Université du Québec
à Rimouski

RÉPONSE À COURT TERME DE LA FAUNE BENTHIQUE AUX APPORTS DE PHYTODÉTRITUS DANS L'OCÉAN ARCTIQUE CANADIEN

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RÉSUMÉ

Les phytodétritus sont considérés comme étant l'une des sources alimentaires les plus importantes pour la faune en milieu profond. Dans les régions polaires, les algues de glace et le phytoplancton sont les principaux producteurs primaires qui peuvent atteindre le domaine benthique. L'étendue, l'épaisseur et la durée de présence du couvert de glace de mer sont fortement affectées par le changement climatique et peuvent altérer la quantité et la qualité de la matière organique qui sédimente. Pour cerner l'utilisation des deux sources de nourriture par les communautés macroendobenthiques, des expériences d'incubations en laboratoire ont été réalisées à partir de sédiments prélevés à trois stations de l'Arctique canadien (la baie de Baffin, le golfe d'Amundsen et la mer de Beaufort). Des diatomées enrichies en ^{13}C et ^{15}N, *Thalassiosira nordenskioeldii* (phytoplancton) et *Synedra hyperborea* (algues de glace), ont été utilisées comme traceurs de l'alimentation par les différents groupes de la macroendofaune. La structure des communautés était différente à chaque site et l'consomation totale des deux sources de nourriture la plus élevée a été mesurée dans la baie de Baffin où l'abondance et la biomasse de macroendofaune étaient plus élevées dans la couche superficielle de sédiments (0-5 cm) et où plus de 70% de la biomasse était représentée par les guildes trophiques de suspensivores/déposivores. Des différences significatives ont été observées dans l'consommation d'algues de glace et du phytoplancton dans la baie de Baffin, avec une consommation préférentielle du phytoplancton. Ces mêmes algues de glace et phytoplancton ont été consommées de manière similaire dans le golfe d'Amundsen et en mer de Beaufort. Ceci semble donc suggérer que les algues de glace ne sont pas consommées préférentiellement. Par conséquent, les communautés macroendobenthiques pourraient être résilientes à une réduction des apports d'algues de glace causés par une diminution de la couverture de glace de mer.

Mots clés: Arctique canadien - Communautés macroendobenthiques - Incubations - Algues de glace et phytoplancton enrichies – Isotopes stables - Changement climatique

ABSTRACT

Phytodetritus is considered as one of the most important food supplies for deep-sea fauna. In polar regions, sea ice algae and phytoplankton are the main primary producers that reach the seafloor. Sea ice cover extension and duration is being affected by climate change and may alter the quantity and quality of food reaching the seafloor (fewer ice algae and more phytoplankton biomass expected). In order to investigate the utilization of both food sources by macroinfaunal communities in different parts of the Canadian Arctic, we conducted on board pulse-chase experiments on sediment cores collected from the Baffin Bay, the Amundsen Gulf, and the Beaufort Sea. Dual-labeled (^{13}C and ^{15}N) diatoms, *Thalassiosira nordenskioeldii* (phytoplankton treatment) and *Synedra hyperborea* (ice algae treatment), were used as tracers of food consumption by macroinfaunal groups. Community structure differed among sites, and the total uptake of both food sources was greater in Baffin Bay. In this station, the highest biomass of macroinfauna was registered and more than 70% of the total biomass was represented by facultative filter feeder-surface/deposit feeders. Significant differences were found in the biomass-specific uptake of ice algae and phytoplankton only at Baffin Bay station, where phytoplankton was more consumed. While at the stations in the Amundsen Gulf and Beaufort Sea, both food sources were equally consumed. This suggest that ice algae are not preferentially uptaken and macroinfaunal communities could be resilient to a decrease in ice algal input to the seafloor inflicted by sea ice reduction.

Keywords: Canadian Arctic – Macroinfaunal community- Pulse chase experiences – Climate change- Enrichment techniques

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INTRODUCTION GÉNÉRALE

L'ÉCOSYSTÈME ARCTIQUE

Des cinq divisions océaniques mondiales, l'océan Arctique est, avec une superficie de près de 14 × 10^6 km^2 (Carroll et Carroll 2003), la composante la plus petite et la moins profonde (profondeur moyenne = 1201 m, Jakobsson 2002). Les plateaux continentaux arctiques constituent 31% de la surface totale des plateaux du monde et avec 53% de l'océan Arctique présente une profondeur inférieure à 200 m (Jakobsson et al. 2004). Le climat extrêmement froid actuel de l'Arctique persiste depuis environ 1,8 millions d'années (Bleil et Thiede 2012) et a donné lieu à l'établissement d'une banquise de glace pluriannuelle permanente qui couvre les bassins océaniques profonds dans la zone centrale de cet océan (Wadhams 2000). Entre cette région et l'océan ouvert et les côtes qui bordent l'arctique, il existe une bande dynamique, biologiquement active de couverture de glace de mer saisonnière nommée zone de glace saisonnière (ZGS) et l'endroit où cette bande de glace rencontre l'océan ouvert est connu sous le nom de zone de glace marginale (ZGM) (Carmack et Wassmann 2006). Ces aires ont été définies en anglais comme « seasonal ice zone » et « marginal ice zone ». La ZGS montre des fluctuations saisonnières marquées avec des valeurs maximales à la fin de l'hiver et interannuelles. Ce système hautement dynamique est extrêmement important pour les communautés polaires, pour les flux de carbone, les courants océaniques et la régulation du climat planétaire (Ferreyra et al. 2004).

PRODUCTEURS PRIMAIRES DANS L'OCÉAN ARCTIQUE

Au sein des écosystèmes marins arctiques, les principaux producteurs primaires se développent en eaux ouvertes (phytoplancton) et à la base de la glace de mer (algues de glace) (Syvertsen 1991, Horner et al. 1992, Hegseth 1998, McMinn et Hegseth 2004, Sakshaug 2004). Des floraisons phytoplanctoniques peuvent être également observées sous la glace de mer (Arrigo et al. 2012, Mundy et al. 2014).

Les algues de glace de mer vivent notamment attachées à la base et à l'intérieur de la glace où elles rencontrent des conditions favorables pour leur floraison au printemps, floraison qui mène à une biomasse substantielle malgré de faibles intensités lumineuses (Leu et al. 2011). La production phytoplanctonique débute, quant-à-elle, au début de l'été quand la glace de mer se met à fondre (Hsiao 1992, Leu et al. 2011). Pendant l'été, les nutriments deviennent limitants pour la croissance phytoplanctonique (Wassmann et Reigstad 2011), mais peuvent conduire à des floraisons épisodiques (Grebmeier et al. 2006). Le découplage temporelle entre la croissance des algues de glace et les floraisons phytoplanctoniques permette un allongement de la saison productive (Leu et al. 2011). Même si la période de production d'algues de glace peut égaler celle du phytoplancton, la biomasse normalisée en fonction de la superficie est généralement inférieure pour les algues de glace (5 – 10 g C m^{-2} an^{-1} vs 12 –50 g C m^{-2} an^{-1}, Legendre et al. 1992, Gosselin et al. 1997). Dans la ZGS, 25% de la production primaire totale annuelle peut être attribuée à des algues de glace (Horner et al. 1992, Hegseth 1998, Gradinger 2009). Par contre, dans l'océan Arctique central la production d'algues de glace peut atteindre 60% de la production primaire totale annuelle (Gosselin et al. 1997).

Le terme phytodétritus est considéré comme étant la matière particulaire dérivée du phytoplancton lorsqu'elle parvient sur les sédiments même si dans les agrégats il y a des cellules vivantes (Brown et Parsons 1972). Dans ce travail nous définissons les phytodétritus comme de la MO produite pendant les événements de production primaire (phytoplancton ou algues de glace) qui atteigment le fond de l'océan. Les pelotes fécales, débris de zooplancton et les fragments de macroalgues ne sont pas considérés dans la définition de phytodétritus.

APPORTS DE MATIÈRE ORGANIQUE DANS L'OCÉAN ARCTIQUE

Les écosystèmes benthiques de l'océan Arctique dépendent principalement des apports en matière organique (MO) produits dans la zone euphotique et, dans certains secteurs, des apports de MO d'origine terrigène (Wassmann 1984, Ambrose et Renaud 1995, Rachold et al. 2004). Une proportion importante (de 48 à 96%) de la MO totale générée dans les eaux de surface peut sédimenter au fond chaque année (Wassmann 1991), contribuant ainsi à un fort couplage pélago-benthique (Grebmeier et Barry 1991, Ambrose et Renaud 1995, Wassmann et al. 2006). Cela pourrait expliquer pourquoi la biomasse benthique de l'Arctique peut être plus élevée qu'à des latitudes inférieures pour des profondeurs et des substrats comparables (Petersen et Curtis 1980, Rowe 1983).

La qualité et la quantité de MO qui arrive au fond après un évènement de production primaire dans la colonne d'eau et/ou dans la glace de mer dépend des taux de broutage zooplancton et de la dégradation microbienne (Wassmann et Reigstad 2011). Si l'abondance zooplanctonique est élevée au moment de la floraison du phytoplancton, la quantité de MO arrivant sur le fond sera moins élevée (« match »)(Wassmann 1998). Inversement, lorsque les floraisons de phytoplancton ne coïncident dans le temps et l'espace avec les pic d'abondance zooplanctonique, la sédimentation de MO sera plus importante (« mismatch ») (p. ex. Sakshaug 2004).

Même si les algues de glace ne constituent pas la majeure partie de la production primaire totale, elles peuvent sédimenter au fond de l'océan sans être consommées dans la colonne d'eau (Coyle et Cooney 1988, Grebmeier et al. 1988, Boetius et al. 2013) et peuvent constituer une source de MO importante pour les organismes benthiques pendant la période précédant à la floraison phytoplanctonique (Ambrose et Renaud 1995, Grebmeier et al. 1995, 2006, Piepenburg et al. 1997, Ritzrau 1997, Ritzrau et Thomsen 1997, Grant et al. 2002, Carroll et Carroll 2003). Des algues de glace ont ainsi été observées à 4400 m de profondeur dans le bassin central arctique (Boetius et al. 2013), et peuvent donc constituer une importante source de nourriture pour les organismes benthiques de profondeur. Elles constituent par ailleurs une nourriture de haute qualité en raison de leur forte teneur en acides gras, surtout en acides gras polyinsaturés (Falk-Petersen et al. 1998), et sont importantes pour les processus de croissance et la reproduction de la faune benthique (Olsen et al. 1991, Müller-Navarra 1995, Brett et Müller-Navarra 1997, Park et al. 2002, Kainz et al. 2004).

EFFECTS DU CHANGEMENT CLIMATIQUE DANS L'ARCTIQUE

La glace de mer Arctique est sensible au réchauffement climatique. Au cours des 11 dernières années, les images satellites ont révélé une diminution accélérée de l'étendue de la glace de mer, avec une étendue minimale (septembre) de 3,39 millions de kilomètres carrés dans l'Arctique pour l'année 2012 (Cole et Rani 2015). De plus, l'épaisseur moyenne des glaces a diminué en 1,75 m, si les registres des années 1980 sont comparés à ceux des 2008 (Kwok et Rothrock 2009). Cette tendance devrait se poursuivre au cours de ce siècle (Cubasch et Meehl 2001) et pourrait ainsi entraîner de profonds changements dans la production primaire (Hegseth 1998, Wassmann et al. 2006, Bélanger et al. 2013), notamment en ce qui trait à la contribution relative des algues de glace et du phytoplancton dans les apports de MO aux organismes benthiques (Carroll et Carroll 2003, Wassmann 2011). Il a été proposé par certains auteurs que la réduction de l'étendue de la couverture de glace pourrait réduire l'intensité du couplage pélago-benthique actuel, avec une transition d'un flux dominant « algues de glace-benthos » vers un flux dominant « phytoplancton-zooplancton » (Carroll et Carroll 2003, Piepenburg 2005), provoquant dès lors une diminution de la quantité et de la qualité de la MO atteignant les fonds marins arctiques. Par contre, d'autres modèles conceptuels prédisent que les algues de glace et le phytoplancton connaîtront une période de floraison encore plus hâtive. Il en résultera une diminution de l'exportation verticale de MO mais avec une répartition plus longue dans le temps (Wassmann 2011). Rysgaard et Glud (2007) proposent, pour leur part, que l'exportation verticale de MO serait accrue avec deux épisodes de transfert, l'un au printemps et l'autre à l'automne en raison de l'allongement de la période d'eaux libres de glace. Cette hypothèse est par contre basée sur des études menées dans un fjord (Young Sound, NE Groenland).

Des modifications rapides dans la qualité et la quantité des apports de MO pourraient entraîner des changements dans l'abondance des espèces et la composition des communautés benthiques. En plus, ces organismes benthiques servent de proies pour des animaux comme certains oiseaux ou mammifères marins qui sont à la recherche de leur nourriture sur le fond, permettant un transfert d'énergie vers les niveaux trophiques supérieurs (Grebmeier et McRoy 1989, Grebmeier et al. 2006, Iken et al. 2010). Par conséquent, des changements sont également dans l'organisation des réseaux trophiques (p. ex. Grebmeier et al. 2006).

EXPÉRIENCES D'INCUBATION À BORD

L'une des stratégies utilisées pour étudier la réponse des organismes benthiques aux apports de MO consiste en des expériences d'incubation de carottes sédimentaires en présence d'une source externe de carbone. Cette technique permet de travailler avec les communautés benthiques qui sont extraites des fonds marins profonds et sont incubées dans un laboratoire à bord avec des conditions semblables à celles qui vivaient. Pour ce faire, des carottes de 10 cm de diamètre sont enfouies 20 cm dans le sédiment extrait avec le carottier à boite, puis ils sont emmenés au laboratoire, sont entièrement remplies avec de l'eau de fond, provenant de la station et sont fermée hermétiquement par un capuchon fourni d'un système d'agitation (barreau aimanté) (Fig. 1). En utilisant des algues enrichies en ^{13}C et ^{15}C comme source externe de matière organique, on peut déterminer en analysant des isotopes stables, quels organismes ont consommé la nourriture ajoutée.

Les résultats de ces expériences peuvent nous donner des indications sur la façon dont les organismes réagissent dans les situations naturelles après une sédimentation du MO au fond. Des expériences de ce genre ont été réalisées dans l'Arctique, mais elles demeurent peu nombreuses et ont concerné à ce jour les seules régions de l'archipel du Svalbard (Sun et al. 2007, 2009), de l'estuaire Kotzebue Sound (McMahon et al. 2006) et plus récemment dans le détroit de Lancaster et la polynie des eaux du Nord (Mäkelä et al. 2017a).

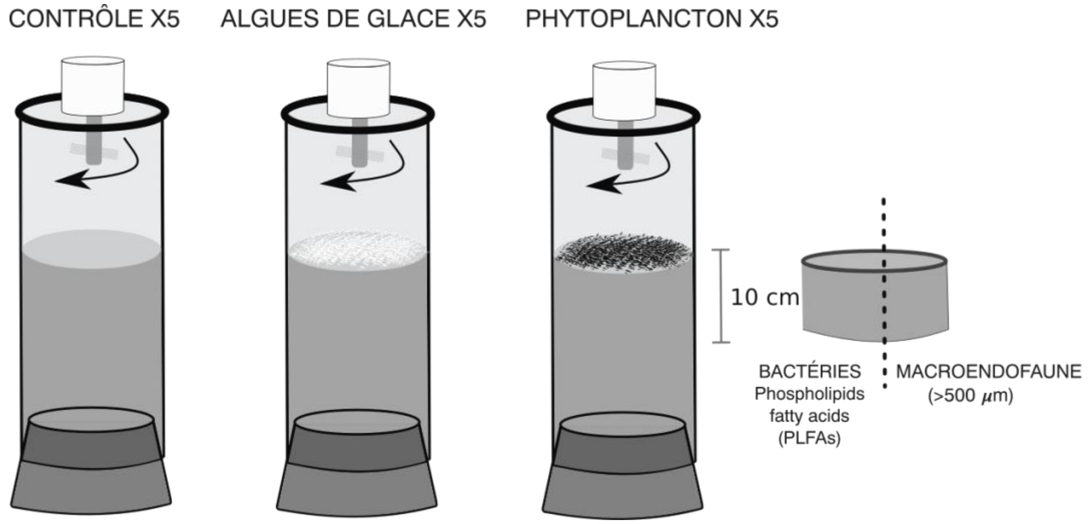


Figure 1 : Configuration des incubations faites en laboratoire à bord du navire. Des carottes sont fermée hermétiquement avec un système d'agitation (barreau aimanté), disposé en haut de chaque carotte qui permet l'homogénéisation de l'eau surnageante.

OBJECTIF GÉNÉRAL DU PROJET

Comprendre la réponse des organismes hétérotrophes aux apports des différents types de matière organique (algues de glace et phytoplancton) est important si l'on veut être en mesure de prédire les effets des changements climatiques sur l'écosystème benthique de l'Arctique. L'objectif principal de ce projet de recherche est d'identifier les réponses à court terme des communautés macroendobenthiques dans différentes régions de l'Arctique canadien aux apports de phytodétritus dérivés d'algues de glace et de phytoplancton. Pour atteindre cet objectif, des incubations à bord du brise-glace NGCC Amundsen ont été réalisées à partir de sédiments prélevés à trois stations de l'Arctique canadien (baie de Baffin, golfe d'Amundsen et le mer de Beaufort). Les trois régions choisies sont situées dans la ZGS où les organismes benthiques sont susceptibles de s'alimenter sur des phytodétritus dérivés d'algues de glace et de phytoplancton. En plus, chaque site présente différentes intensités de production primaire en offrant un scénario idéal pour faire des comparassions entre sites.

OBJECTIVES SPÉCIFIQUES

Le premier objectif spécifique est de déterminer s'il y a une consommation et une assimilation différentielles entre les algues de glace et le phytoplancton par les organismes benthiques. Le deuxième objectif spécifique est de documenter l'existence de différences régionales dans ces processus dans de l'Arctique canadien. Trois hypothèses ont été formulées dans le cadre du premier objectif : la première hypothèse (H1) est que les détritus dérivés des algues de glace seront consommés plus rapidement par les organismes benthiques, en raison des concentrations élevées d'acides gras contenus dans cette source alimentaire. La deuxième hypothèse (H2) est que les organismes benthiques exposés aux détritus dérivés des algues de glace vont mieux consumer cette nourriture dans leur biomasse en raison de sa qualité. Finalement, la troisième hypothèse (H3) est que certains taxa de la macrofaune vont assimiler plus de MO détritique en raison de leur mode d'alimentation. En ce qui concerne le deuxième objectif spécifique, l'hypothèse (H4) est que les organismes benthiques présents dans les environnements moins productifs vont réagir différemment et plus lentement aux apports de MO détritique.

CHAPITRE 1

IMPORTANCE OF SEA ICE ALGAL AND PHYTOPLANKTON DETRITUS AS FOOD SOURCES FOR THREE CONTRASTING MACROINFAUNAL COMMUNITIES OF THE CANADIAN ARCTIC

1.1 INTRODUCTION

Sedimentation of phytodetritus is recognized as the main source of food supply for deep-sea fauna (Billen et al. 1990, Gooday & Turley 1990, Pfannkuche 1993, Smith et al. 1996). In Arctic ecosystems, microscopic algae occurring in sea ice (ice algae) and in the water column (phytoplankton) are known as the main primary producers (Leu et al. 2011), and they form the phytodetrital pool that reaches the sea floor. Ice algae (mostly pennate diatoms) grows at the bottom and within the sea ice column, and reach substantial biomass, particularly during spring (Cota & Horne 1989), while phytoplankton blooms normally occur in early summer after ice breakup (Hsiao 1992, Leu et al. 2015).

In seasonal ice zones (SIZ), where sea ice is present during some part of the year, the underlying benthos could receive both types of phytodetritus. Nevertheless, the amount, nature and timing of sedimenting autotrophic material varies depending of sea-ice cover, current velocities, water depth, the mass of phytodetrital aggregates, and zooplankton grazing rates (Schewe & Soltwedel 2003) among other factors. Although phytoplankton represents the major part of total annual primary production in SIZs (Gosselin et al. 1997, Hegseth 1998, Forest et al. 2011), high ice algal biomass could also be observed during the winter-spring transition (Berge et al. 2015). And some studies reported that a large fraction of ice algae production could quickly sink to the bottom (e.g. Apollonio 1965; Anning 1989; North et al. 2014) due to the low grazing pressure during the blooming period (Lovvorn et al. 2005). This phenomenon is also suggested by observations of large aggregates of ice algae onto the sea floor (Pomeroy et al. 1990, Syvertsen 1991, Yunker et al. 1995, Macdonald et al. 1998, Ambrose et al. 2001, 2005). This suggests that incoming of organic matter (OM) could be an important contribution as early season food source for benthos after the food shortage during the winter (Ambrose et al. 2001, Morata et al. 2013, North et al. 2014).

Among all the effects of climate change in the Arctic, the decrease in extent, thickness, and duration of seasonal sea ice are the most evident and accurately registered (IPCC 2014). With a new climatic regime, less ice cover and more ice-free periods could drastically change the timing, quality and amount of phytodetritus released to bottom sediments. Phytoplankton production could increase during longer ice-free periods (Arrigo et al. 2008, Wassmann 2011), and has already been observed in some areas (Bélanger et al. 2013). Consequently, the biomass of phytoplankton detritus could become higher than that of ice algae due to the loss of sea ice. This phenomenon could provide less nutritious organic matter fluxes to the seafloor since phytoplankton species are considered as a low quality food item compared to ice algae which normally have a higher relative polyunsaturated fatty acids (PUFAs) content (36.9–43.3% vs. 22.6% [Falk-Petersen et al. 1998]; 17-18% vs. 5% [Sun et al. 2007]; 9% vs. 1% [Sun et al. 2009]). PUFAs have important roles in reproduction and growth of marine fauna (Olsen et al. 1991, Müller-Navarra 1995, Kainz et al. 2004) and many benthic organisms must obtain PUFAs from their food. Therefore, the loss of ice algae could impact Arctic food webs (McMahon et al. 2006, Leu et al. 2011) as the sea ice algal-derived lipids are also important for zooplankton (Søreide et al. 2010) and are transferred to higher trophic levels (Brown et al. 2013).

Natural stable isotope analyses showed that ice algae and phytoplankton are assimilated by benthic macrofauna (Hobson & Welch 1995, McMahon et al. 2006, Søreide et al. 2006, Tamelander et al. 2006). However, the stable isotope compositions of ice algae and phytoplankton could be similar and vary among regions making them indistinguishable in many cases (Lovvorn et al. 2005). For this reason, it is not always possible to discriminate both carbon sources from the consumer’s tissue (e.g. Iken et al. 2005). Over the last years, experimental approaches have been developed using ^{13}C-enriched ice algae and phytoplankton species to trace algal assimilation by benthic organisms. These labeled algae can be detected in the consumers allowing estimations of total uptakes by the entire community. The first feeding experiments with shallow benthic communities in the Arctic were made by McMahon et al. (2006) in the Svalbard Archipelago to investigate the consumption of fresh-frozen ice algae, ^{13}C-enriched ice algae and fresh-frozen phytoplankton by the whole community or by individual macrobenthic organisms. Sun et al. (2009) utilized similar experiences with two common benthic species of the Arctic (*Macoma balthica* and *Monoporeia affinis*) collected from the Kotzebue Sound Estuary (2–18 m depth). These authors also performed on board experiences with communities collected from ~200 m depth in northwest Svalbard and the western Barents Sea adding natural phytoplankton and ^{13}C-labeled ice algae (see Sun et al. 2007). Recently, Mäkelä et al. (2017a) presented the first results (North Water Polynya and Lancaster Sound) of a series of pulse-chase experiences performed along the Canadian Arctic, using dual-labeled ice algae and phytoplankton to compare uptakes of deep-sea macroinfauna. Our study provides additional results from three pulse-chase experiments conducted with contrasting benthic communities from Baffin Bay, Amundsen Gulf, and the Beaufort Sea regions, considered as intermediate productive areas. Our main goal was to utilize dual-labeled (^{13}C and ^{15}N) diatoms *Thalassiosira nordenskioeldii* (phytoplankton treatment) and *Synedra hyperborea* (ice algae treatment) to simulate an external food pulse and measure the macroinfauna responses. This approach is also a powerful tool to compare ice algae and phytoplankton uptakes by macrofauna in different regions of the Canadian Arctic where community characteristics can also provide information about the quantity and quality of OM in the different areas. We hypothesized that ice algae uptake would be considerably higher than phytoplankton uptake by macrofauna in all sites, as organisms would prefer a better-quality food source such as ice algae. We also predicted that in the less productive areas macrofauna would have a lower response and uptakes in comparison to high productive regions.

1.2 METHODS

1.2.1 Field sampling

On board pulse-chase experiments were carried out using sediment push cores collected from boxcore casts at three stations (Stn 435, Stn 407 and Stn 177) during ArcticNet 2015 cruise aboard the icebreaker CCGS *Amundsen* (Fig. 2). Stn 435 in the Mackenzie Shelf hereafter referred as Beaufort Sea station, and Stn 407 in the Amundsen Gulf, hereafter defined as Amundsen Gulf station, were located inside the limits of the Cape Bathurst polynya. This polynya which extends over the western part of the Amundsen Gulf and the eastern Beaufort Sea Shelf (Mackenzie Shelf), has medium primary production (90 to 175 g C m^{-2} yr^{-1}; Arrigo & van Dijken 2004) compared to the North Water polynyas (76 to 254 g C m^{-2} yr^{-1}; Klein et al. 2002). Annual particulate organic carbon (POC) fluxes al 200 m were estimated in 1.6–1.8 g C m^{-2} yr^{-1} for the Mackenzie Shelf (near Beaufort Sea station) and 2.4 g C m^{-2} yr^{-1} for Cape Bathurst Polynya (near Amundsen Gulf station) (O'Brien et al. 2006, Forest et al. 2007, Lalande et al. 2009). On the other side, Stn 117 located 20 km from the southeast coast of Baffin Island, referred hereafter as Baffin Bay station, is within an area where annual primary production ranged from 60 to 120 g C m^{-2} yr^{-1} (Sakshaug 2004). Information of POC flux are not available yet, but was considered as intermediate between Beaufort Sea station (higher) and Amundsen Gulf station (lower). All sampling stations are located in the SIZ, where benthic communities can receive both ice algae and phytoplankton food sources.

Near-bottom dissolved oxygen (O_2), temperature (T), and salinity were obtained from the ship's CTD profiler and together with sediment characteristics (e.g. mean grain size, porosity, and organic matter) at each station are given in Table 1.

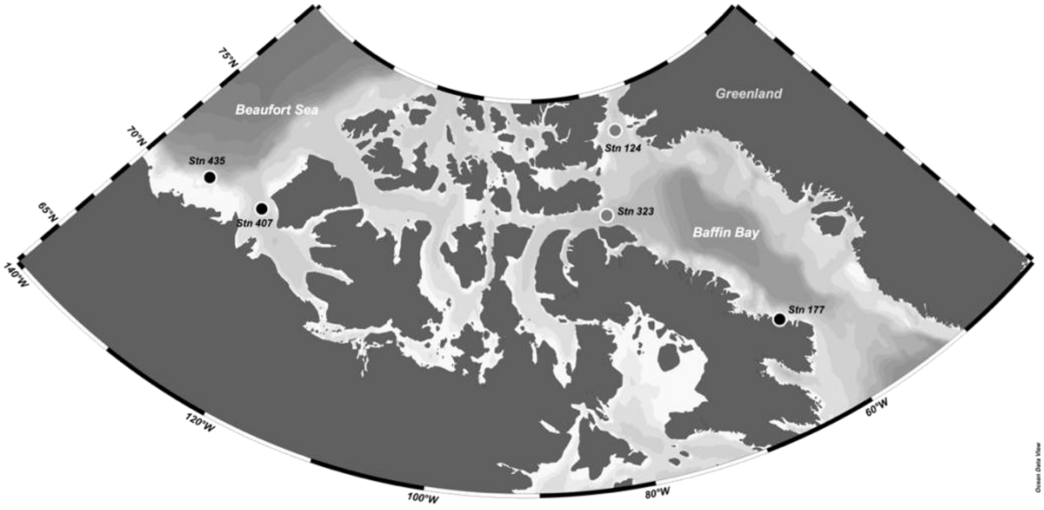


Figure 2: Map of sampled stations in this study (black dots) in the Beaufort Sea (Stn 435), Amundsen Gulf (Stn 407) and Baffin Bay (Stn 177) and stations sampled by Mäkelä et al. (2017) (gray dots).

Table 1: Summary of hydrographic and sediment characteristics for each station

	Beaufort Sea	**Amundsen Gulf**	**Baffin Bay**
ArcticNet 2015 station number	435	407	177
Latitude	71°04.74’N	70°59.62’ N	67°28.430’ N
Longitude	133°37.96’ W	126°03.39’ W	63°41.526’ W
Date sampled	27 August	23 August	25 October
Depth (m)	300	382	376
Bottom T (°C)	0.49	0.37	0.78
Bottom disolved O_2 (ml/l)	6.3	6.4	5.2
Bottom salinity (psu)	34.08	34.83	34.11
MAX Chl *a* in column water (mg /m^3)	0.7	3.34	0.53
Ch*l a* in sediments (mg /m^3)	0.96	0.27	0.48
Sediments OM content (% DW)	8.53	10.60	5.57
Surface sediment δ^{13}C (n = 3)	-25.20 ± 0.09	-23.78 ± 0.20	-22.20 ± 0.28
Surface sediment δ^{15}N (n = 3)	6.17 ± 1.39	7.09. ± 0.49	7.88. ± 1.19
C:N (w/w, n=3)	7.56 ± 0.12	6.96 ± 0.08	7.03 ± 0.84
Median grain size (μm)	15.488	7.299	10.417

1.2.2 Culture of labeled phytodetritus

Before our cruise experiments, axenic clones of ice algal species *Synedra hyperborea* (CCMP 1422, Bigelow Marine Laboratories) and phytoplankton species *Thalassiosira nordenskioeldii* (CCMP 995, Bigelow Marine Laboratories) were cultured in laboratory at 0°C (light:dark=12:12h) in F/2 artificial seawater medium (Grasshoff et al. 1999) amended with 50% ^{13}C-bicarbonate and 50% ^{15}N-nitrate during 21 days. Algae were harvested by centrifugation, freeze-dried and stored at -80°C to produce phytodetritus. The produced algae consisted of 22.3% ^{13}C and 3.0% ^{15}N (C:N ratio of 3.95 w:w) for *Synedra hyperborea* and 21.6% ^{13}C and 4.5% ^{15}N (C:N ratio of 3.52 w:w) for *Thalassiosira nordenskioeldii.* These algal species were selected as a food source because they occur in all study sites (Northern Baffin Bay: Lovejoy et al. 2002, Caron et al. 2004; Amundsen Gulf: Rózańska et al. 2009; Beaufort Sea: Horner & Schrader 1982).

1.2.3 Incubations set-up

Identical experimental protocols were followed in each station. Undisturbed cores (9.4 to 10 cm internal diameter) with about 20 cm of sediment were transported into a dark and controlled temperature room at 3°C, gently filled with ambient bottom water, sealed off with lids containing a magnetic stirrer and allowed to acclimatize for five hours before starting the experiment. Cores were randomly distributed into three treatments with five replicated each: (1) ^{13}C-^{15}N enriched ice algae detritus addition (freeze-dried *Synedra hyperborea),* (2) ^{13}C-^{15}N enriched phytoplankton detritus addition (freeze dried *Thalassiosira nordenskioeldii)* and (3) controls without food addition. To simulate a phytodetritus pulse, each treatment cores received: 425 mg C m^{-2} in Beaufort Sea station, 545 mg C m^{-2} in Baffin Bay station, and 600 mg C m^{-2} in Amundsen Gulf station. These concentrations were determined according to the POC flux estimations in each area and represented around 25% of the total annual POC flux at 200 m depth (Lalande et al. 2009). In the case of Baffin Bay station where POC estimations were not available, an intermediate quantity was used. The amount of algal N added in treatments cores was calculated using the C:N ratios. For ice algae cores, these amounts were 57 (Beaufort Sea station), 73 (Baffin Bay station) and 81 (Amundsen Gulf station) mg N m^{-2}, while in phytoplankton cores these amounts were 88 (Beaufort Sea station), 113 (Baffin Bay station) and 125 (Amundsen Gulf station) mg N m^{-2}. After the addition of food, all cores were incubated for four days in dark conditions.

1.2.4 Sample processing

After removing overlying water, the first top 10 cm of sediment in each core was extracted and was horizontally sectioned by intervals of 0–5 cm and 5-10 cm. Each layer was divided in two; one half was kept for phospholipid fatty acids (PLFAs) analyses (data not shown here) while the other half was used for macrofauna extraction using a 500 μm mesh sieve. Samples were preserved in buffered 4% formaldehyde-seawater solution. In the laboratory, organisms were rinsed in ultra-pure water, counted and categorized in taxonomic groups (mostly family level) under a binocular microscope. Each core (n=15 per station) was used as a replicate for density, biomass, and biodiversity index's calculations (Simpson's, Pielou's evenness, Shannon-Wiener index and taxonomic richness). Determination of the feeding guilds of all taxa identified was done using the available bibliography (WoRMs Editorial Board; Fauchald & Jumars 1979, Link et al. 2013, Mäkelä et al. 2017b) and five functional groups were determined: facultative filter feeder-surface deposit feeder (FF/SDF), obligate filter feeder (FF), predator-scavenger (P/S), subsurface deposit feeder (SSDF) and obligate surface deposit feeder (SDF). In order to avoid contamination, different picking instruments were used for working with labeled and unlabeled samples cores. Identified specimens were oven-dried overnight at 60 °C, encapsulated in pre-weighed tin cups and stored in a desiccator until isotopic analyses. Bivalves were decalcified by adding drops of 1M HCl until bubbling ceased (Yokoyama et al. 2005) and then again dried as above without rinsing. For the Baffin Bay station, several organisms of each taxonomic group were encapsulated together, while for the stations in the Beaufort Sea and Amundsen Gulf, specimens were encapsulated individually for isotopic analysis. In some cases, animals from the same species found in different cores were pooled together to obtain sufficient sample mass for isotope analysis. In these cases, the total uptake was divided by the number of cores pooled. Due to the small size of organisms, guts contents were not emptied, so the isotopic values represent assimilation and ingestion, called in this work as uptake. Samples for sediment δ $^{13}C/C^{12}$ and $^{15}N/N^{14}$ analysis were collected from three control cores and stored at –80°C before processing. Sediments were acidified two times with 1M HCl allowing but dried between acid additions. All samples were simultaneously analyzed for $^{13}C/C^{12}$ - $^{15}N/N^{14}$ at the UC Davis Stable Isotope Facility using using a PDZ Europa ANCA-GSL elemental analyzer (for macrofauna samples) and Micro Cube elemental analyzer (Elementar Analysensysteme GmbH, Germany; for sediment samples), both interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, Uk). The mass spectrometer was calibrated against several replicates of four or more National Institute of Standards and Technology (NIST) standards (bovine liver, glutamic acid, enriched Alanine, IsoLife Enriched Maize, Nylon 5, Nylon 6, Glutamic Acid (GLU), REF5 (KN5)).

1.2.5 Oxygen fluxes

During incubations, dissolved oxygen concentration was measured over periods of 24-hours with a non-invasive optical probe (Fibox 3 LCD- trace V6; PreSens). The flux of oxygen into sediments (SCOC) was estimated from the slope of the linear regression of dissolved oxygen concentration versus time in each core and expressed in mmol m^{-2} d^{-1}. Only linear regressions with $r^2 > 0.8$ were used for SCOC estimations and corrections were applied for the oxygen concentration changes during small volume water replacement during sampling.

1.2.6 Calculations of carbon and nitrogen uptake

Isotope ratios are expressed in the delta notation (δ ‰) as:

$$\delta\text{X}\ (‰) = \left[\left(R_{sample} - R_{reference}\right) - 1\right] x\ 1000 \qquad (1)$$

where X is ^{13}C or ^{15}N, R_{sample} is the ^{13}C/^{12}C or ^{15}N/^{14}N of the sample and $R_{reference}$ is the ^{13}C/^{12}C of the Vienna Pee Dee Belemnite standard (R_{VPDB}=0.0112372) or atmospheric air isotopic ratio (R_{atmN} = 0.0036765) for ^{15}N/^{14}N.

The total amount of C or N of algae uptaken (I $_{algae}$) by macrofauna taxa was calculated by multiplying the excess ^{13}C or ^{15}N (above natural isotope signature of taxa) by specimens C or N content (Moodley et al. 2005) and then adjusted to account for phytodetritus labelling as shown in Eq. (2).

$$I_{algae} = \frac{E * (Specimens\ C\ or\ N\ content)}{At\ \%\ phytodetritus/100} \qquad (2)$$

where Excess (E) is the difference in the fraction (F_{sample}) and the background ($F_{background}$), F is equal to R/$_{(R+1)}$ and R = (δ^{13}C / 1000 + 1) × (R_{VPDB}=0.0112372) or R = (δ^{15}N / 1000 + 1) × (R_{atmN} = 0.0036765). At % phytodetritus represents the percentage of ^{13}C or ^{15}N atoms of the total C or N present in the added labeled algae, which was 53.8 atom % ^{13}C and 45.9 atom % ^{15}N for *Thalassiosira nordenskioeldii* and 60.1 atom % ^{13}C and 36.5 atom % ^{15}N for *Synedra hyperborea*. $F_{background}$ values were calculated using macrofauna in control cores. Specimen´s C or N content expressed as unit of mass was calculated using the output of the isotopic ratio mass spectrometry (IRMS) and the dry mass in mg. The total uptake (I_{algae}) by core was measured adding up all uptakes of organisms present in each core. To get an indicator of uptake efficiency, the biomass-specific uptake was calculated dividing the (I_{algae}) by the total sample weight of the different families (Mäkelä et al. 2017a).

Macrofauna from control cores was used to estimate the natural isotopic values at each station. Only the δ^{13}C values were corrected by adding 1‰ to each δ^{13}C value to minimize the effect of formalin preservation (Sarakinos et al. 2002). The trophic levels (TL) of macrofauna were calculated using the equation:

$$TL_{consumer} = (\delta^{15} N_{consumer} - \delta^{15} N_{sediment}) / 3.8 + 1 \qquad (3)$$

where we assumed a fractionation factor of 3.8 ‰ in the $\delta^{15}N$ value per trophic level. Surface sediment bulk $\delta^{15}N$ signature was used as baseline because it better represents the long term organic matter available for benthos (e.g. Cooper et al. 2013).

For an examination of the trophic structure in each station, the package SIBER (Jackson et al. 2011) available in R software was used to calculate community-wide metrics defined by Layman et al. (2007). Three metrics were calculated in each station using the mean $\delta^{13}C$ and $\delta^{15}N$ of each family sampled in the community: (1) total area (TA) which gives higher values when the community has a larger niche space; (2) mean distance to centroid (CD) that gives a measure of the trophic diversity, with higher values indicating larger trophic separation; and (3) the mean nearest neighbour distance (MNND) providing smaller values when a large proportion of species have similar trophic niche (trophic redundancies).

1.2.7 Statistical analyses

Since the amount of C and N added in the cores differed in each experiment, the stations were considered as independent samples. Statistical comparisons among treatments for the total uptake and biomass-specific uptake were made using t-test analysis (Welch approximation used). Shapiro-Wilk test was used to test normality and homogeneity assumptions were visually examined using residuals vs fitted (predicted) values. Data were log transformed when necessary. When assumptions were not met, Mann-Whitney U-test (nonparametric test) was used. One-way ANOVA, followed by post-hoc Tukey was used to compare differences in SCOC for each treatment. The multivariate community data at the family level (Bray-Curtis similarity matrix created from the fourth-root transformed density and a resemblance matrix of Euclidean distances from biodiversity indexes) was analyzed using permutational multivariate analysis of variance (PERMANOVA) to assess differences between stations. For univariate analysis of density and biomass among stations, an Euclidean distance matrix was used to calculate resemblance before performing PERMANOVA. For both multivariate and univariate analysis, ADONIS (Permutational Multivariate Analysis of Variance Using Distance Matrices) and post hoc-ADONIS (pairwise-ADONIS; Martinez Arbizu 2017) in the vegan package of R (Oksanen et al. 2007) were used. Significance was set at $p \leq 0.05$ for most of the statistical test, however due to the high variability in the uptakes rates the significance for these cases was reported at $p \leq 0.10$, in these cases the exact p value is explicitly stated in the text. All statistical analyses and plots were carried out in R 3.4.0 (R Development Core Team 2014).

1.3 RESULTS

1.3.1 Macroinfaunal community composition

Benthic community assemblages were significantly different among stations (PERMANOVA, $P_{(perm)} < 0.01$, Table 2). At the Baffin Bay station, small Thyasiridae bivalves (mostly smaller than 1.5 mm) and Spionidae polychaetes contributed the highest proportion of the macroinfaunal assemblage, whilst sized polychaetes and nemerteans (> 10 mm) in low densities dominated at Amundsen Gulf and Beaufort stations which were more similar among them (see ANNEX I). The family of bivalves Thyasiridae was the most abundant at Baffin Bay station (46%) but only contributed to 8% of total C biomass (ANNEX II). The polychaetes Spionidae were the second more abundant group (14%) and dominated in terms of biomass representing 28% of total biomass (ANNEX II). At this station, large agglutinated foraminifera (>1 mm) make up 70 and 51% of the total biomass and densities, respectively, however they were excluded from the density and biomass calculations because it was difficult to determine if they were alive at the time of sampling. At the Amundsen Gulf station, the polychaetes *Maldane sarsi/arctica* dominated with 9% of the total density and 19% of the overall biomass (ANNEX II). At the Beaufort Sea station, the most abundant family was the Crustacea Diastylidae (6%); however, all the species occurred at low densities (between 5-3% of the total density, ANNEX II). One large Gnathidae crustacea (4 mm) and six nemerteans accounted for the 52% of the total biomass at this station and Lumbrineridae was the polychaete presenting the highest biomass (8% of total).

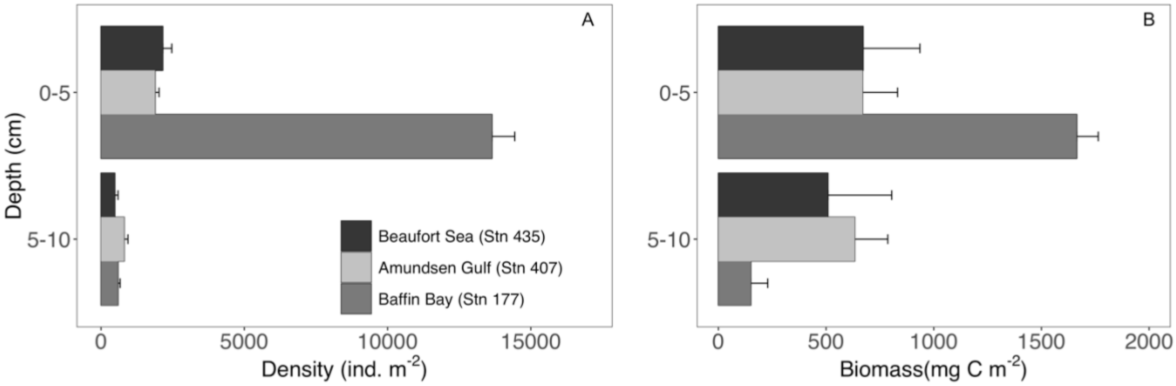


Figure 3: Mean density ± SE (A) and C biomass ± SE (B) by sediment depth in each station, using each core as a replicate (n per station =15)

Univariate PERMANOVA results indicated that the Baffin Bay station had a significantly higher total C biomass compared to the Beaufort Sea and Amundsen stations (Pseudo-F = 9.3177, $p_{(perm)}$= 0.001) in the top 0-5 cm of sediment. Different distribution patterns were also observed in the sediment depth used by organisms. At the Baffin Bay station, 91% of the total biomass was observed in the surface layer (0-5 cm), while in Amundsen Gulf and in Beaufort Sea stations organisms were more equally distributed in both layers (0-5 an 5-10 cm; Fig. 3 B). Pair-wise ADONIS comparisons for biomasses between layers 0-5 and 5 10 cm, showed no significant differences in the Amundsen Gulf station (Pseudo-F =0.002, $p_{(perm)}$= 0.867) and in the Beaufort Sea station (Pseudo-F =0.016, $p_{(perm)}$= 0.711). Different feeding modes dominated in each station (Fig. 4). In the Beaufort Sea station, the predators/scavengers (P/S) dominated with 67.2% of the total biomass. In the Amundsen Gulf station, 43.5% of the organisms were SSDF, 27.7% SDF and 16.1% P/S and in Baffin Bay station, 73.9% of the total biomass was represented by FF/SDF organisms.

Table 2: PERMANOVA results for community assemblages and diversity differences

Source of variation	df	Ms	Pseudo-F	p(perm)
Benthic community assemblages STATION	2	2.16	12.65	**0.001**
Benthic community diversity indices STATION	2	10.62	2.71	0.401

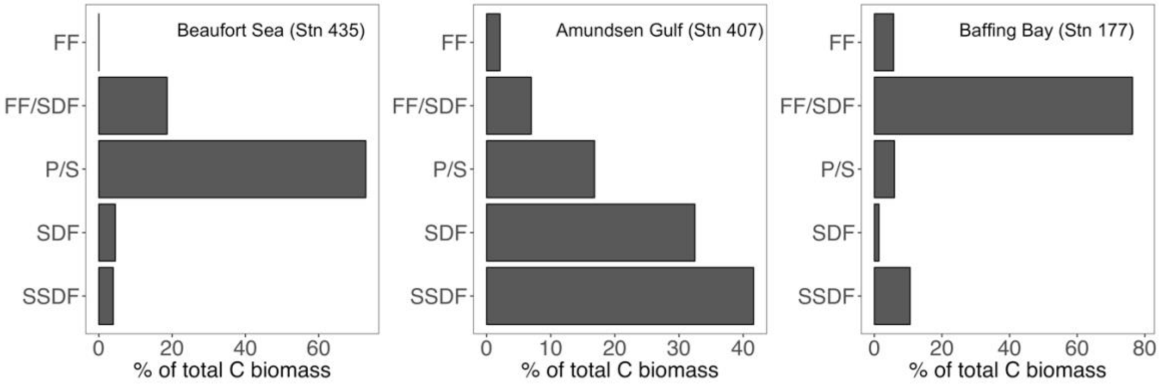


Figure 4: Macroinfaunal feeding guild represented as percentage of the total C biomass in each station. FF= obligate filter feeder, FF/SDF= filter feeder-surface deposit feeder, SDF = obligate surface deposit feeder, SSDF subsurface deposit feeder and P/S= predator-scavenger

PERMANOVA results for diversity indices did not show a significant difference ($p_{(perm)}$=0.072) among stations (Table 2). However, macrofaunal taxa and diversity index were higher at the Amundsen Gulf station (s= 26, H=1.60, simp=0.77, j=0.94) and Beaufort Sea station (s=26, H=1.67, simp=0.78, J=0.97) in contrast with Baffin Bay station (s=19, H=1.15, simp=0.56, J= 0.63).

1.3.2 Sediment community oxygen consumption

In Baffin Bay station the SCOC measured in enriched cores almost doubled, and was significantly different (F=11.27, df=2 $p \leq 0.01$), compared to control cores, but this trend was not observed in the Beaufort Sea where control and treatments cores exhibited similar SCOCs after 4 days (Fig. 5). Phytoplankton cores from Baffin Bay station had higher SCOC values although they were not significantly different from those observed in the ice algae treatment (Tuckey 's comparations p=0.487).

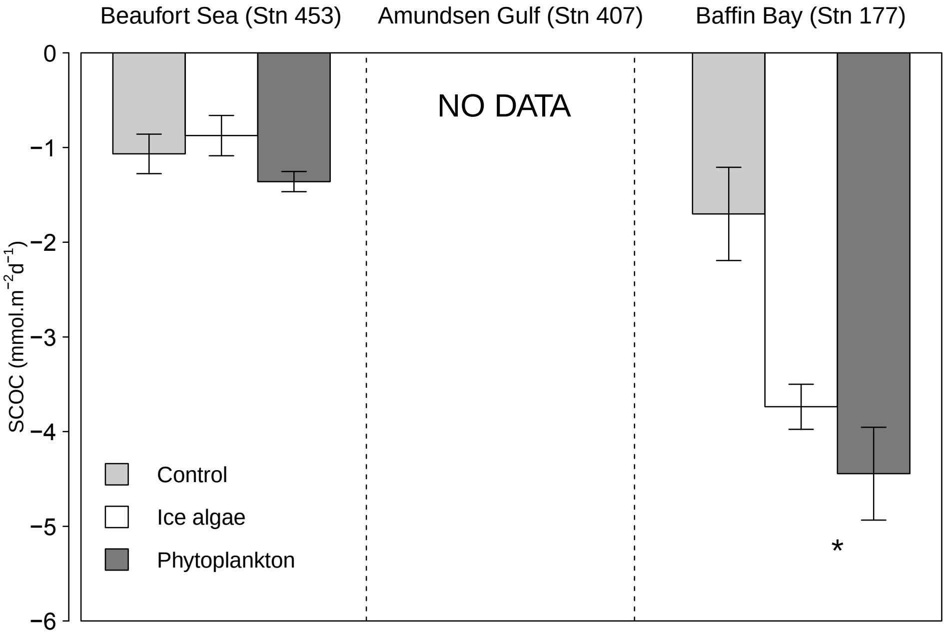


Figure 5: Mean sediment community oxygen consumption (SCOC) for control, ice algae, and phytoplankton cores at Beaufort Sea and Baffin Bay stations. Error bars represent ± SE from 5 cores by treatment. Significant differences are indicated with asterisks: $*p \leq 0.05$

1.3.3 Pulse-chase experiments

Natural isotopic values

The average $\delta^{13}C$ values for all macrofauna in Beaufort Sea, Amundsen Gulf, and Beaufort Sea stations were -24.06 ‰ ± 0.76 SD (ranging from -25.41 ‰ to -22.53 ‰, n=23), -23.43 ± 1.44 SD (ranging from -26.38 ‰ to -20.78 ‰, n=31) and -22.14 ‰ ± 1.16 SD (ranging from -24.92 ‰ to -17.79 ‰, n=24), respectively (Fig. 6). Bulk sediment δ ^{13}C values in

Beaufort Sea station ($\delta^{13}C$ = -25.2 ‰ ± 0.10 SD, n=3) and in Amundsen Gulf station ($\delta^{13}C$ = -23.78 ‰ ± 0.20 SD, n=3) were, respectively 3 ‰ and 1.4 ‰ more negative than in the Baffin Bay station ($\delta^{13}C$ = -22.2 ‰ ± 0.28 SD, n=3). The lowest $\delta\ ^{13}C$ and $\delta\ ^{15}N$ values were found for one SDF polychaeta of the family *Ampharetidae* ($\delta^{13}C$ = -25.41 ‰ and $\delta^{15}N$ = 9.29 ‰) in the Beaufort Sea station. The range in $\delta^{15}N$ of macroinfauna species was ~12 ‰ and the highest $\delta^{15}N$ signature (18.21 ‰) was measured for a Nephtyidae polychaete (*Bipalponephtys neotena)* classified as P/S (Fig. 6). The Thyasiridae and Spionidae were the only families observed at the three stations and exhibited similar $\delta^{15}N$ values, while the $\delta^{13}C$ values presented more variation that may covary with the ^{13}C values found in the sediments at each station. Occasionally, the same species appear in two (n=6) of the three stations sampled. In those cases, most of them presented similar $\delta^{13}C$ and $\delta^{15}N$ values between stations with the exception of Yoldiidae bivalves (Amundsen Gulf and Baffin Bay stations) which $\delta^{15}N$ values were notably different.

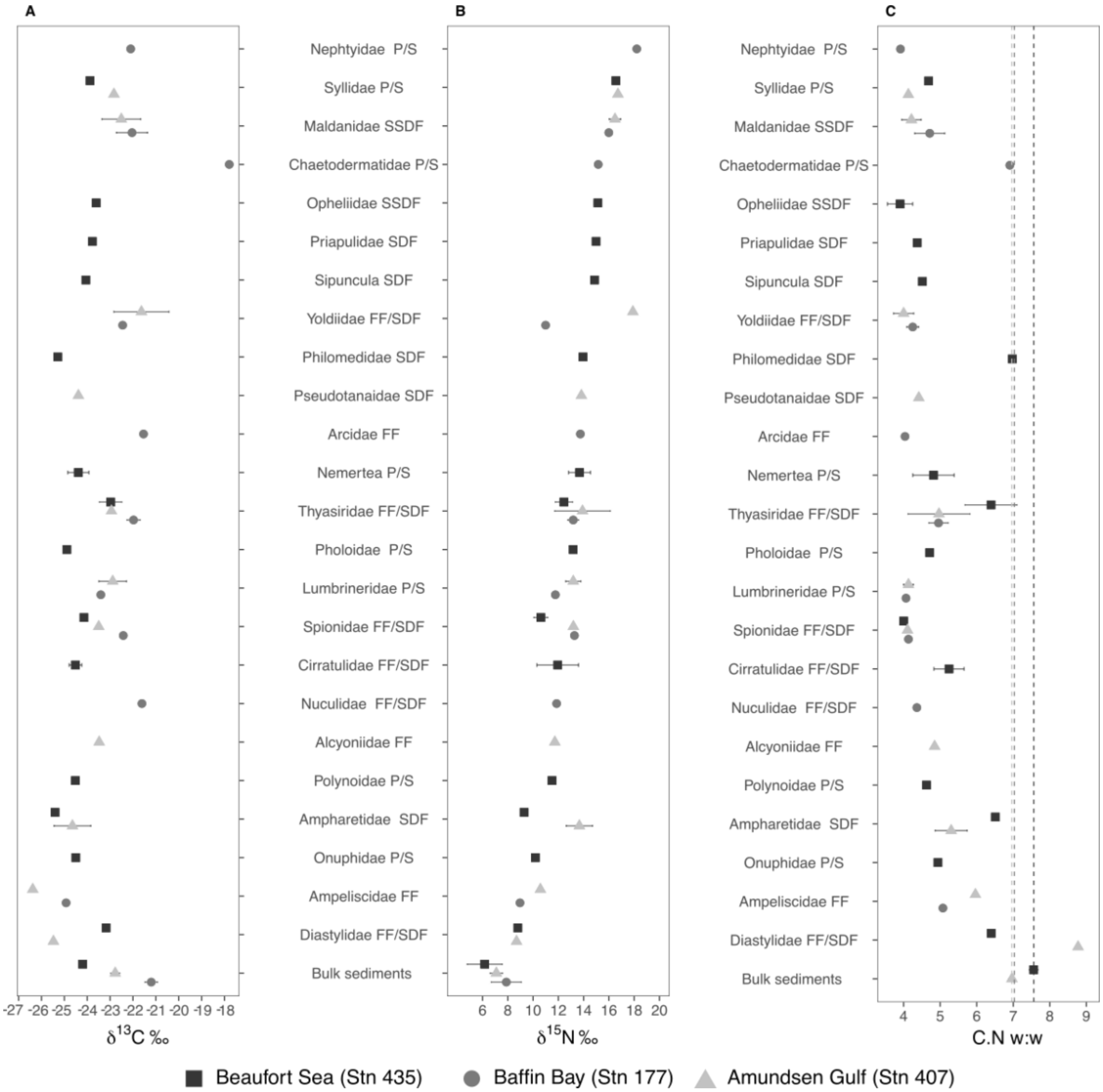


Figure 6: Natural $\delta^{13}C$ (A) and $\delta^{15}N$ (B) values, and C:N ratios (C) of macrofauna taxa and bulk sediment at Beaufort Sea station (square), Amundsen Gulf station (triangle) and Baffin Bay station (circle). Dashed lines represent the sediment C:N ratio. Error bars represent ± Standard deviations. FF= obligate filter feeder, FF/SDF= filter feeder-surface deposit feeder, SDF = obligate surface deposit feeder, SSDF subsurface deposit feeder and P/S= predator-scavenger

Median $\delta^{15}N$ values for the different feeding modes showed little variation among stations (<2‰), except for the FF/SDF in Amundsen Gulf station (Fig. 7). On average, $\delta^{15}N$ values for SSDFs were the highest of all feeding groups, although those for P/S values were similar but with more variability. The FF/SDF organisms in Baffin Bay station and Beaufort Sea station presented the lowest mean $\delta^{15}N$.

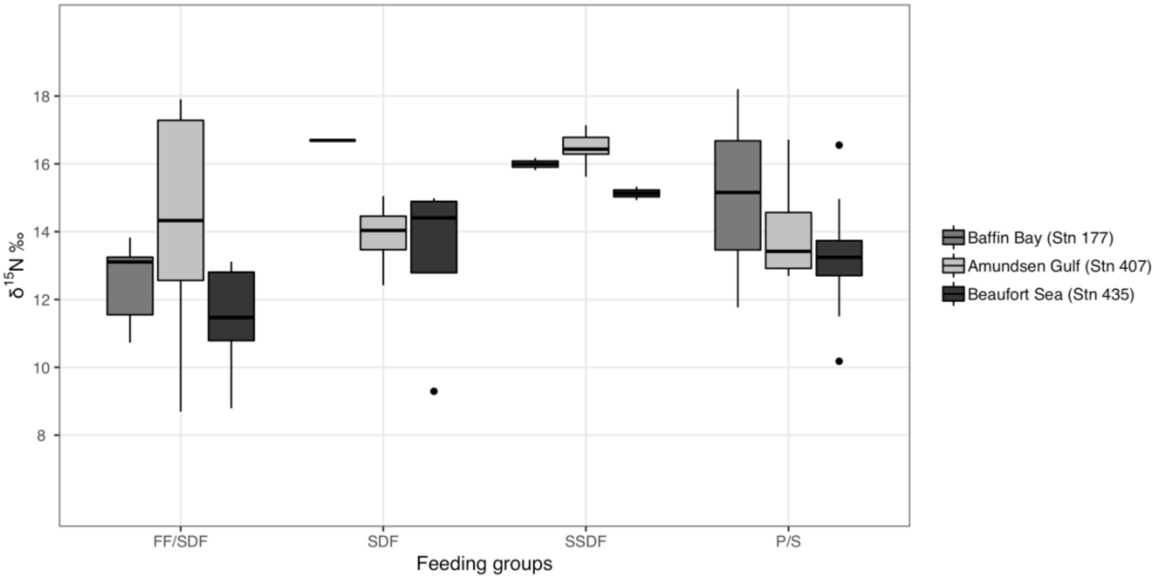


Figure 7: Box plot of background $\delta^{15}N$ signature per macroufauna feeding groups. Median values are indicated by horizontal bars in the box plots; dots outside the boxes represented outliers; box whiskers indicate the 1st and 3rd quartiles and error bars extend to the lowest and highest data value inside a range of 1.5 times the inter-quartile range, respectively. FF/SDF= filter feeder-surface deposit feeder, SDF = obligate surface deposit feeder, SSDF subsurface deposit feeder and P/S= predator-scavenger

The macroinfaunal community in Baffin Bay station presented the highest total convex hull area (TA) and mean distance to centroid (CD) which indicates higher trophic separation (Layman et al. 2007, table 3). The mean nearest neighbour distance (MNND) was also higher in this station indicating lower trophic redundancy (Layman et al. 2007). The Beaufort Sea station presented the lowest TA, CD and MNND, while Amundsen Gulf station showed intermediated values between the Baffin Bay and Beaufort Sea stations and was the station with the highest mean TL.

As we did not find natural δ ^{13}C and δ ^{15}N values higher than -17.7‰ and 18.2‰ respectively, we used δ ^{13}C > -15‰ and 15N > 19‰ to determine which organisms were labeled (evidence of incorporation of ^{13}C or ^{15}N from the labeled phytoplankton or ice algae). Macrofauna incorporated ^{13}C- and ^{15}N- labeled algae after four days of incubation, in all experiments. In Baffin Bay station 97% of the organisms present in the surface layer had enriched δ^{13}C and δ^{15}N values, while in Amundsen Gulf station and Beaufort Sea station only 52% and 35%, respectively. In some cases (one in Baffin Bay station, ten in Amundsen Gulf station and eight in Beaufort Sea station) organisms where only ^{15}N labeled. Only 20% of the organisms presented evidence of labeled algae incorporation for all stations in the deepest layer of sediment (5-10 cm).

Table 3: Community trophic metrics for the sampling station in 2015

	Beaufort Sea station	**Amundsen Gulf station**	**Baffin Bay station**
Mean TL	2.73 ± 0.54	3.01 ± 0.59	2.37 ± 0.54
TL range	1.69 - 3.73	1.42 - 3.85	1.28 - 3.72
TA	13.67	18.64	24.65
CD	2.14	2.36	2.46
MNND	0.81	1.00	1.69

* Mean TL ± SE, TL =Trophic level, TA= total convex hull area covered by all species in δ ^{13}C– δ ^{15}N bi-plot space, CD= mean Euclidean distance of each species to the δ ^{13}C– δ ^{15}N centroid and MNND= mean Euclidean distance to each species nearest neighbor in bi-plot space (Layman et al. 2007)

Ice algae and phytoplankton total C and N uptake rates

Total C and N uptakes by macroinfauna in ice algae and phytoplankton treatments for the 3 stations are represented in Figures 8A and B. Carbon and nitrogen total uptakes were higher in phytoplankton cores for all stations, however statistically significant difference was only found in Baffin Bay station (Table 4). The macroinfaunal community in Baffin Bay station took up 0.23 ± 0.04 and 0.31 ± 0.06% of the total C and N added in ice algae cores, and in phytoplankton cores the C and N uptakes represented 0.42 ± 0.08 and 0.35 ± 0.07% of the total added respectively (Table 5). In Amundsen Gulf station macrofauna took up 0.09 ± 0.03 of the total C and 0.13 ± 0.05% of the total N added in ice algae cores and 0.34 ± 0.20 and 0.33 ± 0.19% of the total C and N added in phytoplankton cores. Two large *Amage* sp. polychaetes (Ampharetidae) present in two phytoplankton cores at this station took up ~ 4 mg C m^{-2} and ~ 2.5 mg N m^{-2} respectively and were the individuals that presented highest uptakes in all our experiments. These polychaetes were responsible of the high variability in the total uptake of phytoplankton (Table 5). Without them, the average uptake was 0.32 ± 0.20 mg C m^{-2} and 0.06 ± 0.04 mg N m^{-2}. Finally, macroinfauna did uptake, 0.07 ± 0.04 and 0.11 ± 0.06% of the total C and N respectively added in ice algae cores and 0.08 ± 0.03 (C) and 0.10 ± 0.03% (N) in phytoplankton cores for the station in the Beaufort Sea.

Table 4: Statistical analysis comparations between ice algal and phytoplankton treatments for the total C and N uptake of the whole community, polychaetes and bivalves.

	Total C uptake			Total N uptake		
Beaufort Sea station	t	df	p	t	df	p
Whole community	-0.269	5.640	0.798	-0.446	6.348	0.671
Polychaetes	0.683	3.784	0.534[a]	0.375	3.776	0.728[a]
Bivalves	-3.038	2.009	**0.092**	-2.932	2.01	**0.099**
Amundsen Gulf station	t	df	p	t	df	p
Whole community	0.103	4.889	0.922 [a]	0.042	5.186	0.968 [a]
Polychaetes	0.233	5.261	0.825[a]	0.151	5.353	0.885 [a]
Bivalves	U=14		0.110	U=15		**0.059**
Baffin Bay station	t	df	p	t	df	p
Whole community	-2.020	5.697	**0.092**	-1.913	6.23	**0.102**
Polychaetes	-2.392	5.658	**0.056**	-2.11	6.127	**0.078**
Bivalves	0.248	5.122	0.814	-0.425	5.736	0.686

* a= log transformation, U=Mann-Whitney U-test, p ≤0.10 significance

Table 5: Mean total C and N uptake and % of the total C and N added in each treatment

Station	Treatment	Mean Total uptake (mg C m^2)	Mean Total uptake (mg N m^2)	% of total C added	% of total N added
Beaufort Sea station	IA	0.23±0.14	0.05±0.03	0.05±0.03	0.09±0.05
	PP	0.34±0.11	0.09±0.03	0.08±0.03	0.1±0.03
Amundsen Gulf station	IA	0.53±0.16	0.1±0.04	0.09±0.03	0.13±0.05
	PP	2.03±1.17	0.42±0.24	0.34±0.2	0.33±0.19
Baffin Bay station	IA	1.25±0.21	0.23±0.04	0.23±0.04	0.31±0.06
	PP	2.26±0.45	0.4±0.08	0.42±0.08	0.35±0.07

* ± Standard error, IA=Ice algae, PP=Phytoplankton

In all stations, polychaetes and bivalves were responsible of the major part of the C and N uptake (Fig 9 A-B). In Baffin Bay station, 70% of the phytoplankton derived C and N was taken up by polychaetes belonging to Spionidae and 15% by Lumbrineridae families. Also, in ice algae cores, Spionids were responsible for the major fraction (57 %) of the total C and N uptake, and bivalves from the family Yoldiidae were second in order with 16 %. All polychaetes together registered a more significant C and N total uptake of phytoplankton than ice algae in Baffin Bay station (Table 4). The total phytoplankton C and N uptake in Amundsen Gulf station was dominated by two large Ampharetidae polychaetes (*Amage* sp.) which pick up 76 %, followed by Spionidae with 17 %. For ice cores in the same station, the contribution to total C and N uptakes were 35% for Maldanidae, 22% for Spionidae, 22% for Ampharetidae and 14.7% for Yoldiidae. All bivalves together showed a significantly higher total N uptake of ice algae than phytoplankton in this station (p=0.059, table 4). However, ice algae cores average biomass values were considerably higher 167.42 vs 43.93 mg Dry weight (DW) m^{-2} (but not significantly different, t = 1.425; df = 6.381; p≥ 0.05). The lowest total uptakes were observed in Beaufort Sea station, where Spionidae was almost the unique family that took up C and N in the ice algae cores with 94% of the total uptake followed by 3% for Mytilidae bivalves. The total phytoplankton derived C and N uptake was produced by Yoldiidae (41%), Mytilidae (23%) and the soft coral Alcyoniidae (17%). The bivalves presented a significantly higher C and N uptake of phytoplankton in this station (p=0.092, Table 5), but biomass was significantly higher in this treatment (t=-2.725; df= 3.822; p≤0.05) which could influence the uptake results.

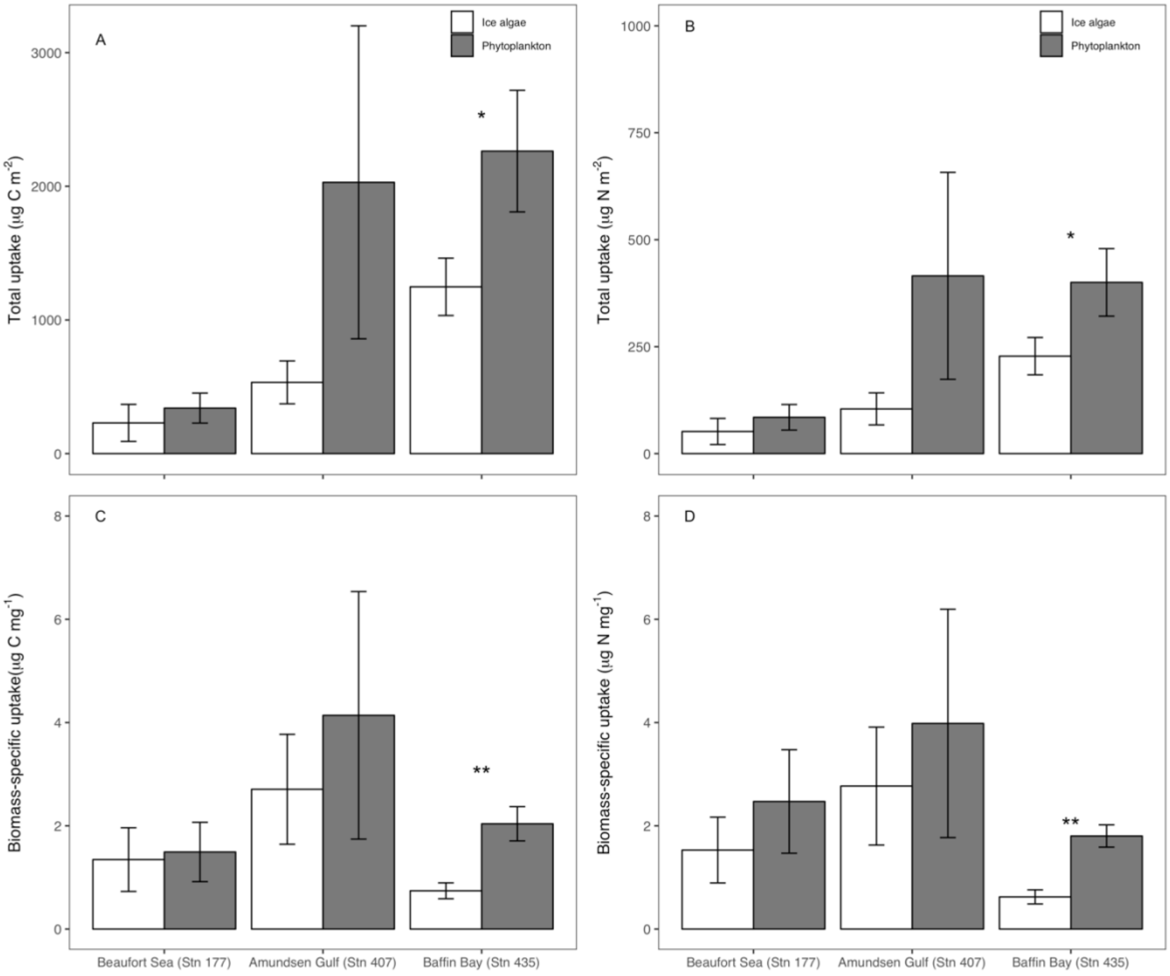


Figure 8: Mean ± (SE) ice algae and phytoplankton total C and N uptake (A-B) and mean (±SE) ice algae and phytoplankton total C and N biomass-specific uptake (C-D) by macroinfaunal communities at Beaufort Sea, Amundsen Gulf and Baffin Bay stations. Significant differences are indicated with asterisks: $*p \leq 0.10$ $**p \leq 0.05$

Total uptakes of ice algae and phytoplankton in the Baffin Bay and Beaufort Sea stations were dominated by FF/SDF organisms, while in the Amundsen Gulf station the SDF organisms (mostly due to the *Amage* sp. polychaetes) were the ones that presented the highest phytoplankton uptakes (ANNEX VI). When statistical tests were possible, no significant differences were found in the total C and N uptake between treatments for the different feeding guild (ANNEX VII).

Biomass-specific uptake of ice algae and phytoplankton C and N

Biomass-specific uptake of phytoplankton derived C and N was on average higher than that of ice algae counterpart at all stations (Fig 8 C-D). This difference was only significantly higher in the Baffin Bay station (Table 7). The highest average values of biomass-specific uptake were found in Amundsen Gulf station (2.42 ± 1.14 μg C mg^{-1} and 2.46 ± 1.28 μg N mg^{-1} for ice algae and 4.16 ± 2.39 μg C mg^{-1} and 3.99 ± 2.21 μg N mg^{-1} for phytoplankton). In all stations, polychaetes from the family Spionidae and Yoldiidae bivalves where amongst the top three dominant species in terms of biomass-specific uptakes (Table 6). Only Spionidae in Beaufort Sea station and Yoldiidae in Amundsen Gulf station showed higher biomass-specific uptakes in ice algae cores vs phytoplankton; however, in most cases few samples could be measured due to the low biomass of the organisms which prevented any statistical comparison. The highest C and N biomass-specific uptakes were 20.34 ± 2.71 μg C mg^{-1} and 20.65 ± 12.09 μg N mg^{-1} registered by the polychaetes Spionidae and Ampharetidae respectively in phytoplankton treatment at Amundsen Gulf station. Finally, polychaetes and bivalves in Baffin Bay station had significantly higher biomass-specific C and N uptake in phytoplankton cores (Table 7).

Table 6: Mean ± SE (n) biomass-specific C and N uptake of the top 3 species by station

		Beaufort Sea station		**Amundsen Gulf station**		**Baffin Bay station**	
Family	Treatment	μg C mg^{-1}	μg N mg^{-1}	μg C mg^{-1}	μg N mg^{-1}	μg C mg^{-1}	μg N mg^{-1}
Yoldiidae	PP	9.40±8.44$_{(2)}$	15.82±14.01$_{(2)}$	0.042 $_{(1)}$	0.03$_{(1)}$	3.94±0.45$_{(5)}$	4.01±0.85$_{(5)}$
	IA	0.02±0.003$_{(2)}$	0.02±0.006$_{(2)}$	9.60$_{(1)}$	10.35$_{(1)}$	1.77±0.82$_{(5)}$	1.60±0.71$_{(5)}$
Spionidae	PP	1.36±1.26$_{(2)}$	1.41±1.34$_{(2)}$	20.35±2.71$_{(2)}$	16.28±0.11$_{(2)}$	3.18±1.09$_{(5)}$	1.22±0.36$_{(5)}$
	IA	8.60±0.70$_{(2)}$	8.06±0.94$_{(2)}$	19.03±9.30$_{(2)}$	18.68±11.92$_{(2)}$	2.23±0.57$_{(5)}$	1.05±0.28$_{(5)}$
Ampharetidae	PP	-	-	18.32±11.48$_{(3)}$	20.65±12.10$_{(3)}$	-	-
	IA	-	-	2.94±2.37$_{(3)}$	2.92±2.56$_{(3)}$	-	-
Lumbrineridae	PP	-	-	-	-	3.91±2.41$_{(4)}$	2.74±1.53$_{(4)}$
	IA	-	-	-	-	0.48±0.15$_{(4)}$	0.40±0.12$_{(4)}$
Mytilidae	PP	5.55$_{(1)}$	8.81$_{(1)}$	-	-	-	-
	IA	5.04$_{(1)}$	9.71$_{(1)}$	-	-	-	-

* number between parenthesis () represents the number of samples analysed

Table 7: Statistical analysis comparations between ice algal and phytoplankton treatments for the biomass-specific C and N uptake of the whole community, polychaetes and bivalves.

	Biomass-specific C uptake			Biomass-specific N uptake		
Beaufort Sea station	t	df	p	t	df	p
Whole community	0.372	5.603	0.724	-0.357	6.906	0.732
Polychaetes	0.451	4.459	0.673^{a}	0.582	4.762	0.587^{a}
Bivalves	-1.761	3.320	0.168	-1.744	3.111	0.176
Amundsen Gulf station	t	df	p	t	df	p
Whole community	-0.003	7.242	0.997 ^{a}	U=14		0.841
Polychaetes	0.087	5.679	0.933^{a}	0.112	5.787	0.914^{a}
Bivalves	0.636	3.144	0.568	0.712	3.078	0.526
Baffin Bay station	t	df	p	t	df	p
Whole community	-3.457	5.241	**0.017**	-4.719	7.401	**0.002**
Polychaetes	-2.191	5.881	**0.071^{a}**	-2.415	4.391	**0.067**
Bivalves	-2.3924	7.343	**0.046**	-2.330	6.812	**0.054**

* a= log transformation, U=Mann-Whitney U-test, $p \leq 0.10$ significance

With the exception of Amundsen Gulf station, where SDF feeding guild presented the higher biomass-specific uptake of phytoplankton (due to the large *Amage* sp.), FF/SDF was the feeding mode that consumed the most of both algal sources in all stations. In Baffin Bay station, *Lumbrineris* sp. Polychaetes, which are described as P/S, showed an important biomass-specific uptake of phytoplankton. No significant differences were found in the biomass-specific C and N uptake between treatments for the different feeding guilds (ANNEX VI).

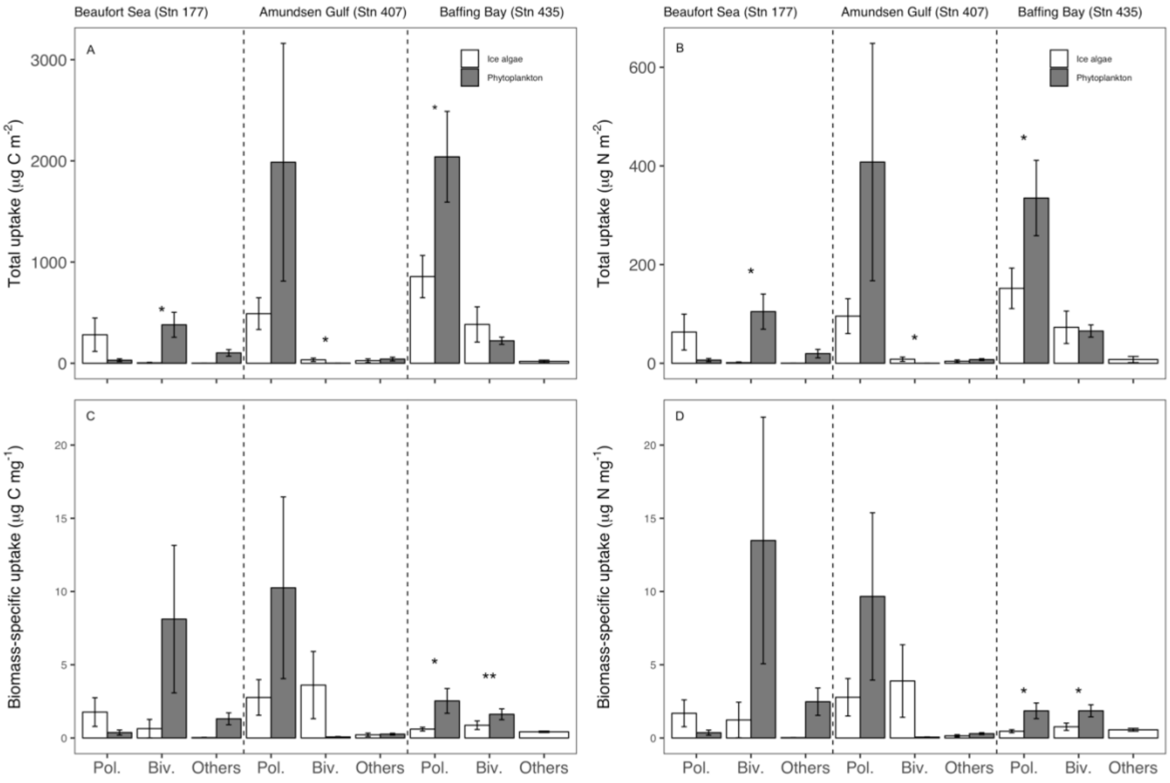


Figure 9: Mean (±SE) ice algae and phytoplankton total C and N uptake (A-B) and mean (±SE) ice algae and phytoplankton total C and N biomass-specific uptake (C-D) by polychaetes (Pol.), bivalves (Biv.) and other (Others) taxa at Beaufort Sea, Amundsen Gulf, and Baffin Bay stations. Significant differences are indicated with asterisks: $^*p \leq 0.10$ $^{**}p \leq 0.05$

Calculations of biomass-specific C:N uptake ratio

The ratio of biomass-specific C uptake to biomass N uptake was used to investigate the preferences for N and C by macroinfaunal groups (Fig. 10). Values at the three stations ranged from 0.5 to 1.8 and were lower than phytoplankton (3.52) and ice algae (3.95) C:N ratios suggesting that all macrofauna groups preferred the N uptake compared to C. Natural C:N of macrofauna are also presented in Figure 6-C and range between 4-9.

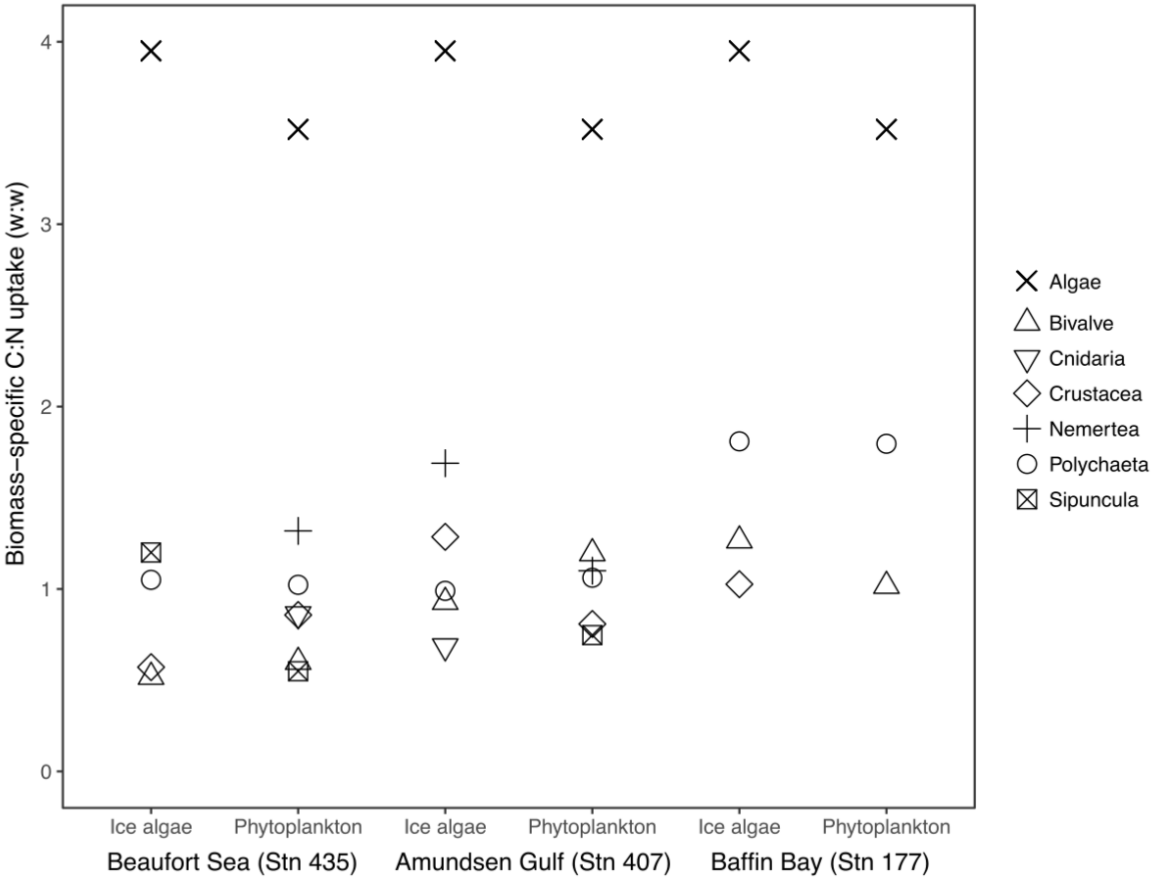


Figure 10: Biomass-specific C:N ratios of individual taxa and labeled algae (x) at Beaufort Sea, Amundsen Gulf and Baffin Bay stations.

1.4 DISCUSSION

Experimental considerations

Our study focused on the macroinfaunal community feeding ecology excluding mobile epifauna, due to sampling methods and large-size foraminifera for which it was not possible to know whether they were alive at the time of sampling. Therefore, the C an N uptake measured in this study could not be considered as representing the global responses because not all of the faunal components were taken into account. This is particularly the case in the Baffin Bay station where high densities and biomasses of large size foraminifera were observed. They could have contributed to a significant part to the C and N uptake since they are known to rapidly consume phytodetritus (Moodley et al. 2002).

Working with *ex situ* incubations implies that sediment could suffer decompression and warming effects during the extraction. However it has been accepted that above 1000 m depth decompression in sediments are not so pronounced (Hensen et al. 2006). Our experiments were conducted using cores sampled at no more than 400 m, so we are confident that the effects of decompression were minimal. Surely, *in situ* labeling experiments are more precise than *ex situ,* but the artefacts and logistic high costs in Arctic studies made the utilization of *in situ* benthic landers difficult.

Finally, it is important to note that the macroinfaunal uptake measured in our experiments reflect more the C and N isotopic values of the faunal gut content than those in their tissues. Indeed, the short duration of our experiments may not be enough to allow the complete incorporation of C and N in the organism's tissues.

Macroinfaunal community

Macrofauna density and biomass recorded in this study are consistent with other studies in the same region (Conlan et al. 2008, 2013, Bodil et al. 2011, Mäkelä et al. 2017b). The highest density of macrofauna organisms in this study (13644.44 ind. m^{-2} ± 794.47 SE) was observed in the 0-5 cm sediment layer at the Baffin Bay station. Thomson

(1982) sampled stations between 251 to 500 m depth, located at ~ 300 km north of Baffin Bay station and using a 1 mm mesh he collected 1482 ind. m^{-2} which is substantially lower than the values we reported. This discrepancy may be due to the different size mesh used. Indeed, an important part of the abundant species in Baffin Bay station, such as Thyasiridae and Spionidae was smaller than 1 mm. Mäkelä et al. (2017b) using the same sampling methodology but in a deeper station (709 m) in the North Water Polynya registered similar densities (10538 ± 860 ind. m^{-2}), which are considered as the highest densities for the Arctic Ocean. The second station in terms of density was Amundsen Gulf station with 2155.5 ind. m^{-2} ± 313.5 (SE) in the 0-5 cm sediment layer. In the same area, Conlan et al. (2008) reported 2577.9 ind. m^{-2} ± 730 (SE) from 11 stations and a 0.4 mm mesh, which is consistent with our results. The Beaufort Sea station corresponds to the Beaufort Sea slope, where Conlan et al. (2008) recorded 828.1 ind. m^{-2} ± 212.1 (SE) averaging from 7 stations and we collected 1888.8 ind. m^{-2} ± 136.7 (SE). This discrepancy could be part of the variability found among stations. In terms of biomass, the highest value found in this study was on the surface layer of Baffin Bay station (2115.1 mg C m^{-2} ± 127.4 SE or 5148.5 mg DW m^{-2} ± 292.3 SE) and is close to the previous measurements of biomass for 251-500 m depth in central Baffin Bay (Thomson 1982). Amundsen Gulf (1890.3 mg C m^{-2} ± 280.7 SE) and Beaufort Sea (1233.8 mg C m^{-2} ± 334.7 SE) stations presented low biomass values according to Conlan et al. (2013) for the same area.

Macroinfaunal community structure differed among stations. This was expected for Baffin Bay station vs Amundsen Gulf/Beaufort Sea stations due to distance locations. However, the Amundsen Gulf and Beaufort Sea stations (~300 km separation) were expected to be more similar considering that other studies did not find differences between the community structure of Amundsen Gulf and the Beaufort slope of similar depths (Conlan et al. 2008). The most perceptible difference was the occurrence of abundant species belonging to Thyasiridae, Spionidae and Yoldiidae families with low individual biomass in Baffin Bay station. This contrasts with low density of large deep burrowing Maldanidae polychaetes (*Maldanidae sarsi/artica*) in Amundsen Gulf station and Crustacea and Nemertea in Beaufort Sea station. Although there are many factors controlling benthic community density, biomass and structure (e.g. water depth, grain size, current velocity, oxygen concentration, sedimentation rate, competition, predation, etc.), some studies concluded that food supply is one of the most important factors (Grebmeier et al. 1989, Cochrane et al. 2009, Carroll & Ambrose 2012). Pearson and Rosenberg (1978) used a succession model and predicted that sites with increasing OM concentrations lead to increasing densities, dominance of a few species (< diversity) and low individual biomass per species of benthic macrofauna. Ruhl et al. (2008) also found that increases in POC flux could decrease equitability. Thus, it could be speculated that the macroinfauna community found in Baffin Bay station could be structured by a higher quality or amount of OM supply in comparison with Amundsen Gulf and Beaufort Sea stations. The dominance of FF/SDF organisms in Baffin Bay station, that could selectively feed and take advantage of high quality food that settles to the seafloor, may also reflect the greater amounts of OM that arrives to this station. High macroinfaunal densities in the uppermost sediment layers has also been suggested to indicate a large amount of OM transported by currents (Flach & Heip 1996, Dauwe et al. 1998). In contrast to Baffin Bay station where almost all the organisms were on the first 5 cm of sediment, in the stations Amundsen Gulf and Beaufort Sea biomass was distributed along both layers of sediment (0-5 and 5-10 cm). This could indicate sites with scarce or episodically food supply as it has been proposed that organisms may migrate beneath the sediment surface to store food safe from competitors (Jumars et al. 1990). High density of Spionid polychaetes in Baffin Bay station may also indicate OM enrichment as this taxon was found to be dominant in deep-sea regions subjected to high quantities of OM inputs (Galeron et al. 2009, Cunha et al. 2011, Paterson et al. 2011). Finally, the abundant large size agglutinated foraminifera (>5000 ind. m^{-2}) in the epifaunal habitat of Baffin Bay station compared to very low density in the other two stations may be indicative of higher OM inputs in Baffin Bay station, as several studies demonstrated coupling between phytodetritus and foraminifera densities (Smart & Gooday 1997, Wollenburg & Kuhnt 2000, Gooday & Hughes 2002, Fontanier et al. 2003, Schewe & Soltwedel 2003, Mohan et al. 2011). Initially, for the planning of these experiences, Amundsen Gulf station inside of Cape Bathurst Polynya was considered as the station with the highest POC fluxes at 200 m depth (2.08- 12.8 g C m^{-2} y^{-1}; Forest et al. 2007), which is close to the POC fluxes registered in the North Water Polynya (1.0~ 13.8 g C m^{-2} y^{-1};Sampei et al. 2004). However, Forest et al. (2011) concluded that heterotrophs could retain ~ 97% of the primary-produced C in the water column, reason why the sedimentation and benthic C demand at 400 m depth in the central Amundsen Gulf (near to our station) are low, and benthic community composition seems not to be altered by the polynya (Conlan et al. 2008). Baffin Bay station, where POC fluxes estimations weren't available in the area, was considered as an intermediate station with respect to POC fluxes, but this station actually could be the one that receives the highest quantity and/or quality of OM. Another explanation for these contrasted macroinfaunal assemblages may be related to the sedimentation and deposition of mineral material coming from glacial bays near Baffin Bay station. Wlodarska-Kowalczuk & Pearson (2004) found that Yoldiid and Thyasirid bivalves were more abundant in glacial bays while in the central basin with lower inorganic sedimentation these bivalves were replaced by tube-building polychaetes.

Sediment community Oxygen consumption (SCOC)

Metabolic activity after phytodetrital pulses might not always be evident in SCOC calculations (see Mäkelä et al. 2018). In some cases, SCOC increases occur several weeks after the natural phytodetritus pulses (Pfannkuche 1993, Drazen et al. 1998, Smith et al. 2002), and the amount of OM addition in experiments could influence the enhanced of SCOC, where low carbon loads may be difficult to detect (Moodley et al. 2005). In our experiments on Baffin Bay station we observed that SCOC estimations in treatment cores duplicated the ones in control cores, but in the Beaufort Sea station control and treatment cores presented similar values of SCOC. This differential response could be due to the fact that macroinfaunal communities in both stations were distinct and few organisms in Beaufort Sea station did uptake labeled phytodetritus to produce substantial SCOC increases. Witte et al. (2003) using *in situ* experiments also observed an instantaneous increase in SCOC (two times greater than controls) after an algal addition.

Natural isotopic values

A substantial difference in sediment $\delta^{13}C$ values among sites was observed with an enrichment from the West to the East. Lowest $\delta^{13}C$ values in the surface sediment were registered in Beaufort Sea station (-25.20 ± 0.09 ‰) on the Beaufort Shelf and this may be due to a terrigenous influence from Mackenzie River flow, which could be around 10% of the annual POC flux in this area (O'Brien et al. 2006). These values are similar to those reported by Dunton et al. (2006) and Conlan et al. (2008). The station in the Amundsen Gulf presented sediment $\delta^{13}C$ values around -23.7 ‰ suggesting that this station was more influenced by a higher ocean-based carbon supply with higher $\delta^{13}C$ values. On the east side, Baffin Bay station showed the highest $\delta^{13}C$ values in the sediment for this study (-22.20 ± 0.28 ‰). This may reflect the effect that Baffin Bay region is not directly affected by river inputs. It could be also considered that different particulate organic matter (POM) $\delta^{13}C$ values for distant geographic regions could be reflected in the different sediments values for Amundsen Gulf and Baffin Bay stations. Roy et al. (2015) observed the same geographic gradient with more terrigenous sediment ^{13}C values measured in western regions and closer to marine derived values in eastern regions (extreme values considered were: for terrestrial regions $\delta^{13}C$=-27‰; Magen et al. 2010 and for marine regions $\delta^{13}C$ = - 20.4‰; Kuzyk et al. 2010).

Making inferences of the possible food sources input at the time of sampling in this study is difficult because no in situ measurements of POM isotopic values were performed and a large variability between ice-algae POM and pelagic phytoplankton POM has been observed between seasons and regions (Tremblay et al. 2006, Gradinger 2009). Despite this, the sediment $\delta^{13}C$ values could be used as a proxy of the isotopic composition of sedimented POM produced in the water column, assuming that early diagenesis process are constant or cause insignificant isotopic variations compared to the primary sedimentary signal (Freudenthal et al. 2001). Also, changes on the satable isotope ratios of organic carbon due to early diagenetic processes are usually smaller in oxic sediments (Tyson 1995) and Magen et al. (2010) found that isotopic values of sediments from Beafourt Sea and Amundsen Gulf were nearly invariant due to this process. If organisms were consuming carbon from the OM in the sediment the difference between the sediment stable isotope values and the consumer should be around 0 to 2 ‰ (McTigue et al. 2015). In the present study, this difference was smaller than 2 ‰ at all stations suggesting that OM in the sediment is the primary source of carbon for macroinfaunal organisms. In some cases, consumer values were not enriched compared to the sediment δ^{13}C values and this may indicate that they were consuming fresher material. Surface sediments C:N ratios lower than 7 (w:w) could indicate a deposit of labile carbon on the seafloor (Schonberg et al. 2014). In Baffin Bay and Amundsen Gulf stations C:N ratio in the sediment was 7.03 and 6.96 respectively indicating that the OM available at the time of sampling in these stations was of higher quality than in Beaufort Sea station (C:N = 7.56), although these difference are not so pronounced.

Spionoids polychaetes and Thyasiridae bivalves presented similar δ^{13}C and δ^{15}N values among the three stations, suggesting that they have similar feeding niche in all stations. On the contrary, Yoldiidae bivalves showed different δ^{15}N values in Amundsen Gulf station (17.89 ± 0.01 ‰) and in Baffin Bay station (10.99 ± 0.21 ‰) illustrating that this species may select fresher particles from the seafloor surface that are isotopically lighter or they may utilize the ones buried in the sediment. Hence, species that may alter the type of food could present different trophic level depending on the food they are using.

The low δ^{15}N values of FF/SDF and SDF in comparison to SSDF and P/S suggest that organisms that filtrate or consume detritus from the surface sediments occupy a lower trophic position and that they first access to labile POM. On average, SSDF presented the highest δ^{15}N values of all the feeding guilds. Gontikaki et al. (2011) also observed the highest natural δ^{15}N values in SSDF polychaetes in a sub-Arctic region and they attribute this difference to prolonged periods of starvation or consumption of degraded OM. Both explanations could apply here, as SSDF were mostly found in the deeper layer of sediment (5-10 cm) where bacterial degradation of POM may produce OM with higher δ^{15}N values (Freudenthal et al. 2001) or where they could result in a gradual δ^{15}N enrichment caused by the excretion of light nitrogenous products during long times of nutritional stress and starvation (Gannes et al. 1997, Adams & Sterner 2000).

Community-wide metrics reflected that the Baffin Bay station has the higher trophic separation (↑CD) and lower trophic redundancy (↑MNND) in the food chain. Which means that this station is characterized by more species with different trophic ecologies making the food web more diverse. The larger trophic level range was also registered in Baffin Bay food chain and this may be governed by a tighter pelagic-benthic coupling compared to the Beaufort Sea and the Amundsen stations where food chains lengths were shorter and may reflect a dependence on more refractory OM.

Ice algae and phytoplankton C and N uptakes

Our results showed that after four days of sediment incubations in all the stations, macroinfaunal organism uptake both, ice algae and phytoplankton. This is consistent with other studies that found that arctic benthic organisms can rapidly respond to phytoplankton and ice algae inputs (McMahon et al. 2006, Renaud et al. 2007, Sun et al. 2007, 2009, Mäkelä et al. 2017a). However, responses were not the same at each station, in Baffin Bay station macroinfauna community obtain the highest total uptakes, phytoplankton detritus was significantly more consumed and almost all the organisms in treatment cores ingested the added food. The explanation for the higher total uptakes found in Baffin Bay station compared to Amundsen Gulf and Beaufort Sea stations could be associated with the higher biomass and density in the surface layer (0-5cm). This observation agrees with previous research showing that consumption of OM is related to consumer biomass (e.g. Woulds & Cowie 2007, Hunter et al. 2012). In addition, the different community structure found in each station may explain the different total uptakes and percentages of labeled organisms. High density of FF/SDF organisms in Baffin Bay station, that are normally the first to access and process the deposited OM (Bender & Davis 1984, Levin et al. 1999, Aberle & Witte 2003), contrasted with the dominance of P/S in Beaufort Sea station and SSDF in Amundsen Gulf station that could need more than 4 days to access to labeled food, may explain the different percentages of organisms that consumed phytodetritus. This agrees with the hypothesis that the structure of macrofauna assemblage influences OM processing (Witte, Aberle, et al. 2003, Sweetman & Witte 2008, Hunter et al. 2012). Total uptake seems to be strongly correlated with the biomass in each station, a pattern also shown in most of the feeding experiences that were developed using the same type of labeled algae in the Canadian Arctic (Table 8). In addition, the comparison of Lancaster Sound station (Stn 323, Mäkelä et al. 2017a) and Amundsen Gulf station (Stn 407), even though there are depth differences, could reflect the importance of the community structure in the C and N uptake. These stations received the same amount of C and presented similar biomass, however, the uptake in Stn 323 was higher (Table 8). This could be associated with the dominance of FF/SDF in Lancaster Sound station vs the dominance of SSDF in Amundsen Gulf station.

Table 8: Macroinfauna density, biomass and C uptake of ice algae (IA) and phytoplankton (PP) at five different stations in the Canadian Arctic using the same sampling protocol.

REGION (Station)	**Density** (Ind. m^{-2})	**Biomass** (mg C m^{-2})	**Depth** (m)	**C added** (mg C m^{-2})	**IA C uptake** (mg C m^{-2})	**% of the total C added**	**PP C uptake** (mg C m^{-2})	**% of the total C added**
North Baffin Bay (Stn 124)[a]	10952	3190 ± 432	709	1475	7.9 ± 1.8	0.5 ± 0.1	4.3 ± 0.9	0.3 ± 0.1
Lancaster Sound (Stn 323)[a]	8355	2110 ± 345	794	600	3.1 ± 1.0	0.5 ± 0.2	3.3 ± 0.4	0.6 ± 0.1
Baffin Bay (Stn 177)[b]	14000± 795	2208 ± 549	376	545	1.25 ± 0.21	0.2 ± 0.03	2.27 ± 0.45	0.4 ± 0.08
Amundsen Gulf (Stn 407)[b]	2644± 191	1890 ± 1087	382	600	0.53 ± 0.16	0.1± 0.03	2.02 ± 1.17	0.3 ± 0.2
Beaufort Sea (Stn 435)[b]	2444 ± 297	1234 ± 1297	300	425	0.29 ± 0.16	0.1 ± 0.04	0.34 ± 0.11	0.1 ± 0.03

*IA= Ice algae, PP=Phyotoplankton, [a] Mäkelä et al. (2017a), [b] this study

Biomass-specific uptake was used to evaluate our original hypothesis that ice algae were consumed in a larger fraction than phytoplankton. Contrary to the total uptake, this measure allows to interpret results without being influenced by the different community core biomass. Our results showed that both ice algae and phytoplankton were consumed equally by the whole community at two of the three stations and in Baffin Bay station the C and N biomass-specific uptake of phytoplankton was significantly greater than ice algae and this led to the rejection of our initial hypothesis that ice algae are a preferential food. Comparable results were found for a similar community by Mäkelä et al. (2017a) at a deeper station in the Lancaster Sound polynya, 900 km north from Baffin Bay station where phytoplankton detritus also presented higher total and biomass-specific uptake (Table 8). Possibly the organisms in those areas are used to consume this type of food that was naturally available at the sampling season (summer) and this may be reflected in the feeding experiments. In addition, it has been proposed that suspension feeders could be more efficient at consuming suspended phytoplankton than ice algae that normally forms aggregates (McMahon et al. 2006). However, it was not possible to show, in our experiments, the exact reason for this preference. Feeding experiments with both labeled phytodetritus together in the same treatment are clearly warranted to verify whether there is a preference (e.g. Sun et al. 2009).

Among the taxa that presented high biomass-specific C and N uptakes (Table 6), ampharetids and spionids polychaetes where the ones with greater values and this agrees with other studies that classified them as efficient feeders of ^{13}C labeled algae (Aberle & Witte 2003, Woulds & Cowie 2007, Mäkelä et al. 2017a). Two large Ampharetidae polychaetes (*Amage* sp.) were responsible for the 76% of total phytoplankton C and N uptake while two small *Prionospio* sp. uptake 17% of the total phytoplankton derived C and N for the same treatment in Amundsen Gulf station. However, their biomass-specific uptakes were similar, demonstrating that size does not affect their efficiency to uptake algae. Levin et al. (1999) also found that small and large infaunal have similar access to phytodetritus. *Prionospio* sp. was registered in all stations, although in Baffin Bay station was 6 times more abundant. Nevertheless, the highest biomass-specific uptakes were found when this species was present in low density (Amundsen Gulf station), suggesting that they become more efficient when they are present in small numbers. *Prionospio* sp. is present along all the Arctic and has been proposed as an important ecosystem engineer (Mäkelä et al. 2017a). In this study, we showed that even if they are in low densities, they still play an important role in the OM processing. Our feeding experiments showed that spionids in Baffin Bay station utilized ice algae and phytoplankton equally, in agreement with the results of Mäkelä et al. (2017a). Only in Beaufort Sea station a higher biomass-specific uptake of ice algae was observed by spionids, but we cannot conclude due to the low number of samples (n=2 for each treatment). Lumbrineridae is the only family defined as carnivores (Fauchald & Jumars 1979) that presented an important biomass-specific C and N uptake, however, it has been proposed that this family can change the feeding mode to deposit feeder depending on the available food (MacDonald et al. 2012). In this study, it seems that Lumbrineridae polychaetes in Baffin Bay station were deposit feeders and became a significant labeled algae consumer. This is also supported by the low $\delta^{15}N$ values (~ 12 ‰) found for this polychaetes in the control cores. This is in accordance with Link et al. (2013) who identified the Lumbrineridae species, *Lumbrineris tetraura* as a major organisms that explain variation in benthic function.

1.5 CONCLUSIONS

The main objective of this study was to compare the ice algae and phytoplankton uptakes by different macroinfaunal communities among three regions in the Canadian Arctic. We did not find any evidence of a significant higher consumption of ice algae detritus compared to its phytoplankton counterpart. This leads us to conclude that benthic macroinfaunal have no a preference and take advantage of both OM sources, and that they will be more vulnerable to the quantity rather than to the quality of OM reaching the floor. This means that communities could be resilient to the projected changes of ice algae reduction.

Also, this study showed that the macroinfaunal community structure in Baffin Bay station, dominated by small FF/SDF feeders and with a high trophic diversity seems to be associated to the amount of OM that reaches the seafloor. Probably, this site receives higher amounts of OM than Amundsen Gulf station, even if both areas have similar estimations of primary production (Arrigo & van Dijken 2004). In Amundsen Gulf station the community structure and uptakes results suggest that macroinfaunal community could be more adapted to lower or sporadically food inputs. Most of the organisms are SSDF with an average trophic level of 3, and they penetrated deeper into the sediment to exploit OM. This supports the idea by Forest et al. (2011) that this region in the Amundsen Gulf could retained a great part of the primary production in the water column (due to zooplankton ingestion) and less OM ends at the bottom. At the Beaufort Sea station, the community structure, again, seemed to be related to the low amounts of OM reaching the bottom. The high trophic redundancy (dominance of P/S organisms) and a less diverse food web structure suggests that organisms at this station depended on refractory OM. The amount of MO that reaches the bottom can define the structure of the communities in these environments. Hence, future changes in primary production altering OM export to the seabed could significantly change these communities.

CONCLUSION GÉNÉRALE ET PERSPECTIVES

Les principaux objectifs de ce projet de recherche étaient : (1) de déterminer s'il y a une consommation différente des algues de glace et du phytoplancton par les organismes macroendobenthiques; et (2) de documenter l'existence des différences régionales dans ces processus au sein de l'Arctique canadien. Ce mémorie a réussi à répondre à ces objectifs avec succès et a fourni des données pour un projet global qui cherche à mieux comprendre les effets possibles du changement climatique sur les organismes benthiques. En plus, les résultats sont en accord avec d'autres travaux publiés recensement, aidant à réaffirmer les conclusions.

Nous avons montré que contrairement à notre hypothèse initiale, qui était que les algues de glace seraient davantage consommées que le phytoplancton en raison de leur teneur élevée en acides gras, les algues de glace ne sont pas davantage consommées que le phytoplancton aux trois stations étudiées. Le phytoplancton était même davantage consommé que les algues de glace à la station 177 (baie de Baffin). Ces observations sont comparables à celles faites dans la polynie Lancaser Sound par (Mäkelä et al. 2017a). Fait intéressant à souligner, les familles d'invertébrés les plus largement représentées dans ces deux régions étaient les Spionidae et les Thyasiridae. L'utilisation préférentielle de cette source de nourriture pourrait refléter cette prédominance d'invertébrés au sein des communautés. Les Spionidae et les Thyasiridae sont des organismes qui peuvent alterner leur mode d'alimentation de suspensivores à déposivores. Ces organismes pourraient être mieux adaptés pour l'utilisation de cette nourriture phytoplanctonique qui se présente moins sous la forme d'agrégats que les algues de glace dans la phase de sédimentation (McConnaughey et McRoy 1979, Hobson et al. 1995, McMahon et al. 2006). Notre étude ne permet pas de tester cette hypothèse. Pour tester s'il existe une préférence alimentaire, il conviendrait de mettre en œuvre des expériences d'incubations incluant simultanément ces deux sources de nourriture (p. ex. Sun et al. 2009).

Les expériences réalisées à partir de sédiments prélevés à trois stations de l'Arctique canadien, présentant des profondeurs similaires mais composées de communautés différentes, nous ont permis de comparer les réponses des différentes communautés aux conditions expérimentales similaires. Il est important de connaître les réponses des différentes communautés benthiques de l'Arctique pour avoir une vision plus globale des effets possibles au futur changement climatique. Les trois régions étudiées couvrent un large spectre géographique dans l'Arctique canadien et représentent des aires qui ont été largement étudiées au cours des dernières années. La dominance d'espèces appartenant aux groupes fonctionnels des filtreurs (FF) et des déposivores de surface (SDF) à la station située dans la baie de Baffin pourrait traduire l'existence de flux de carbone détritique importants comparativement aux stations de la mer de Beaufort et du golfe d'Amundsen. À ces stations, la contribution plus élevée (biomasse) des déposivores de sub-surface (SSDF) et des prédateurs/charognards (P/S) pourrait suggérer des apports en nourriture moins importants dans ces régions, favorisant ainsi les organismes capables d'obtenir leur énergie de la matière organique enfouie dans les sédiments, les prédateurs et les charognards.

Plusieurs études portant sur les impacts causés par les changements climatiques sur la faune benthique suggèrent que la diminution de l'étendue de la couverture de la glace de mer de la glace va modifier les flux de MO vers le fond (Carroll et Carroll 2003, Piepenburg 2005, Carmack et Wassmann 2006, Bluhm et Gradinger 2008, Leu et al. 2011, Wassmann 2011, Wassmann et Reigstad 2011, Kędra et al. 2015). De plus longues périodes d'eaux libres de glace pourraient ainsi favoriser la production phytoplanctonique, et certaines études ont déjà montré des augmentations significatives des niveaux de production primaire au cours des dernières années (Bélanger et al. 2013). Si les niveaux de biomasse des algues de glace diminuent et la production primaire pélagique augmente, alors les organismes benthiques pourraient recevoir principalement des détritus dérivés du phytoplancton. Nos résultats suggèrent que les effets ne seront pas aussi prononcés pour les organismes macroendobenthiques puisqu'ils consomment préférentiellement du phytoplancton et dans une plus grande proportion que les algues de glace. La macrofaune pourrait donc bénéficier avantageusement de plus grands apports de matière organique détritique d’origine phytoplanctonique. Il convient cependant de mentionner que cette matière organique en sédimentation peut être également être consommée par la zooplancton ce qui modifiera ultimement la nature et/ou l’amplitude de ces flux de matière atteignant la surface des sédiments.

Les expériences d’incubation réalisées dans ce travail sont les premières dans ces régions de l’Arctique canadien et fournissent des informations importantes pour mieux comprendre les réponses de la faune à différents types de phytodetritus. Les résultats ont mis en évidence la capacité des organismes macroendobenthiques à consommer le phytodétritus lorsqu'il arrive sur les sédiments et les différentes réponses selon les structures communautaires.

À l'avenir, il serait nécessaire d’analyser l’incorporation de la matière organique par les bactéries pendant les expériences d’incubation, car elles ont tendance à jouer un rôle très important (voir Mäkelä et al. 2018). Aussi, il serait important d'améliorer certaines questions expérimentales, telles que la taille des carottes de sédiments qui, parfois, ne recèlent pas suffisamment de biomasses d'invertébrés pour les analyses isotopiques. Ce dernier pourrait améliorer le nombre d'échantillons analysés et permettre des résultats statistiques plus solides. Aussi la plus grande taille des carottes inclura également la mégafaune qui peut être trouvée dans de grandes densités. De cette façon, les résultats comprendront tous les membres donnant une image plus réelle de la situation. En plus, avec l'utilisation d'organismes plus grande, il serait possible de vider les tubes digestifs des organismes pour analyser juste l’assimilation et non l’assimilation + ingestion.

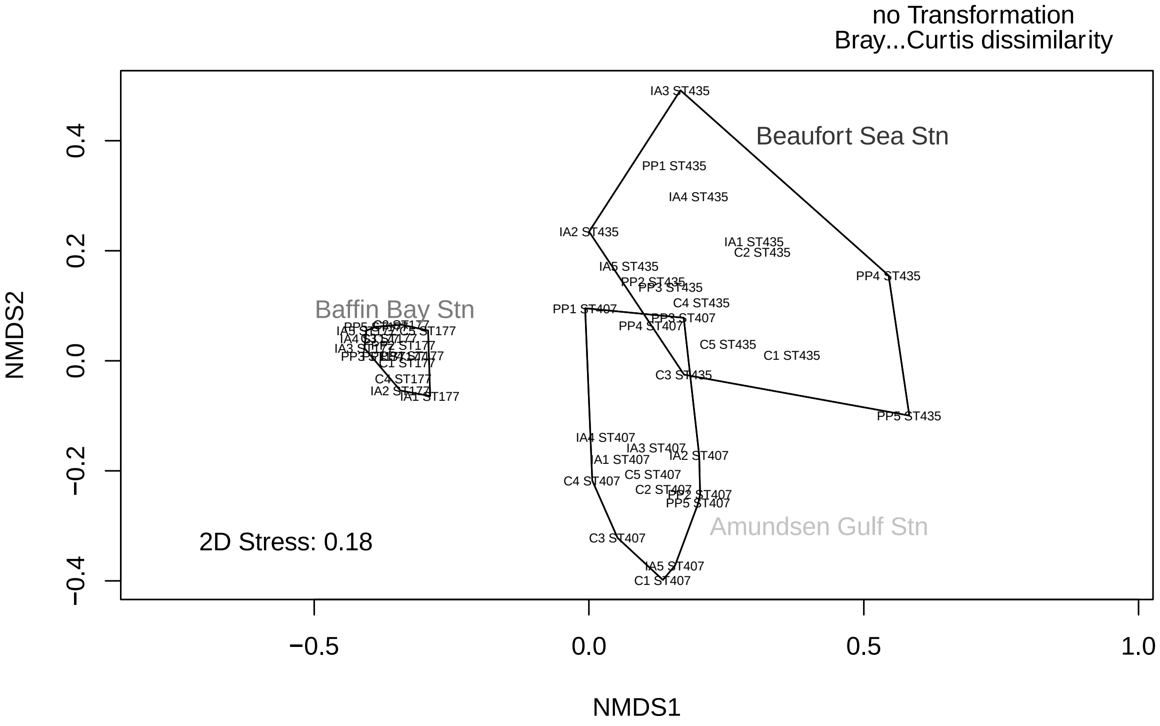
Autant que les algues utilisées dans cette étude (*Thalassiosira nordenskioeldii* et *Synedra hyperborea*) soient communes dans l'Arctique, il serait intéressant d'utiliser d'autres espèces pour comparer les résultats.

Par ailleurs, l’utilisation des modèles de mélange mixte avec les signatures isotopiques naturelles de la macroendofaune et les sources disponibles, permettrait une meilleure interprétation sur les sources de carbone consommeés au moment de l'échantillonnage (voir Mäkelä et al. 2017b). Toutefois, il serait nécessaire de collecter des données d'algues de glace et du phytoplancton en même temps que les données de la faune benthique pour établir un lien plus concret, puisque la signature isotopique des algues de glace et du phytoplancton peut varier selon la zone et la saison (Tremblay et al. 2006, Gradinger 2009).

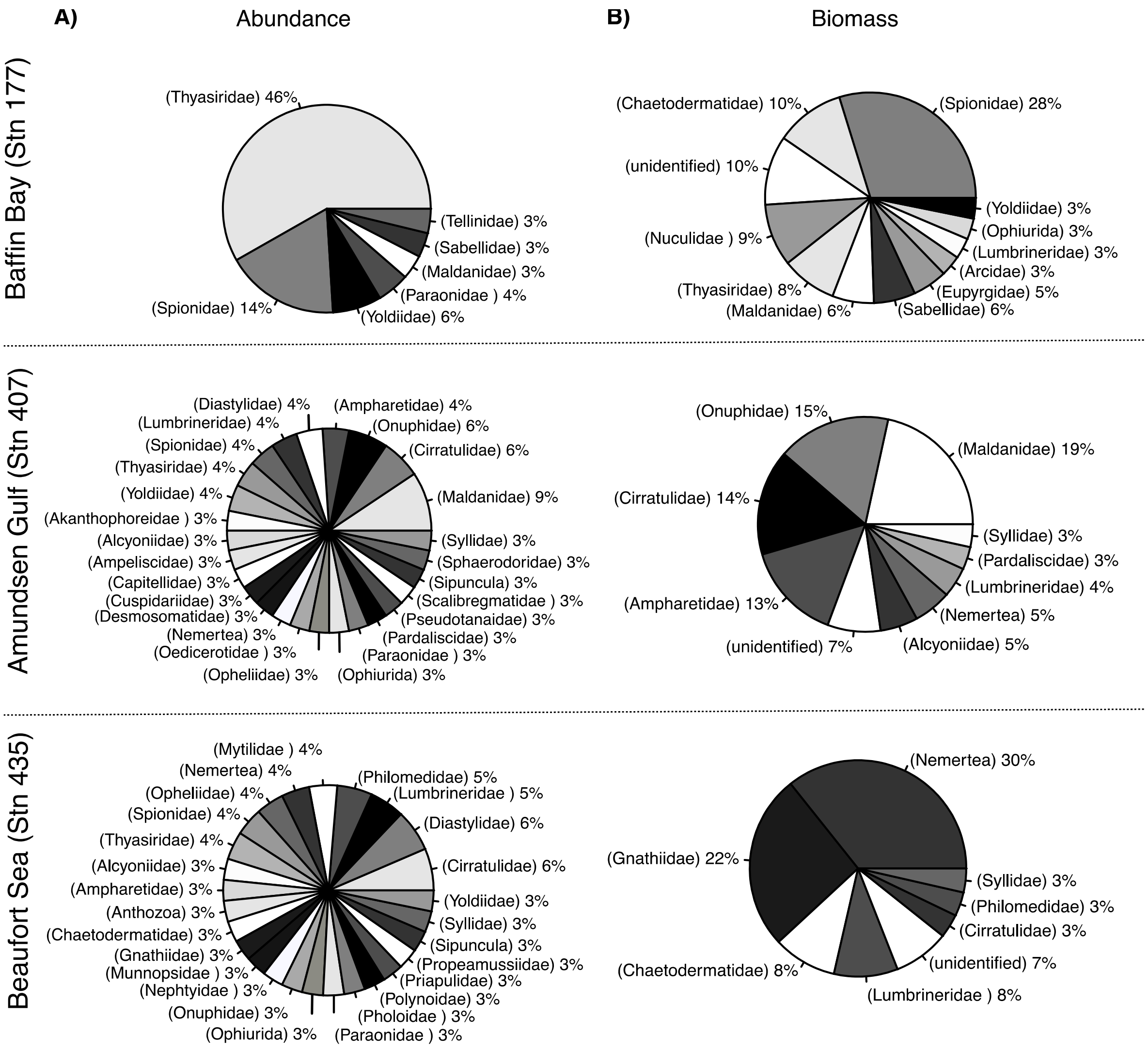
Finalement, l'utilisation des « Landers » pour réaliser les mêmes expériences, mais avec des conditions *in situ* serait idéale pour améliorer les résultats obtenus. Contrairement aux expériences *ex situ*, les conditions environnementales sont identiques auxquelles les organismes sont habitués. Ceci empêche la perturbation de la faune causée par l'extraction (l'augmentation de la température, la réduction de la pression, etc.) qui pourrait affecter aux résultats de l'alimentation. Bien que cette méthodologie soit la plus appropriée, les coûts et les complications logistiques de sa mise en œuvre rendent difficile son utilisation dans l'Arctique.

ANNEXES

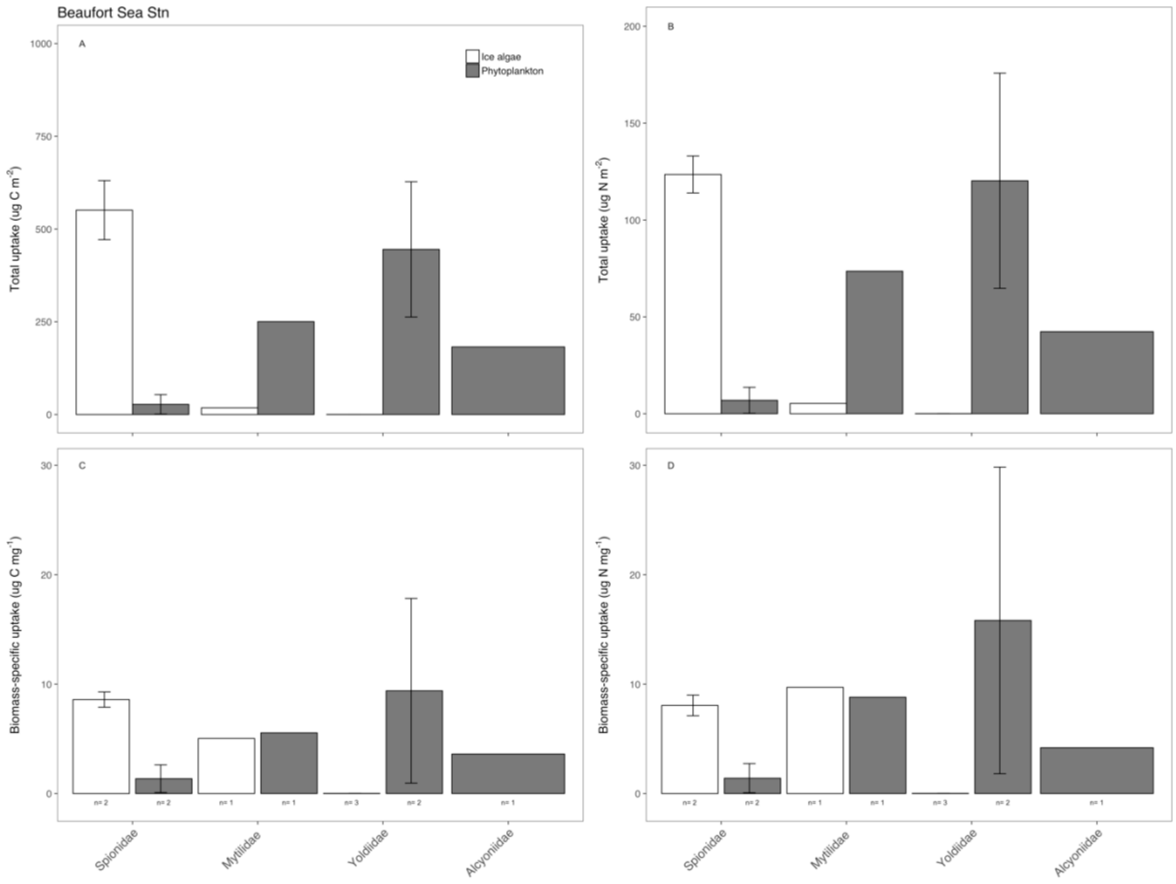
ANNEX I : Non-metric Multidimensional Scaling (MDS) plot of community similarities (cores as replicates) based in species density and composition in each station.



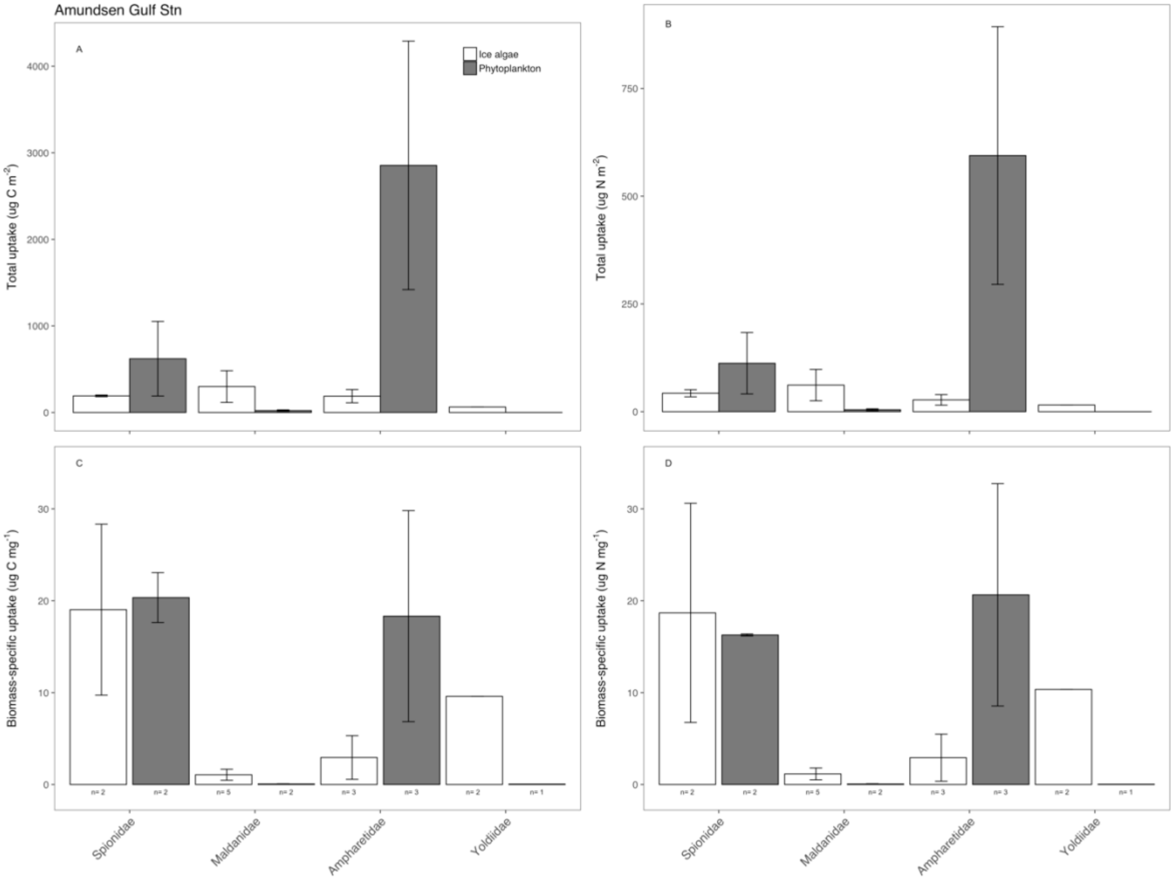
ANNEX II Relative (A) abundance and (B) biomass at the three sations sampled.



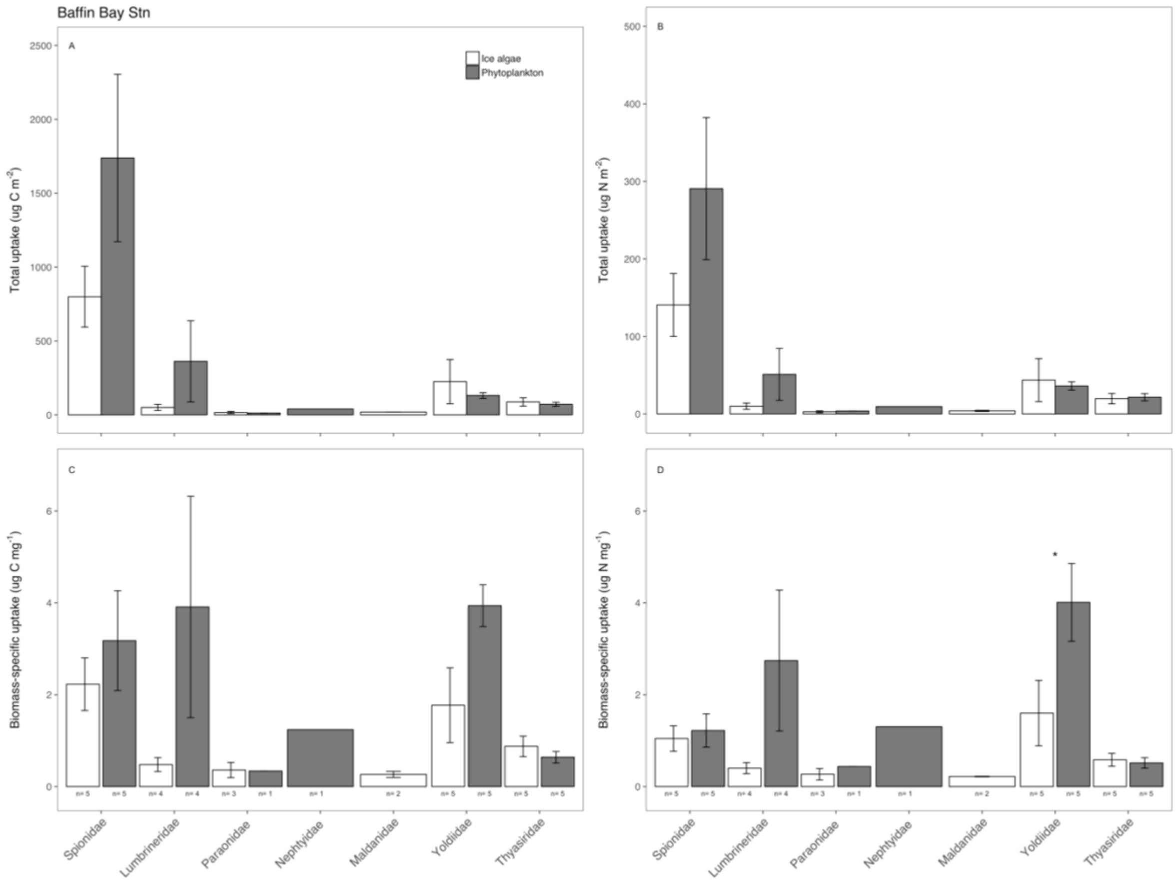
ANNEX III : Mean (±SE) ice algae and phytoplankton total C and N uptake (A-B) and mean (±SE) ice algae and phytoplankton total C and N biomass-specific uptake (C-D) by family at the Beaufort Sea station (Stn 435).



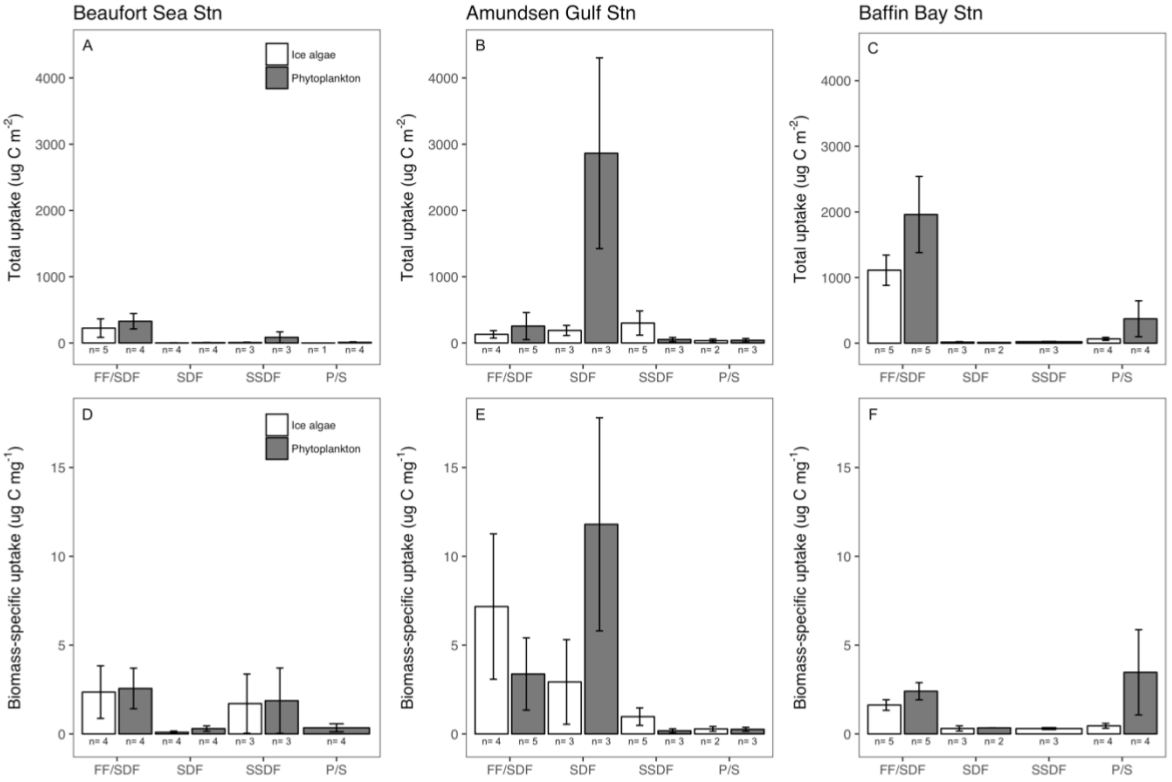
ANNEX IV Mean (±SE) ice algae and phytoplankton total C and N uptake (A-B) and mean (±SE) ice algae and phytoplankton total C and N biomass-specific uptake (C-D) by family at the Amundsen Gulf station (Stn 407).



ANNEX V : Mean (±SE) ice algae and phytoplankton total C and N uptake (A-B) and mean (±SE) ice algae and phytoplankton total C and N biomass-specific uptake (C-D) by family at the Baffin Bay station (Stn 177).



ANNEX VI Mean (±SE) ice algae and phytoplankton total C and N uptake (A-B-C) and mean (±SE) ice algae and phytoplankton total C and N biomass-specific uptake (D-E-F) by feeding mode at the Beaufort Sea, Amundsen Gulf and Baffin Bay stations.



ANNEX VII Total C and N uptake statistical analysis for feeding modes. FF/SDF= filter feeder-surface deposit feeder, SDF = obligate surface deposit feeder, SSDF subsurface deposit feeder and P/S= predator-scavenger.

	Beaufort Sea station						**Amundsen Gulf station**						**Baffin Bay station**					
	Total C uptake			Total N uptake			Total C uptake			Total C uptake			Total N uptake			Total C uptake		
	t	df	p	t	df	p	t	df	p	t	df	p	t	df	p	t	df	p
FF/SDF	-0.245	5.423	0.816	-0.451	5.965	0.668	U=13		0.556	U=11		0.905	-1.358	5.230	0.230	-1.442	5.612	0.203
SDF	-0.775	5.860	0.468[a]	-1.181	3.798	0.306	-0.688	2.689	0.546[a]	-1.001	2.743	0.397[a]	-	-	-	-	-	-
SSDF	-0.939	2.0175	0.446	-0.929	2.018	0.450	F=0.044	1	0.841	F=0.134	1	0.727	-	-	-	-	-	-
P/S	-	-	-	-	-	-	-	-	-	-	-	-	-0.747	5.431	0.486[a]	-0.887	5.813	0.410[a]

ANNEX VIII Mean (±SE) ice algae and phytoplankton total C and N uptake (A-B-C) and mean (±SE) ice algae and phytoplankton total C and N biomass-specific uptake (D-E-F) by feeding mode at the Beaufort Sea, Amundsen Gulf and Baffin Bay stations.

	Beaufort Sea station						**Amundsen Gulf station**						**Baffin Bay station**					
	Biomass-specific N uptake			Biomass-specific C uptake			Biomass-specific N uptake			Biomass-specific N uptake			Biomass-specific C uptake			Biomass-specific N uptake		
	t	df	p	t	df	p	t	df	p	t	df	p	t	df	p	t	df	p
FF/SDF	0.096	4.529	0.927	-0.774	5.912	0.468	0.670	6.061	0.527	0.819	4.996	0.449	-1.368	6.668	0.216	-1.523	7.183	0.171
SDF	-1.182	5.982	0.281[a]	-0.830	5.833	0.439[a]	-0.978	3.816	0.386[a]	-0.955	3.804	0.396[a]	-	-	-	-	-	-
SSDF	0.0182	3.997	0.986[a]	U=7		0.4	1.211	5.698	0.273[a]	1.238	5.599	0.265[a]	-	-	-	-	-	-
P/S	-	-	-	-	-	-	-	-	-	-	-	-	-1.105	5.213	0.317[a]	-1.350	5.533	0.229[a]

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