comm. 1	Comm. 2	
Ophiuridae	2.47	1.72	29.01
Porifera	0.08	1.73	13.68
Strongylocentrotidae	0.05	0.98	10.41
Antedonidae	0.00	0.32	3.85
Ophiopholidae	0.03	0.50	3.57
Solasteridae	0.00	0.26	3.09
Nephtheidae	0.03	0.32	2.75
Thoridae	0.01	0.19	2.71
Actiniaria	0.18	0.05	2.57
Communities 1 and 3			
	Comm. 1	Comm. 3	
Ophiuridae	2.47	0.29	31.36
Strongylocentrotidae	0.05	1.59	13.69
Actiniaria	0.18	0.13	4.45
Balanidae	0.00	0.70	3.53
Porifera	0.08	0.18	3.49
Pectinidae	0.00	1.02	3.48
Oregoniidae	0.05	0.34	3.06
Gorgonocephalidae	0.00	0.25	2.97
Yoldiidae	0.22	0.02	2.90
Astartidae	0.10	0.06	2.35
Communities 2 and 3			
	Comm. 2	Comm. 3	
Ophiuridae	1.70	0.29	17.80
Strongylocentrotidae	0.98	1.59	16.78
Porifera	1.73	0.18	13.19
Antedonidae	0.32	0.16	5.00
Gorgonocephalidae	0.27	0.25	4.44
Balanidae	0.10	0.70	3.62
Pectinidae	0.02	1.02	3.56
Solasteridae	0.26	0.06	3.45
Thoridae	0.19	0.12	3.30

Annexes B - Chapitre 2

Table S2. 1. List of taxa issued from: Cusson et al., 2007, ArcticNet (2010), the Hudson Bay System study (BaySys, Pierrejean et al. submitted), the Bridging Global Change, Inuit Health and the Transforming Arctic Ocean project (BriGHT) and from the global database Ocean Biogeographic Information system OBIS (OBIS, 2020).

Phylum	**Class**	**Family**	**Species**
Arthropoda	**Malacostraca**	Acanthonotozomatidae	*Acanthonotozoma inflatum*
		Ampeliscidae	*Ampelisca* sp.
			Ampelisca eschrichtii
			Ampelisca macrocephala
			Ampeliscidae
			Byblis sp.
			Byblis gaimardii
			Haploops sp.
			Haploops laevis
			Haploops robusta
			Haploops setosa
			Haploops tubicola
		Aoridae	Aoridae
		Arcturidae	*Arcturus baffini*
		Aristiidae	*Aristias tumidus*
		Atylidae	*Atylus carinatus*
			Nototropis smitti
			Nototropis smittii
		Calliopiidae	*Calliopius laeviusculus*
			Cleippides tricuspis
			Halirages fulvocinctus
			Halirages nilssoni
		Caprellidae	*Aeginina longicornis*
			Caprella dubia

	Caprella septentrionalis
	Metacaprella horrida
Chaetiliidae	*Saduria sabini*
	Saduria sibirica
Crangonidae	*Argis dentata*
	Argis lar
	Crangonidae
	Sabinea sarsii
	Sabinea septemcarinata
	Sclerocrangon boreas
	Sclerocrangon ferox
Diastylidae	Diastylidae
	Diastylis sp.
	Diastylis cornuta
	Diastylis goodsiri
	Diastylis rathkei
	Diastylis spinulosa
Dulichiidae	*Dyopedos* sp.
	Dyopedos hirticornis
Epimeriidae	*Epimeria (Epimeria) loricata*
Eusiridae	Eusiridae
	Eusirus cuspidatus
	Rhachotropis aculeata
	Rhachotropis inflata
	Rhachotropis oculata
Gammarellidae	*Gammarellus homari*
Gammaridae	*Gammarus oceanicus*
Idoteidae	*Synidotea bicuspida*
	Synidotea marmorata
Ischyroceridae	*Ericthonius megalops*
	Ericthonius tolli
	Ischyrocerus anguipes
	Ischyrocerus commensalis

	Ischyrocerus latipes
	Ischyrocerus megacheir
Janiroidea incertae sedis	*Tole* sp.
	Tole laciniata
	Tole spinosa
Leptanthuridae	*Calathura brachiata*
Lysianassidae	Lysianassidae
	Onisimus normani
Melitidae	*Megamoera dentata*
	Melitidae
	Quasimelita formosa
Melphidippidae	*Melphidippa goesi*
Munnopsidae	*Munnopsis typica*
	Munnopsurus giganteus
	Munnopsurus sp.
Oedicerotidae	*Acanthostepheia malmgreni*
	Arrhis phyllonyx
	Oediceros borealis
	Oediceros saginatus
	Oedicerotidae
	Paroediceros lynceus
	Paroediceros propinquus
	Rostroculodes longirostris
Oregoniidae	*Hyas* sp.
	Hyas coarctatus
Paguridae	*Pagurus pubescens*
Pandalidae	*Pandalus borealis*
	Pandalus montagui
Paramphithoidae	*Paramphithoe hystrix*
Pardaliscidae	*Pardalisca cuspidata*
Pleustidae	*Neopleustes pulchellus*
	Parapleustes assimilis
	Pleustes (Pleustes) panoplus

	Pleustidae
	Pleusymtes pulchella
Pontogeneiidae	*Pontogeneia inermis*
	Rozinante fragilis
Pontoporeiidae	*Pontoporeia femorata*
Sergestidae	*Eusergestes arcticus*
Stegocephalidae	*Stegocephalus inflatus*
Stenothoidae	*Metopa glacialis*
Thoridae	*Eualus* sp.
	Eualus belcheri
	Eualus fabricii
	Eualus gaimardii
	Eualus macilentus
	Lebbeus sp.
	Lebbeus groenlandicus
	Lebbeus polaris
	Spirontocaris sp.
	Spirontocaris arcuata
	Spirontocaris cf. intermedia
	Spirontocaris intermedia
	Spirontocaris liljeborgii
	Spirontocaris phippsii
	Spirontocaris spinus
Tryphosidae	*Lepidepecreum serraculum*
	Lepidepecreum umbo
	Paratryphosites abyssi
Unciolidae	*Unciola leucopis*
Uristidae	*Anonyx* sp.
	Anonyx laticoxae
	Anonyx lilljeborgi
	Anonyx nugax
	Anonyx sarsi
	Centromedon pumilus

			Onisimus sp.
			Onisimus littoralis
			Onisimus sextonae gr.
			Tmetonyx cicada
			Tmetonyx similis
	Pycnogonida	Callipallenidae	*Pseudopalene brevicollis*
		Nymphonidae	*Boreonymphon* sp.
			Boreonymphon abyssorum
			Boreonymphon robustum
			Nymphon brevirostre
			Nymphon elegans
			Nymphon helleri
			Nymphon hirtipes
			Nymphon hirtum
			Nymphon longimanum
			Nymphon longitarse
			Nymphon schimkewitschi
			Nymphon serratum
			Nymphon sluiteri
			Nymphon stroemi
			Nymphonidae
		Phoxichilidiidae	*Phoxichilidium femoratum*
	Thecostraca	Balanidae	*Balanus* sp.
			Balanus balanus
			Balanus crenatus
			Semibalanus balanoides
Brachiopoda	**Rhynchonellata**	Cancellothyrididae	*Terebratulina retusa*
		Hemithirididae	*Hemithiris psittacea*
		Laqueidae	*Glaciarcula spitzbergensis*
Bryozoa	**Bryozoa**	Bryozoa	Bryozoa
	Gymnolaemata	Alcyonidiidae	*Alcyonidium* sp.
			Alcyonidium disciforme
			Alcyonidium pseudosciforme

		Bryocryptellidae	*Cystisella saccata*
			Porella compressa
			Porella struma
		Bugulidae	Bugulidae
		Calloporidae	*Callopora craticula*
			Cauloramphus cymbaeformis
			Tegella armifera
		Candidae	*Aquiloniella scabra*
			Notoplites sp.
			Scrupocellaria sp.
		Celleporidae	Celleporidae
			Celleporina sp.
		Eucrateidae	*Eucratea loricata*
		Flustridae	*Sarsiflustra* sp.
			Securiflustra securifrons
		Hippothoidae	*Celleporella hyalina*
		Microporidae	*Microporina articulata*
		Myriaporidae	*Leieschara* sp.
			Myriapora sp.
		Smittinidae	*Smittina* sp.
			Smittoidea propinqua
		Umbonulidae	*Posterula sarsii*
			Rhamphostomella sp.
			Rhamphostomella costata
			Umbonulidae
	Stenolaemata	Lichenoporidae	*Disporella hispida*
Chordata	**Ascidiacea**	Ascidiacea	Ascidiacea
		Ascidiidae	*Ascidia* sp.
			Ascidia callosa
			Ascidia obliqua
		Molgulidae	*Molgula griffithsii*
			Molgulidae
		Pyuridae	*Boltenia echinata*

			Boltenia ovifera
			Halocynthia pyriformis
		Styelidae	*Cnemidocarpa rhizopus*
			Styela coriacea
			Styela gelatinosa
			Styela rustica
			Styelidae
Cnidaria	**Anthozoa**	Actiniaria	Actiniaria
			Metridioidea
		Actiniidae	*Bolocera tuediae*
		Actinostolidae	*Glandulactis spetsbergensis*
			Stomphia coccinea
		Amphianthidae	*Stephanauge* sp.
		Hormathiidae	*Allantactis parasitica*
		Metridioidea	Metridioidea
		Nephtheidae	*Duva florida*
			Gersemia sp.
			Nephtheidae
	Hydrozoa	Campanulariidae	*Campanularia* sp.
			Rhizocaulus verticillatus
		Campanulinidae	*Calycella syringa*
			Cuspidella humilis
		Haleciidae	*Halecium* sp.
		Hydrozoa	Hydrozoa
		Sertularellidae	Sertularellidae
		Sertulariidae	Sertulariidae
	Staurozoa	Lucernariidae	*Lucernaria* sp.
Echinodermata	**Asteroidea**	Asteriidae	Asteriidae
			Icasterias panopla
			Leptasterias sp.
			Leptasterias (Hexasterias) polaris
			Leptasterias groenlandica
			Urasterias lincki

		Benthopectinidae	*Pontaster tenuispinus*
		Ctenodiscidae	*Ctenodiscus crispatus*
		Echinasteridae	*Henricia* sp.
		Pterasteridae	*Pteraster* sp.
			Pteraster militaris
			Pteraster pulvillus
		Solasteridae	*Crossaster* sp.
			Crossaster papposus
	Crinoidea	Antedonidae	*Heliometra glacialis*
	Echinoidea	Strongylocentrotidae	*Strongylocentrotus* sp.
	Holothuroidea	Cucumariidae	*Cucumaria frondosa*
		Dendrochirotida	Dendrochirotida
		Eupyrgidae	*Eupyrgus scaber*
		Holothuroidea	Holothuroidea
		Myriotrochidae	*Myriotrochus rinkii*
		Psolidae	*Psolus fabricii*
	Ophiuroidea	Amphilepidida	*Ophiopus arcticus*
		Amphiuridae	*Amphiura* sp.
			Amphiura sundevalli
		Gorgonocephalidae	*Gorgonocephalus* sp.
			Gorgonocephalus arcticus
		Ophiacanthidae	*Ophiacantha bidentata*
		Ophiolepididae	Ophiolepididae
		Ophiopholidae	*Ophiopholis aculeata*
		Ophiopyrgidae	*Stegophiura nodosa*
			Stegophiura stuwitzii
		Ophiuridae	*Ophiocten sericeum*
			Ophiura robusta
			Ophiura sarsii
			Ophiuridae
		Ophiuroidea	Ophiuroidea
Mollusca	**Bivalvia**	Arcidae	*Bathyarca glacialis*
		Astartidae	*Astarte* sp.

Cardiidae	*Ciliatocardium ciliatum*
	Parvicardium pinnulatum
Cuspidariidae	*Cuspidaria glacialis*
	Cuspidaria subtorta
Hiatellidae	*Hiatella arctica*
Lyonsiidae	*Lyonsia arenosa*
	Lyonsia hyalina
Myidae	*Mya pseudoarenaria*
	Mya truncata
Mytilidae	*Crenella faba*
	Dacrydium sp.
	Musculus sp.
	Musculus discors
	Musculus glacialis
	Musculus niger
	Mytilus sp.
Nuculanidae	*Nuculana* sp.
	Nuculana minuta
	Nuculana pernula
Nuculidae	*Ennucula tenuis*
Pectinidae	*Chlamys islandica*
Pectinoidea	Pectinoidea
Propeamussiidae	*Similipecten greenlandicus*
Tellinidae	*Macoma* sp.
	Macoma calcarea
	Macoma moesta
Thyasiridae	*Genaxinus eumyarius*
	Thyasira gouldi
	Thyasiridae
Yoldiidae	*Portlandia arctica*
	Yoldia sp.
	Yoldia amygdalea
	Yoldia hyperborea

		Yoldiella sp.
		Yoldiella intermedia
		Yoldiella lenticula
		Yoldiella lucida
		Yoldiidae
Gastropoda	Buccinidae	Buccinidae
		Buccinum sp.
		Buccinum belcheri
		Buccinum ciliatum
		Buccinum ciliatum sericatum
		Buccinum finmarkianum
		Buccinum glaciale
		Buccinum hydrophanum
		Buccinum micropoma
		Buccinum scalariforme
		Colus sp.
		Colus holboelli
		Colus pubescens
		Colus sabini
		Neptunea despecta
		Plicifusus kroeyeri
	Cancellariidae	*Admete viridula*
	Capulidae	*Ariadnaria borealis*
	Cylichnidae	*Cylichna alba*
		Cylichnoides occultus
	Dendronotidae	*Dendronotus* sp.
	Lepetidae	*Lepeta caeca*
	Littorinidae	*Littorina saxatilis*
	Lottiidae	*Testudinalia testudinalis*
	Mangeliidae	*Curtitoma* sp.
		Curtitoma decussata
		Curtitoma incisula
		Oenopota elegans

			Oenopota pyramidalis
			Propebela sp.
			Propebela nobilis
			Propebela turricula
		Margaritidae	*Margarites costalis*
			Margarites groenlandicus
			Margarites helicinus
			Margarites olivaceus
			Margarites sordidus
		Muricidae	*Boreotrophon truncatus*
			Scabrotrophon fabricii
		Naticidae	*Euspira pallida*
		Nudibranchia	Nudibranchia
		Philinidae	*Philine* sp.
		Trochidae	Trochidae
		Turridae	Turridae
		Turritellidae	*Tachyrhynchus erosus*
		Velutinidae	*Piliscus commodus*
	Polyplacophora	Ischnochitonidae	*Stenosemus albus*
		Tonicellidae	*Boreochiton ruber*
			Tonicella marmorea
	Scaphopoda	Gadilidae	*Siphonodentalium lobatum*
Nemertea	**Nemertea**	Nemertea	Nemertea
Porifera	**Demospongiae**	Myxillidae	*Myxilla (Myxilla) incrustans*
		Polymastiidae	*Polymastia* sp.
			Polymastia hemisphaerica
			Tentorium semisuberites
	Porifera	Porifera	Porifera
Sipuncula	**Sipuncula**	Sipuncula	Sipuncula
	Sipunculidea	Phascolionidae	*Phascolion* sp.

Table S2. 2. Set of environmental variables used in the hierarchical modelling species community under future environmental conditions. Modified from Assis et al. (2017).

Variables	**Units**	**Range RCP4.5**	**Source**	**Resolution**
Max. bottom temperature	°C	0.48 – 12.49	CCSM4, HadGEM2-ES, MIROC5 (Bio-ORACLE v2)	5 arcmin
Min. bottom salinity	-	11.74 – 33.35	CCSM4, HadGEM2-ES, MIROC5 (Bio-ORACLE v2)	5 arcmin
Depth	m	0 – 527	GEBCO (Bio-ORACLE v2)	5 arcmin
Substratum type	-	Coarse – Mud – Mixed	Modified from Henderson (1989) and Pelletier (1986)	5 arcmin
Mean ice thickness	m	0.03 – 0.38	CCSM4, HadGEM2-ES, MIROC5 (Bio-ORACLE v2)	5 arcmin

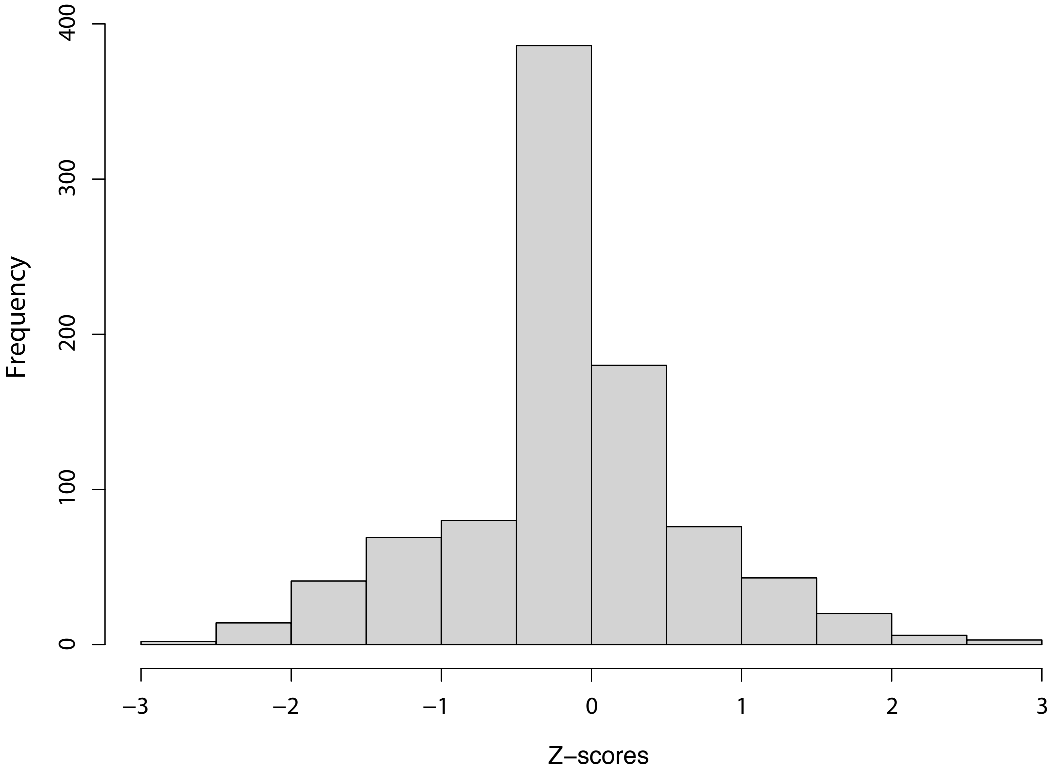

Figure S2. 1. Z-score distribution issued from Geweke diagnostics

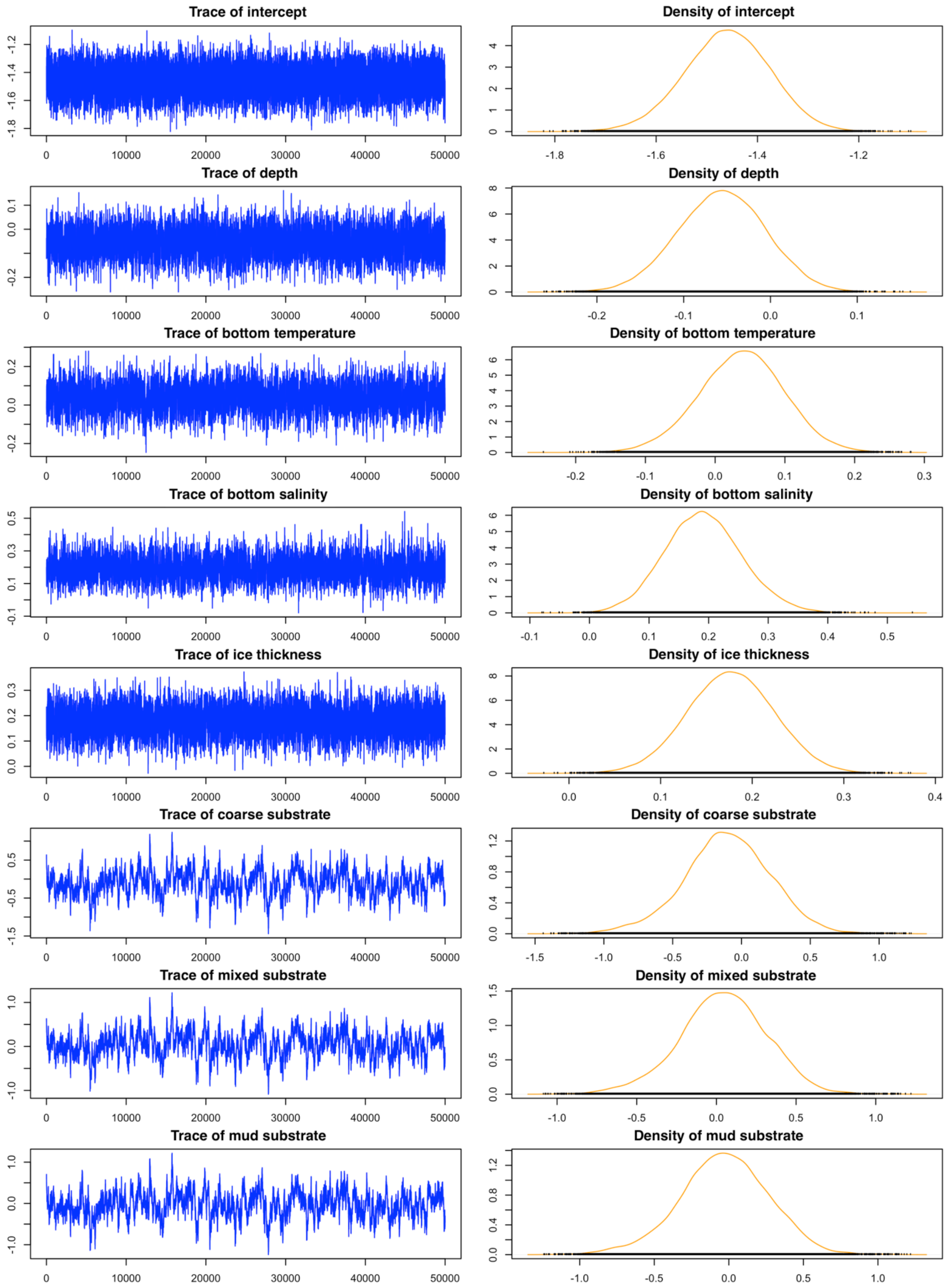

Figure S2. 2. Markov chain Monte Carlo and density plots for intercept and each parameter.

Annexes C - Chapitre 3

Table S3. 1. The table presents all taxa identified during this study and the accorded functional traits. For details on functional traits modalities, see Table 3.1.

Class	Species/Taxon	Motility	Body size	Feeding type	Bioturbation
Polychaeta	*Abyssoninoe hibernica*	M	M	CSc	B
Malacostraca	*Aceroides latipes*	M	M	C	B
Malacostraca	*Akanthophoreus gracilis*	L	S	DDt	S
Gymnolaemata	*Alcyonidium pseudodisciforme*	S	M	F	E
Malacostraca	*Ampelisca eschrichti*	L	M	F	S
Polychaeta	Ampharetidae spp.	S	M	D	UC/DC
Polychaeta	*Ancistrosyllis groenlandica*	M	L	C	B
Malacostraca	Aoridae spp.	L	M	F	S
Polychaeta	*Aphelochaeta* sp.	L	L	D	B
Gastropoda	*Ariadnaria borealis*	M	L	F	S
Polychaeta	*Aricidea* sp.	L	M	D	S
Polychaeta	*Aricidea suecica*	L	M	DF	S
Ascidiacea	*Ascidiacea*	S	M	F	S
Malacostraca	*Astacilla boreaphilis*	M	L	F	B
Bivalvia	*Astarte* sp.	L	L	F	S
Bivalvia	*Bathyarca* sp.	S	M	F	S
Bivalvia	*Bivalvia*	L	M	F	B
Malacostraca	*Brachydiastylis resima*	M	M	DF	S
Malacostraca	*Byblis* sp.	L	L	F	S
Polychaeta	*Ceratocephale loveni*	M	L	D	B
Actinopterygii	*Chaetodermis* sp.	M	L	CO	B
Ascidiacea	*Ciona intestinalis*	S	L	F	E
Polychaeta	Cirratulidae spp.	L	L	D	S
Polychaeat	*Cirrophorus* sp.	L	L	D	S
Malacostraca	Corophiidae spp.	L	M	F	S
Hydrozoa	*Corymorpha* sp.	S	M	F	E
Polychaeta	*Cossura* sp.	M	M	D	S
Malacostraca	*Cumella* sp.	M	S	C	S
Malacostraca	*Desmosomatidae* spp.	M	S	DDt	B
Bivalvia	*Ennucula tenuis*	M	M	D	S
Polychaeta	*Eteone* sp.	M	L	CSv	B
Malacostraca	*Eudorella emarginata*	M	M	DF	S
Malacostraca	*Eudorella* sp.	M	M	DF	S
Malacostraca	*Eudorellopsis integra*	M	M	DF	S
Malacostraca	*Eurycope* sp.	M	L	DtO	S
Polychaeta	Eusyllinae spp.	M	L	C	B
Gastropoda	*Frigidoalvania janmayeni*	L	M	D	S
Polychaeta	*Galathowenia* sp.	L	M	D	S
Polychaeta	*Glycera capitata*	M	L	C	B
Polychaeta	*Glyceriformia*	M	L	C	B

Table S3.1. continued

Class	Species/Taxon	Motility	Body size	Feeding type	Sediment reworking
Anthozoa	*Halcampa* sp.	L	M	C	S
Polychaeta	*Harmothoe* sp.	M	L	C	B
Malacostraca	*Harpinia serrata*	M	M	Dt	S
Malacostraca	*Harpinia* sp.	M	M	Pr	S
Malacostraca	*Hemilamprops cristatus*	M	M	Dt	S
Malacostraca	*Heterotanais* sp.	L	S	Dt	S
Bivalvia	*Hiatella arctica*	L	L	F	E
Holothuroidea	*Holothuroidea*	M	M	D	S
Hydrozoa	*Hydrozoa*	S	L	FCO	S
Malacostraca	*Ischnomesus* sp.	M	L	DDt	S
Malacostraca	*Leptostylis* sp.	M	M	Dt	S
Malacostraca	*Leucon (Atyloleucon) pallidus*	M	M	DFDt	S
Malacostraca	*Leucon (Leucon) nasica*	M	M	DFDt	S
Malacostraca	*Leucon (Leucon) nasicoides*	M	M	DFDt	S
Malacostraca	Leucothoidae spp.	L	M	F	S
Polychaeta	*Levinsenia gracilis*	L	M	D	UC/DC
Bivalvia	*Macoma calcarea*	L	L	DF	B
Polychaeta	*Maldane sarsi*	S	L	D	UC/DC
Malacostraca	*Desmosoma lineare*	M	S	D	B
Polychaeta	*Maldane* sp.	S	L	D	UC/DC
Polychaeta	*Melinna elisabethae*	L	L	D	UC/DC
Malacostraca	*Metopa* sp.	M	S	C	S
Polychaeta	*Micronephthys minuta*	M	S	C	S
Bivalvia	*Montacutinae* spp.	S	M	F	B
Malacostraca	*Munna acanthifera*	M	M	Dt	B
Malacostraca	*Munna fabricii*	M	M	Dt	B
Malacostraca	Munnopsidae spp.	M	M	Dt	B
Bivalvia	*Musculus discors*	S	L	F	S
Bivalvia	*Musculus* sp.	S	L	F	S
Polychaeta	*Myriochele* sp.	L	M	D	S
Nematoda	*Nematoda*	M	S	D	S
Polychaeta	*Neoamphitrite* sp.	L	L	D	UC/DC
Polychaeta	*Nephtys ciliata*	M	L	C	B
Polychaeta	*Nephtys* sp.	M	M	C	B
Polychaeta	*Nicomache lumbricalis*	S	L	D	UC/DC
Bivalvia	*Nuculana pernula*	L	L	D	S
Malacostraca	Oedicerotidae spp.	M	M	C	S
Clitellata	*Oligochaeta*	M	L	D	B
Ophiuroidea	*Ophiacantha bidentata*	M	L	FDDt	S
Ophiuroidea	Ophiuroidea spp.	M	L	DSc	S
Malacostraca	*Orchomenella* sp.	M	L	Sc	S
Ostracoda	*Ostracoda*	M	S	DCSc	S
Polychaeta	*Owenia* sp.	L	L	DF	UC/DC
Polychaeta	Oweniidae spp.	L	L	DF	UC/DC
Polychaeta	*Paramphinome* sp.	M	L	CSc	B
Malacostraca	*Paraoediceros lynceus*	M	M	C	B

Table S3.1. continued

Class	Species/Taxon	Motility	Body size	Feeding type	Sediment reworking
Polychaeta	Paraonidae spp.	L	M	D	S
Asteroidea	*Paxillosida*	M	L	CD	S
Sipunculidea	*Phascolion* sp.	L	L	Dt	S
Polychaeta	*Pholoe* sp.	M	S	C	S
Polychaeta	*Pista maculata*	S	L	D	UC/DC
Porifera	*Porifera*	S	L	F	E
Bivalvia	*Portlandia* sp.	L	M	D	B
Polychaeta	*Prionospio* sp.	L	M	DF	UC/DC
Polychaeta	*Protomystides* sp.	M	L	C	B
Polychaeta	*Pseudoscalibregma parvum*	M	L	D	B
Polychaeta	*Pseudoscalibregma* sp.	M	L	D	B
Malacostraca	*Pseudosphyrapus anomalus*	M	M	C	S
Malacostraca	*Pseudotanais* sp.	L	M	D	S
Malacostraca	*Rostroculodes kroyeri*	M	L	C	S
Polychaeta	*Scoletoma impatiens*	M	L	C	B
Polychaeta	*Scoletoma* sp.	M	L	C	B
Malacostraca	*Centraloecetes* sp.	L	M	D	S
Ophiuroidea	*Stegophiura nodosa*	M	L	CDt	S
Malacostraca	Stenothoidae spp.	M	M	C	S
Polychaeta	Syllidae spp.	M	M	C	S
Polychaeta	*Syllis* sp.	M	M	C	S
Malacostraca	*Tanaidacea*	L	S	Dt	S
Polychaeta	Terebellidae spp.	S	L	D	UC/DC
Polychaeta	*Terebellides stroemii*	S	L	D	UC/DC
Polychaeata	Terebellinae spp.	S	L	D	UC/DC
Rhynchonellata	*Terebratulina* sp.	S	L	F	E
Bivalvia	*Thyasira* sp.	L	M	F	UC/DC
Bivalvia	Thyasiridae spp.	L	M	F	UC/DC
Malacostraca	*Typhlotanais* sp.	L	S	D	S
Gastropoda	Velutininae spp.	M	L	C	S
Bivalvia	*Yoldiella* sp.	L	M	D	S
Polychaeta	Maldanidae spp.	S	L	D	UC/DC

Table S3. 2. Variability explained by individual axes and relationships between RDA axes and variables from redundancy analysis of benthic fluxes against environmental drivers.

	Axis 1	Axis 2
Variation out of total variation		
Proportion explained	0.28	0.15
Cumulative proportion	0.28	0.43
Variation out of fitted variation		
Proportion explained	0.66	0.34
Cumulative proportion	0.66	1.00
Relations between RDA axes and constraining variables		
Depth	0.99	-0.03
Sand	0.30	-0.95

Table S3. 3. Variability explained by individual axes and relationships between RDA axes and variables from redundancy analysis of benthic fluxes against diversity indices.

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
Variation out of total variation						
Proportion explained	0.36	0.15	0.07	0.03	0.01	0.00
Cumulative proportion	0.36	0.51	0.58	0.61	0.62	0.62
Variation out of fitted variation						
Proportion explained	0.58	0.25	0.11	0.05	0.02	0.00
Cumulative proportion	0.58	0.83	0.94	0.98	1.00	1.00
Relations between RDA axes and constraining variables						
CWM.UCDC	0.83	0.08	0.19	-0.02	-0.49	-0.16
CWM.Sessile	0.64	-0.004	0.70	-0.19	0.18	-0.14
FEve	-0.42	-0.60	0.26	0.44	-0.05	-0.45
CWM.Surficial	-0.43	-0.32	-0.04	-0.03	-0.07	0.84
CWM.Mobile	-0.58	-0.32	0.22	0.54	0.47	0.03
S	0.87	-0.09	-0.39	0.24	0.16	0.05