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Drivers of trophic ecology and food web structure of epibenthic communities exposed to different sea-ice concentrations across the Canadian Arctic Ocean

Thèse

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

Québec, Canada

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Résumé

La diminution de la couverture de glace de mer due au réchauffement de l'Arctique pourrait entraîner des changements complexes et indéterminés dans l'apport en nourriture qui pourraient altérer le fonctionnement des écosystèmes marins de l'Arctique. Les organismes benthiques sont des membres essentiels du réseau trophique de l'Arctique et constituent une source de nourriture importante pour les consommateurs des niveaux trophiques supérieurs. Dans l'océan Arctique, les consommateurs benthiques dépendent en grande partie des pulsations saisonnières de l'approvisionnement en nourriture provenant du phytoplancton (c.-à-d. la communauté pélagique) et des algues de glace de mer (c.-à-d. la communauté sympagique), mais nous ignorons encore comment les changements de la productivité primaire pourraient influer sur la dynamique trophique benthique. Afin de prévoir les tendances futures de la dynamique et du fonctionnement des écosystèmes, il est de plus en plus important de comprendre les facteurs environnementaux et biologiques qui influencent les interactions trophiques, les régimes alimentaires des consommateurs benthiques, et la cooccurrence des espèces dans les régions sujettes à des changements environnementaux rapides. En utilisant de multiples marqueurs trophiques, trois études connexes ont été réalisées et présentées dans cette thèse dans le but de (i) déterminer les facteurs qui influencent l'écologie trophique et la structure du réseau trophique benthique; (ii) quantifier la contribution relative du carbone sympagique dans le régime alimentaire des consommateurs benthiques et établir le rôle de la concentration de glace de mer dans le régime alimentaire des consommateurs benthiques et la structure du réseau trophique; et (iii) déterminer le rôle des individus dans les interactions trophiques et la structure du réseau trophique benthique.

Dans le chapitre 1, nous avons étudié la structure du réseau trophique de la communauté macrobenthique à l'échelle de l'Arctique pancanadien afin de déterminer les facteurs influençant la dynamique des niches écologiques. Nous avons trouvé que la niche écologique fluctuait entre les régions présentant des concentrations différentes de glace de mer (SIC) sous l'effet d'une série de facteurs, notamment les conditions environnementales, les ressources disponibles et les pressions biotiques comme la prédation et la compétition. Les résultats ont mis en évidence une réduction de la richesse isotopique (c.-à-d. longueurs et largeurs de chaînes trophiques plus courtes) associée aux zones ayant des concentrations de glace de mer faibles et élevées, ce qui suggère une homogénéité et une faible variabilité des ressources consommées par les organismes. En revanche, nous avons observé une augmentation de la richesse isotopique (c.-à-d. une niche plus étendue) dans les zones de

glace avec une concentration de glace de mer modérée, ce qui correspond à une plus grande hétérogénéité dans les sources de nourriture basale et des consommateurs utilisant des niches trophiques individuelles. Nos résultats appuient l'idée que la glace de mer est un facteur déterminant important de la dynamique et de la structure du réseau trophique benthique dans l'océan Arctique canadien.

Dans le chapitre 2, les régimes alimentaires de la macrofaune benthique des grands fonds marins et la structure de son réseau alimentaire ont été étudiés dans la région de la baie de Baffin. Nous sommes les premiers à combiner des biomarqueurs lipidiques de type isoprénoïdes hautement ramifiés (HBI) avec des rapports d'isotopes stables ($\delta^{13}C$, $\delta^{15}N$) pour mieux comprendre la relation entre la disponibilité des sources de carbone dans les sédiments et l'assimilation et le transfert du carbone sympagique dans le réseau alimentaire benthique. Les HBI ont révélé une corrélation entre la consommation par les organismes benthiques de carbone organique particulaire dérivé de la glace de mer et les concentrations de glace de mer. D'après nos résultats, les diminutions de la quantité de carbone sympagique atteignant les fonds marins pourraient entraîner des changements temporels dans la composition des régimes alimentaires des consommateurs benthiques, les affectant de différentes manières selon leur guilde alimentaire et leur degré de plasticité alimentaire, ce qui pourrait alors affecter la dynamique du transfert de carbone.

Dans le chapitre 3, les isotopes stables ($\delta^{13}C$, $\delta^{15}N$) ont été utilisés en conjonction avec l'approche des ellipses bayésiennes pour explorer les tendances spatiales des niches isotopiques quant à leur chevauchement et à leur largeur pour trois ophiures cooccurrentes: *Ophiacantha bidentata*, *Ophiocten sericeum* et *Ophiopleura borealis*, dans des régions arctiques spécifiques de la baie de Baffin (BB), de l'archipel arctique canadien (CAA), et de la polynie des eaux du Nord (NOW). Les différences de disponibilité et de diversité des aliments à l'échelle locale ont entraîné la variabilité de l'utilisation des ressources entre les stations au niveau individuel, ce qui a affecté les interactions trophiques, les chevauchements de niche et les structures de niche isotopique des ophiures. Nous avons observé un plus grand chevauchement de niches dans la région hautement productive de NOW, où les consommateurs présentaient une sélectivité alimentaire similaire, tandis que les régions présentant une plus grande concentration de glace de mer présentaient une augmentation de la ségrégation des niches. Enfin, les résultats ont mis en évidence que les ophiures pourraient être des espèces écologiques critiques gouvernant la dynamique, le fonctionnement et la stabilité des réseaux alimentaires benthiques dans l'océan Arctique.

Abstract

Declines in sea-ice cover due to the Arctic warming could lead to complex and undetermined changes in food supply that could alter negatively the functioning of Arctic marine ecosystems. Benthic organisms are essential members of the Arctic food web, constituting an important food source for higher-trophic level consumers. In the Arctic Ocean, benthic consumers depend mainly on seasonal pulses of food supply from phytoplankton (i.e., pelagic) and sea ice-associated algae (i.e., sympagic community), yet it is still unknown how changes in primary productivity might affect benthic trophic dynamics. In order to predict future trends in ecosystem dynamics and functioning, it is becoming increasingly important to understand the environmental and biological drivers influencing trophic interactions, benthic consumer diets, and species co-occurrence in regions subject to rapid environmental changes. Using multiple trophic markers approaches, three inter-related studies were performed here with the ultimate purpose of (i) determine the drivers of trophic ecology and benthic food web structure; (ii) quantify the relative contribution of sympagic carbon in benthic consumers' diets and establish the role of sea-ice concentration (SIC) in benthic consumers' diets and food web structure; and (iii) determine the role of individuals in trophic interactions and benthic food web structure.

In Chapter 1, the food web structure of the macrobenthic community was studied at a Pan-Canadian Arctic scale to identify drivers of ecological niche dynamics. The ecological niche fluctuated between areas with different SIC by a series of drivers including environmental conditions, resource supply, and biotic pressures such as predation and competition. Results highlighted a reduction in the isotopic richness (i.e., shorter chain length and width) linked to ice areas with low and high SIC, suggesting homogeneity and low variability of resources consumed by organisms. In contrast, an increase in isotopic richness (i.e., broad niche) was observed in ice areas with moderate SIC, implying higher heterogeneity in basal food sources and consumers using individual trophic niches. Our results support the idea that sea ice is an important driver of benthic food web dynamics and structure across the Canadian Arctic Ocean. In Chapter 2, deep-sea benthic macrofauna diets and food web structure were studied in the Baffin Bay region. We were the first at combining highly branched isoprenoid (HBI) lipid biomarkers and stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$) to better understand the relationship between the availability of carbon sources in sediments and the assimilation and transfer of sea-ice algae carbon through the benthic food web. Highly branched isoprenoid (HBI) biomarkers revealed a correlation between sea ice-derived particulate organic carbon (Sympagic carbon or SC) consumption in benthic organisms and sea-ice concentrations. Based on our results, decreases in the quantity of SC reaching the seabed could lead to temporal changes in the composition of benthic consumer diets, affecting them in different ways according to their feeding guilds and degree of dietary plasticity that could, in turn, affect carbon transfer dynamics. In Chapter 3, stable isotopes ($\delta^{13}C$, $\delta^{15}N$) in conjunction with the Bayesian ellipses approach were used to explore spatial trends in population isotopic niche width and overlap of three coexisting ophiuroids: *Ophiacantha bidentata, Ophiocten sericeum,* and *Ophiopleura borealis*, in specific Arctic regions of Baffin Bay (BB), Canadian Arctic Archipelago (CAA), and North Water Polynya (NOW). Differences in the availability and the diversity of local food items drove variability of resource utilization across stations at the individual-level, which in turn affected trophic interactions, niche overlaps, and isotopic niche structures of ophiuroids. A greater niche overlap was associated with the highly productive region of NOW, where consumers exhibited similar food selectivity, whereas regions with more sea-ice concentration (SIC) showed an increase in niche segregation. Finally, results highlighted that brittle stars could be critical ecological species driving dynamics, functioning and stability of benthic food webs in the Arctic Ocean.

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$\delta^{13}C$:	stable isotope ratios of carbon
$\delta^{15}N$:	stable isotope ratios of nitrogen
BC:	Baffin Current
BB:	Baffin Bay
CAA:	Canadian Arctic Archipelago
CB:	Cape Bathurst polynya
CD:	mean distance to centroid
Chl *a*:	chlorophyll *a*
CR:	$\delta^{13}C$ range in the convex hull
FYI:	first year ice
GM:	sediment textual group – gravelly mud
HBIs:	highly branched isoprenoid lipid biomarkers
HBI II:	di-unsaturated HBI (often referred as diene) and proxy for sympagic OM
HBI III:	tri-unsaturated HBI (often referred as triene) and proxy for pelagic OM
H-Print:	highly branched isoprenoid-fingerprint
IDis:	isotopic dispersion
IDiv:	isotopic divergence
IEve:	isotopic evenness
IUni:	isotopic uniqueness
iOM:	ice organic matter
OM	organic matter
IRich:	isotopic richness
IP_{25}:	monounsaturated HBI and proxy for sympagic OM in the Arctic Ocean
$IPSO_{25}$:	monounsaturated HBI and proxy for sympagic OM in the Antarctic Ocean
LS-BI:	Lancaster Sound-Bylot Island polynya
M:	sediment textual group – mud
MIZ:	marginal ice zone
MNND:	mean nearest-neighbor distance in the convex hull
MYI:	multiyear ice
NOW:	North Water Polynya
NPP:	net primary production
NR:	$\delta^{15}N$ range in the convex hull
POM:	particulate organic matter
SC:	sympagic carbon
SCM-POM:	subsurface chlorophyll maximum particulate organic matter
SD:	standard deviation
SDNND:	standard deviation of the mean nearest-neighbor distance in the convex hull
SEA:	standard ellipse area
SEAb:	Bayesian estimation of the standard ellipse area
SEAc:	sample-size corrected standard ellipse area
SGSM:	sediment textual group – slightly gravelly sandy mud
SIA:	stable isotope analysis
SIBER:	stable isotope Bayesian ellipses in R
SIC:	sea-ice concentration
SM:	sediment textual group – sandy mud
SPOM:	suspension particulate organic matter

SST:	sea surface temperature
TA:	total area of the convex hull
TP:	trophic position
VMS:	Viscount-Melville Sound polynya
WGC:	West Greenland Current

“The Arctic Ocean and the sea ice is our Nunaat - our homeland.” – Okalik Eegeesiak, chair of the Inuit Circumpolar Council.

Dedication

To God, my parents, my lovely grandfather, who I miss dearly, my family and wonderful Marylise, for always loving and supporting me.

À Dieu, mes parents, mon cher grand-père, qui me manque beaucoup, à ma famille et à ma merveilleuse Marylise, pour votre amour et soutien.

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Preface

Our planet is undergoing a period of many climatic changes that can transform the world as we know it today. Currently, on a global scale, there is an attempt of governments around the world to reduce anthropogenic emissions beyond 1°C in order not to overcome a warming of more than 1.5°C in the coming decades. However, the current global warming (between 0.8°C and 1.2°C) above pre-industrial levels is already affecting ecosystems that could buffer such climatic changes, including high latitude polar regions. The Arctic region is facing a warning two to three times faster than the global average. As a result, changes in the phenology, thickness and extent of sea ice are some of the most evident signs of the effects of climate change in the region. Sea ice plays an important role influencing the onset of the primary production, and the magnitude and composition of the organic matter exported to the benthic community. Ongoing climatic warming could induce shifts in the flux of particulate organic matter to the seafloor in the future, affecting food stability for benthic consumers, dietary patterns, food web dynamics, and ecosystem functioning. Despite this, very little is known about the response of benthic fauna to changes in time, type, quantity and quality of resources, and the implications that these changes could have on Arctic marine food webs and the stability of the ecosystem. The present research sought to increase our knowledge about the trophic ecology of the benthic community under the influence of different sea-ice conditions, with the goal of understanding the response of consumers to the predicted sea-ice reductions and the implications for benthic food webs and their stability.

The present thesis consists of five different sections: a general introduction, three chapters written in the form of scientific articles, and a general discussion. The entirety of this thesis has been written in English with abstracts translated into French. I am the lead author responsible for all aspects of the research described in the three chapters of this thesis, including formulating research questions, separation and identification of the samples, lipids extraction, stable isotope and HBI data analyses, and preparation of the manuscripts, comprising figures, maps and tables. My supervisor and co-supervisor, Philippe Archambault (Université Laval) and Christian Nozais (Université du Québec à Rimouski), respectively, contributed to conception and design of the project and drafted and/or revised the three chapters that are included in the thesis. The results obtained during this thesis have been the subject of oral and scientific posters presentations at national and international congresses. The full citations of the articles published or in process of publication are as follows:

List of publications:

Yunda-Guarin, G., Brown, T.A., Michel, L.N., Saint-Béat, B., Amiraux, R., Nozais, C. and Archambault, P. (2020). Reliance of deep-sea benthic macrofauna on ice-derived organic matter highlighted by multiple trophic markers during spring in Baffin Bay, Canadian Arctic. *Elem Sci Anth*. 8: 1. DOI: https://doi.org/10.1525/elementa.2020.047 (Chapter 2).

Yunda-Guarin, G, Michel, L.N., Nozais, C. and Archambault, P. (in press). Interspecific differences in feeding selectivity shape isotopic niche structure of three ophiuroids in the Arctic Ocean. *Marine Ecology Progress Series*. DOI: https://doi.org/10.3354/meps13965 (Chapter 3).

Publications in preparation:

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Brown, T.A., Koch, C.W., Ruiz-Gonzalez, C., Maccorquodale, M., **Yunda-Guarin, G**., Loseto, L.L., Rosenberg, B., Hussey, N.E., Ferguson, S.H. and Yurkowski DJ. Year-round utilization of sea ice-associated carbon in Arctic ecosystems.

Pedro, S., Lemire, M., Hoover, C., Saint-Béat, B., Janjua, M.Y., Herbig, J., Geoffroy, M., **Yunda-Guarin, G**., Moisan, M-A., Boissinot, J., Little, M., Chan, L., Babin, M., Kenny, T-A. and Maps, F. A (scientific) ecological perspective of the structure and function of the Western Baffin Bay Coastal and Shelf Ecosystem.

Conference Research Presentations

Oral presentations:

Yunda-Guarin G, Brown T.A, Nozais C, Archambault P (2020) Sea ice-derived organic carbon: A dominant food source for deep sea benthic consumers in Spring, Baffin Bay, Canadian Arctic. Sixth International Symposium on Arctic Research, ISAR-6, Tokyo, Japan.

Yunda-Guarin G, Brown T.A, Nozais C, Archambault P (2019) Sea ice-derived organic carbon: a dominant food source for deep sea benthic consumers in a marginal Arctic region, Baffin Bay. Green Edge Annual Scientific Meeting. Nice, France, 5–7 November.

Yunda-Guarin G, Archambault P, Nozais C, Massé G (2018) Étude de la structure du réseau trophique benthique dans l'océan Arctique Canadien. Colloque de biologie, Laval Université. Québec, Canada, 21–22 March.

Yunda-Guarin G, Archambault P, Nozais C, Massé G (2018) Influence of sea-ice depletion on the epibenthic food web structure and resilience in the Canadian Arctic. Green Edge Annual Scientific Meeting. Paris, France, 6–8 February.

Poster presentations:

Yunda-Guarin G, Archambault P, Brown T.A, Nozais C, Massé G (2018) Ecological approach of the importance of sea ice algae as a carbon source to the deep-sea benthic food web using sea ice proxy biomarkers and stable isotope analyses in Baffin Bay, Canadian Arctic. ArcticNet Annual Scientific Meeting, Ottawa, Ontario, Canada.

Yunda-Guarin G, Archambault P, Brown T.A, Nozais C, Massé G (2018) Tracing deep sea macrobenthic trophodynamics using sea ice proxy biomarkers and stable isotopes analysis in Baffin Bay, Canadian Arctic. Québec-Océan, Annual Scientific Meeting, Rivière-du-Loup, Québec, Canada.

Yunda-Guarin G, Archambault P, Nozais C, Massé G (2018) Food web structure of the epibenthic community at the sea ice edge in Baffin Bay, Canada**.** 4th World Conference on Marine Biodiversity, Montreal, Canada.

Yunda-Guarin G, Archambault P, Nozais C, Massé G (2017) Benthic trophodynamics in areas influenced by seasonal sea-ice depletion in Baffin Bay, Arctic. Arctic Change Annual Scientific Meeting. Québec city, Québec, Canada.

Yunda-Guarin G, Archambault P, Nozais C, Massé G (2017) Influence of seasonal sea-ice depletion on Arctic marine epibenthic communities in an area located between mid-western Greenland and Canada's Baffin Island, Baffin Bay. Québec Océan Annual Scientific Meeting. Rivière-du-Loup, Québec, Canada.

General introduction

Sea-ice dynamics and ecosystem productivity in the Arctic Ocean

Polar oceans represent about one fifth of Earth's surface. At both poles, ocean ecosystems are highly influenced by seasonal changes in sea-ice cover (Barnes and Tarling, 2017). With an area of approximately 14.06 million km² and an average depth of 1,038 meters, the Arctic Ocean is the smallest and shallowest of the world's five oceans (Figure 1). The sea ice area in the Arctic ranges from a minimum of about 4 million km^2 in September (Meredith et al., 2019; Stroeve et al., 2008), after which month it starts forming to reach a maximum of about 15 million km^2 in March (Bhatt et al., 2014; Shokr and Sinha, 2015). Arctic sea ice is made up of a mixture of first-year ice (FYI) and multi-year ice (MYI; more than one year old) (Stroeve et al., 2008). In the Arctic Ocean, sea-ice dynamics change seasonally, where ice growth or decay is primarily a response to surface air and water temperatures. At the same time, wind and current patterns are the main driving forces moving sea ice (Timmermans and Marshall, 2020).

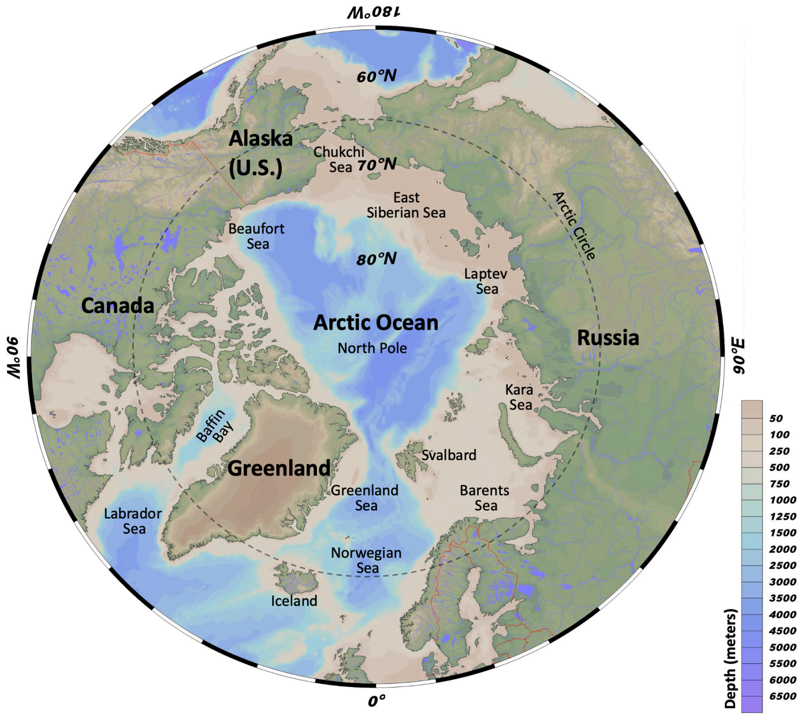


Figure 1. Map of the Arctic Ocean, including bathymetry, and surrounding seas.

The Canadian Arctic Ocean can be divided into several regions with specific sea-ice dynamics and conditions. The annual timing of sea-ice formation and retreat play an essential role in the functioning of the Canadian Arctic ecosystem. For instance, sea-ice dynamics plays an important role in biological processes such as the primary pelagic and benthic production (Clark et al., 2015; Gradinger, 2009; Legendre et al., 1992). Furthermore, sea ice provides substrate and habitat for ice-associated species such as ice diatoms and a great variety of viruses, bacteria, protists, meio- and macrofauna (Goutte et al., 2014; Horner, 1985). Offshore Arctic marine ecosystems are mainly sustained by seasonal pulses of food supply from phytoplankton (i.e., pelagic or open water community) and sea ice-associated algae (i.e., sympagic community) (Figure 2; Søreide et al., 2006; Tamelander et al., 2009). Moreover, macroalgal detritus (e.g., McMeans et al., 2013; Renaud et al., 2015) and terrestrial organic matter (e.g., Bell et al., 2016) are important basal food resources for coastal Arctic marine ecosystems. During the spring and early summer, when light conditions and supply of inorganic nutrients are favorable, a limited period of high primary production begins with the first bloom of sea ice-associated algae followed by a bloom of phytoplankton (Leu et al., 2015). Primary production first increases along the marginal ice zone (MIZ), where the retreating ice edge leads to a better stability of the water column (Michel et al., 2015). Sea-ice algae growth season begins in April, providing the first spring carbon input to benthic invertebrates and higher trophic levels that depend on benthos (Figure 2; Grebmeier et al., 2006). The duration of phytoplankton and ice algae production is comparable, but in terms of biomass, the phytoplankton production generally exceeds that of sea-ice algae (Leu et al., 2011). Depending on the latitude and sea-ice cover conditions, the sympagic community is responsible for different net contributions in primary production ranging from 0.002 to 20g m^{-2} $year^{1}$ of carbon, representing <1–26% of the total primary production in regions with seasonal sea-ice cover (Gosselin et al., 1997; Gradinger, 2009). In regions with FYI, annual phytoplankton production is higher than its ice algal counterpart with an average of 12 to 50g m^{-2} $year^{-1}$ of carbon (Gosselin et al., 1997). Meanwhile, in areas dominated by MYI pack, ice algae represented the major contributions to the total primary production (approximately 57%) in the central Arctic Ocean (Gosselin et al., 1997). Contrary to sea-ice algae production, phytoplankton net primary production (NPP) in some regions of the Arctic Ocean is increasing rapidly (~20%), as a result of reductions in sea-ice concentration (~ 9% per decade), changes in sea-ice phenology, and the resulting increase in the amount of light penetrating the surface layer of the ocean. Consequently, longer periods without sea ice are favoring the formation of propitious and more enduring habitats for the growth of phytoplankton cells (Arrigo and van Dijken, 2015).

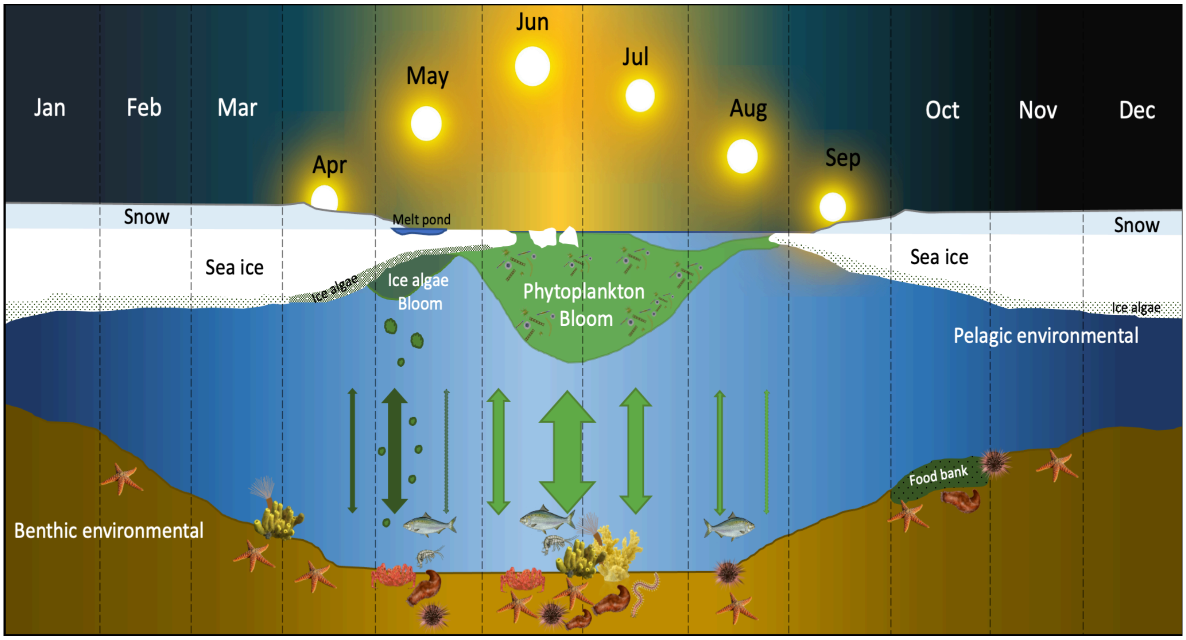


Figure 2. Schematic illustration of seasonal offshore primary production in the Arctic Ocean. In the figure, the size of the arrows represents the strength of the coupling: sympagic-benthic coupling (dark-green arrows) and pelagic-benthic coupling (light-green arrows). The strength of the coupling varies according to latitude, biological production and oceanographic conditions. The illustration represents the seasonal development of sea-ice algae and phytoplankton blooms in the Arctic Ocean (75°N) under current sea-ice conditions. The present illustration is based on manuscripts from Ardyna and Arrigo (2020) and Wassmann (2011).

The Arctic benthic community and its interactions with the pelagic habitat

Benthic fauna is an important component of marine ecosystems (Jędruch et al., 2019). They play an essential role in key ecosystem processes such as fueling higher trophic levels, driving biogeochemical cycles, bioturbation and nutrient remineralization processes, organic carbon sequestration, and provide biogenic habitats (Canuel et al., 2007; Ehrnsten et al., 2019). The structure of benthic community varies substantially in geographical scale due to ecological and biological drivers (e.g., species interactions, resource availability, seasonality) (Sokołowski et al., 2012). Environmental gradients (e.g., temperature, salinity, depth, currents, sediment type, bottom topography) strongly influence the distribution and taxonomic composition of the benthos (Kędra et al., 2013; Roy et al., 2014). Sedimentary processes are important for benthic communities at different depths, essentially because they are linked to the vertical flux of particulate organic matter (POM) produced by primary pelagic producers (Sweetman et al., 2017). Benthic fauna depend largely upon the supply of organic carbon from euphotic zone for their food (Figure 2 and 3; Gallagher et al., 1998; Grebmeier and Barry, 1991), thus benthic communities are sensitive to changes in the timing, nature, quality or abundance of nutrients (Ruhl et al., 2008). Hence, variations in the input of these nutrients could compromise pelagic-sympagic-benthic coupling processes, trophic dynamics, and community stability (Findlay et al., 2015; Griffiths et al., 2017).

The sympagic-pelagic-benthic couplings (Figure 2 and 3) refer to the set of interactions between pelagic and benthic habitats in which exchanges of energy, mass, and nutrients are produced (Griffiths et al., 2017). In the Arctic Ocean, these couplings play a fundamental role by supporting essential ecosystem processes such as the energy transfer in food webs (Griffiths et al., 2017). The relative importance of the pelagic versus the sympagic community depends on the season and geographical latitude (Legendre et al., 1992). Likewise, the complexity of the pelagic-benthic or sympagic-benthic coupling and fluctuations in the vertical export of POM varies considerably according to biological (e.g., magnitude of primary production) and physical gradients (e.g., sea-ice dynamics and water masses) (Lalande et al., 2009; Renaud et al., 2007). In addition, top-down regulation through zooplankton and bacterial population strongly influences the amount and quality of organic matter reaching the benthos (Tamelander et al., 2006; Wassmann et al., 1996). However, the set of interactions between the pelagic and benthic habitats is sensitive to ecological or environment changes, and its nature and intensity could be diminished by disturbances related to the global warming in the Arctic Ocean (Reid and Valdés, 2011). For example, sea-ice algae NPP, which is considered as an important high-quality food source for a high range of wildlife from the Arctic (Brown et al., 2018; Koch et al., 2020a), could decrease in some Arctic's regions due to reductions in sea-ice concentration (Arrigo and van Dijken, 2015).

The benthic food webs in a changing environment: food web structure, characteristics and assessment

A food web (see Figure 3) represents the networks formed by the set of feeding interactions between organisms, populations, or aggregate trophic units that share an ecosystem and describes the exchange of matter between compartments (Layman et al., 2015). Food webs provide a framework for integrating population dynamics, community structure and ecosystem processes (Layman et al., 2015). The structure of the food web is a key feature of the ecosystem that is useful to describe ecological interactions between species and their ecosystem, energy flow pathways, feeding relationships, and functional role of organisms in the food web (Renaud et al., 2015). In a food web, individuals are grouped into feeding types (i.e., primary, omnivorous, and high consumers) or according to the positions they occupy (i.e., trophic level). Variations in the structure of the food web is influenced by ecosystem size, resource availability, assembly history, disturbances, and biotic interactions (Baiser et al., 2012; Post, 2007). The number of trophic levels is a widely used metric in studies related to the dynamics of the food web and the structuring of the ecosystem through trophic cascades (Zanden and Fetzer, 2007). A food chain length is a term used to express the number of trophic links between primary producers and the top predators and is a fundamental ecosystem variable determining ecosystem functioning (Zanden and Fetzer, 2007). Arctic's benthic food webs consist of no more than 4 to 5 trophic levels (TLs) (Sokołowski et al., 2012). In arctic marine food webs, variations in the strength of energy flux pathways must vary in space and time across gradients of environmental change affecting the benthic food web topology (Post, 2017). Thus, in response to the quantity of resources, weak energy channels induced broader food chain lengths, while strong energy flux channels favored narrow food chain lengths (Ward and McCann, 2017).

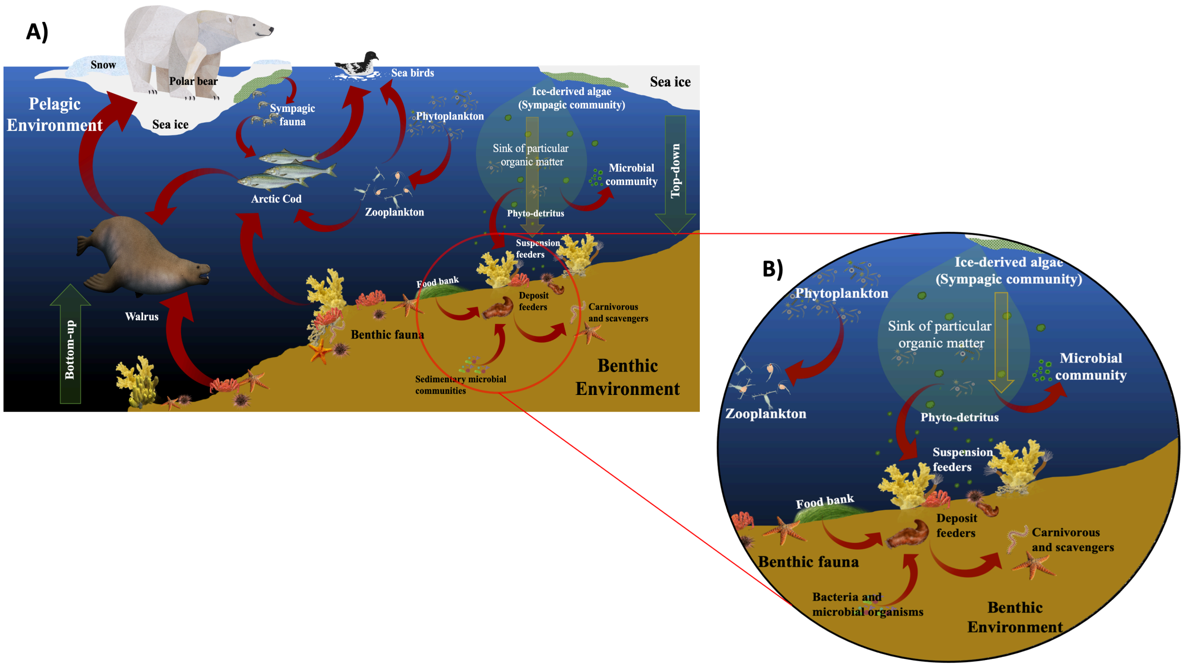


Figure 3. Schematic representation of an Arctic Ocean food web. The red arrows represent the set of feeding interactions between organisms and populations in a general Arctic Ocean food web (A and B). Phytoplankton and ice-derived algae are the main carbon sources sustaining offshore pelagic and benthic communities (yellow arrow). On the seafloor, food banks and bacterially reworked organic matter represent an important food source for benthic consumers (B).

For ecological and conservation purposes, it is important to understand the functioning (i.e. the causes and consequences) of food web structure since it provides insights into ecosystem structure and stability (Beckerman et al., 2006). In the Arctic Ocean, the dynamics and functioning of the food web are linked to multiple environmental drivers, among which sea-ice is one of the main components influencing the development of main primary producers (i.e., sympagic algae and phytoplankton), patterns in organic matter inputs, and the amount of energy transfer through trophic levels (Clark et al., 2015; Gradinger, 2009; Legendre et al., 1992; Pabi et al., 2008). Despite this, only few studies have investigated the effects of sea ice on food web structure and trophic interactions in the Arctic Ocean (e.g., Kortsch et al., 2019; Pratte et al., 2019; Yunda-Guarin et al., 2020). These studies found a relationship between sea-ice conditions and changes in species' ecological niches. Such studies could provide an opportunity to infer the effects of sea-ice depletion in food web functioning. The Canadian Arctic Ocean can be divided into several regions with specific sea ice dynamics and conditions, which make this region a natural setting against which to test the effects of sea-ice decline on the availability of different carbon sources for benthic consumers and food web functioning.

Assessment of consumers' diets and food web structure using stable isotopes and lipid biomarkers

Different analytical approaches such as lipid biomarkers, stable isotopes analyses (SIA), and fatty acids analyses have previously been used to better understand the complexity of the benthic food web, trophic relationships, carbon transfer, and dietary patterns of benthic consumers in the Arctic Ocean (Søreide et al., 2013; Yunda-Guarin et al., 2020). Among these approaches, stable carbon and nitrogen isotope ratio analyses are commonly employed in research related to individuals' trophic ecology (Boecklen et al., 2011). Indeed, this approach is one of the main tools in the study of the structure and dynamics of food webs because it provides time and space-integrated insights into trophic relationships (Layman et al., 2012). To assess the food web structure, the nitrogen isotope ($\delta^{15}N$) ratio is used to estimate the trophic level of consumers in relation to their food sources because it integrates the assimilation and the transfer of energy through all different trophic pathways (see Figure 4 below; Chikaraishi et al., 2009). Indeed, a $\delta^{15}N$ enrichment ranging between 3 and 4‰ can be observed from one TL to the next (DeNiro and Epstein, 1980; Post, 2002). In contrast, the carbon isotope ($\delta^{13}C$) ratio is used to establish the reliance of the consumers to different food sources (Figure 4; Peterson and Fry, 1987). Carbon isotope ratios ($\delta^{13}C$) vary substantially among primary producers but change very little with trophic transfers (Layman et al., 2007a).

Recently, advances in stable isotope analyses allow the estimation of community-wide characteristics providing quantitative information on resources and habitats used by consumers that helps characterize aspects of the trophic niche of individuals (Jackson et al., 2011; Layman et al., 2007a). The isotopic niche is one of the most widely used approaches in food web studies to describe the dietary ecology of individuals, diversity of resources, and the habitats used by consumers (Bearhop et al., 2004; Reid et al., 2016). In addition, community-wide measures of the trophic niche is a useful tool to obtain quantitative estimates of the degree of vulnerability of a community to changes in the trophic structure (Divine et al., 2015). More recently, Bayesian mixing models (based on carbon and nitrogen isotope ratios) have gradually become a valuable method for transferring isotopic data into estimates of food source contributions from diverse components of consumer diets (Smith et al., 2013).

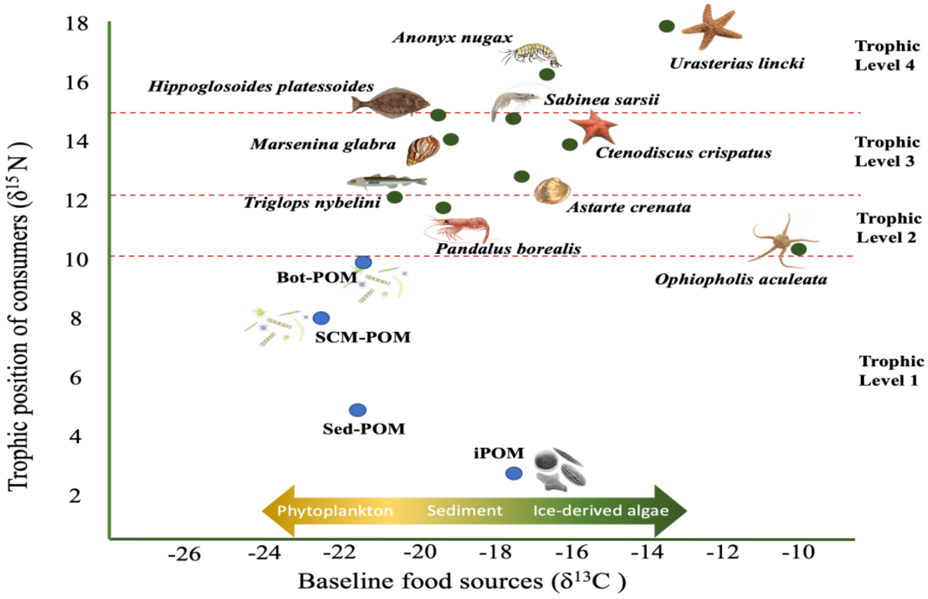


Figure 4. Schematic representation of a trophic model based on the nitrogen and carbon (δ^{15}N - δ^{13}C) isotopic composition of benthic consumers in a deep station influenced by high sea-ice concentration. The color of the arrow indicates differences in the amount of contribution of each basal food source: subsurface chlorophyll maximum (SCM-POM; yellow), bottom water particulate organic matter (Bot-POM; yellow), surface sediment particular organic matter (Sed-POM; yellow-green gradient), and ice-derived algae (iPOM; green). The isotopic values from the primary sources are indicated by blue dots and the isotopic values from the benthic fauna are indicated by green dots. The vertical (δ^{15}N) and horizontal (δ^{13}C) isotopic dimensions, trophic levels, primary producers, and benthic consumers are represented in the trophic model. The present scheme is based on isotopic data collected in the present thesis from deep stations (> 200 meters) in Baffin Bay, 2016 during spring.

In food web studies, novel approaches that use multiple trophic markers (e.g., fatty acids and stable isotope ratios) have opened new research avenues in the study of the trophic ecology of species in the Arctic giving new insights in food web dynamics and species ecology (e.g., Budge et al., 2008; Parzanini et al., 2018). Lipid molecules have been widely used as biochemical markers in Arctic food web and nutritional studies, due to the biochemical specificity on the synthesis of fatty acids by organisms (e.g., Budge et al., 2007; Parzanini et al., 2018; Søreide et al., 2013). Some of the essential fatty acids (EFAs) are not synthesized by aquatic invertebrates and they are obtained through their nutrition. Thus, variations in lipids composition change in relation to the diet of the animal (Gaillard et al., 2015). Among lipids, sterols and EFAS are part of a series of essential nutrients that are vital in physiological processes of marine organisms (Parrish, 2013). They play a vital role as source of energy and as structural and functional components of cell membranes (Gaillard et al., 2015). The marine food webs are characterized by different levels of specific fatty acids, particularly by long chain of polyunsaturated fatty acids (PUFA) (Søreide et al., 2013). In the Arctic, fatty acids are synthesized mainly by phytoplankton (Budge et al., 2007). However, ice algae congregations contain a higher percentage of PUFA than phytoplankton, turning it into a significant source of higher food quality for low trophic levels (Søreide et al., 2010). Although benthic species have relatively low lipid content compared to zooplankton and ice algae, they represent a considerable source of essential PUFA, playing an important role in the marine Arctic food web (Legeżyńska et al., 2014). Changes in the environment induced by climate anomalies can negatively affect the physiology of aquatic organisms, altering the composition of fatty acids and decreasing the quality of the food sources and the lipid transfer in the Arctic marine ecosystem (Gaillard et al., 2015; North et al., 2014).

For the Arctic Ocean, there are still very few studies that have investigated the importance of ice-derived carbon source in the diets of benthic consumers and food web dynamics, and more importantly, how sea-ice depletion could affect the quantity and quality of this resource for benthic communities. Recently, the use of highly branched isoprenoids alkene lipids (HBIs), produced only by diatoms, have been shown to be an important tool in studies related to polar food webs and tracers of ice-derived carbon in consumers. For example, the HBI termed IP_{25} (Belt et al., 2007) and its homolog, the HBI II named diene, have been used as proxies of sea ice-derived organic carbon (Figure 5) in the environment (e.g., Brown et al., 2016; Xu et al., 2006), including within Arctic benthic organisms (Brown et al., 2012; Brown and Belt, 2012; Koch et al., 2020a). In contrast to sea-ice proxies, a tri-unsaturated HBI III named triene, has been proposed as a proxy for pelagic organic matter (phytoplankton) in open water regions (Figure 5; Belt, 2018; Belt et al., 2019). In the Arctic, the presence and abundance of IP_{25} ice proxy, in marine organisms, is connected with periods of major sea-ice algae biomass (Brown et al., 2017a). Different degradation rates are associated with the number of double bonds of each HBI. For example, while IP_{25} has the lowest degradation rates among alkenes (Belt and Müller, 2013), the HBI III is more susceptible to degradation in both the water column and sediments (Belt et al., 2019). Based on the relative abundances of pelagic (III) and sympagic (IP_{25}, II) lipid biomarkers, quantitative approximations of the relative proportions of SC transfer through different trophic levels have been calculated (e.g., Brown et al., 2018; Brown and Belt, 2017) revealing the importance of each organic carbon source in the diet of different organisms across the Arctic food web.

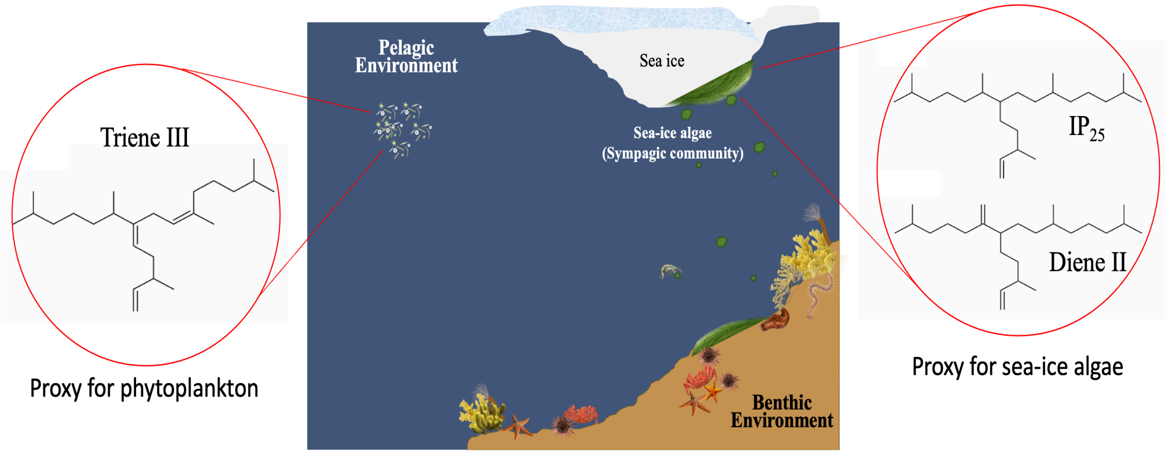


Figure 5. Schematic representation of the highly branched isoprenoid (HBI) alkenes used as proxies of sea ice-derived algae and phytoplankton. The molecular structures of sea-ice diatoms from the sympagic community (IP_{25}, Diene II; right) and of phytoplankton diatoms (Triene III, left) HBIs commonly used in the Arctic Ocean.

Effects of climate change on the Arctic Ocean ecosystem

Current global warming is most evident and intense in the polar areas (Meredith et al., 2019). In recent decades, a rapid increase of the Arctic surface air temperatures (SAT) is causing the Arctic region to warm two to three times faster than the global average (Francis et al., 2017; Meredith et al., 2019; Post et al., 2019). The accelerated reduction in both thickness and extent of sea ice is one of the most evident signs of the effects of climate change in the Arctic Ocean ecosystem (Cavalieri et al., 1997; Wadhams, 1990). Since the 1970s, when passive microwave satellites began to acquire systematic measurements in the Arctic Ocean, sea-ice cover exhibited accelerated reductions, particularly during the summer months (Figure 6; Comiso et al., 2008; Stroeve et al., 2008). In concordance with the Arctic's SAT intensification, predictive models estimated a continuous increase in ocean and atmospheric temperatures in the next 50 to 100 years (Johannessen et al., 2004; Sweetman et al., 2017).

In addition, due to global warming, a decrease in the thickness of the MYI and shortening in the duration and extent of the FYI is happening in the Arctic Ocean (Polyakov et al., 2010). In this context, from 1979 to 2006, the Arctic summer minimum sea-ice extent declined substantially (25%), with the record-low extent reached on September 2012 (Boé et al., 2009). Likewise, the winter maximum sea-ice extent has decreased with the lowest satellite record registered in March 2017 (Gascard et al., 2019). More recently, the second lowest annual minimum Arctic sea-ice extent (3.74 million km^2) was observed on September 2020, whereas on March 2020 the 11th lowest annual maximum sea-ice extent (15.05 million km^2) was recorded (Figure 6; Perovich et al., 2020). MYI extent has declined rapidly (14%) over the last decades (Johannessen et al., 2004) to make up less than 15% of summer sea-ice extent in 2010, and its area of coverage experienced a net loss of over 50% in summer in areas such as the Beaufort Sea between 1993 and 2009 (Kwok and Cunningham, 2010). A steady increase in temperatures and a continued decrease in sea-ice extent could render the Arctic Ocean seasonally ice-free by 2040 (AMAP, 2021; Kędra et al., 2015).

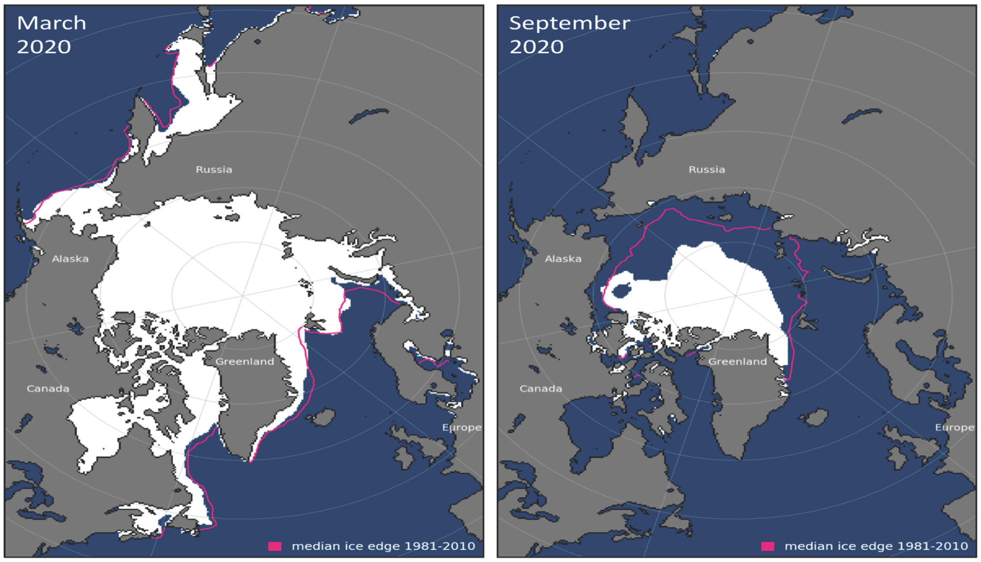


Figure 6. Illustration of the monthly average of sea-ice extent during the months of sea-ice maximum extent in March (left) and sea-ice minimum extent in September (right) in the Arctic Ocean. The magenta line indicates the median ice extent in March and September, respectively, during the period of 1981–2010. Maps are from NSIDC at http://nsidc.org/data/seaice_index (Fetterer et al., 2002).

Arctic's warming has also been accompanied by changes in the freshwater Arctic outflows and inflows (Arnell, 2005; Pemberton and Nilsson, 2016), decreases in the salinity concentration (Curry et al., 2011), variations in circulation regimes (Proshutinsky et al., 2015), differences in water stratification (Pemberton and Nilsson, 2016; Rudels et al., 1991), changes in upwelling and nutrient concentrations (Tremblay et al., 2011), increases in runoff and hydrological cycle (Greene et al., 2008), and alterations in biogeochemical cycles (Cai et al., 2010).

Effect of climate change on ecosystem functioning and services

Evidence suggests that climate change impacts on populations and communities are increasing, affecting availability of resources, biological processes, functioning of ecosystems and services such as carbon sequestration (Divine et al., 2015). For instance, as a result of climate change, the conditions for growth of primary producers is changing affecting their biomass and composition (Blais et al., 2017). Thereby, a decrease in the net ice-algae production and an increase in the net phytoplankton production are expected in the coming decades (Figure 7; Leu et al., 2011). Likewise, changes in the annual timing of sea-ice melt onset has allowed the ocean surface to absorb more solar radiation, delaying the onset of freezing in autumn (Arrigo, 2013; Post, 2017) affecting phytoplankton dynamics (Ardyna and Arrigo, 2020). As a result, a second phytoplankton bloom is possible in autumn (Waga and Hirawake, 2020). Furthermore, climate change can also alter the proportion of POC exported to the seabed by increasing grazing pressure from pelagic consumers, especially in areas with reduced sea ice in summer (Hansen et al., 2003). Consequently, changes in the timing, intensity and spatial distribution of nutrients in the Arctic Ocean are expected (Wassmann, 2011). As benthic organisms are highly dependent on the food supply from primary producers, changes in the nature and quantity of the carbon sources could impacts benthic trophodynamics, species composition, diversity, production, and carbon couplings (Griffiths et al., 2017; Link et al., 2013). Similarly, climatic alterations may affect consumption patterns and diet quality of consumers by altering the taxonomic and biochemical composition of the primary resources (Leu et al., 2011). As a result of these environmental and ecological changes, threats to the stability of ecosystems, biodiversity, and traditional Inuit livelihoods are expected in the future Arctic Ocean (Carroll and Carroll, 2003; Post et al., 2019).

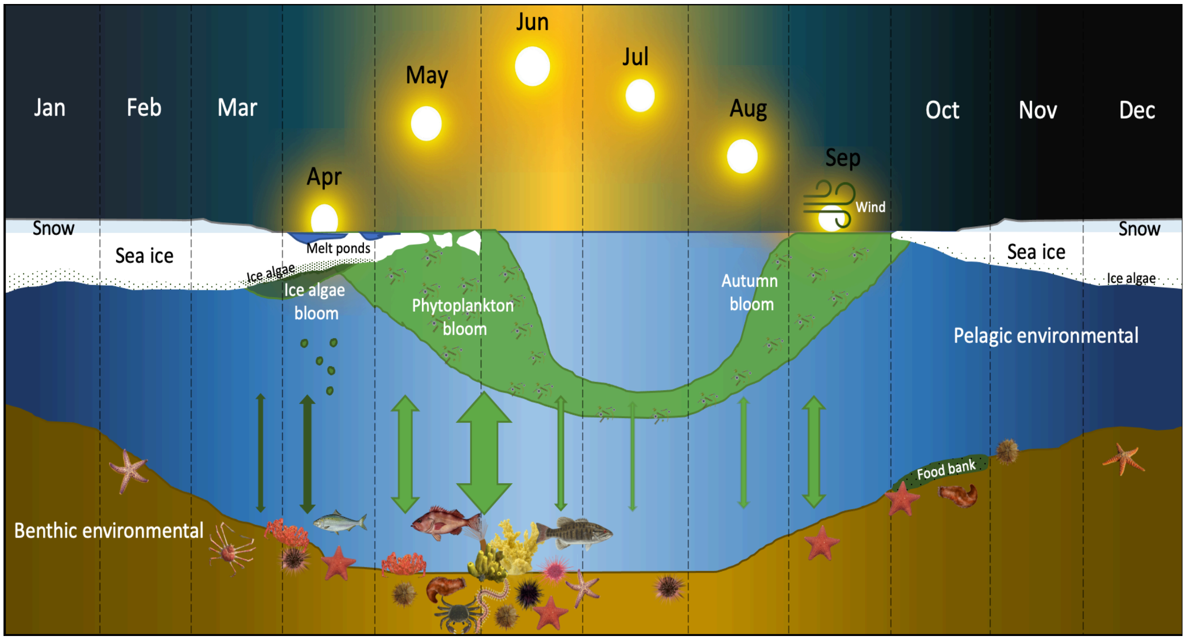


Figure 7. Schematic illustration of changes in seasonal offshore primary production in the Arctic Ocean due to Arctic warming and consequences for the benthic community. In the figure, the size of the arrows represents the strength of the couplings: sympagic-benthic coupling (dark-green arrows) and pelagic-benthic coupling (light-green arrows). The strength of the coupling varies according to latitude, biological production and oceanographic conditions. The illustration represents the probable variation in water column production due to changes in the duration and extent of seasonal sea ice (Ardyna and Arrigo, 2020; Kahru et al., 2016), which could in turn weaken pelagic-benthic coupling processes (Olivier et al., 2020). In addition, a warming Arctic Ocean will allow a longer phytoplankton growth season, which can induce an increase in benthic biomass in some northern parts of the Arctic Ocean (Cochrane et al., 2009). Similarly, a northward expansion of boreal species is expected (Kortsch et al., 2015). The present illustration is based on manuscripts from Ardyna and Arrigo (2020) and Wassmann (2011).

Resilience of Arctic Ocean food webs to environmental changes

In ecology, one of the biggest challenges is to predict the adaptive capacity of a system to remain stable when faced with various disturbances (Frid and Caswell, 2016), and to understand the consequences of environmental change towards ecological functioning (Timpane-Padgham et al., 2017). Because of global warming and ocean acidification, the marine ecosystems are experiencing rapid and pervasive changes in species diversity and composition that could alter the magnitude of energy flows in marine food webs affecting ecosystem processes (Murphy et al., 2016; Ullah et al., 2018). Species diversity is a key component to maintaining the system's integrity due to the different roles that organisms play in communities and food web processes (Worm and Duffy, 2003). Community attributes (e.g., biomass, abundance, and richness) and species identity are fundamental aspects influencing ecosystem functions and services (Piccini et al., 2020). However, the mechanisms by which species loss affects the ecosystem functioning and how marine food webs may respond to future climate change are not clear (Rosenfeld, 2002; Ullah et al., 2018).

In studies related to climate change and its effects on communities, understanding the food web structure is essential to evaluate the capacity of the ecosystem to remain stable under external disturbances. The vulnerability and resilience of food webs to disturbances can be better understood by measuring complementarity aspects of species realized niches (i.e., the origin of the carbon used by consumers and their trophic position within the food chain) using the *n*-dimensional niche concept (Hussey et al., 2014; Layman et al., 2007b). The ecological resilience – defined as the capacity of an ecosystem to absorb change, recover and adapt after a disturbance (Griffith et al., 2019; Holling, 1973) – is influenced by numerous factors, such as the magnitude and duration of the disturbance, the elasticity of the food web, and the strength of interactions (Bölter and Müller, 2016). For example, in a food web, redundancy is connected to species that share attributes and can perform similar ecological roles, conferring more elasticity and resilience to the ecosystem (Greenfield et al., 2016; Rosenfeld, 2002). In food web studies, the isotopic niche space is a useful approach to characterise the isotopic niche and assessing the redundancy of communities facing environmental changes (Divine et al., 2015). In addition, species richness, functional diversity and number of taxa are variables that are widely used to estimate functional changes in an ecosystem (Törnroos et al., 2015). Recently, new metrics (isotopic divergence, dispersion, evenness and uniqueness) using a dual-isotope framework (i.e., δ^{13}C- δ^{15}N space) and based on the functional diversity approach could give additional clues to understand the food web (Cucherousset and Villéger, 2015). They are useful because metric values are not affected by the number of individuals analyzed (Cucherousset and Villéger, 2015).

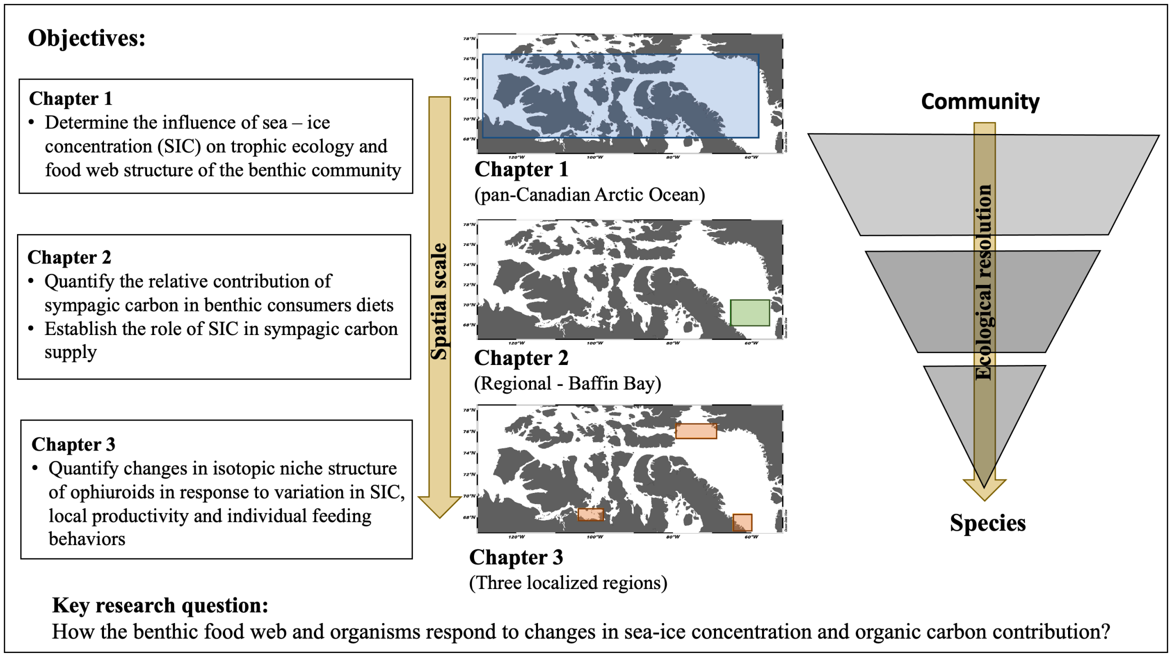
Objectives and thesis structure

The main objective of this research was to increase our understanding of the trophic ecology of benthic communities in the Canadian Arctic Ocean. Specifically, this research aimed to answer how benthic food web and organisms respond to changes in sea-ice concentrations and organic carbon inputs, and how these changes could affect consumers' diets, trophic interactions, carbon transfer, benthic food web structure and its redundancy. In addition, the main objectives for each chapter were to: (i) determine the influence of sea-ice concentration (SIC) on trophic ecology and food web structure of the benthic community; (ii) quantify the relative contribution of sympagic carbon in benthic consumers diets and establish the role of sea-ice concentration in benthic fauna diets and food web structure; and (iii) quantify changes in isotopic niche structure of ophiuroids in response to variation in SIC, local productivity and individual feeding behaviors.

In order to increase our understanding of the environmental and biological factors driving epibenthic food web structure and trophic interactions, this thesis was divided into three different chapters in which the benthic food web was studied at different spatial scales (localized, regional, and pan-Canadian Arctic Ocean) and ecological scales (individual and community; Figure 8). In Chapter 1, environmental drivers (i.e., sea ice, depth, productivity) of epibenthic food web structure were studied. We quantified aspects of the ecological niche of the benthic communities exposed to different sea-ice concentrations (SIC) across the Canadian Arctic Ocean. Using a combination of traditional community-wide metrics (i.e., convex hulls and ellipses) and recent isotopic diversity indices (i.e., Cucherousset and Villéger, 2015) the following hypotheses were tested: (i) the isotopic composition of food sources and benthic fauna will be largely influenced by gradients of SIC and the nature of the resources, (ii) the isotopic niche size will vary according to extrinsic factors (i.e., SIC and ecosystems productivity), in which a narrow niche size is linked to higher SIC areas and to high-productive ecosystems. In this framework, we also hypothesize that among the polynyas sampled, the narrowest niche will be associated with the most productive polynya (i.e., NOW), and (iii) an increase in the isotopic redundancy will be associated with a simplification of the niche structure (i.e., shorter chain length and width) linked with high-productive ecosystems where consumers use a low range of resources.

In Chapter 2, changes in trophic interactions and ecological niche structure were studied across areas with different sea-ice concentrations and sympagic carbon inputs. A novel combination of methods, ice-derived algae lipid biomarkers and stable isotope analyses, was used to analyze the importance of ice-derived carbon as a food source for deep-sea benthic consumers. In addition, the implications of changes in the input of sympagic carbon sources on the structure and dynamics of the benthic food web in the Baffin Bay region were studied. The following hypotheses were tested: (i) sea-ice cover is the primary environmental driver of contribution and geographic distribution of sympagic carbon on the seabed; (ii) sympagic carbon is the most important baseline food source supporting benthic consumers during spring in areas close to the MIZ; and (iii) deep benthic food web dynamics and structural variability are directly linked with both depth and availability of food sources.

Finally, Chapter 3 focused on three different species of ophiuroids on a localized scale with the objective of understanding the individual mechanisms (e.g., inter-individual dietary flexibility) that support feeding interactions and influence food web structure. Particularly, changes in the isotopic niche structure of ophiuroids were examined in response to variation in sea-ice conditions, productivity, and individual-level in feeding behavior. These coexisting ophiuroids were chosen as models to test the following hypotheses: (i) depending on sea-ice concentrations, patterns in species niche structure (i.e., segregation and overlap of niches) will change across regions, where a higher overlap of niches will be linked to regions with more SIC due to brittle stars exploiting more similar food items; (ii) changes in the isotopic niche width of ophiuroids will be closely related to sediment $\delta^{13}C$ carbon composition and individual feeding behaviors, in which niche width reduction will be linked to regions with higher abundance of resources where consumers ingest the more abundant sources; and (iii) a decrease in niche overlap will be associated with regions with higher heterogeneity of resources in which brittle stars can use a higher spectrum of resources.



Objectives:

Chapter 1
- Determine the influence of sea – ice concentration (SIC) on trophic ecology and food web structure of the benthic community

Chapter 2
- Quantify the relative contribution of sympagic carbon in benthic consumers diets
- Establish the role of SIC in sympagic carbon supply

Chapter 3
- Quantify changes in isotopic niche structure of ophiuroids in response to variation in SIC, local productivity and individual feeding behaviors

Key research question:
How the benthic food web and organisms respond to changes in sea-ice concentration and organic carbon contribution?

Figure 8. Schematic representation of the thesis structure for the three chapters relating to community levels and spatial scales.

Chapter 1. Quantifying aspects of the trophic and isotopic ecology of benthic communities exposed to different sea-ice concentrations across the Canadian Arctic Ocean

1.1 Résumé

La glace de mer est l'un des facteurs environnementaux les plus importants qui façonnent la production primaire et les flux d'apports de matières organiques dans les communautés benthiques de l'océan Arctique. Les fluctuations des apports de matières organiques influent sur les relations trophiques et les transferts d'énergie. Toutefois, les modifications dans la concentration de la glace de mer induites par le réchauffement de la planète pourraient entraîner des changements importants dans les interactions trophiques, affectant en bout de ligne le fonctionnement des réseaux trophiques de l'Arctique. Malgré les préoccupations croissantes quant à la nécessité de comprendre les réactions des espèces et des réseaux trophiques à la rapide perte de glace de mer, seules quelques études ont abordé ce sujet jusqu'à présent. Notre étude a examiné l'écologie trophique et isotopique des communautés macrobenthiques dans des zones présentant différentes concentrations de glace de mer dans l'océan Arctique canadien, en utilisant l'analyse d'isotopes stables en combinaison avec de multiples mesures de niche écologique à l'échelle de la communauté. D'après nos données, les niches écologiques de la communauté benthique varient en fonction des interactions complexes entre les conditions environnementales, les ressources disponibles et les pressions biotiques comme la prédation et la compétition. Nos résultats ont mis en évidence une réduction de la richesse isotopique (c.-à-d. des longueurs et largeurs de chaînes trophiques plus courtes) dans les zones à concentrations de glace de mer faibles et élevées, ce qui suggère une homogénéité des ressources et une faible diversité des aliments ingérés par les individus. En revanche, on a observé une augmentation de la richesse isotopique (c.-à-d. une niche trophique plus grande) dans les zones ayant des concentrations de glace de mer modérées, ce qui sous-entend une plus grande hétérogénéité des ressources alimentaires de base et des consommateurs utilisant des niches trophiques individuelles. Enfin, nos résultats suggèrent une réduction de la redondance isotopique dans les zones à concentrations de glace de mer élevées. Nos résultats appuient l'idée que la glace de mer est un facteur important dans la dynamique du réseau trophique benthique et renforcent le besoin urgent d'étudier plus à fond les

effets du déclin de la concentration de glace de mer sur le fonctionnement du réseau trophique arctique.

1.2 Abstract

Sea ice is one of the most critical environmental drivers shaping primary production and fluxes of organic inputs to benthic communities in the Arctic Ocean. Fluctuations in organic inputs influence trophic relationships and energy cascades. However, changes in sea-ice concentration (SIC) induced by global warming could lead to important shifts in trophic interactions, ultimately affecting Arctic food webs functioning. Despite the increasing concern over the need to understand benthic species and food web responses to rapid sea-ice loss, only a few studies have addressed this topic so far. This study investigated the trophic and isotopic ecology of epibenthic communities in areas with different SIC across the Canadian Arctic Ocean, using stable isotope analysis in combination with multiple community-wide niche metrics. Based on our data, ecological niches of the benthic community varied according to complex interactions between environmental conditions, resource supply, and biotic pressures such as predation and competition. Our results highlighted a reduction in isotopic richness (i.e., shorter chain length and width) in low and high SIC areas, suggesting homogeneity of resources and low range of diversity of food items ingested by individuals. In contrast, an increase in isotopic richness (i.e., broad niche) was observed in the moderate SIC area, implying higher heterogeneity in basal food sources and consumers using individual trophic niches. Finally, our findings suggested a reduction in the isotopic redundancy in ice areas with high SIC. Our results support the idea that sea ice is an important driver of benthic food web dynamics, and reinforce the urgent need for further investigations of the effects of declining sea ice on Arctic food web functioning.

1.3 Introduction

Arctic marine ecosystems are experiencing rapid and widespread changes due to increases in the average surface air temperature (Bhatt et al., 2014). As a result of this warming, the minimum multi-year sea-ice extent has been decreasing at a rate of 13.1% per decade, reaching its second-lowest minimum in September 2020, and its seventh-lowest maximum annual sea-ice extent in March 2020 (Perovich et al., 2020). In addition, there are trends towards an early onset period of sea-ice melt (2 days per decade) and delays in refreezing time (2.3 days per decade) (Post, 2017; Stroeve et al., 2014). Changes in the primary production of the Arctic Ocean are linked with decreases in sea ice (i.e., thickness and concentration), alterations in sea-ice phenology, and changes in the intensity of the stratification of the water column (Ardyna et al., 2020), which could yield alterations in the timing, magnitude, and delivery of the produced organic matter across water depths in the coming decades (Lafond et al., 2019; Leu et al., 2011). Hence, changes in primary production and delivery could lead to rapid shifts in the composition, abundance, and richness of the benthic community because benthic species rely mainly on ice-associated (i.e., sympagic) and water column (i.e., phytoplankton) microalgae sources (Roy et al., 2014). Furthermore, in marine Arctic food webs, fluctuations in the input of resources due to advances or delays in sea-ice melt could control consumers' diets and the biomass of individuals at lower trophic levels, affecting the timing of species interactions across trophic levels (Post, 2017). Despite this, only a few studies have investigated the response of species and marine food webs to changes in sea ice and carbon supply in the Arctic Ocean (e.g., Post, 2017; Yunda-Guarin et al., 2020).

One of the biggest challenges in ecology is predicting the adaptive capacity of a system to maintain functional integrity when faced with various disturbances and understanding the consequences of environmental shifts towards ecosystem functioning and services (Frid and Caswell, 2016). To address this challenge, stable isotope analysis (SIA) is an important tool that could be used to understand the effects of anthropogenic activities on food webs. For example, stable isotope ratios of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) have been used extensively for the investigation of the trophic ecology of marine species (Middelburg, 2014), and to track carbon transfer pathways in food webs (Peterson and Fry, 1987), revealing aspects of trophic structure and dependencies on various basal food items. Indeed, SIA is one of the main tools in food web ecology because it provides time and space-integrated insights into trophic relationships (Layman et al., 2012). $\delta^{15}N$ ratios are typically used to estimate the trophic level (TL) of consumers in relation to food sources (Post, 2002), whereas $\delta^{13}C$ ratios are used to establish the relative contribution of food sources in the diet of consumers and energy pathways (Layman et al., 2007a). The nitrogen isotope ratio increases by about 2.3‰ for each trophic level in aquatic ecosystems, whereas the carbon isotope trophic shift value is 0.4‰ (McCutchan et al., 2003). Advances in SIA allowed to estimate community-wide measures of the isotopic niche (i.e., the area occupied by individuals in a $\delta^{13}C$ - $\delta^{15}N$ space) providing quantitative information on resources and habitat use that helps characterize aspects of the ecological niche space (Jackson et al., 2011; Layman et al., 2007a). The community-wide measures, initially proposed by Layman et al. (2007a), consist of a quantitative approach to investigate different aspects of trophic ecology and food web structure, which is composed by six metrics (see methodology section). Recently, new metrics using a dual-isotope framework (i.e., $\delta^{13}C$- $\delta^{15}N$ space) and based on the functional diversity approach could give additional clues to understand the food web functioning (Cucherousset and Villéger, 2015).

The isotopic niche, a low-dimensional specification of the “Hutchinsonian ecological niche” (Hutchinson, 1957), represents the fraction of the isotopic niche area (in δ-space) occupied by consumers (Martínez Del Rio et al., 2009; Newsome et al., 2007), and helps in the analysis of patterns of interactions at various ecological resolutions (Shipley and Matich, 2020). The isotopic niche is a valuable approach to obtain quantified differences in ecological niches and is a useful conceptual tool to estimate variations in the trophic redundancy (degree of dietary overlap among taxa within a food web) of a community in response to changes in the trophic structure (Layman et al., 2007a). The characteristics of the niche vary according to intrinsic and extrinsic factors (Costa-Pereira et al., 2017; Shipley and Matich, 2020). For example, the seasonal phenology in sea-ice concentration and ecosystem productivity have been shown to influence the dimensions of the isotopic niche in benthic communities in polar regions (e.g., Lesser et al., 2020; Michel et al., 2019; Yunda-Guarin et al., 2020). While, inter-individual levels of dietary specialization and interspecific competition may also drive niche dynamics (e.g., Araújo et al., 2009; Evans et al., 2005; Semmens et al., 2009).

Based on the assumption that feeding linkages are the main factor structuring food webs and that sea ice is a key factor influencing the onset of primary production and supply of resources to benthic communities, we focused our analyses on studying the influence of sea-ice concentration (SIC, defined here as the fraction of an area covered by sea ice) on trophic ecology and food web structure of the benthic community. Using stable isotopes ($\delta^{15}N$, $\delta^{13}C$) and a combination of metrics of isotopic niche structure, we examined variation in the ecological niche of the benthic community at the pan-Canadian Arctic scale and tested the following hypotheses: i) the isotopic composition of food sources and benthic fauna will be largely influenced by gradients of SIC and the nature of the resources, ii) the isotopic niche size will vary according to extrinsic factors (i.e., SIC and ecosystems productivity), in which a narrow niche size is linked to higher SIC areas and to high-productive ecosystems. In this framework, we also hypothesize that among the polynyas sampled (Figure 1.1), the narrowest niche will be associated with the most productive polynya (i.e., NOW), and iii) an increase in the isotopic redundancy will be associated with a reduction of isotopic niche size (i.e., shorter chain length and width) linked with high-productive ecosystems where consumers use a low range of resources.

1.4 Materials and Methods

1.4.1 *Study area and sampling methods*

Located across the Canadian Arctic Ocean, the studied areas, namely Baffin Bay (BB), Lancaster Sound (LS) and the Canadian Arctic Archipelago (CAA) (Figure 1.1) are characterized by large inter-annual variations in primary productivity and sea-ice conditions (Stein and Macdonald, 2004). BB is a semi-enclosed ocean located between Baffin Island and western Greenland. It is partially covered by sea ice, excluding the ice-free months of August and September (Tang et al., 2004). Even if the ice breaks in the spring, LS is never completely ice-free, as first-year ice and multi-year ice continue to move from west to east until the formation of new ice in September (Welch et al., 1992). The CAA is made up of a larger number of islands and channels and the sea ice component consists of a mixture of both first-year and multi-year ice (Kwok, 2006). Multi-year ice is mostly located in Western CAA and can represent more than 50% of the total ice-covered area prior to melting (Howell et al., 2013). The Beaufort Sea can be divided into two ice regimes: the Alaskan Beaufort Shelf in the west and the Canadian Beaufort Shelf in the east (Carmack and Wassmann, 2006). The Canadian Beaufort Sea and the Amundsen Gulf are strongly influenced by terrigenous carbon inputs from different rivers, including the Mackenzie River that discharges freshwater (approximately 340 km^3 y^{-1}) to the Arctic Ocean (Macdonald et al., 1999). Sea-ice conditions in the Beaufort Sea vary according to the season. In the Beaufort Sea, winter sea ice can be categorized in three regimes: the offshore pack ice (composed of mobile annual and multiyear sea ice), the coastal landfast sea ice, and the Cape Bathurst polynya (Barber and Hanesiak, 2004).

The CAA region contains four of the polynyas analyzed in this study (i.e., CB: Cape Bathurst polynya, LS-BI: Lancaster Sound-Bylot Island polynya, NOW: North Water polynya, and VMS: Viscount-Melville Sound polynya). Polynyas are areas of reduced ice cover or open water enclosed by consolidated ice (Smith and Rigby, 1981). Arctic polynyas exhibit a marked interannual variability in sea-ice dynamics, and the initial timing moment of formation, the persistence of open water, and the productivity vary considerably across polynyas (Arrigo and van Dijken, 2004; Grebmeier and Barry, 2007). For example, until recently, the NOW was considered as one of the largest and most biologically productive polynyas in the Arctic Ocean, where production reached >250 g C m^{-2} y^{-1} (Klein et al., 2002; Stirling, 1997; Tremblay et al., 2006b). By comparison, primary productivity was ranging from 23 to 49 g C m^{-2} y^{-1} in the Canadian Shelf between Beaufort Sea and Amundsen Gulf

(Forest et al., 2011; Lavoie et al., 2009; Martin et al., 2013), 90 to 175 g C m^{-2} y^{-1} in the Cape Bathurst polynya (Arrigo and van Dijken, 2004), and 56 g C m^{-2} y^{-1} in Lancaster Sound (Welch et al., 1992).

A total of 35 stations ranging in depth from 35 to 789 m were sampled between August 2011 and July 2016 during three different oceanographic campaigns: 2011 (Roy et al., 2015), 2014 (Friscourt, 2016), and 2016 (Yunda-Guarin et al., 2020; Figure 1.1). At each station, epibenthic specimens, surface sediments, and suspended particulate organic matter (SPOM) were collected aboard the Canadian research icebreaker CCGS *Amundsen*. Epibenthic fauna were collected using an Agassiz trawl with an opening of 1.5 m and a net mesh size of 40 mm, with a 5 mm cod-end liner. A box core (0.25 m^2) sampling was undertaken to collect sediment samples (upper 1 cm). For each box core, surface sediments (Sed-POM) were collected for pigment content (using 10 ml truncated syringes of an area of 1.5 cm^2) and stable isotopes analyses (using 60 ml truncated syringes of an area of 5 cm^2). In addition, suspension particular organic matter (i.e., SCM-POM and Bot-POM) sources were collected at two depths, 10 meters above the seafloor (Bot-POM) and in the subsurface chlorophyll maximum (SCM-POM) using a CTD-Rosette with 12 L Niskin-type bottles. Water samples for SPOM were filtered onto 21 mm Whatman GF/F glass-fiber filters (nominal pore size 0.7 µm) pre-combusted at 450°C for 5 h. After collection, all samples, including filters, were immediately frozen at –20°C for further isotopic analyses. In surface sediments, the quantification of chlorophyll *a* (chl *a*) concentration was carried out at Université Laval (Quebec, Canada) following modified protocol of Riaux-Gobin and Klein (1993) and Link et al. (2011).

To assess the possible effects of sea-ice concentration (SIC) on the ecological niche structure, sampled stations were arbitrarily grouped into three sea-ice condition categories: i) fifteen stations with low SIC (<10% of SIC) located within or in the vicinity of polynyas; ii) ten stations with moderate SIC (>10 to 50% of SIC) situated in the CAA and BB; and iii) eleven stations with high SIC (>50% of SIC) located mainly in BB (Figure 1.1). Additional information about individual sampling stations can be found in Supplementary Table S1.1.

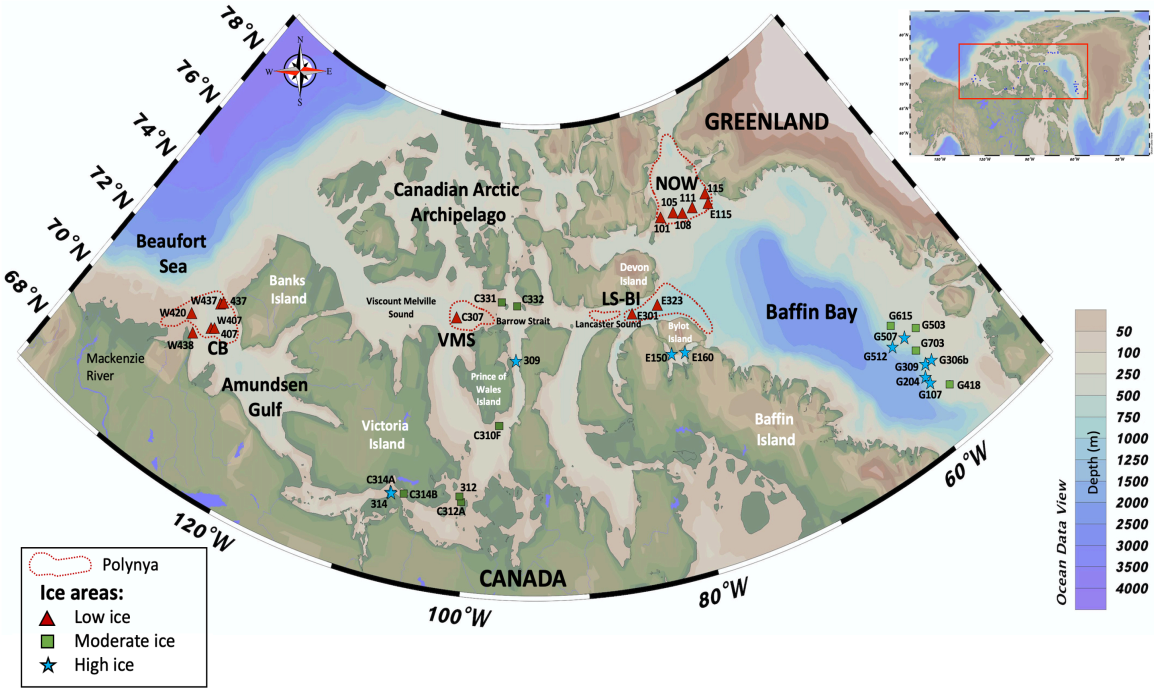


Figure 1.1. Location of sampling stations with bottom bathymetry. Sampled stations were grouped into three ice areas according to the average sea-ice concentration (SIC) estimated over a 30-day period prior to sampling: low (red triangles, <10% of SIC), moderate (green squares, >10 to 50% of SIC), and high (blue stars, >50% of SIC). Polynyas are represented by a red dotted line and their names are indicated by abbreviations in capital letters (CB: Cape Bathurst polynya, LS-BI: Lancaster Sound-Bylot Island polynya, NOW: North Water polynya, VMS: Viscount-Melville Sound polynya). The approximate location and delimitation areas of the polynyas were based on Barber and Massom (2007) and Roy et al. (2015).

1.4.2 *Sea-ice concentration data*

Satellite sea-ice concentrations (SIC) data was derived from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data with polar stereographic projection at a grid cell size of 25 × 25 km, and downloaded from the National Snow and Ice Data Center, NSIDC (Cavalieri et al., 1996). The average percentage SIC at each station was calculated for a period of 30 days prior to sampling. This period was considered relevant in this study, since isotopic values of tissues in invertebrates with Arctic distribution (e.g., *Alitta virens*, *Onisimus litoralis*, *Mytilus edulis*, and *Macoma calcarea*) showed metabolic turnover rates of the organic matter assimilated by benthic consumers of approximately 30 days (Dubois et al., 2007; Kaufman et al., 2008; McMahon et al., 2006; Olive et al., 2003).

1.4.3 *Carbon and nitrogen stable isotope analysis*

Stable isotope ratios ($\delta^{13}C$ - $\delta^{15}N$) were measured in a total of 664 benthic specimens. Benthos samples were freeze-dried at –50°C. Afterward, they were ground and homogenized to a fine powder with mortar and pestle. When necessary, samples were acidified (HCl 1M) to remove inorganic carbon before the stable carbon isotopic ($\delta^{13}C$) analysis. Filters for the analysis of SPOM isotopic signatures were freeze-dried for 48h, fumed with saturated HCl vapors for 24h, and dried at 60°C for 24h before conducting isotope analyses. Sediments and benthic organisms were freeze-dried, acidified with an aqueous solution of 1N HCl until bubbling ceased and dried at 60°C for 24h. Unacidified samples were used to assess the stable nitrogen isotopic ($\delta^{15}N$) composition.

Stable carbon and nitrogen isotope ratios were measured in the Oceanography Laboratory at Laval University and at the Marine Chemistry and Mass Spectrometry Laboratory of University of Quebec at Rimouski (UQAR), Canada, with a continuous-flow isotope ratio mass spectrometry (CF-IRMS) in the continuous-flow mode (Thermo Electron ConFlo III) using an ECS 4010 Elemental Analyzer/ZeroBlank Autosampler (Costech Analytical Technologies). Replicate measurements of international standards (USGS40 and USGS41 from the International Atomic Energy Agency; B2151 from Elemental Microanalysis) established measurement errors ≤ 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$. Standards were calibrated against the international references Vienna PeeDee Belemnite (PDB) for carbon and atmospheric air (N_2) for nitrogen. Stable isotope ratios were expressed in delta (δ) units ($\delta^{13}C$; $\delta^{15}N$) as parts per mil (‰) differences from a standard reference material: $\delta X\,(‰) = \left[\frac{(\text{Rsample} - \text{Rstandard})}{\text{Rstandard}}\right] \times 1000$, where X is ^{13}C or ^{15}N of the sample and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

1.4.4 *Trophic position of benthic consumers*

Based on the trophic position (TP) for each benthic consumer, we studied the relative assimilation and transfer of carbon across the benthic community, assuming a constant enrichment factor (Δ) of 2.3‰ per trophic level in aquatic consumers (McCutchan et al., 2003). The surface sediment bulk $\delta^{15}N$ signature was used as a baseline to estimate the trophic level for each consumer. Benthic epifauna were categorized into three different groups, higher level consumers (including secondary, tertiary, or upper consumers as well as scavengers (TP ≥ 3), omnivores (3 > TP > 2), and primary consumers (TP ≤ 2), using Equation 1:

$$\mathrm{TP} = \frac{\delta^{15}\mathrm{N\ consumer} - \delta^{15}\mathrm{N\ base}}{\Delta^{\delta^{15}\mathrm{N}}} + \lambda \qquad \text{Equation 1}$$

where $\delta^{15}N_{Consumer}$ is $\delta^{15}N$ of the benthic consumers, $\delta^{15}N_{base}$ is the nitrogen isotope ratio of sediments for each ice area studied (Figure 1.1), namely the base of the food chain, $\Delta\delta^{15}N$ is the trophic enrichment factor between successive trophic levels, and $\lambda = 1$ is the trophic position of "baseline". The sediment baseline was estimated using the mean $\delta^{15}N$ calculated for each ice area, while $\delta^{13}C$ was used as a proxy to establish the dependence of benthic epifauna on different food sources.

1.4.5 *Statistical analyses*

All statistical analyses were carried out in R (v3.6.1, R Studio v1.1.456). Mixed linear models were fit using the *nlme* package (v.3.1-140) (Pinheiro et al., 2021). The normality of residuals was tested by examining the characteristic Quantile-Quantile (QQ) plot (Zuur et al., 2007). If residual normality and homoscedasticity assumptions were not met, dependant variables were log-transformed. Models comprised only main effects and two-way interaction effects. $\delta^{13}C$ and $\delta^{15}N$ models were run against depth, sea-ice concentration, ice areas, and epibenthic consumer groups (GC; primary consumers, omnivores, and high consumers) as fixed factors and both region (i.e., CAA, BB, and Cape Bathurst, Lancaster Sound-Bylot Island, North Water, Viscount-Melville Sound polynyas) and sampling year as random factors to account for the variability they incurred. Nonsignificant two-way interaction effects were trimmed to increase model fit. Significant effects implicating categorical factors (ice areas and consumer groups) were further analysed with Tukey post-hoc using the *emmeans* package (v2.27-61) (Lenth and Lenth, 2018).

1.4.6 *Trophic structure: community-wide metrics and isotopic diversity assessment*

At the community level, the quantification of different aspects of the ecological niche structure and isotopic diversity of the benthic community between ice areas was completed using two different approaches. Firstly, community-wide metrics (i.e., convex hulls and ellipses) based on the relative position of groups or individuals in multivariate isotopic space were used to describe different aspects of trophic ecology and food web structure according to the ecological niche of each benthic community using stable isotope data (Jackson et al., 2011; Layman et al., 2007a). Among Layman's metrics, the total convex hulls area (TA) represents the amount of isotopic space filled by the group of consumers, providing a proxy of the niche width and the range of resources and habitats used by consumers (Bearhop et al., 2004). The δ^{15}N and δ^{13}C ranges (NR and CR, respectively) were used to quantify the total realized niche breadth in the horizontal and vertical dimensions of the iso-space (Layman et al., 2007a). The mean distance to centroid (CD) gives a measure of the average degree of trophic diversity within a community. The mean nearest-neighbor distance (MNND) providing a measure of density and clustering of species within the community, and the standard deviation of MNND (SDNND) provides a measure of evenness of spatial density and packing (Layman et al., 2007a). Besides the Layman's metrics, the core isotopic niche of each epibenthic community was calculated to infer characteristics of community structure and niche width using the standard ellipse area in the R "SIBER" package (Jackson et al., 2011). The probabilistic method of Jackson et al. (2011) was used to estimate the mode and the credible interval of the Bayesian-simulated Standard Ellipse Areas (SEAb, expressed in ‰^{2}; Jackson et al., 2011) and the sample size-corrected standard ellipse area (SEAc, expressed in ‰^{2}). SEAC is a more robust approach that encompasses the core (around 40%) of the isotopic data within each community, therefore is less sensitive to sample size and isotopic outliers, providing a better and more comparable description of the isotopic niche area of a community (Jackson et al., 2011).

Secondly, different facets of the isotopic diversity were measured using four different indices: isotopic dispersion (IDis), divergence (IDiv), evenness (IEve), and uniqueness (IUni) defined by Cucherousset and Villéger (2015). Isotopic diversity indices were measured in the two-dimensional isotopic spaces providing data on isotopic diversity and redundancy of the benthic community (Cucherousset and Villéger, 2015). Briefly, IDiv index measures the amount of isotopic space occupied by an assemblage of species taking into account their distribution within the convex hull. IDis index estimates the variation or dispersion of a set of weighted values in iso-space and divides it by the distance to the gravity center. IEve index quantifies the regularity in the distribution of the species through the shortest spanning tree that connects all points in the isotopic space. Finally, IUni index measures the average distance of each species to the nearest neighbor. Therefore, it is a measure of the packing density of species in stable isotope space (for further description, see Cucherousset and Villéger, 2015).

For the first part of the analyses, stable isotope values of consumers were used without any transformation to examine variations on aspects (e.g., isotopic richness, NR, CR) of the ecological niche structure of the benthic community within each ice area. Then, when calculating the isotopic diversity indices, stable isotope values of consumers were homogenized in each ice area using the mean-correction method recommended by Le Bourg (2020). This method reduced the potential biases of isotope values between sampling stations caused by spatial and temporal differences in sample collection (for a review, see Le Bourg, 2020). It consists of taking the isotopic mean $\bar{X}$ ($\delta^{13}C$ or $\delta^{15}N$) of each individual i and subtract it to the result of the subtraction between the station mean s for that isotopic value and the overall mean of all stations combined z. The result of the equation is the mean corrected value $\bar{X}c$ for the individual, Equation 2:

$$\bar{X}c = \bar{X}i - (\bar{X}s - \bar{X}z) \qquad \text{Equation 2}$$

Additionally, the multidimensional isotopic space ($\delta^{15}N$ and $\delta^{13}C$) was standardized (i.e., scaled between 0 and 1) to have equal importance in the index's calculation for each axis and to remove the potential scaling discrepancies present in δ-space across ice areas (Cucherousset and Villéger, 2015).

1.5 Results

1.5.1 *Stable isotope composition of basal food sources and epibenthic trophic groups*

Baselines food sources displayed a wide range of isotope signatures among ice areas with contrasting ice conditions (Table 1.1; Figure 1.2). Overall, the basal pelagic SCM-POM (mean SCM-POM ‰ ± SD = –25.9‰ ± 1.3, n= 32) and Bot-POM (mean Bot-POM ‰ ± SD = –25.8‰ ± 3.1, n= 21) were more ^{13}C-enriched under low SIC, while basal Sed-POM was, on average, more ^{13}C-enriched than pelagic baseline POM sources regardless of the SIC (Figure 1.2). Linear models showed a significant effect of depth ($P < 0.001$) and the interactive effects between depth and SIC ($P < 0.001$) on the $\delta^{13}C$ isotopic composition of Sed-POM (Table S1.2).

The basal Sed-POM showed the most ^{15}N-depleted (mean Sed-POM ‰ ± SD = 5.4‰ ± 1.6, n= 38) and ^{15}N- enriched values (mean Sed-POM ‰ ± SD = 7.0‰ ± 1.3, n= 19) in low and moderate ice areas, respectively. Based on linear models, a significant effect of both depth ($P < 0.001$) and SIC ($P < 0.01$) and an interactive effect between these environmental variables were detected on the $\delta^{15}N$ isotopic composition of Sed-POM (Table S1.2). Finally, linear models did not find a significant effect of depth or SIC on $\delta^{13}C$ and $\delta^{15}N$ isotopic values for the other basal food sources of SPOM between ice areas (Table S1.2).

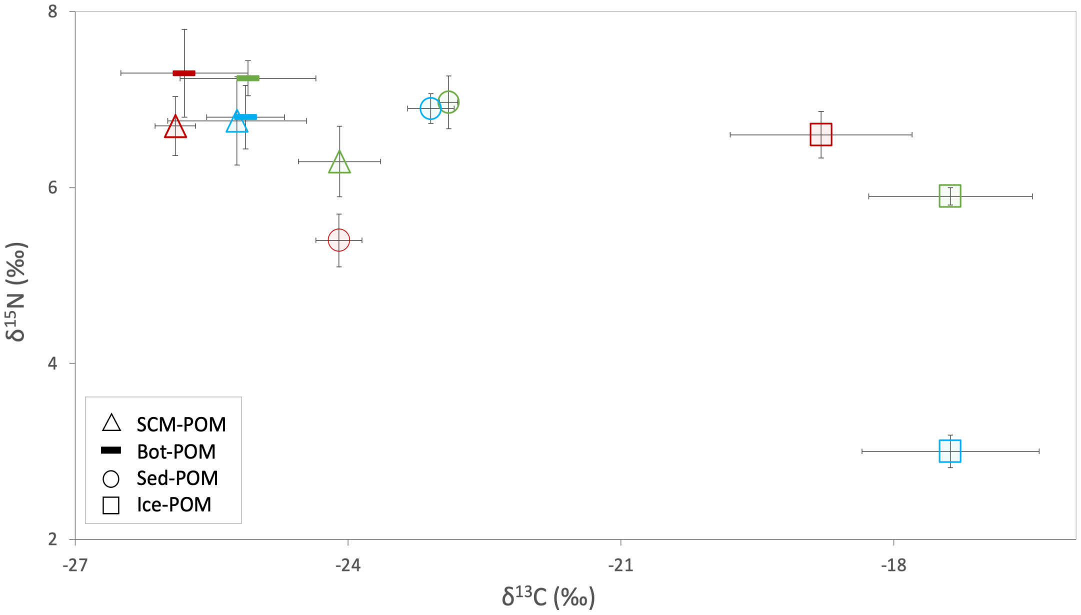


Figure 1.2. Biplot of carbon (δ^{13}C) and nitrogen (δ^{15}C) composition of basal food sources. Isotopic δ^{13}C and δ^{15}N composition (mean ± SE) of basal food sources in ice areas with low SIC (red); ice areas with moderate SIC (green), and areas with high SIC (blue) concentration. Basal food sources: subsurface chlorophyll maximum (triangle, SCM-POM), bottom water particulate organic matter (rectangle, Bot-POM), surface sediment particular organic matter (circle, Sed-POM), and ice particulate organic matter (square, iPOM). Ice-POM data are from Beaufort Sea (Pineault et al., 2013), Baffin Bay (Yunda-Guarin et al., 2020), the NOW (Tremblay et al., 2006a), and Allen Bay/Resolute Passage (Gosselin and Mundy, unpublished data).

Benthic fauna under areas with contrasting ice conditions displayed a wide range of isotopic composition in this study (Figure 1.3; Table S1.5). The average benthic fauna δ^{13}C composition was –19.0 ± 1.7‰ (range from –24.1‰ to –14.7‰) in ice areas with low SIC, –18.4 ± 2.1‰ (range: –23.8‰ to –13.5‰) in ice areas with moderate SIC, and –18.1 ± 1.9‰ (range from –21.7‰ to –13.4‰) in ice areas with high SIC. Among the benthic fauna studied the most ^{13}C-enriched values corresponded to the echinoderm *Ophiacantha bidentata* (high consumer) in high SIC areas (–13.4‰), while the most depleted in ^{13}C were hydrozoans of the family Sertulariidae (omnivorous consumer) in low SIC areas (–24.1‰). Among benthic groups, primary consumers in low SIC areas were the most depleted group in δ^{13}C values (mean δ^{13}C‰ ± SD = –20.3‰ ± 1.4, n= 34), whereas high consumers in high SIC areas were the most enriched in δ^{13}C (mean δ^{13}C‰ ± SD = –17.6‰ ± 1.7, n= 114). Besides, linear models showed a significant effect of SIC on the δ^{13}C isotopic composition of benthic consumers (P <0.001). However, the effect of SIC on the δ^{13}C is more significant in high

Table 1.1. Isotopic composition of baseline food sources measured in samples collected at different locations in the Canadian Arctic Ocean

			Suspended-POM						Sediment-POM		
Region[a]	Station	Sea-ice[b] condition	n[c]	δ^{15}N (‰)[d] SCM-POM	δ^{13}C (‰)[e] SCM-POM	n[c]	δ^{15}N (‰)[d] Bot-POM	δ^{13}C (‰)[e] Bot-POM	n[c]	δ^{15}N (‰)[d] Sed-POM	δ^{13}C (‰)[e] Sed-POM
CB	407	Low	2	4.5 ± 1.0	–25.8 ± 0.0	2	6.3 ± 3.3	–27.1 ± 0.1	2	5.7 ± 1.1	–23.6 ± 0.1
CB	437	Low	2	9.4 ± 0.0	–25.8 ± 0.2	2	7.7 ± 0.7	–28.1 ± 1.7	2	6.5 ± 0.4	–24.8 ± 0.6
CB	W.420	Low	2	5.4 ± 0.5	–27.6 ± 0.0	2	5.4 ± 0.5	–27.6 ± 0.0	3	2.1 ± 0.3	–27.4 ± 0.2
CB	W.437	Low	2	4.7 ± 0.0	–27.4 ± 0.0	0	N/A[f]	N/A	3	5.7 ± 0.5	–24.9 ± 0.3
CB	W.438	Low	2	6.5 ± 0.3	–28.1 ± 0.0	0	N/A	N/A	3	2.1 ± 0.6	–28.3 ± 0.2
CB	W.407	Low	2	6.9 ± 0.2	–25.6 ± 0.2	1	13.3	–28.5	3	6.6 ± 0.3	–25.0 ± 0.1
VMS	C.307	Low	2	6.5 ± 0.9	–25.5 ± 0.1	1	8.5	–31.3	3	7.0 ± 0.4	–22.9 ± 0.2
LS-BI	E.301	Low	2	5.5 ± 0.5	–24.9 ± 0.2	1	7.6	–26.8	3	6.0 ± 0.0	–22.8 ± 0.2
LS-BI	E.323	Low	2	5.5 ± 0.3	–24.2 ± 0.2	2	8.2 ± 0.73	–24.9 ± 0.0	3	6.3 ± 0.1	–23.0 ± 0.1
NOW	115	Low	3	8.4 ± 2.3	–25.5 ± 0.1	4	5.8 ± 2.2	–26.4 ± 1.8	2	5.7 ± 0.8	–22.5 ± 0.6
NOW	111	Low	3	7.5 ± 0.7	–25.7 ± 1.5	2	9.0 ± 0.6	–22.2 ± 1.8	2	6.3 ± 0.4	–22.3 ± 0.3
NOW	101	Low	2	7.6 ± 1.5	–24.0 ± 1.0	3	6.4 ± 0.8	–21.2 ± 3.0	2	5.8 ± 0.2	–22.6 ± 0.0
NOW	105	Low	2	5.9 ± 0.6	–25.0 ± 0.3	0	N/A	N/A	2	4.7 ± 0.3	–22.5 ± 0.6
NOW	108	Low	2	9.4 ± 2.1	–26.0 ± 1.1	0	N/A	N/A	2	5.9 ± 0.1	–22.4 ± 0.1
NOW	E.115	Low	2	5.2 ± 0.1	–27.6 ± 0.1	1	7.3	–26.6	3	5.7 ± 0.4	–23.2 ± 0.2
CAA	C.331	Moderate	2	6.5 ± 3.0	–24.9 ± 0.1	1	7.3	–22.0	3	5.8 ± 0.8	–23.2 ± 0.3
CAA	C.310F	Moderate	2	6.4 ± 0.2	–23.2 ± 0.0	1	7.5	–27.6	3	8.0 ± 1.0	–22.5 ± 0.6
CAA	C.312A	Moderate	2	7.3 ± 0.0	–23.6 ± 0.1	2	7.3 ± 0.1	–23.8 ± 0.3	3	6.4 ± 1.0	–23.1 ± 0.1
CAA	312	Moderate	3	5.5 ± 0.5	–23.5 ± 0.1	2	6.6 ± 0.6	–26.4 ± 1.1	2	6.5 ± 0.1	–23.0 ± 0.1
CAA	C.314B	Moderate	2	4.1 ± 0.1	–26.9 ± 0.2	1	8.6	–27.3	3	8.8 ± 0.5	–23.9 ± 0.1
CAA	C.332	Moderate	2	7.1 ± 0.4	–24.9 ± 0.0	1	6.8	–23.5	3	6.8 ± 0.1	–22.2 ± 0.1
CAA	314	High	2	6.8 ± 1.4	–25.3 ± 2.1	2	6.4 ± 0.0	–26.1 ± 1.0	2	7.2 ± 0.4	–22.1 ± 0.2
CAA	C.314A	High	2	5.6 ± 0.0	–24.8 ± 0.1	2	7.2 ± 0.1	–24.0 ± 0.3	3	7.2 ± 0.3	–23.4 ± 0.1
CAA	309	High	2	6.3 ± 1.2	–29.2 ± 1.2	2	7.2 ± 1.8	–24.8 ± 0.6	2	7.1 ± 0.7	–23.0 ± 0.6
BB	G.418	Moderate	0	N/A	N/A	0	N/A	N/A	1	4.8	–22.6
BB	G.615	Moderate	1	8.5	–20.1	0	N/A	N/A	1	7.4	–21.9
BB	G.107	High	1	6.7	–22.0	0	N/A	N/A	0	N/A	N/A
BB	G.204	High	1	9.1	–21.9	0	N/A	N/A	0	N/A	N/A
BB	G.306b	High	1	10.4	–21.4	0	N/A	N/A	1	5.8	–21.4
BB	E.150	High	1	6.5	–26.1	1	5.0	–24.1	3	6.3 ± 0.6	–24.4 ± 0.7
BB	E.160	High	2	5.8 ± 0.1	–26.2 ± 0.1	1	8.1	–26.9	3	7.2 ± 0.3	–22.8 ± 0.1

[a] Regions of sampling collection: Baffin Bay (BB), Canadian Arctic Archipelago (CAA), Cape Bathurst polynya (CB), Viscount-Melville Sound-Lancaster Sound-Bylot Island polynya (VMS-LS-BI), and North Water polynya (NOW).

[b] Sea-ice condition in ice areas: low ice (≤10% of SIC), moderate ice (>10 to 50% of SIC), and high ice (>50% of SIC).

[c] Number of total samples per station used for subsurface chlorophyll maximum particulate organic matter (SCM-POM), bottom water particulate organic matter (Bot-POM), and surface sediment particulate organic matter (Sed-POM) for stable isotope analyses.

[d] Mean values ± standard deviation of δ^{15}N (‰).

[e] Mean values ± standard deviation of δ^{13}C (‰).

[f] N/A indicates data not available.

SIC areas (Table S1.3). No effect of depth alone on $\delta^{13}C$ isotopic composition of consumers was detected (P value = 0.42; Table S1.3).

The average $\delta^{15}N$ composition in benthic fauna was 12.8 ± 2.8‰ (range from 4.6‰ to 19.4‰) in ice areas with low SIC, 12.8 ± 3.2‰ (range of 5.4‰ to 21.3‰) in ice areas with moderate SIC, and 13.4 ± 2.8‰ (range from 6.4‰ to 20.5‰) in ice areas with high SIC. Among benthic species, the sea stars *Stephanasterias albula* and *Korethraster hispidus* (high consumers) were the most ^{15}N-enriched species in ice areas with high (21.3‰) and moderate (20.5‰) SIC, respectively. In contrast, the species of echinoderms *Ophiocten sericeum* and *Ophiura robusta* (primary consumers) were the most ^{15}N-depleted in areas with low SIC with $\delta^{15}N$ of 4.6‰ and 5.9‰, respectively. Among benthic groups, primary consumers in low SIC areas were the most depleted group in $\delta^{15}N$ values (mean $\delta^{15}N$‰ ± SD = 7.9‰ ± 1.0, n= 34), whereas high consumers in moderate SIC areas were the most enriched in $\delta^{15}N$ (mean $\delta^{15}N$‰ ± SD = 15.4‰ ± 1.9, n= 106). Linear models indicated that seafloor depth was an important variable affecting $\delta^{15}N$ isotopic composition for consumers (P <0.001; Table S1.4).

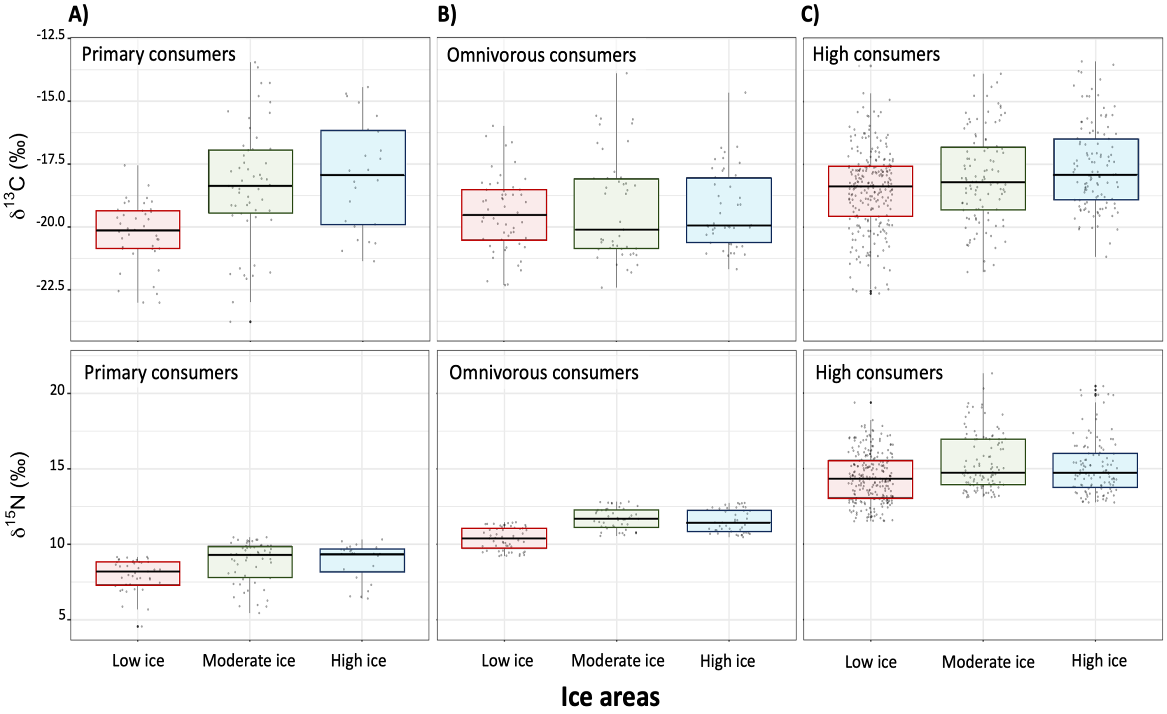


Figure 1.3. Boxplot showing the stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) of epibenthic consumer groups under contrasted sea-ice conditions. Stable isotope data ($\delta^{13}C$ and $\delta^{15}N$) of benthic consumers are shown in ice areas with different sea-ice concentration (SIC): low ice (<10%

of SIC; red), moderate ice (>10 to 50% of SIC; green), and high ice (>50% of SIC; blue). Benthic consumers were grouped according to their trophic levels (see methodology). The middle part of the box, or the "interquartile range," represents the middle quartiles (or the 75th minus the 25th percentile). The black line in the box represents the median. Points beyond the lines represent outliers in the data set and black points are individual isotopic values of benthic consumers.

1.5.2 *Epibenthic food web structure based on community-wide metrics*

Bayesian estimates of SEAs and Layman's multidimensional metrics found differences in the ecological niche structure of benthic communities between ice areas (Figure 1.4; Table 1.2). The convex hull area of benthic communities ranged from 76.37 in the ice areas with moderate SIC to 55.68 in the ice areas with high SIC (Figure 1.4, Table 1.2). Based on the data, the largest niche width (CR = 9.01) corresponded to the ice areas with moderate SIC, whereas the shortest niche width (CR = 6.51) was related to the ice areas with high SIC. In addition, a short niche length was found in the ice areas with low SIC (NR = 10.42) compared to ice areas with moderate and high SIC (NR = 14.44 and 13.55, respectively). Furthermore, data showed an increase in both the distance to the centroid (CD = 3.18) and the standard deviation of MNND (SDNND = 0.49) in the ice areas with moderate SIC, whereas the mean nearest-neighbor distance (MNND = 0.61) was greater in the ice areas with high SIC (Table 1.2). Bayesian standard ellipse areas revealed similar patterns in niche size to those observed with Layman's metrics for the benthic community (Figure 1.4, Table 1.2), showing a wider isotopic niche width (SEAc = 18.54) in the ice areas with moderate SIC, whereas a narrow niche width was found in the ice areas with high SIC (SEAc = 12.51; Table 1.2).

Among benthic groups, multidimensional metrics showed a similar pattern in the ecological niche size, indicating that the broadest niche corresponded to high consumers in ice areas with low SIC, whereas omnivorous consumers in ice areas with high SIC showed the narrowest niche (Table 1.2; Figure S1.1). In addition, the greatest trophic separation (CD = 2.29) and mean nearest-neighbor distance (MNND = 0.80) corresponded to primary consumers in ice areas with moderate SIC (Table 1.2).

Table 1.2. Results of the quantitative community-wide niche metrics of the whole epibenthic communities and three epibenthic trophic groups (high consumers, omnivorous consumers, primary consumers) under contrasting sea-ice conditions. Maximum values are in bold.

Metric	**Ice areas**[a]		
	Low ice	**Moderate ice**	**High ice**
Whole epibenthic community			
***Convex hulls metrics* (‰)**			
Nitrogen range (NR)	10.42	**14.44**	13.55
Carbon range (CR)	7.87	**9.01**	6.51
Convex hull area (TA)	58.12	**76.37**	55.68
Distance to centroid (CD)	2.90	**3.18**	2.60
Mean nearest-neighbor distance (MNND)	0.52	0.58	**0.61**
Standard deviation of MNND (SDNND)	0.36	**0.49**	0.44
***Standard ellipse metrics* (‰^{2})**			
Ellipse area (TA)	56.00	**76.35**	55.71
Standard ellipse area (SEAb)	12.68	**18.26**	12.30
Standard ellipse area core (SEAc)	12.87	**18.54**	12.51
Epibenthic trophic group			
***Convex hulls metrics* (‰)**			
High consumers			
Nitrogen range (NR)	6.48	7.10	**7.65**
Carbon range (CR)	6.47	7.00	5.84
Convex hull area (TA)	**38.96**	33.67	30.82
Distance to centroid (CD)	2.15	2.14	2.13
Mean nearest-neighbor distance (MNND)	0.52	0.52	0.51
Standard deviation of MNND (SDNND)	0.41	0.41	0.34
***Standard ellipse metrics* (‰^{2})**			
Ellipse area (TA)	**37.68**	33.67	30.83
Standard ellipse area (SEAb)	8.55	8.52	8.73
Standard ellipse area core (SEAc)	8.75	8.72	8.91
Omnivorous consumers			
Nitrogen range (NR)	2.12	1.90	2.01
Carbon range (CR)	5.79	7.34	4.96
Convex hull area (TA)	8.62	10.61	6.79
Distance to centroid (CD)	1.35	1.99	1.29
Mean nearest-neighbor distance (MNND)	0.50	0.59	0.47
Standard deviation of MNND (SDNND)	0.40	0.50	0.24
***Standard ellipse metrics* (‰^{2})**			
Ellipse area (TA)	8.63	10.59	6.81
Standard ellipse area (SEAb)	3.12	4.26	2.67
Standard ellipse area core (SEAc)	3.28	4.54	2.84
Primary consumers			
Nitrogen range (NR)	2.24	4.55	3.41
Carbon range (CR)	5.30	**9.01**	6.24
Convex hull area (TA)	7.26	21.54	9.24
Distance to centroid (CD)	1.33	**2.29**	2.15
Mean nearest-neighbor distance (MNND)	0.54	**0.80**	1.21
Standard deviation of MNND (SDNND)	0.45	**0.92**	0.49
***Standard ellipse metrics* (‰^{2})**			
Ellipse area (TA)	7.27	21.52	9.25
Standard ellipse area (SEAb)	3.09	**9.40**	6.96
Standard ellipse area core (SEAc)	3.33	**10.08**	8.12
***Sea-ice concentration* (%)**	0 – 10%	> 10 – 50%	> 50%

[a] Sea-ice concentration (SIC) across ice areas: low ice (≤10% of SIC), moderate ice (>10 to 50% of SIC), and high ice (>50% of SIC).

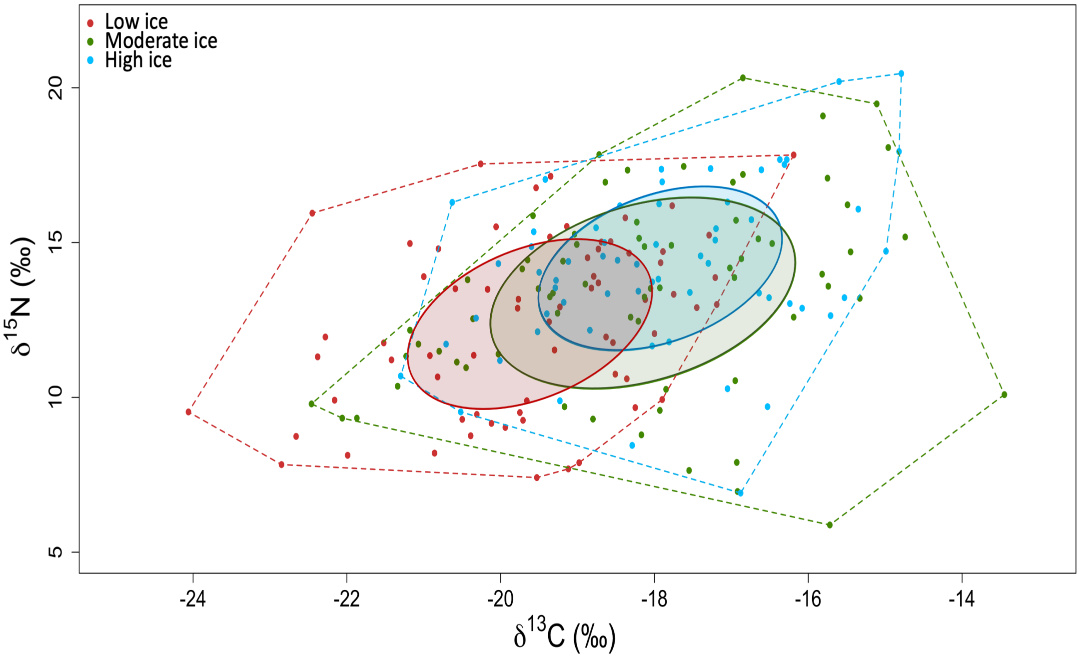


Figure 1.4. Biplot illustrating the isotopic niche structure of the whole epibenthic community under contrasted sea-ice conditions. The positions occupied by benthic fauna in the isotopic space are represented by dots in the δ^{13}C - δ^{15}N biplot. Isotope data of benthic fauna are shown in areas with different sea-ice concentrations (SIC): low ice (≤10% of SIC; red), moderate ice (>10 to 50% of SIC; green), and high ice (>50% of SIC; blue). The representation of the ellipses (shaded area within solid lines) encloses the size-corrected standard ellipse area (SEAc, fits 40% of the data). The representation of the convex hull area (dashed lines) encloses the isotopic richness of the benthic community for each sea-ice condition.

1.5.3 *Trophic and isotopic ecology of the whole epibenthic community based on isotopic diversity indices*

Among the three ice areas, isotopic diversity indices denote variations in the trend of distribution of the isotopic values of epibenthic consumers in the iso-space area of the convex hulls (Figure 1.5). For example, under moderate ice conditions, the epibenthic community registered the highest values of isotopic divergence (IDiv = 0.721) and isotopic dispersion (IDis = 0.488), which indicated that isotopic values of organisms had a wide distribution, far from the center of gravity at the edges of the convex hulls. In turn, the lowest IDis values, often referred to as centroid distance or CD (Layman et al., 2007a), was recorded in both low and high SIC areas (IDis = 0.363 and 0.362, respectively), which suggested an approximation of the isotopic values of organisms to the center of gravity of the convex hulls area. Isotopic eveness (IEve), comparable to the standard deviation of nearest neighbor distance or SDNND (Layman et al., 2007a), showed slight differences in IEve values between ice areas, displaying the highest value for the ice area with moderate SIC (IEve = 0.745), whereas the lowest value was found in the ice area with low SIC (IEve = 0.72). In this context, IEve tended to 0 when most of the organisms are packed within a small area of the stable isotope space, while IEve tended to 1 when organisms were evenly distributed in the stable isotope space. Finally, the isotopic uniqueness (IUni), used here as a proxy to estimate of the redundancy of the benthic community between ice areas, exhibited the lowest value in the ice area with low SIC (IUni = 0.197), aiming to a higher overlap of isotopic values between organisms and suggesting a greater redundancy of the benthic community in this ice area (Table 1.2).

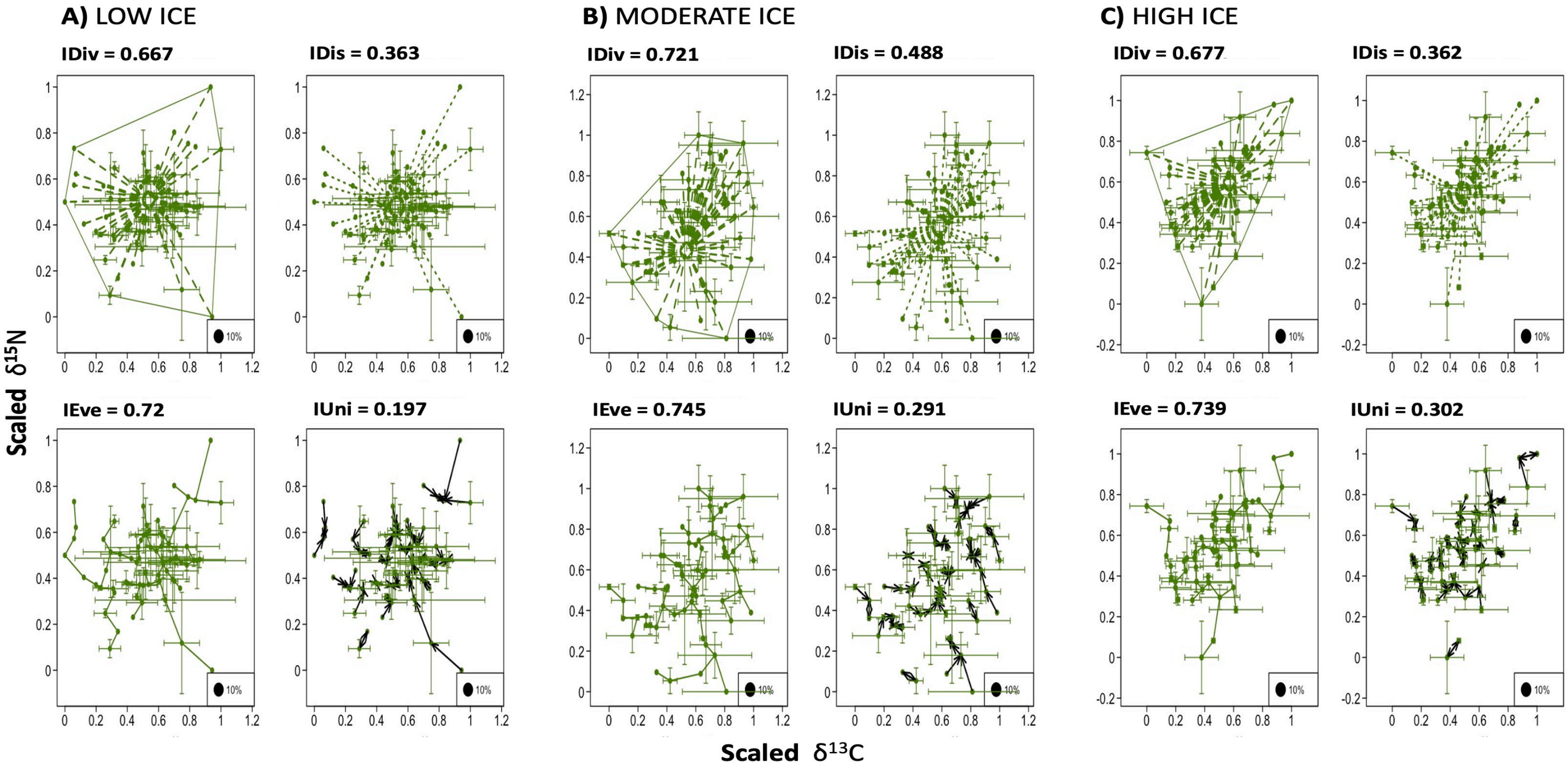


Figure 1.5. Biplots illustrating the isotopic diversity indices of the whole epibenthic community under contrasted sea-ice conditions. Biplots represent the mean scaled isotopic diversity indices: isotopic divergence (IDiv), dispersion (IDis), evenness (IEve), and uniqueness (IUni) of the whole epibenthic community. Isotope data of epibenthic fauna are shown in areas with different sea-ice concentrations (SIC): **A)** low ice (≤10% of SIC), **B)** moderate ice (>10 to 50% of SIC), and **C)** high ice (>50% of SIC). Isotopic positions of the epibenthic fauna are represented by green dots in each panel. In each area, epibenthic community $\delta^{13}C$ and $\delta^{15}N$ values are scaled between 0 and 1 to account for potentially different isotope variability in basal food resources (Cucherousset and Villéger, 2015).

1.6 Discussion

1.6.1 *Sea ice influencing food resource availability and isotopic composition*

Sea ice is a critical environmental component that indirectly affects dietary patterns in consumers by controlling the timing, magnitude, and distribution of organic carbon that sustains Arctic benthic communities (Norkko et al., 2007). In this context, sea ice, together with other abiotic components such as temperature and depth, is perhaps one of the main abiotic drivers influencing the isotopic composition of benthic consumers. Our results indicated spatial variability in the $\delta^{13}C$ isotopic composition of both food items and epibenthic consumers between ice areas. In sediments, the most ^{13}C-depleted values (less than –28.0‰) were found in low SIC areas of Beaufort Sea, while the most ^{13}C-enriched values were associated with sediments from high and moderate SIC areas. Similarly, suspended POM sources (i.e., SCM-POM and Bot-POM) exhibited more ^{13}C-depleted values linked to low SIC areas in Beaufort Sea. Depletion in $\delta^{13}C$ values observed in Beaufort Sea suggested an increase in the deposition of terrigenous sources ($\delta^{13}C$ values ranged from –26.0 to –28.0‰) in areas under the influence of large rivers (Bell et al., 2016). The $\delta^{13}C$ epibenthic consumers' composition showed the occurrence of different trophic pathways, among which epibenthic fauna was mostly sustained by a mix of ice-derived algae and phytoplankton sources ($\delta^{13}C$ values ranged from –19.0 to –24.0‰; Stein and Macdonald, 2004). $\delta^{13}C$ values found in the epibenthic fauna showed spatial differences in the isotopic composition of baseline carbon inputs according to varying SIC, and the use of a high range of carbon sources by epibenthic consumers, thereby highlighting their considerable capacity to switch diets between ice areas. For example, primary consumers found below low SIC areas had the most ^{13}C-depleted average in isotopic composition, suggesting some reliance on phytoplankton or terrestrial origin sources (Bell et al., 2016). In contrast, primary consumers from high SIC areas had the most ^{13}C-enriched average in isotopic composition, suggesting a greater reliance on ice-derived carbon and/or the assimilation of alternative sources, including reworked organic material by sedimentary microbial communities (Iken et al., 2005; Mäkelä et al., 2017a).

Our data did not support the first hypothesis, which indicated that sea-ice conditions were a significant driver influencing $\delta^{15}N$ composition in sources and in consumers. Instead, according to linear models, depth was an important environmental variable influencing $\delta^{15}N$ variation. An increase in $\delta^{15}N$ in benthic consumers is commonly related to depth (Stasko et al., 2018b), however, we observed that some benthic species (e.g., *Ophiocten sericeum* and *Ophiura robusta)* were the most ^{15}N-depleted in deep stations. Since the isotopic composition in epibenthic consumers reflects a time-integrated average of the resources assimilated by invertebrates (Bearhop et al., 2004), ^{15}N-depleted values could indicate that consumers ingested/assimilated a series of food items reworked in benthic food banks for a more extended period. Furthermore, the ^{15}N-depleted composition could be related to the ingestion/assimilation of cyanobacteria or other N_2-fixing microorganisms (Karlson et al., 2014). Based on our results, sea-ice conditions represented only one of the abiotic factors that drove changes in the δ^{15}N composition in consumers. However, our findings highlighted that sea ice is a crucial driver influencing changes in the δ^{13}C composition of consumers by possibly affecting the timing, quantity, and nature of the organic carbon inputs. The phenology of the cycles is changing faster in the Arctic Ocean due to climate change; more empirical studies are needed that assess how variations in physical and chemical properties of the environment may affect the ecosystem functioning, services, and stability.

1.6.2 *Epibenthic food web characteristics across ice areas*

Sea ice has also been documented to be an important component of the Arctic Ocean influencing: the degrees of connectivity between the benthic and the pelagic habitats, the trophic interactions, the nutrient cascades, and therefore food web structure (Post et al., 2000; Post, 2017). Likewise, sea-ice dynamics may be closely correlated with seasonality in the range of resources (i.e., prey diversity), which may influence the degrees of competition and variability in dietary and foraging patterns of specialization among species (Araújo et al., 2011; Costa-Pereira et al., 2019). In agreement with our second hypothesis, community-wide niche metrics showed multidimensional niche variation of the benthic community across ice areas. However, the broader niche was interestingly associated with moderate SIC areas, whereas a simplification of the niche structure (i.e., shorter chain length and width) was linked to low and high SIC areas (Figure 1.4). Our results agree with previous studies that highlighted a similar pattern in benthic food web simplification linked to differences in sea-ice cover in the Arctic (Yunda-Guarin et al., 2020) and the Antarctic Oceans (e.g., Michel et al., 2019; Norkko et al., 2007). These studies indicated that a greater reliance of benthic invertebrates on sympagic algae in regions with greater ice cover, induced reductions in the ecological niche size of the benthic community. In this context, a tight δ^{13}C dispersion (low CR ranges) suggested homogeneity of resources and consumers' assimilation of analogous resources (i.e., in nature and isotopic composition). In contrast, a broad δ^{13}C dispersion suggested a higher heterogeneity in basal food sources and/or the assimilation of food items with a greater difference in $\delta^{13}C$ isotopic composition (Wang et al., 2020). Similarly, when comparing the isotopic niche structure across epibenthic groups, primary consumers and omnivores showed a similar trend to those observed for the entire community, exhibiting narrow $\delta^{13}C$ ranges associated with ice areas with low and high SIC (Supplementary Figure S1.1). Hence, the reduction of niche breadth observed in systems with less diversity of prey could be related to an increase in the number of specialists on the same sort of resources available in the sediment (Costa-Pereira et al., 2019; Yunda-Guarin et al. in press). Instead, a broader niche breadth, observed in systems with a greater diversity of resources, suggested an increase in the number of generalist species with intraspecific inclinations towards a particular diet or foraging behavior (Yunda-Guarin et al. in press).

Niche metrics also showed variations in the food chain length highlighting a broader $\delta^{15}N$ dispersion (high NR ranges) associated with ice areas with moderate SIC and a simplification of the food web structure (i.e., shorter chain length) linked to ice areas with low and high SIC (Figure 1.4). Previous studies suggested that food chain lengths are largely influenced by the amount of energy exchanges between trophic levels, which are controlled by ecosystem size, productivity, and disturbance episodes (e.g., Post, 2007; Post et al., 2000; Ward and McCann, 2017). Therefore, in Arctic marine food webs, variations in the strength of energy flux pathways must vary in space and time across gradients of environmental change affecting the benthic food web topology (Post, 2017). Thus, in response to the quantity of resources, weak energy channels induced great food chain lengths, while strong energy flux channels favored narrow food chain lengths (Ward and McCann, 2017). However, according to differences in organic matter input, benthic groups were affected differently by the effect of energy cascades through the trophic levels, with secondary and tertiary consumers showing a reduction in the width of their isotopic niche (Table 1.2; Supplementary Figure S1.1). Likewise, variations in the food chain length of the benthic community may also reflect changes in the isotopic composition of resources related to alterations in the biochemical characteristics of the organic matter due to abiotic degradation processes (Rontani et al., 2016). Thus, with depth and depending on the nature and the residence time of the organic inputs in the water column, sinking particles should experience different stages of degradation. Among these, ice-derived carbon may experience less degradation time due to faster sinking rates associated with the formation of aggregate structures (Rapp et al., 2018; Rontani et al., 2016).

1.6.3 *Ecosystem primary productivity variability and changes in the isotopic niche size*

Based on Hutchinson's original conceptualization of the 'fundamental niche'(Hutchinson, 1957), a novel approach supported the idea of a positive relationship between reductions in the isotopic niche size and overlap associated with high-productivity ecosystems (Lesser et al., 2020). On this basis, we hypothesized a similar trend in the isotopic ecology of the benthic community, predicting niche size reductions associated with high-productive ice areas (i.e., polynyas in low SIC areas). We also examined variations in the isotopic niche size between polynya's ecosystems, predicting the narrowest niche associated with the most productive polynya (i.e., NOW). Community-wide metrics supported our second hypothesis, highlighting a reduction in the isotopic niche size (lower SEAc, TA, and CD) of the benthic community associated with the polynyas. However, metrics revealed a narrow niche associated with ice areas with high SIC (Figure 1.4), despite these areas being less productive than the polynyas (e.g., primary production in BB range from 60 to 120 g C m^{-2} y^{-1}; Stein and Macdonald, 2004). Our results suggested that changes in resource availability might be an important factor influencing the strength of species interactions (e.g., predation and competition), feeding strategies, species-specific dietary specialization, and thus isotopic niche sizes. Hence, in regions of higher seasonal productivity, a substantial influx of organic matter could be associated with an increase in the number of deposit feeders and a reduction in the number of omnivores (i.e., including carnivores or scavengers) that depended mainly on the most favorable energy resource (Evans et al., 2005; Michel et al., 2019). Therefore, narrower niches were related in our study to polynyas and less productive ice areas with a significant seasonal contribution of a specific carbon source such as ice-derived algae (Yunda-Guarin et al., 2020). On the contrary, in less productive regions, a greater breadth of the niche could be related to an increase in the predation pressure across trophic levels, the assimilation of a wider range of prey items, or a high degree of species-specific dietary specialization (Robinson and Strauss, 2020; Yunda-Guarin et al. in press).

Regarding the polynyas, our results denoted niche reductions along a west-to-east gradient, exhibiting a narrow niche associated with NOW (SEAc = 6.01), and broader niches associated with CB and VMS-LS-BI polynyas (SEAc = 15.17 and 8.03; respectively) (Supplementary Figure S1.2). Our results are compatible with Mäkelä et al. (2017) who, while studying variations in the benthic food web structure in two polynyas (i.e., NOW and LS), highlighted a shorter food web length associated with the more productive polynya of NOW. Based on the isotopic data, variations in the isotopic niche of the polynyas may reflect a seasonal relationship between productivity, pelagic-benthic coupling strength, environmental changes, and fluctuations in the contribution and use of resources by consumers (Kędra et al., 2012). For example, a broad niche size in CB polynya could be linked to differences in the use of terrestrial and marine organic resources by consumers along a geographic/depth gradient that affected $\delta^{13}C$ and $\delta^{15}N$ composition in consumers and thus, the trophic niche structure (Bell et al., 2016; Divine et al., 2015; Dunton et al., 1989). Similarly, a broad isotopic niche in LS polynya was connected with a greater assimilation of reworked organic material by invertebrates that was depleted in ^{13}C (Mäkelä et al., 2017). These results highlighted that niche architecture is extremely dynamic across the Arctic Ocean, varying geographically and seasonally due to a connection of intrinsic and extrinsic mechanisms that influence the isotopic composition, trophic interactions, and energy channels.

1.6.4 *Isotopic diversity indices and epibenthic niche redundancy*

In our study, isotopic diversity indices (IDis, IDiv, and IEve) suggested changes in the isotopic ecology of the benthic community, denoting differences in the trend of distribution of isotopic values between ice areas (Figure 1.5). On one side, IDis and IDiv indicated that species had a wider isotopic dispersion in moderate SIC areas. In contrast, slight differences in IDis and IDiv were found in low and high SIC areas, in which the isotopic dispersal of species was closer to the center of gravity of the convex hull. On the other hand, IEve suggested that consumers tended towards an even distribution in the stable isotope space in all the ice areas. Thus, an even and wide distribution in isotope space observed with isotopic diversity indices suggested that epibenthic consumers could be largely composed of generalist and opportunistic species that depend mainly on the most abundant temporary resources. However, depending on the availability of food sources, narrow food webs were mainly composed of consumers sharing an isotopically similar trophic niche. In contrast, an increase in the trophic plasticity was mediated by a greater number of species occupying different trophic niches. On this basis, decreases in the food supply could translate into a greater divergence of species-specific individual niches as a strategy to reduce competition and the lack of resources (Yunda-Guarin et al. in press).

Isotopic uniqueness (IUni) suggested spatial gradients in isotopic redundancy of the benthic community, highlighting a gradual decrease in isotopic redundancy from low SIC to high SIC areas. IUni results were consistent with community-wide niche metrics that showed a lower isotopic redundancy (i.e., lower MNND values) associated with the polynyas. These results are particularly interesting since similar patterns in the assemblage of individuals in the isotopic space (i.e., lower

IEve, IDiv and IDis) were observed in ice areas with low and high SIC; therefore, we expected homogeneous redundancies between these types of ice areas. Furthermore, such variation in IUni suggested that the isotopic redundancy of the community could change in space even during periods of high biological productivity. For example, in polynyas, the great availability of resources could induce consumers to feed on a narrow spectrum of $\delta^{13}C$ sources, reducing predation and intra- and interspecific competition, promoting the coexistence of species and increasing redundancy in the community (Brind'Amour and Dubois, 2013). However, in less productive ecosystems, even with an increase in the contribution of seasonal food supply, predation episodes and increased competition can be more recurrent and intensify over time, promoting species feeding instead on different sources, thus reducing the redundancy in the community (Comte et al., 2016). Based on our results, changes in biotic interactions (e.g., levels of competition and predation) in response to variations in the abundance of resources stood out as one of the main drivers of trophic redundancy. Consequently, shifts towards future variation in composition and abundance of resources due to climate change could impact trophic interactions and transfer of nutrients potentially inducing changes in food web functioning in Arctic Ocean ecosystems.

1.7 Conclusions

The responses of food webs to changes in several environmental drivers are still poorly understood. In this study, stable isotope values showed changes in the isotopic composition of benthic invertebrates and sources according to SIC gradients, suggesting that a large portion of the benthic carbon pool was from marine origin. However, in ice areas from the Beaufort Sea, isotopic composition showed some influence of terrestrial organic matter in food web structure. Community-wide metrics and isotopic diversity indices showed similar trends relating to the characteristics of the ecological niche structure, providing evidence that sea-ice condition is an important environmental variable influencing the niche structure of the benthic community. Our results showed that narrow niches were associated with high and low SIC areas, suggesting that benthic consumers relied on fewer food items in these areas. In contrast a broad niche was linked to ice areas with moderate SIC implying that consumers relied on a greater diversity of sources. Besides sea-ice conditions, gradients of seasonal food availability also induced variability in niche structures. Our results suggested that epibenthic fauna had a marked response to the phenology of the carbon inputs. Accordingly, in high-productive ice areas (e.g., polynyas) high availability of resources might promote the exploitation of the most energetically rich sources, inducing a shorter food chain length where consumers shared similar feeding guilds and trophic levels. On the contrary in low-productive ice areas, decreases in food availability induced species to exploit a bigger range of energy resources, promoting broader niches, weaker energy channels, predation pressure, and greater interspecific competition. Finally, our results showed spatial differences in the isotopic redundancy of the benthic community along a SIC gradient, underlying a gradual decrease in the redundancy from low to high SIC areas. Variations in isotopic redundancy reflected changes in prey availability and biotic interactions, connecting more stable food webs to ecosystems with greater stability in food inputs and phenological cascades.

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Chapter 2. Sea ice-derived organic carbon: a key food source shaping benthic food web structure and influencing diets of deep-sea benthic consumers during spring, Baffin Bay, Canadian Arctic Ocean

2.1 Résumé

Les organismes benthiques dépendent principalement des pulses saisonniers de matières organiques des producteurs primaires. Dans l’Arctique, le déclin de la glace dû au réchauffement climatique pourrait entraîner des changements dans cet apport alimentaire ce qui aurait des effets encore inconnus sur la dynamique trophique benthique. Pour cette étude, nous avons étudié les régimes alimentaires des consommateurs benthiques et la structure du réseau trophique au printemps 2016 à des stations dont la profondeur variait de 199 à 2111 m dans une région de la baie de Baffin qui est recouverte de glace pendant une partie de l’année. Cette recherche est la première à combiner deux méthodes connues impliquant des biomarqueurs de lipides isoprénoïdes hautement ramifiés (HBI) et des rapports d’isotopes stables ($\delta^{13}C$, $\delta^{15}N$) afin de mieux comprendre la relation entre la disponibilité des sources de carbone au printemps sur le fond marin et leur assimilation et leur transfert dans le réseau trophique benthique. Le carbone organique provenant des algues de glace de mer (carbone sympagique, SC) était une source alimentaire importante pour les consommateurs benthiques. Les analyses des biomarqueurs lipidiques ont révélé une contribution relative élevée de SC dans les sédiments (SC % ± écart type = 86 % ± 16,0; n = 17) et dans les tissus benthiques des consommateurs (SC % ± écart type = 78 % 19,7; n = 159). Nous avons également détecté un effet des concentrations de glace de mer sur la contribution relative de SC dans les sédiments et chez les consommateurs benthiques. L’analyse de regroupement a divisé la région étudiée en trois zones différentes selon les proportions relatives de SC assimilées par le macrofaune benthique. Nous avons observé une variation du réseau trophique benthique entre les zones, avec une augmentation de la largeur de la niche écologique dans les zones où la concentration de glace de mer est moindre, ce qui indique une plus grande diversité des sources de carbone assimilées par les consommateurs. Dans les zones où la concentration de glace de mer est plus élevée, la plus grande disponibilité de SC a accru le rôle écologique que jouent les consommateurs primaires dans le transfert plus important de nutriants vers les niveaux trophiques supérieurs. D’après nos résultats, le SC est une source d’énergie importante pour le benthos des grands fonds de l’Arctique dans la baie de Baffin, de sorte que les changements de la phénologie printanière des glaces de mer pourraient modifier la structure du réseau trophique benthique.

2.2 Abstract

Benthic organisms depend primarily on seasonal pulses of organic matter from primary producers. In the Arctic, declines in sea ice due to warming climate could lead to changes in this food supply with as yet unknown effects on benthic trophic dynamics. Benthic consumer diets and food web structure were studied in a seasonally ice-covered region of Baffin Bay during spring 2016 at stations ranging in depth from 199 to 2111 m. We used a novel combination of highly branched isoprenoid lipid biomarkers and stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$) to better understand the relationship between the availability of carbon sources in spring on the seafloor and their assimilation and transfer within the benthic food web. Organic carbon from sea ice (sympagic carbon [SC]) was an important food source for benthic consumers. The lipid biomarker analyses revealed a high relative contribution of SC in sediments (mean SC% ± SD = 86% ± 16.0, n = 17) and in benthic consumer tissues (mean SC% ± SD = 78% ± 19.7, n = 159). We also detected an effect of sea-ice concentrations on the relative contribution of SC in sediment and in benthic consumers. Cluster analysis separated the study region into three different zones according to the relative proportions of SC assimilated by benthic macrofauna. We observed variation of the benthic food web between zones, with increases in the width of the ecological niche in zones with less sea-ice concentration, indicating greater diversity of carbon sources assimilated by consumers. In zones with greater sea-ice concentration, the higher availability of SC increased the ecological role that primary consumers play in driving a stronger transfer of nutrients to higher trophic levels. Based on our results, SC is an important energy source for Arctic deep-sea benthos in Baffin Bay, such that changes in spring sea-ice phenology could alter benthic food-web structure.

2.3 Introduction

In the Arctic Ocean, the functioning of the food web is linked to the dynamics of sea ice (Kędra et al., 2015). Indeed, the development of marine primary production, based on unicellular microalgae associated with sea ice (i.e., sympagic or ice algae) and with the water column (i.e., phytoplankton; (Frey et al., 2018), is strongly influenced by sea-ice dynamics. During spring, when the snow melts and sea ice becomes more transparent, the growth of sea-ice algae provides the first substantial carbon input to the food web, being consumed by sea-ice fauna, zooplankton, and benthic organisms (Nozais et al., 2001; Tremblay et al., 2006; Link et al., 2011). Depending on latitude and sea-ice conditions in regions with seasonal sea-ice cover, sympagic primary production rates range from 2×10^{-3} to 20 g C m^{-2} $year^{-1}$, representing 1 to 26% of total production in these areas (Gosselin et al., 1997; Leu et al., 2011; Tamelander et al., 2009). Up to 6.5 g C m^{-2} $year^{-1}$ of particulate organic matter originating from this production sinks into the deep ocean (Boetius et al., 2013). As a result, sea ice constitutes a natural regulator of energy transfer through trophic links (North et al., 2014; Calizza et al., 2018) and strengthens pelagic-benthic coupling (Piepenburg, 2005).

The response of marine food webs to variations in the organic carbon cycle is one of the fundamental issues in the changing Arctic Ocean, due to the sensitivity of food webs to changes in the magnitude and direction of energy flow (Findlay et al., 2015). For a long time the deep (below 200-m water depth) seafloor ecosystem was considered largely unaffected by the human footprint (Bluhm et al., 2011). Evidence suggests, however, that deep-sea ecosystems can be influenced by climate-driven seasonal and interannual changes taking place in shallower waters (Glover et al., 2010); for example, climate change may affect the availability of carbon resources across different depths in the ocean (Divine et al., 2015). As benthic communities depend primarily on seasonal pulses of organic matter that reach the seabed, variations in the timing or quantity of this food supply can influence interactions, abundance, and distribution of benthic fauna (Collin et al., 2011; Roy et al., 2014; Vedenin et al., 2018), with consequences for food web functioning that are not yet fully understood (Griffiths et al., 2017; Jeffreys et al., 2013; Kędra et al., 2015; Mäkelä et al., 2017b; North et al., 2014; Van Oevelen et al., 2011). Some benthic fauna seem to be able to change diet rapidly and ingest a wide range of food sources (e.g., plant detritus, animal carcasses, bacteria, and fungi; Gage, 2003), which makes identifying the sources of carbon and assessing proportions ingested by consumers difficult (Kelly and Scheibling, 2012). The absence of such information can hinder accurate predictions of the response of benthic consumers to changes in food supply. Although the organic matter originating from the water column is already known to be an essential food source for benthic fauna at different depths, studies of the transfer of sympagic carbon (SC) to deep benthic consumers are scarce (e.g., Link et al., 2011; Boetius et al., 2013; Jeffreys et al., 2013). Recently, novel approaches that use multiple trophic markers (e.g., fatty acids and stable isotope ratios) have opened new research avenues in the attempt to differentiate with more accuracy the proportions of organic matter sources in the environment (Leu et al., 2020) and in consumers (Budge et al., 2008; Wang et al., 2015).

Highly branched isoprenoids (HBIs) are lipid biomarkers found frequently in marine and lacustrine sediments (Belt et al., 2007; Brown and Belt, 2016; Volkman et al., 1994). Among HBIs, a mono-unsaturated HBI termed IP_{25} (Belt et al., 2007) and its homolog, a di-unsaturated HBI II (diene, often referred to as $IPSO_{25}$ in the Antarctic), have been used as proxies of SC in the environment (Brown et al., 2016; Xu et al., 2006), notably in Arctic benthic organisms (Brown et al., 2013, 2012; Brown and Belt, 2012). In contrast with sea-ice proxies, a further tri-unsaturated HBI (often referred to as HBI III or triene), has been proposed as a promising proxy for pelagic organic matter (phytoplankton) in the region of open waters near the marginal ice zone (MIZ) in polar regions (Belt, 2018; Belt et al., 2019). Based on the relative abundances of pelagic (III) and sympagic (IP_{25}, II) lipid biomarkers, quantitative estimates of the relative proportions of SC transfer through different trophic levels have been calculated (Brown et al., 2017a, 2017b, 2018; Brown and Belt, 2017), revealing the importance of each organic matter source in the diet of different organisms across the Arctic food web. For example, the HBI-fingerprint, or "H-Print," is an index that has been used to estimate the relative contribution of both sympagic and pelagic carbon sources (Brown et al., 2014).

Besides lipid markers, carbon and nitrogen stable isotope ratios are effective tools for the study of the structure and dynamics of food webs, as they provide time- and space-integrated insights into trophic relationships (Layman and Allgeier, 2012). Because of an often consistent gradual ^{15}N-enrichment of 2.3‰ per trophic step in aquatic environments (McCutchan et al., 2003), nitrogen isotope ratios ($\delta^{15}N$) are used to estimate the trophic level of consumers. On the other hand, with a 0 to 2‰ of ^{13}C-enrichment per trophic step, carbon isotopes ratios ($\delta^{13}C$) are typically used to establish the dependence of benthic macrofauna on different food sources (Renaud et al., 2015). Original multidimensional metrics were made to represent the total extent of the ecological diversity using stable isotopes only (Layman et al., 2007a). In the present study, HBI lipid biomarkers were coupled quantitatively with stable isotopes to generate community-wide niche proxies combining insights from both methods. To our knowledge, this approach is unique in the literature. Metrics derived from this kind of analysis can give additional clues to understand changes in food web structures in areas exposed to marked seasonal changes in sea-ice phenology and primary productivity.

To assess the relative importance of SC as a food source to deep benthic communities, we conducted a field investigation of macrobenthos in areas near the marginal ice zone. Baffin Bay provides an ideal natural laboratory to investigate the effects of sympagic production availability on benthic food web structure and functioning. In Baffin Bay, sea ice starts forming in late autumn and reaches maximum extent around March, with ice melt beginning as early as April (Stern and Heide-Jørgensen, 2003). Excluding the ice-free months between August and September, Baffin Bay is always moderately covered by sea ice (Tang et al., 2004). Ocean currents and the atmospheric temperature influence the extent and formation of sea ice in the south of Baffin Bay (Stern and Heide-Jørgensen, 2003). On its eastern side, the West Greenland Current moves warm Atlantic waters northward along the western coast of Greenland (Bi et al., 2019). On its western side, the Baffin Current carries cold Arctic waters and sea ice southward along the east coast of Baffin Island, towards the Labrador Sea (Figure 2.1 A; (Bi et al., 2019). This distinct longitudinal gradient in sea-ice concentration thus presents an important feature against which to test the effects of sea-ice decline on the availability of different carbon sources for deep benthic consumers and how further ice loss could affect deep communities around the Arctic. Moreover, this region is undergoing one of the most significant declines in sea ice in the Canadian Arctic Ocean, as the sea-ice extent was reduced by 102,000 km^2 between 1968 and 2018 (Environment and Climate Change Canada, 2019). As a result of changes in atmospheric and oceanic temperatures, with an earlier onset of sea-ice melt in spring (4.6 days per decade; AMAP, 2018), a continuous reduction in sea-ice thickness and extent (10–15% in spring by 2080) is predicted in Baffin Bay (AMAP, 2018). Using an innovative coupling of sea-ice algae lipid biomarker and stable isotope analyses, the following hypotheses were tested: (i) sea-ice cover is the primary environmental driver of contribution and geographic distribution of SC on the seabed; (ii) SC is the most important baseline food source supporting benthic consumers during spring in areas close to the MIZ; and (iii) deep benthic food web dynamics and structural variability are directly linked with both depth and availability of food sources.

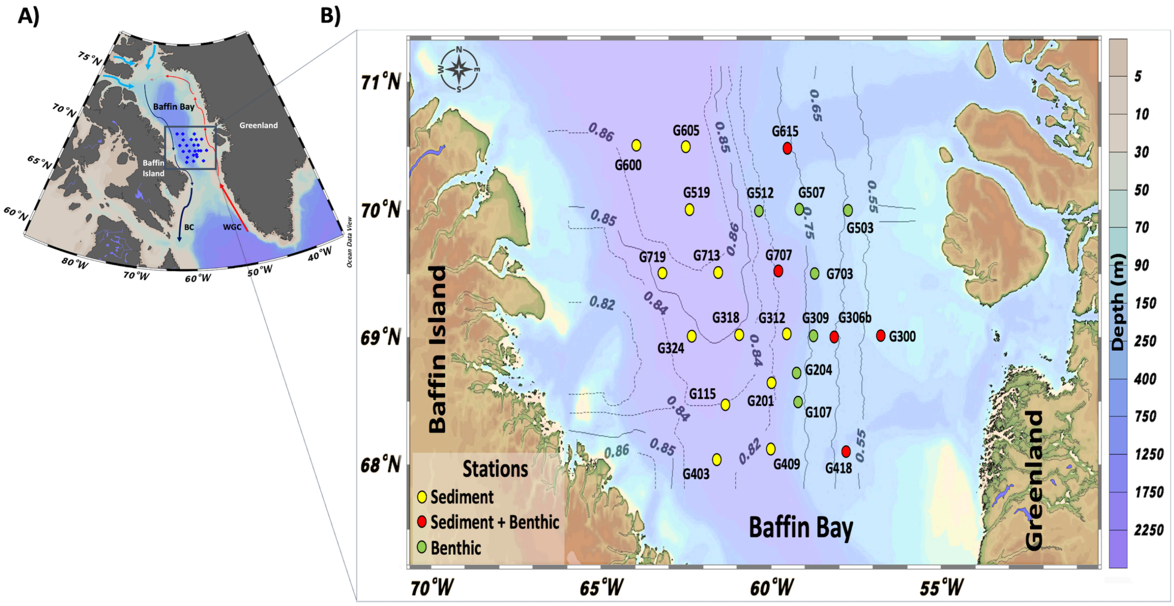

Figure 2.1. Location of the sampling stations with bathymetry gradients. Red arrows show the northward-flowing West Greenland Current (WGC) and blue arrows show the southward-flowing Baffin Current (BC; map A). Coloured points show sampling stations (11 June to 10 July 2016) for sediment only (yellow), both sediment and benthic macrofauna (red), and benthic macrofauna only (green; map B). The average sea-ice concentrations, ranging from 0 to 100% (expressed here between 0 and 1; gray lines), in the spring (1 April to 30 June between 1998 and 2017) were derived from the National Snow and Ice Data Center (https://nsidc.org/data/nsidc-0051).

2.4 Materials and Methods

2.4.1 *Study area and sampling collection*

This study was conducted on board the Canadian research icebreaker CCGS *Amundsen* in Baffin Bay (Figure 2.1 A). Twenty-four stations near the MIZ were sampled for sediments and macrofauna from 11 June to 10 July 2016, within the framework of the Green Edge project (www.greenedgeproject.info). Station depths ranged from 199 to 2111 m. Epibenthic fauna were collected at 12 stations (Figure 2.1 B: red and green coloured stations) using an Agassiz trawl with an opening of 1.5 m and a net mesh size of 40 mm. Box core (0.25 m^2) sampling was undertaken to collect surface sediment samples (upper 1 cm) at 17 stations (Figure 2.1 B: red and yellow-colored stations). For each box core, six sediment sub-cores were collected for sediment pigment content (with 10-ml truncated syringes of an area of 1.5 cm^2), granulometry, organic carbon content, HBIs, and stable isotope analyses (with 60-ml truncated syringes of an area of 5 cm^2). Ice blocks containing fresh sympagic algae were collected at three stations (G115, G318, and G409; Figure 2.1 B). After collection, all samples were frozen immediately at –20°C for further analysis. Sediment porosity was estimated by measuring the mass loss of the wet sediment dried at 60°C; total organic matter (OM) content was determined as the ash-free dry weight after combustion (500°C) and converted to total OM in the sediment. Chlorophyll *a* (Chl *a*) content was determined fluorometrically following the protocol of Riaux-Gobin and Klein (1993). Water samples were collected 10 m above the seafloor using a CTD-Rosette with 12-L Niskin-type bottles to determine the isotopic composition of the suspended particular organic matter (SPOM) close to the bottom. The water was filtered onto pre-combusted filters (450°C for 5 h) of 21-mm diameter Whatman GF/F glass-fiber filters (nominal pore size of 0.7 μm).

2.4.2 *Extraction and quantification of HBI lipid biomarkers*

In the laboratory, benthic macrofauna were separated, weighed and identified to the lowest taxonomic resolution possible. A total of 648 individuals were processed for the extraction and quantification of HBIs. Due to their small size, some individuals had to be pooled by species per station resulting in 249 samples processed for subsequent HBI measurements (Table S2.1). Lipid extraction and quantification of surface sediment samples were carried out for 17 stations. Processed samples that did not contain all three types of HBIs were discarded from the analyses, as a combination of sympagic and pelagic HBIs is required to calculate the "H-Print" biomarker index (Equation 1) and the percentage of sympagic carbon (Equation 2).

The extraction of HBIs was carried out at Laval University, Québec, Canada, while the HBI analyses were done in the marine ecology and chemistry laboratory at the Scottish Association for Marine Science, Scotland, following established techniques (Belt et al., 2012). Molecular structures of HBI alkenes measured in this study (IP_{25}, diene and triene) can be found in Figure S2.1. HBIs were analyzed by gas chromatography-mass spectrometry and quantified by measuring the mass spectral intensities for each HBI in selective ion monitoring (SIM) mode (Brown et al., 2017a). The data were obtained and analyzed using the Agilent ChemStation software.

2.4.3 *Sympagic carbon quantification*

To quantify the contribution of sympagic algae as a food source, the "H-Print" biomarker index was calculated combining the analytical intensities of three HBI biomarkers, IP_{25} (*m/z* 350.3), II (*m/z* 348.3) and III (*m/z* 346.3), into a single index, according to Equation 1 (Brown and Belt, 2017). High values of H-Print (> 50%) are associated with pelagic carbon, and lower values (<50%) are associated with sympagic carbon.

$$\text{H-Print (\%)} = \frac{\text{Pelagic HBI (III)}}{\text{Sympagic HBIs } (\text{IP}_{25} + \text{II}) + \text{Pelagic HBI (III)}} \times 100 \qquad \text{Equation 1}$$

To estimate the relative proportion of SC in sediments and benthic fauna, we used Equation 2 proposed by Brown et al. (2018). It is based on a previously established calibration that converts the H-Print values into estimates of SC (Brown and Belt, 2017). To calculate the relative proportion of organic matter derived from sea ice (ice organic matter, iOM), we used Equation 3 whereby the organic matter percentage in sediments (OM, %) is multiplied by the SC estimation from Equation 2.

$$\text{Sympagic carbon (SC, \%)} = 101.08 - 1.02 \times \text{H-Print (\%)} \qquad \text{Equation 2}$$

$$\text{Ice organic matter (iOM, \%)} = \text{SC (\%)} \times \text{OM (\%)} \qquad \text{Equation 3}$$

2.4.4 *Carbon and nitrogen stable isotope analyses*

Sediments and benthic fauna that had been previously treated (i.e., lipid extraction) for HBI analyses were freeze-dried at –50°C and ground to a fine powder with mortar and pestle. HCl was used to remove carbonates prior to stable carbon isotopic ($\delta^{13}C$) analysis. Surface sediment and organisms with significant carbonate structures, e.g., echinoderms, were soaked in 1 N HCl until bubbling ceased. The stable nitrogen isotopic ($\delta^{15}N$) composition was determined on non-acidified samples to avoid the alteration of $\delta^{15}N$ values (Roy et al., 2015). Stable nitrogen isotope ratios were measured using a continuous-flow isotope ratio mass spectrometer (Thermo Electron Delta Advantage) in the continuous-flow mode (Thermo Electron ConFlo III) with an ECS 4010 Elemental Analyzer/ZeroBlank Autosampler (Costech Analytical Technologies) in the laboratory of oceanography at Laval University, Quebec, Canada. Replicate measurements of international standards (USGS40 and USGS41 from the International Atomic Energy Agency; B2151 from Elemental Microanalysis) established measurement errors of ≤ 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$. Stable isotope ratios are expressed in delta (δ) units ($\delta^{13}C$, $\delta^{15}N$) as the per mil (‰) difference with respect to standards: δX (‰) = $[(R_{sample} - R_{standard})/R_{standard}] \times 10^3$, where X is ^{13}C or ^{15}N of the sample and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Standards were calibrated against the international references Vienna PeeDee Belemnite (PDB) for carbon and atmospheric air (N_2) for nitrogen.

2.4.5 *Trophic level and origin of carbon*

Based on the trophic position (TP) for each benthic consumer, we studied the relative assimilation and transfer of SC across the benthic community assuming a constant enrichment factor (Δ) of 2.3‰ per trophic level in consumers of aquatic environments (McCutchan et al., 2003). The surface sediment bulk $\delta^{15}N$ signature was used as a baseline in the estimation of the trophic level for each consumer. Benthic macrofauna were categorized into three different groups, high consumers (including secondary, tertiary, or upper consumers as well as scavengers (TP ≥ 3), omnivores (3 > TP > 2) and primary consumers (TP ≤ 2), using Equation 4:

$$\mathrm{TP} = \frac{\delta^{15}\mathrm{N\ consumer} - \delta^{15}\mathrm{N\ base}}{\Delta^{\delta^{15}\mathrm{N}}} + \lambda \qquad \text{Equation 4}$$

Where $\delta^{15}N_{Consumer}$ is $\delta^{15}N$ of the benthic consumers, $\delta^{15}N_{base}$ is the nitrogen isotope ratio of the base of the food chain or "sediment baseline", $\Delta\delta^{15}N$ is the trophic enrichment factor between successive trophic levels, and $\lambda = 1$ is the trophic position of "baseline". The sediment baseline was estimated using the mean $\delta^{15}N$ calculated for the 17 sediment stations. Carbon isotopes ratios ($\delta^{13}C$) were used to establish the dependence of benthic macrofauna on different food sources.

2.4.6 *Sea-ice concentration data*

Satellite sea-ice concentration (SIC) data were derived from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data and downloaded from the National Snow and Ice Data Center (Cavalieri et al., 1996). Spring (1 April to 30 June) sea-ice concentrations at each station were averaged for the period of 1998 to 2017, expressed in percentages, and the standard deviation was calculated. Such averaged spring SIC was considered relevant in this study because benthic consumers have access to sedimentary carbon deeper than the top ~ 1 mm deposited in 2016. Consequently, the lipid signature in animals likely represents several years of accumulated carbon.

2.4.7 *Statistical analyses*

All statistical analyses and graphical procedures were performed using R (R Core Team, 2019) and Ocean Data View version 5.1.7 (https://odv.awi.de), respectively. The normality of residuals was examined using Q-Q plots. Linear models were employed to evaluate simultaneously the effect of environmental variables (i.e., depth and sea-ice concentration) and their interactions on percentages of SC found in both sediment and benthic consumer samples. Furthermore, linear models were used to predict the relationship between SC (%) found in sediments and SC (%) assimilated by the benthic macrofauna across stations. A cluster analysis using the Euclidean dissimilarity index was performed to identify groups and classify the benthic stations according to the relative proportion of SC assimilated by the benthic macrofauna. Box plots of the relative percentage of SC found in benthic macrofauna were made to visualize concordance with the hierarchical clustering analysis. To compare variations in the relative assimilation of SC (%) by benthic consumers across species and stations, a Tukey's test was run following an analysis of variance (ANOVA). Finally, using Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al., 2011), standard ellipses and convex hulls were created to study interspecific ecological niche variations in the $\delta^{15}N$ versus SC iso-space. The niche space is a measure used in food web studies to describe both the amounts of resources and the habitats used by animals (Reid et al., 2016). In this context, convex hulls represent the full range of resources used by benthic consumers, whereas standard ellipses, which are bivariate equivalents of standard deviation, represent the core isotopic niche, i.e., resources most commonly used by consumers.

2.5 Results

2.5.1 *Spatial distribution and relative contribution of sympagic carbon in sediments*

Satellite observations between the years 1998 to 2017 showed a spatial trend in the average spring sea-ice concentration (SIC) in the region studied (Figure 2.1). As expected, we observed more variability in SIC (Table 2.1) in the eastern region of the study area where the warmer West Greenland Current induces later ice formation and earlier ice breakup (Figure 2.1 A–B). Sediment samples were comprised of four different textural groups; i.e., slightly gravelly sandy mud, sandy mud, gravelly mud, and mud. The percentages of OM across all sediments ranged from 1.75 to 6.47% (Table 2.1), with no apparent relationship to textural group (linear model; F = 4.06, p-value = 0.13), although linear model indicated that gravel (F = 11.15, p-value <0.01) and mud (F = 16.62, p-value <0.001) had an effect on OM percentage found in sediment. Lower percentages of OM in sediments were recorded in the southeastern stations, while higher percentages were recorded in the western stations of Baffin Bay (Table 2.1). A linear model showed a significant effect of both depth (F = 30.87, p-value <0.001) and sea-ice concentration (F = 75.94, p-value <0.001) on OM percentage in sediment, but no interactive effects between these environmental variables were detected.

HBI biomarkers indicated that all surface sediments contained both sympagic (IP_{25}, II) and pelagic (III) lipids. In addition, the relative contribution of sympagic carbon to the sediments ranged from 37 to 98% (mean SC% ± SD = 86% ± 16.0, n = 17; Table 2.1; Figure S2.2). Based on a linear model, SIC had a significant effect on the relative contribution of SC in sediment (F = 118.51, p-value <0.001), whereas no significant effects of depth alone or in combination with SIC were detected on sympagic carbon. Lowest SC percentages in sediments were found in the shallower southeastern stations of Baffin Bay (Table 2.1; Figure S2.2). The greatest relative contribution of SC was encountered in the western stations of the study area, revealing a gradient of decreasing SC values from the west to the east of Baffin Bay. A similar pattern of decreasing sea-ice concentration was observed from west to east in the sampled area (Table 2.1; Figure S2.2). In addition to HBI biomarkers, Chl *a* concentrations reflected higher algal (sympagic and/or pelagic) biomass in areas with less sea-ice concentrations in the southeast and lower algal biomass in the west (Table 2.1). By combining OM with relative proportions of sympagic carbon (sympagic versus pelagic; H-Print), we calculated the maximum theoretical percentage value of sympagic organic matter (iOM) available for benthic consumption in the sediment stations sampled. This value ranged from 9 to 63% (Table 2.1). Accordingly, with maximum sedimentary OM of 6.47% (64.7 mg OM g^{-1} dry weight) and maximum iOM content in sediment of 62.6% (based on HBI biomarker estimates), Baffin sediments could contain no more than 40 mg iOM g^{-1} dry weight.

2.5.2 *Relative contribution of sympagic carbon to benthic macrofaunal diets*

Approximately two-thirds of the benthic samples contained both sympagic (IP_{25}, II) and pelagic (III) HBIs. Regardless of the taxonomic group, benthic macrofauna showed a wide assimilation of SC (i.e., varying between 16 and 99%; mean SC% ± SD = 78% ± 19.7, n = 159) in most of the study area (Table 2.2; Figure S2.3). Also, the relative proportion of SC assimilated by the benthic fauna varied significantly among species (F = 3.91, df = 70, p-value <0.001) and stations (F = 7.40, df = 11, p-value <0.001). The lowest SC percentages were found in samples from the fish *Lumpenus lampretaeformis* (26%), the hermit crab *Pagurus pubescens* (25%), and the sea star *Hippasteria phrygiana* (16%; Table S2.1). The brittle star *Ophiacantha bidentata* and the sea star *Pseudarchaster parelii* had the highest percentages of SC found among consumers (almost 100%).

Table 2.1. Surface sediment dataset derived from sediment stations collected in Baffin Bay in 2016

Station	Depth (m)	Date[a] sampling	Latitude[b] (N)	Longitude[b] (W)	SIC[c] (%)	H-Print[d] (%)	SC[e] (%)	OM[f] (%)	iOM[g] (‰)	$\delta^{13}C$[h] (‰)	$\delta^{15}N$[h] (‰)	Chl *a*[i] ($\mu g\ g^{-1}$)	Textural group[j]	Gravel (%)	Sand (%)	Mud (%)
G300	**199**[k]	17/06/2016	69.00	–56.79	**43 ± 40**	**63.1**	**36.8**	2.5	**9.3**	–21.3	5.1	**668**	SM	0.0	20.2	79.8
G418	384	28/06/2016	68.11	–57.77	63 ± 30	40.0	60.2	**1.8**	10.5	–22.6	**4.8**	249	SGSM	0.3	44.9	54.9
G306b	309	18/06/2016	68.99	–58.15	71 ± 30	27.6	72.9	**1.8**	13.0	–21.4	5.8	49	SGSM	1.5	**48.3**	**50.2**
G615	615	05/07/2016	70.50	–59.52	76 ± 30	7.0	94.0	3.1	29.2	–21.9	7.4	61	SM	0.0	20.3	79.7
G312	1455	19/06/2016	69.01	–59.56	82 ± 20	10.7	90.2	5.2	46.7	–21.9	8.6	34	M	0.0	**10.0**	**90.0**
G707	1427	08/07/2016	69.51	–59.81	80 ± 20	12.1	88.7	4.6	40.4	–21.3	7.0	47	SM	0.0	11.5	88.5
G201	1321	14/06/2016	68.63	–59.95	83 ± 20	11.3	89.5	5.5	49.2	–21.8	8.0	112	SM	0.0	22.7	77.3
G409	1407	26/06/2016	68.11	–60.00	81 ± 20	11.0	89.8	5.2	46.6	–22.2	7.8	37	SGSM	1.4	18.6	80.0
G318	1777	20/06/2016	69.01	–60.95	85 ± 20	21.6	79.1	5.6	44.6	**–22.7**	9.4	11	GM	5.2	11.0	83.8
G115	1719	13/06/2016	68.46	–61.35	84 ± 20	8.0	92.9	5.1	47.2	–21.2	7.5	58	SGSM	1.2	19.1	79.8
G713	1898	09/07/2016	69.50	–61.58	86 ± 10	6.5	94.5	4.9	46.0	–22.2	9.6	17	GM	8.0	15.7	76.3
G403	1675	25/06/2016	68.03	–61.60	82 ± 20	6.6	94.3	5.0	47.6	**–18.8**	9.0	12	GM	6.6	13.3	80.1
G324	1897	21/06/2016	69.00	–62.36	85 ± 20	6.6	94.3	6.2	58.7	–21.6	8.9	15	GM	**17.3**	16.6	66.2
G519	2008	02/07/2016	70.00	–62.42	**87 ± 10**	6.9	94.0	5.6	52.4	–22.0	9.6	16	GM	12.8	12.4	74.8
G605	2007	04/07/2016	70.50	–62.52	**87 ± 10**	4.6	96.3	5.9	56.6	–21.8	9.8	46	SGSM	0.9	16.2	82.9
G719	1951	10/07/2016	69.50	–63.23	85 ± 10	4.2	96.8	**6.5**	**62.6**	–21.6	**9.8**	**10**	GM	6.4	15.0	78.7
G600	**2111**	03/07/2016	70.51	–63.99	**87 ± 10**	**2.8**	**98.3**	6.0	59.1	–21.9	9.3	25	GM	12.3	22.5	65.2

[a] Date sampling (day/month/year).

[b] Sampling locations (longitudinal arrangement from east to west of Baffin Bay).

[c] Mean values (± SD), average sea-ice concentration in spring between the years 1988 and 2017 (n= 30).

[d] HBI-fingerprint or "H-Print" carbon source index (H-print > 50% is associated with pelagic carbon, and H-print < 50% is associated with sympagic carbon).

[e] SC = sympagic carbon.

[f] OM = organic matter (% of sediment mass).

[g] iOM = ice organic matter (% of OM content in sediment)

[h] Stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$).

[i] Chl *a* = Chlorophyll *a*.

[j] Sediment textual groups: slightly gravelly sandy mud (SGSM), sandy mud (SM), gravelly mud (GM) and mud (M).

[k] The minimum and maximum values obtained are shown in bold.

Based on the relative proportion of SC assimilated by benthic macrofauna, a hierarchical clustering grouped benthic stations geographically into three zones (A to C; Figure 2.2 A). The proportion of SC assimilated by the benthic macrofauna varied among these zones, progressively decreasing southeastwards (Figure 2.2 B, C). The average spring sea-ice concentration ranged from 43% in the southeast to 84% in the northwest (Figure 2.2 C; Table 2.2).

Based on linear models, at stations where both sediments and benthic macrofauna were sampled (Figure 2.1), a significant effect was found between SC available in sediments and SC assimilated by benthic macrofauna (F = 33.64, p-value <0.001). In addition, linear models indicated a significant effect of both sea-ice concentration (F = 43.21, p-value <0.001) and depth (F = 9.52, p-value <0.01) and interactive effect of these environment variables (F = 5.25, p-value < 0.05) on the SC assimilated by benthic consumers. Highest mean SC values found in benthic fauna (mean SC% ± SD = 94% ± 9.6, n = 15) were recorded at the westernmost station G512 (Figure 2.2 C; Table 2.2).

Table 2.2. Sampling details and trophic marker measurements in benthic macrofauna from stations collected in Baffin Bay

Stations	Depth (m)	Date[a]	Latitude[b] (N)	Longitude[b] (W)	SIC[c] (%)	n[d]	SC[e] (%)	n[f]	$\delta^{13}C$[e] (‰)	$\delta^{15}N$[e] (‰)
G300	**199**[g]	17/06/2016	69.00	–56.79	**43 ± 40**	12	**59 ± 31.3**	22	–18.1 ± 1.4	13.4 ± 1.8
G503	301	29/06/2016	70.00	–57.76	65 ± 30	8	71 ± 10.2	20	–18.1 ± 1.3	13.5 ± 2.1
G418	384	28/06/2016	68.11	–57.77	63 ± 30	10	61 ± 28.8	14	–18.3 ± 1.8	13.1 ± 1.2
G306b	309	18/06/2016	68.99	–58.15	71 ± 30	8	61 ± 7.9	12	–19.4 ± 1.1	13.8 ± 2.3
G703	520	07/07/2016	69.50	–58.72	74 ± 30	26	74 ± 19.4	36	**–17.0 ± 1.9**	**14.7 ± 3.5**
G309	360	18/06/2016	69.00	–58.74	71 ± 30	2	78 ± 27.7	11	–18.6 ± 1.5	13.5 ± 2.2
G507	294	30/06/2016	70.01	–59.12	77 ± 30	29	79 ± 12.5	41	–17.8 ± 1.8	13.1 ± 2.1
G107	403	11/06/2016	68.50	–59.18	79 ± 20	4	65 ± 8.6	6	**–19.7 ± 1.0**	13.3 ± 2.3
G204	445	15/06/2016	68.71	–59.26	75 ± 30	5	65 ± 23.5	12	–18.4 ± 1.3	13.9 ± 1.3
G615	615	05/07/2016	70.50	–59.52	76 ± 30	18	88 ± 8.4	23	–17.2 ± 2.2	**12.3 ± 3.2**
G707	**1427**	08/07/2016	69.51	–59.81	80 ± 20	22	92 ± 5.7	31	–18.8 ± 1.7	15.0 ± 2.3
G512	605	01/07/2016	70.00	–60.36	**84 ± 20**	**15**	**94 ± 9.6**	20	–18.3 ± 1.8	14.1 ± 3.3

[a] Date sampling (day/month/year).
[b] Sampling location (longitudinal arrangement from east to west of Baffin Bay).
[c] Mean value ± standard deviation (SD) for sea-ice concentration in spring over the years 1988 to 2017 (n= 30).
[d] Number of samples analyzed per station for sympagic carbon calculations.
[e] Mean values ± SD.
[f] Number of samples analyzed per station for stable isotope ratio analyses.
[g] The minimum and maximum values obtained are shown in bold.

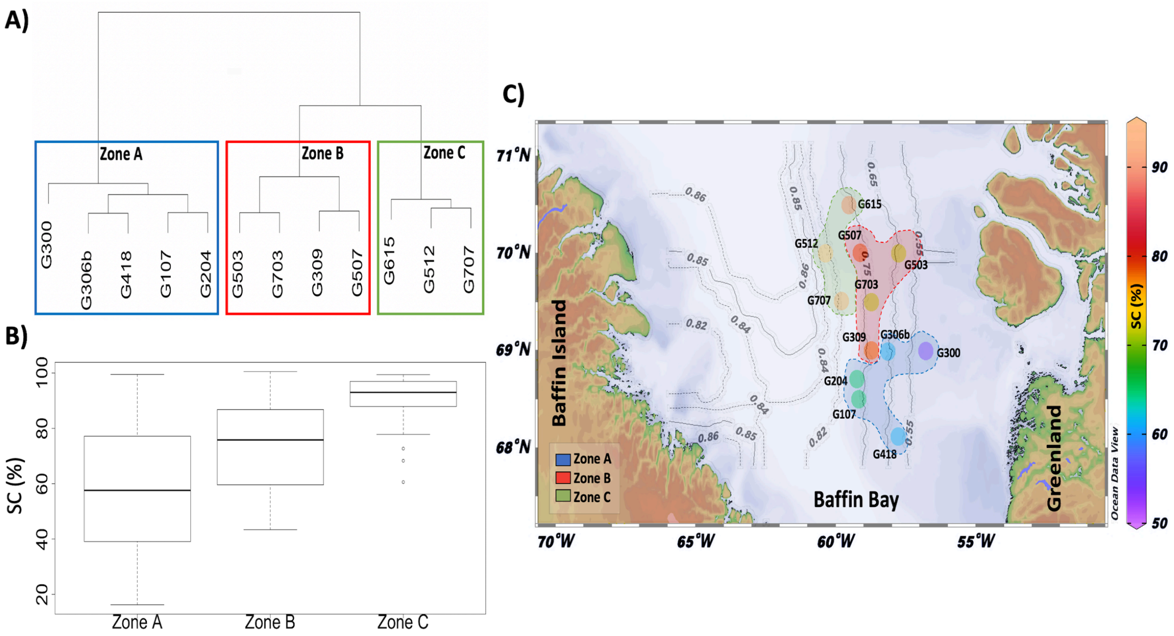

Figure 2.2. Cluster analysis performed on relative proportion of sympagic carbon assimilated by benthic macrofauna. Cluster analysis resulted in three different zones (A); boxplot of the relative abundance of sympagic carbon (SC) assimilated by the deep benthic fauna sampled in the three zones resulting from the hierarchical clustering analysis (B); and spatial distribution and relative percentage of SC assimilated by the benthic community across the benthic stations (C). The average sea-ice concentration, ranging from 0 to 100% (expressed here between 0 and 1; gray lines), derived from the National Snow and Ice Data Center in spring (1 April to 30 June) between 1998 and 2017 in Baffin Bay, Canadian Arctic.

2.5.3 *Food web structure and transfer of sympagic carbon across benthic macrofauna*

HBI lipid biomarkers and δ^{15}N values of the benthic macrofauna revealed distinct niche spaces between zones (Figure 2.3). Convex hulls showed a decrease in niche width (trophic diversity) from Zones A to C. Moreover, the relative position of these hulls showed that the highest assimilation of SC by macrofauna was located in Zone C (where SC ranged between 61 and 99%; mean SC% ± SD = 91% ± 8.1, n = 55) and the lowest in Zone A (where SC ranged between 16 and 97%; mean SC% ± SD = 61% ± 23.7, n = 39). In contrast, intermediate values of SC assimilated by macrofauna were found in Zone B (where SC ranged between 54 and 99%; mean SC% ± SD = 76% ± 15.8, n = 65).

Likewise, ellipses (core niche spaces) for Zones A and C showed almost no overlap, suggesting important differences in the assimilation of SC by benthic macrofauna in these regions (Figure 2.3). Benthic macrofauna displayed a wide range of isotopic signatures (Table S2.1). Differences in $\delta^{15}N$ values were observed across species (F = 18.27, df = 70, p-value <0.001) and reflected in the high variability of trophic levels occupied by the consumers. Trophic markers highlighted variations in the extent of the niche space along the $\delta^{15}N$ axis between the different zones (Figure 2.3). Convex hulls and ellipses showed a trend of increasing niche length from Zones A to C, relating the shortest niche length to Zone A ($\delta^{15}N$ values from 10.7 to 17.9‰) and the longest to Zone C ($\delta^{15}N$ values from 6.1 to 20.5‰). In Zone B, $\delta^{15}N$ values ranged from 8.8 to 19.2‰ (Figure 2.3).

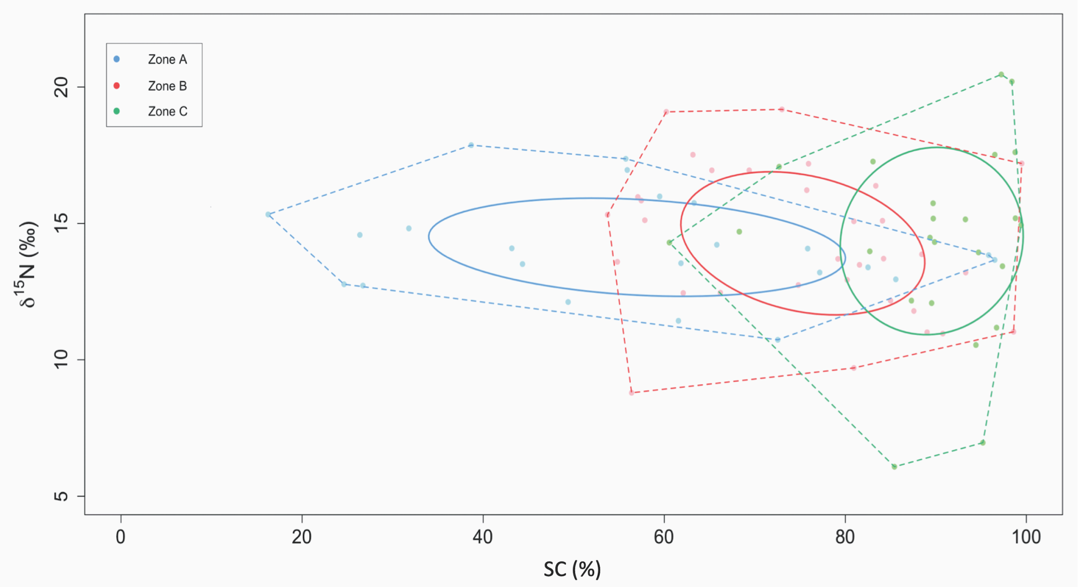

Figure 2.3. Biplot illustrating the ecological niche characteristics of the benthic community for each zone. Convex hulls (dashed lines) and standard ellipses (full lines) represent the niche space, sympagic carbon (SC%) versus $\delta^{15}N$, for three different zones in Baffin Bay (11 June to 10 July 2016): Zone A (blue), Zone B (red), and Zone C (green) (Figure 2.2). Convex hulls represent the full range of the ecological niche area of resources used by benthic consumers, while ellipses represent the core niche area used by consumers.

Differences in the ecological niche space across groups of benthic consumers (i.e., primary, omnivorous, and high consumers) and zones were observed (Figure 2.4). In Zone A, SC ranged from 61.6 to 72.5% in primary consumers, from 24.6 to 96.5% in omnivorous consumers, and from 16.3 to 75.8% in high consumers. In Zone B, SC ranged from 56.4 to 98.6% in primary consumers, from

54.8 to 93.2% in omnivorous consumers, and from 53.7 to 99.5% in high consumers. In Zone C, SC ranged from 85.4 to 96.7% in primary consumers, from 87.3 to 97.4% in omnivorous consumers, and from 60.6 to 99.4% in high consumers (Figure 2.4).

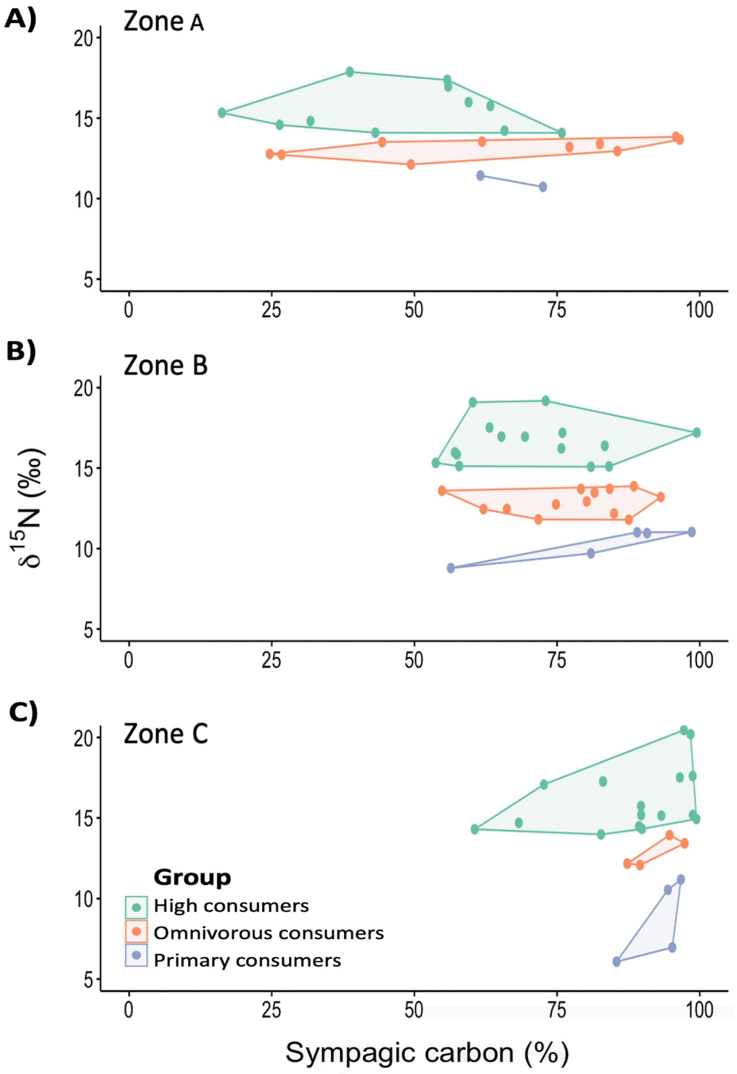

Figure 2.4. Biplots illustrating the ecological niche characteristics of the different benthic consumer groups. Convex hulls (full lines) represent the ecological niche space, δ^{15}N versus sympagic carbon (SC%), for three different groups of benthic consumers: high (green), omnivorous (orange), and primary (blue), in three different zones in Baffin Bay, 11 June to 10 July 2016.

Likewise, the values of δ^{15}N varied across zones and consumer groups. In Zone A, δ^{15}N values ranged from 10.7 to 11.4‰ in primary consumers, from 12.1 to 13.8‰ in omnivorous consumers, and from

14.1 to 17.9‰ in high consumers. In Zone B, $\delta^{15}N$ values ranged from 8.8 to 11.0‰ in primary consumers, from 11.8 to 13.9‰ in omnivorous consumers, and from 15.1 to 19.2‰ in high consumers. Finally, in Zone C, $\delta^{15}N$ values ranged from 6.1 to 11.2‰ in primary consumers, from 12.1 to 13.9‰ in omnivorous consumers, and from 14.0 to 20.5‰ in high consumers (Figure 2.4). We noted a greater variability of $\delta^{15}N$ values in both primary and high consumers in Zone C compared to the other zones.

To assess the origin of carbon, amount of resources, and habitat used by benthic macrofauna, we analyzed $\delta^{13}C$ values of consumers and food web baselines (i.e., SPOM, fresh sympagic algae, and sediment). Surface sediments were slightly enriched in carbon isotopes compared to SPOM. $\delta^{13}C$ values ranged from –23.8 to –20.1‰ in SPOM, from –22.7 to –18.8‰ in sediments, from –20.7 to –13.4‰ in fresh sympagic algae, and from –18.6 to –18.1‰ in wracks of the macroalga *Fucus vesiculosus*, found only at station G418 in Zone A. Macrofaunal $\delta^{13}C$ values ranged from –21.5 to –12.9‰. Values of $\delta^{13}C$ in benthic macrofauna ranged from –21.2 to –13.6‰ in Zone A, from –21.2 to –12.9‰ in Zone B, and from –21.5 to –13.7‰ in Zone C (Figure 2.5). Among macrofauna, the sea stars *Icasterias panopla* and *Urasterias lincki* were the most ^{13}C-enriched in this study ($\delta^{13}C$ = –12.9‰ and –13.6‰, respectively). None of the benthic macrofauna analyzed was ^{13}C-depleted to $\delta^{13}C$ values lower than –22‰, which would have reflected a higher consumption of phytoplankton or SPOM. Differences in the shape of density distribution $\delta^{13}C$ values were observed (Figure 2.5), which reflect changes in relative importance of carbon sources used by consumers. The largest peak of $\delta^{13}C$ values was detected in Zone A, the second highest $\delta^{13}C$ peak in Zone B, and the lowest $\delta^{13}C$ peak in Zone C. A secondary peak of $\delta^{13}C$ was evidenced in all three zones, but was more pronounced in Zone C. The $\delta^{13}C$ values from the benthic macrofauna showed similar ranges in all zones studied, but the most positive $\delta^{13}C$ values corresponded mostly to Zones B and C (Figure 2.5).

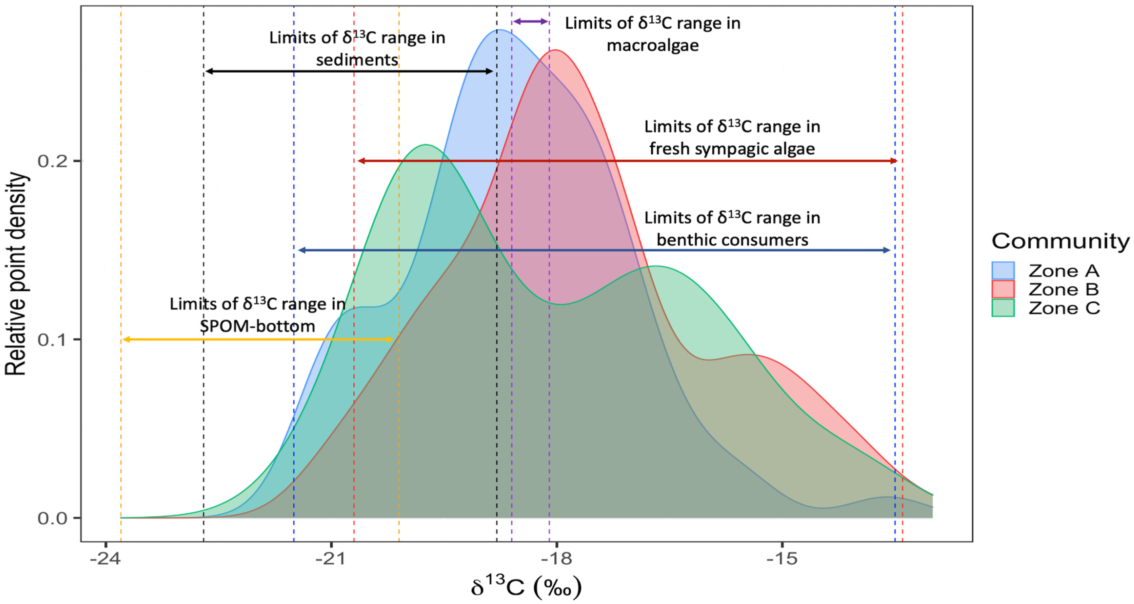

Figure 2.5. Density plot of δ^{13}C of the benthic community measured in Baffin Bay in spring 2016. Limits of δ^{13}C range are also shown for different baseline items: SPOM (yellow arrows), fresh sympagic algae (red arrows), sediment (black arrows), macroalgae (purple arrows), and benthic consumers (blue arrows). The consumer δ^{13}C measurements are from the three different zones of the study.

2.6 Discussion

2.6.1 *Influence of sea-ice concentration and depth on distribution and availability of sympagic carbon in sediment*

We found a significant relationship between sea-ice concentration and sympagic carbon, associated with a decreasing gradient in the relative contribution of SC from the western to eastern side of Baffin Bay. Our results also revealed a latitudinal SC gradient between the southeast and northwest stations, with SC increasing towards the northernmost stations. Independently of hydrographic conditions, we detected a significant effect of sea-ice concentration on the relative contribution and distribution of SC in sediment. Previous studies that explored how benthic food webs responded to changes in sea ice and primary food supply highlighted the critical role that sea ice plays in Antarctic food webs (Michel et al., 2019; Norkko et al., 2007; Rossi et al., 2019). Also, lipid biomarker studies denoted how latitudinal patterns in sea-ice conditions and seasonality influenced the abundance and distribution of HBI lipids in different Arctic regions (Koch et al., 2020b; Navarro-Rodriguez et al., 2013; Ribeiro et al., 2017). In Baffin Bay, Stoynova et al. (2013) studied the distribution of HBI lipids and observed diminishing abundances of IP_{25} (sympagic carbon proxy) in areas with less sea-ice concentration towards the south of the Bay. Our data showed a similar trend, highlighting that among the studied environmental parameters, sea-ice concentration has a significant effect on the relative contribution and distribution of SC on the seafloor. Therefore, changes in sea-ice concentration during spring could have had a significant impact on sediment SC contents.

High SC percentages occurred at all of our stations. Previous work has shown that the abiotic degradation (e.g., Type II photodegradation and autoxidation; for a review, see Rontani and Belt, 2019) of HBI lipids increases with the number of unsaturations, and, therefore, degradation rate constants of tri-unsaturated HBIs (e.g., pelagic HBI) are higher than those of the mono-unsaturated HBIs IP_{25} (sympagic HBI) (first order type II photodegradation rate constant of 1.0×10^{-2} and 1.7×10^{-5} h^{-1} and first order autoxidative rate constant of 3.2×10^{-1} and 1.0×10^{-3} h^{-1} for IP_{25} and HBI III, respectively; Rontani et al., 2011; Rontani et al., 2014). Because the calculation of SC is based on a ratio of HBI of uneven reactivity where the most subject to degradation is the pelagic HBI, degradation of organic matter could lead to over-estimation of SC percentages. Therefore, for similar sinking rates, organic particles should experience more degradation the deeper they sink, which could cause deeper sampling sites to present higher SC percentages compared to shallower sites. However, as one of the major abiotic degradation processes (Type II photodegradation) is limited to the euphotic zone where the light necessary for this process is available (Amiraux et al., 2017; Rontani et al., 2016), the residence time of a particle within the euphotic zone should dictate its degradation rather than its travel time to sediment. Hence, for a same euphotic zone thickness, the degradation state of HBIs as well as the potential overestimation of SC between deep and shallow sampling sites should be relatively similar. Moreover, the use of pelagic and sympagic HBIs in a ratio is not a specificity of the SC percentage. The phytoplankton-IP_{25} index (PIP_{25}; Müller et al., 2011) represents another HBI-based index based on a ratio of IP_{25} and HBI III (Belt, 2018). By providing robust Arctic palaeo sea-ice reconstructions (Kim et al., 2019; Smik et al., 2016), this index suggests that the degradation of HBI III within the water column or sediment is reduced or at least close to that of IP_{25}. Thus, the high SC percentages observed in our deep stations should likely be derived from a relatively higher contribution of sympagic than pelagic POM rather than a preferential degradation of the pelagic biomarker. The $\delta^{13}C$ values support this interpretation, as we found the most positive $\delta^{13}C$, suggesting the strongest link with sympagic source values, in the deepest stations.

2.6.2 *Relative contribution of sympagic carbon in benthic macrofauna diets*

Sea-ice lipids are known to be transferred through pelagic food webs upwards to the highest trophic levels in both Arctic (Brown et al., 2017a; 2017b; 2018) and Antarctic ecosystems (Goutte et al., 2013). However, only few studies have shown the presence of HBI lipids in organisms associated with the seafloor (Brown et al., 2012; Brown and Belt, 2012; Koch et al., 2020a). Our results showed that both sea ice and pelagic HBI lipids were found in two thirds of the benthic samples analyzed. It is possible that the absence of certain HBIs (pelagic or/and sympagic) in the other third of the benthic samples could be a consequence of the tiny size of organisms, dietary preferences, rates of reactivity of HBIs, and short residence time of HBI lipids following ingestion by consumers (Koch et al., 2020a). In addition, environmental factors (e.g., nutrient availability; see Brown et al., 2020) influence the amount of HBIs produced by algae, which in turn could indirectly influence the presence or absence of HBIs in consumers. The SC quantification, combined with other trophic marker analyses, represents a novel approach to address questions related to the assimilation and transfer of HBI lipids through the benthic food web. However, more studies using this approach are necessary to conclude how biological, environmental and chemical processes could affect their detection in sediment and organisms.

Even if the assimilated contributions of SC varied between species present at each station, the average SC (%) found in sediments and SC (%) assimilated by benthic macrofauna across stations did not differ notably. This suggests that the relative abundance of SC assimilated in spring by benthic consumers could be explained partly by the relative abundance of SC available on the seabed (Tables 2.1 and 2.2), although benthic consumer identity (i.e., taxonomic group) or feeding strategy (i.e., functional group) could also play a role (see below). Consumption pathways of organic matter across the benthic community have been documented previously in the Arctic (Hobson et al., 2002; Mäkelä et al., 2017b; McTigue and Dunton, 2014), showing variations in the utilization of phytoplankton or sympagic carbon sources across regions and time. However, studies that investigated the role of sea-ice-derived carbon in benthic diets during spring indicated that SC and bacterially reworked organic matter represented the most important food sources for benthic consumers (Kohlbach et al., 2019; North et al., 2014). Regardless of how we addressed the analysis of the carbon assimilation and transfer through benthic consumers (i.e., HBI and/or stable isotope analyses), the spread of values showed similar results, among which benthic consumers exhibited strong patterns in SC assimilation in response to gradients of SC values. Hence, SC (%) assimilated by deep benthic fauna increased towards sites with higher sea-ice concentration during the spring in the northwest of Baffin Bay.

Based on our results, we highlight sympagic carbon as an important food source in the diet of different benthic taxa in springtime.

2.6.3 *Food web structure and transfer of sympagic carbon*

Trophic markers revealed shifts in the ecological niche space (i.e., niche width) of the benthic community across zones. Decreases in niche width from Zones A to C suggested a greater diversity of carbon sources used by consumers in Zone A. Our results showed that percentages of SC available for benthic consumption is a determining factor shaping the ecological niche space. Thus, the most significant differences in niche space corresponded to areas with strong differences in SC percentages (Figure 2.3). Across trophic groups, changes in the niche space revealed variations in SC assimilation by benthic macrofauna. Omnivorous and primary consumers relied the most on SC in all zones, showing the narrowest niche space in Zone C. On the other hand, high consumers showed low to moderate assimilation of SC in Zone A, with a high increase in SC assimilation in Zones B and C. In addition to variations in the niche width, $\delta^{15}N$ range was greater in both primary and high consumers from Zone C, compared to Zones A and B. Although percentages of SC available for the consumption of benthic macrofauna should vary over the seasons and regions (Boetius et al., 2013), benthic consumers can specialize on the consumption of some available basal resources, which is ultimately reflected in the food web structure (Rossi et al., 2019). Likewise, changes in the ecological niche can reflect mechanisms adopted by the different groups to ingest different food sources (Iken et al., 2001). For example, primary consumers adapted to feed on more selective food items occupied a restricted ecological niche space and the lowest trophic positions in this study. This result means that aside from environmental conditions that influence the availability of food sources, changes in the benthic food web could be a reflection of the plasticity of those benthic consumers that can ingest different carbon sources efficiently (Mäkelä et al., 2017b). For instance, *Rossia megaptera*, a cephalopod, shifted from a high trophic level in Zone A (high consumers) to a lower trophic level (omnivorous) in Zone B. In addition, our data suggest that high availability of SC may influence the transfer efficiency of this basal source.

The $\delta^{13}C$ values from the benthic community revealed differences in resource assimilation between zones, indicating that consumers probably depend on multiple baseline items, among which sympagic algae provide one of the main carbon inputs for consumers in spring. Very positive $\delta^{13}C$ values (typically linked to consumption of ice algae) were found mainly in benthic fauna from Zones B and C, suggesting that at the time of sampling the SC resource might be used less commonly by benthic fauna in Zone A (Figure 2.5). Some studies have proposed a link between ^{13}C-enriched benthic invertebrates and the consumption of organic material that has been reworked by microbes (Amaro et al., 2019; Gradinger and Bluhm, 2020; Michel et al., 2016). Therefore, unaccounted resources (e.g., from bacteria) may also have influenced isotopic compositions in consumers. Likewise, increases of δ^{15}N with depth in both sediments and benthic fauna may be linked to biological and chemical processes, including microbial consumption and degradation of OM in the water column (Macko and Estep, 1984; Stasko et al., 2018b) and remineralization (Feder et al., 2011; Lehmann et al., 2019), that could influence nitrogen isotopic compositions across benthic macrofauna. However, for some surface deposit feeders (e.g., the arthropod *Diastylis rathkei*) we found exceptionally low δ^{15}N values (at the same level of the baseline/sediment δ^{15}N values), coinciding with previous findings (Iken et al., 2005; Renaud et al., 2011). The cause for these depleted ^{15}N values remains unexplained in this study, but ^{15}N depletions may have been influenced by the isotopic composition of unknown baseline sources, such as cyanobacteria or other N_2-fixing microorganisms (Karlson et al., 2014). Based on our results, the benthic food web is supported by several carbon sources. In springtime, however, sympagic algae and probably microbially degraded organic matter seem to have important functions in supporting and shaping the benthic food web. Although this study gives some clues about the functioning of the benthic food web, many questions remain to be resolved, including the role of microbial communities in deep benthic food webs. Continued study of how temporal and spatial changes in basal resource inputs, including reworked material, impact nutrient transfer and food web structure is needed, particularly in areas with notable changes in sea-ice concentration.

2.6.4 *Climate change, consumer diets, and food web structure*

The quantity of POC that reaches the polar seabed influences deep benthic community structure and plays an essential role in shaping patterns and trends in biomass, density, and macrobenthic production (Degen et al., 2015; Grebmeier and Barry, 1991). Coinciding with reductions in sea-ice cover and warming waters, shifts in both benthic biomass and species composition have been described for some Arctic regions, suggesting that climate change may also impact biological diversity in these deep-sea ecosystems (Grebmeier et al., 2018; Rybakova et al., 2019). Predictions point to future alterations in primary production in the Arctic Ocean due to a reduction in sea-ice extent and changes in its phenology (Tedesco et al., 2019). As a result, the quality and quantity of the organic matter that reaches the seafloor will be impacted negatively by taxonomic and biochemical alterations and by increased grazing pressure in the pelagic zone (Jeffreys et al., 2013) which could in turn weaken pelagic-benthic coupling processes (Olivier et al., 2020) and the efficiency of energy transfers across food webs (Post, 2017). In terms of food quality, Leu et al. (2011) found that sympagic primary production is generally of better nutritional quality than pelagic production. Moreover, sympagic production is better conserved because of its higher sinking rates (avoiding most of the abiotic degradation that occurs in euphotic zones) and frequent mismatch with the onset of grazing activity. Hence, an increase in phytoplankton production due to an earlier onset of sea-ice melt will not necessarily imply more food for deep benthic communities. Instead, climate change may reduce the size of phytoplanktonic cells (Li et al., 2009) and lower the overall quality and quantity of some primary food sources. Here, we established a connection between contrasting sea-ice conditions and changes in deep benthic consumer diets and food web structure. Our results denoted a link between niche sizes and diversity of food sources, highlighting a reduction in niche size when food diversity decreased. As an increase in the diversity of basal sources leads to temporal stability in the supply of organic carbon to food webs, food restrictions (i.e., decrease of diversity) could lead to the temporal instability of the system (Wing et al., 2012). Likewise, preference for ice algae as food was reflected in niche sizes. Narrower niches were associated with primary and omnivorous consumers in regions with a major abundance of SC. Consumer food preferences may be linked to feeding mode and the ability of animals to capture, handle, and digest food, and to the energy value that this resource represents for consumers (Araújo et al., 2011). Thus, instead of revealing lesser adaptability to ingest different kinds of food sources, narrow niche may reflect the strategies adopted by consumers to ingest food of great nutritional value. Finally, ellipses and $\delta^{13}C$ values indicated that the resource most commonly used by consumers was ice algae. A reduction in the availability of SC could increase both intraspecific and interspecific competition and predation among the consumers, ultimately affecting structure, dynamics, and seasonal stability of deep-sea benthic food webs in the Canadian Arctic.

2.7 Conclusions

Quantifying the importance of SC as a food source in the Arctic is an increasingly important research objective as sea-ice extent and thickness continue to decline. The present study represents the first analysis of the transfer of sea-ice and pelagic lipids through a diverse range of benthic species at different depths and sea-ice conditions, supporting the idea that SC is an important energy subsidy for deep benthic communities that could be disrupted in the years to come. Climate change will drive food quality and availability in the future Arctic Ocean, which can affect the transfer of matter and energy to high-level consumers, including commercial fish and Inuit people. Also, a greater disparity in the formation and melting period of sea ice could lead to consequences not yet defined in cycles of production and delivery of OM to benthic fauna. Changes in the quantity of sympagic OM available to benthic consumers and/or the timing of its availability could disrupt the life cycles of benthic organisms and affect lower benthic trophic levels. Such disruption could in turn induce changes in ecosystem functioning at different levels in the Arctic food web. The use of lipid biomarkers in the quantification of SC assimilated by benthic consumers proved to be a powerful technique that could enhance our understanding of deep benthic communities. Also, the novel combination of HBIs with stable isotope ratios ($\delta^{15}N$; $\delta^{13}C$) was shown to be a suitable method in the study of the benthic food web structure. Our results indicated considerable assimilation of SC by benthic consumers during spring/early summer, providing estimates of SC assimilated by benthic consumers in areas with different dynamics in sea-ice cover. Regardless of depth, our results showed that the relative contribution and distribution of SC in the seabed was regulated mainly by sea-ice cover. In this study, availability of food sources and ecological strategies (i.e., diversity of resources and habitats used by animals) adopted by benthic consumers were major drivers shaping the benthic food web structure across sampled sites. As benthic fauna are key members of the organic carbon cycle, further long-term studies encompassing all four seasons over multiple years would be beneficial to establishing how variations in sea-ice phenology can influence food supply and nutrient transfers among Arctic benthos. Decreases in spring sea-ice concentrations with alterations in timing, quantity, and origins of the organic matter that reach the seafloor could lead to temporal changes in the nutritional composition of benthic consumer diets, which in turn could impact the structure and functioning of these ecosystems. In response to Arctic warming, raising our capacity to detect the ecological impacts of continued sea-ice decline is a fundamental priority, requiring more empirical studies that explicitly test the effects of sea-ice reduction on biological responses and the resilience of the ecosystem.

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Chapter 3. Trophic ecology of brittle stars (Echinodermata: Ophiuroidea): ecological niche differentiation induced by food availability and interspecific feeding behavior, Canadian Arctic Ocean

3.1 Résumé

La compréhension des mécanismes qui soutiennent les interactions alimentaires et la cooccurrence des espèces dans les régions soumises à des changements environnementaux rapides est de plus en plus importante pour prédire les tendances futures de la dynamique des populations. Cependant, il n'y a encore que trop peu de données disponibles sur l'écologie trophique pour de nombreuses espèces benthiques qui pourraient nous aider à mieux comprendre les interactions trophiques et les rôles trophiques à l'échelle individuelle. Ici, des isotopes stables (δ^{13}C, δ^{15}N), en conjonction avec l'approche bayésienne, ont été utilisés pour explorer les tendances spatiales quant à la largeur des niches isotopiques de la population et leur chevauchement pour trois ophiures syntopiques de l'Arctique (Echinodermata : Ophiuroidea) : *Ophiacantha bidentata*, *Ophiocten sericeum* et *Ophiopleura borealis*, dans la baie de Baffin (BB), l'archipel Arctique canadien (CAA) et la polynie des eaux du Nord (NOW). Les ophiures étudiées ont présenté une grande plasticité quant à leurs comportements de recherche de nourriture, dévoilant un régime alimentaire très adaptable entre individus. Toutefois, les différences dans la composition de carbone ont entraîné la variabilité observée dans l'utilisation des ressources au niveau individuel entre les stations, ce qui a affecté les interactions trophiques, le chevauchement des niches et l'étendue des niches isotopiques des populations d'ophiures. Le chevauchement des niches était plus élevé dans la région très productive de la polynie NOW, où les consommateurs sélectionnaient les mêmes aliments. Les régions où la concentration de glace de mer était plus élevée ont montré quant à elles une ségrégation accrue des niches. Dans l'ensemble, les résultats suggèrent que la taille des niches isotopiques reflète les réactions populationnelles et individuelles des consommateurs aux fluctuations relatives à la disponibilité de nourriture et peut-être à la compétition passée, toutes les deux induites par les caractéristiques océanographiques locales. Cette étude représente la première description de l'écologie trophique d'ophiures grâce à l'utilisation de niches isotopiques dans trois régions différentes de l'océan Arctique canadien.

3.2 Abstract

Understanding the mechanisms that support feeding interactions and species co-occurrence in regions subject to rapid environmental changes is becoming increasingly important to predict future trends in population dynamics. However, there is still little information available on the trophic ecology for many benthic species to help us better understand trophic interactions and individual trophic roles. Here, we used stable isotopes ($\delta^{13}C$, $\delta^{15}N$) in conjunction with the Bayesian ellipses approach to explore spatial trends in population isotopic niche width and overlap of three syntopic Arctic brittle stars (Echinodermata: Ophiuroidea): *Ophiacantha bidentata, Ophiocten sericeum,* and *Ophiopleura borealis*, in the Baffin Bay (BB), the Canadian Arctic Archipelago (CAA), and the North Water Polynya (NOW). These three coexisting ophiuroids displayed great interspecific plasticity in foraging behaviors, and showed a high degree of inter-individual dietary flexibility. However, differences in surface carbon composition drove the variability of resource utilization at the individual level across stations, which in turn affected trophic interactions, niche overlaps, and isotopic niche breadth of ophiuroids. Greater niche overlap was found in the highly productive region of NOW, where consumers exhibited similar food selectivity, whereas an increased in niche segregation occurred in regions with more sea-ice concentration (SIC). These results suggested that the isotopic niche size reflected the consumers' population and individual responses to fluctuations in food availability and possibly past competition, both induced by local oceanographic features. This study represents the first description on the trophic ecology of brittle stars species using the isotopic niche approach in the Canadian Arctic Ocean. Our study indicated that niche parameters of ophiuroids can respond quickly to ecological and environmental gradients, which suggested an important adaptability of these species facing multiple stressors.

3.3 Introduction

Arctic marine offshore ecosystems are mainly sustained by seasonal organic carbon pulses from phytoplankton (i.e., open water algae) and sympagic (i.e., ice-associated algae) communities (Tamelander et al., 2009). When light conditions and inorganic nutrient supply are favorable during spring, the beginning of a limited period of sea-ice algal production begins, followed by a phytoplankton bloom (Hegseth, 1998; Leu et al., 2015, 2011). The duration of phytoplankton and ice algal production is comparable, but in terms of biomass, phytoplankton generally exceeds sea-ice algae (Leu et al., 2011). Once the organic matter is produced, the vertical export of particulate organic matter (POM) varies considerably during seasons and among regions according to biological and physical processes (e.g., zooplankton grazing pressure, microbial processes), which ultimately control the final amount and quality of POM that reaches the benthos (Herndl and Reinthaler, 2013).

The Arctic is warming faster than any other region on Earth (AMAP, 2017). As a result, the Arctic seascape changes abruptly, exhibiting accelerated reductions in the thickness and extent of sea ice, with predictions estimating a seasonally ice-free Arctic Ocean by 2040 (Comiso et al., 2008; Kędra et al., 2015). Sea ice plays a vital role in the Arctic Ocean ecosystem by mediating physical and biological processes such as the primary production (Gradinger, 2009; Hunt et al., 2002; Ramírez et al., 2017), but also by serving as a habitat for a large number of organisms (e.g., from bacteria to marine mammals) and as a base substrate for ice algae (Garrison, 1991; Werner, 2006). Consequently, sea ice loss may affect the magnitude of the set of interactions between habitats (i.e., sympagic-pelagic and sympagic-benthic coupling) in which exchanges of energy, mass, or nutrients occur (Wassmann and Reigstad, 2011). Benthic fauna depends largely upon the supply of organic carbon from primary producers (pelagic and sympagic), thus benthic consumers and food web structure are sensitive to changes in the timing, nature, quality, or abundance of nutrients (Kędra et al., 2012). Therefore, the knowledge of the ecological and biological mechanisms that drive trophic ecology and support species co-occurrence is important to predict how environmental changes may affect trophic interactions, species coexistence, and food web dynamics.

In the Arctic Ocean, the benthic community structure varies significantly due to ecological (e.g., species interactions, resource availability, seasonality) and environmental gradients (e.g., temperature, salinity, depth, currents, sediment type, bottom topography) (Kędra et al., 2013; Roy et al., 2014). Ecological drivers that include niche complexity coupled with species interactions shape benthic composition and influence the transfer of energy through trophic levels (Collin et al., 2011; Roy et al., 2014). Stable isotope analysis (SIA; carbon and nitrogen), which provides time- and space-integrated insight on diet and habitat use by consumers, has emerged as a common approach to examine the structure and dynamics of ecological communities and carbon flow in food webs (Jackson et al., 2011; Layman et al., 2007a; Post, 2002). In turn, the use of the isotopic niche, a low-dimensional specification of the “Hutchinsonian niche” (Hutchinson, 1957), which consists of the area occupied by individuals in the isotopic niche space, has served to analyze patterns of interactions in various ecological resolutions (Shipley and Matich, 2020), and to interpret levels of dietary specialization of individuals (Araújo et al., 2007; Karlson et al., 2015). The characteristics of the niche vary according to intrinsic (e.g., intra and interspecific competition) and extrinsic factors (e.g., sea-ice cover, resource availability, seasonality) that influence the dimensions of the niche (Costa-Pereira et al., 2017; Shipley and Matich, 2020). Furthermore, individual levels of dietary specialization within a population may drive the variability of the niches (Araújo et al., 2009; Semmens et al., 2009).

The high densities of ophiuroids, often observed in dense aggregations, make them the most common components of benthic assemblages in the Arctic Ocean (e.g., Piepenburg and Schmid, 1996; Starmans *et al.*, 1999; Sejr *et al.*, 2000; Brooks *et al.*, 2007). With approximately 73 species recorded, brittle stars (Echinodermata: Ophiuroidea) are present in a wide geographic and bathymetric distribution (Ravelo et al., 2017; Stöhr et al., 2012). Among the brittle stars studied, *Ophiacantha bidentata,* is a widespread arctic-boreal ophiuroid with a circumpolar distribution that can switch from deposit to suspension feeding depending of food availability (Brooks et al., 2007). The ophiuroids *Ophiocten sericeum,* and *Ophiopleura borealis* have been described as endemic Arctic species, and they are considered mobile deposit or predator-scavenger feeders (Gallagher et al., 1998; Paterson et al., 1982; Piepenburg and Schmid, 1996). Due to the high densities that ophiuroids can reach, it is believed that this group is prone to play a fundamental role in the functioning of the ecosystem by increasing the number of trophic links and maintaining trophic cascades in food webs (Pearson and Gage, 1984). In general, brittle stars have been suggested to be opportunistic facultative deposit or suspension feeders (Jangoux, 1982). However, according to changes in the availability of resources, ophiuroids display wide-ranging trophic flexibility using more than one feeding mode (Brooks et al., 2007; Pearson and Gage, 1984).

Even though we have expanded our knowledge about the diet of brittle stars in the Arctic (e.g., Graeve *et al.*, 1997; Gallagher *et al.*, 1998), there are still many knowledge gaps in the trophic ecology of most ophiuroids and how they coexist using the same resources while avoiding interspecific competition. In the present study, we examined changes in the isotopic niche structure of ophiuroids in response to variation in sea-ice conditions, local productivity, and individual-level differences in feeding behavior. Three species of coexisting ophiuroids were chosen as models to test the following hypotheses: (1) depending on sea-ice concentrations (SIC), patterns in species niche structure (i.e., segregation and overlap of niches) will change across regions, where a higher overlap of niches will be linked to regions with more SIC due to brittle stars exploiting more similar food items; (2) changes in the isotopic niche width of ophiuroids will be closely related to sediment δ^{13}C carbon composition and individual feeding behaviors, in which niche width reduction will be linked to regions with higher abundance of resources where consumers ingest the more abundant sources; and (3) a decrease in niche overlap will be associated with regions with higher heterogeneity of resources in which brittle stars can use a higher spectrum of resources.

3.4 Material and methods

3.4.1 *Study area*

Baffin Bay (Figure 3.1) is a semi-enclosed ocean basin located between Baffin Island and western Greenland that connects the Arctic Ocean and the northwest Atlantic Ocean (Dunlap and Tang, 2006; Hamilton and Wu, 2013). Annual sea ice development in Baffin Bay begins in late autumn and reaches its maximum extent around March (Stern and Heide-Jørgensen, 2003). Excluding the ice-free months between August and September, Baffin Bay is partially covered by sea ice (Tang et al., 2004). The Canadian Arctic Archipelago to the north-west of Baffin Bay extends over an area of 3.3×10^6 km^2, and comprises a large number of islands and channels between Banks Island in the west and Baffin and Ellesmere Islands in the east (Melling, 2002). In this region, the sea ice component is a mixture of both first-year and multi-year ice (MYI; Kwok, 2006). The perennial MYI, located almost entirely on Queen Elizabeth Islands, Western Parry Channel and M'Clintock Channel, can represent more than 50 % of the total area covered by ice before the melt season (Howell et al., 2013). The North Water Polynya is located between Greenland and Canada on the northern end of Baffin Bay. This region is characterized by low SIC and exhibits one of the highest levels of primary productivity recorded for the Arctic Ocean (Barber et al., 2001). Polynyas are areas of open water or with minimal sea-ice coverage surrounded by a contiguous ice pack (Barber and Massom, 2007).

3.4.2 Sample collection

On board the Canadian research icebreaker CCGS Amundsen, fifteen stations were visited from August 19 to September 1, 2018 and from July 20 to August 23, 2019 to collect sediment and brittle stars (i.e., *O. bidentata, O. sericeum,* and *O. borealis*) in three different Canadian Arctic regions (Figure 3.1). Brittle stars were found and collected at 9 of the 15 stations (Table 3.2, Table S3.1) for subsequent SIA using an Agassiz trawl with an opening of 1.5 m and a net mesh size of 40 mm. In addition, surface sediment samples were collected from 13 stations (Table 3.1), from the upper 1 cm of a box core (0.25 m^2). From each box core, sediments were collected for SIA (one sample per station) using 60-ml truncated syringes and for pigment content analysis (three samples per station) using 10-ml truncated syringes. Since carbon isotope ratios ($\delta^{13}C$) vary substantially among primary producers, but changes little between each trophic level (0-1 ‰; Peterson & Fry 1987, Post 2002, Layman et al. 2007), the carbon isotopic composition of surface sediment was used in the present study as a proxy to determine the relative contribution of primary carbon food sources in the diet of ophiuroids. In addition, sediment surface chlorophyll *a* concentration (Chl *a*), a short-term proxy of productivity, was carried out at Laval University, Quebec, following the modified protocols of Riaux-Gobin and Klein (1993) and Link et al. (2011). After collection, all samples were frozen for subsequent SIA and pigment analyses.

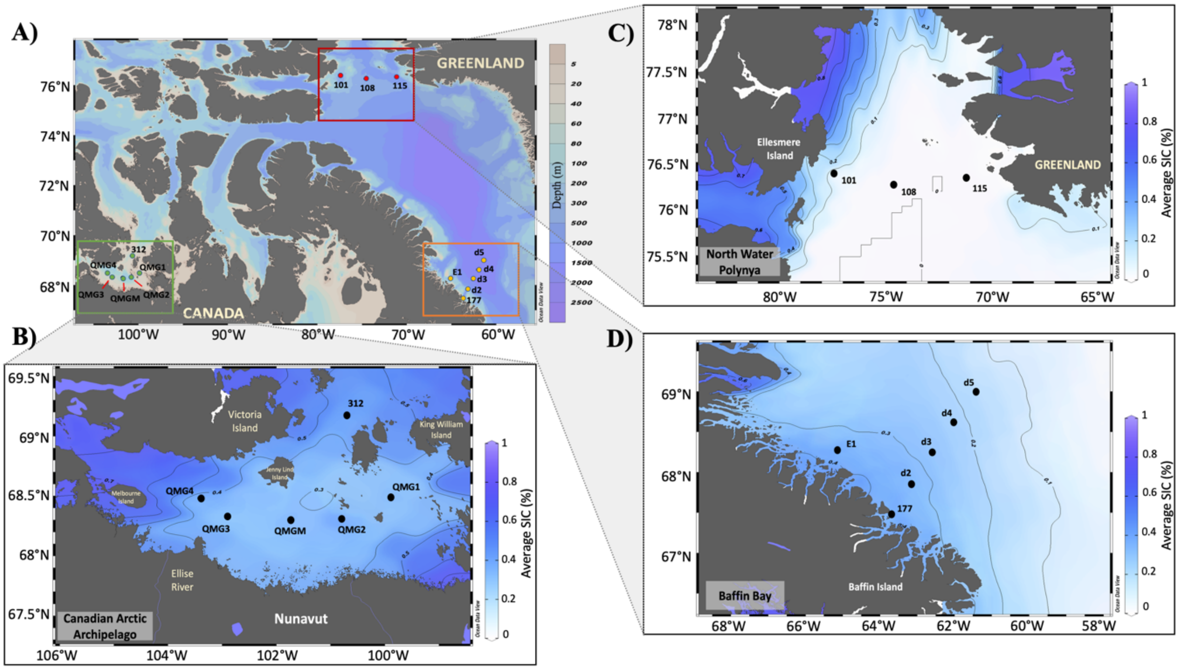

Figure 3.1. Location of sampling stations with bathymetric gradients. Red dots represent the stations in the North Water Polynya, green dots in the Canadian Arctic Archipelago, and orange dots in the Baffin Bay (map A). The average sea-ice concentrations for the regions studied (maps B-D), ranging from 0 to 100 % (expressed here between 0 and 1; gray lines), in the summer (June to August, between 2018 and 2019) were derived from the National Snow and Ice Data Center (https://nsidc.org/data/nsidc-0051).

3.4.3 Stable isotope analyses

Sediment and brittle stars samples were freeze-dried at –50°C and ground to a fine powder with mortar and pestle. For sediments, carbonates were removed using 1 N HCl until bubbling ceased. For brittle stars, a total of 92 individuals were used for SIA (Table S3.1). Lipid extraction was carried out in brittle stars using a solution of dichloromethane: methanol (2:1). Then, brittle stars samples were decarbonated by exposing them to HCl vapors for 48 h in an airtight container. After acidification, to verify the total removal of carbonate in the samples, drops of acid were applied to dried material (champagne test) to check that no more bubbles (i.e., CO_2 that would be produced by the chemical dissociation of the carbonates) formed.

Stable nitrogen and carbon isotope ratios were measured using a continuous-flow isotope ratio mass spectrometer (Thermo Electron Delta Advantage) in the continuous-flow mode (Thermo Electron ConFlo III) with an ECS 4010 Elemental Analyzer/ZeroBlank Autosampler (Costech Analytical Technologies) in the oceanography laboratory at Laval University, Quebec, Canada. Replicate measurements of international standards (USGS40 and USGS41 from the International Atomic Energy Agency; B2151 from Elemental Microanalysis) established measurement errors of ≤ 0.2 ‰ for $\delta^{13}C$ and $\delta^{15}N$. Stable isotope ratios were expressed in delta (δ) units ($\delta^{13}C$, $\delta^{15}N$) as the per mil (‰) difference with respect to standards: δX (‰) = $[(R_{Sample} - R_{Standard})/R_{Standard}] \times 10^3$, where X is ^{13}C or ^{15}N of the sample and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Standards were calibrated against the international references Vienna PeeDee Belemnite (VPDB) for carbon and atmospheric air for nitrogen.

3.4.4 Trophic positions

The estimation of trophic positions (TP) was used to characterize the functional role of individuals in brittle star species. The TP of ophiuroids was estimated using the 'OneBaseline' model in the Bayesian tRophicPosition package (Quezada-Romegialli et al., 2018) using the following equation:

$$\delta^{15}N_c = \delta^{15}N_b + \Delta N\,(TP - \lambda)$$

Where $\delta^{15}N_c$ corresponds to the nitrogen stable isotope value of the consumer for which TP is estimated, $\delta^{15}N_b$ represents the nitrogen isotope ratio of surface sediment bulk organic matter for each region studied; ΔN corresponds to the trophic discrimination factor (TDF) for nitrogen, and λ the TP of baseline sources. Trophic position of basal primary producers was set to 1.0, meaning that $TP \leq 2$ (low-trophic-level) represents primary consumers, > 2 $TP < 3$ (intermedium-trophic-level) represents secondary consumers (e.g., omnivores), and $TP \geq 3$ (high-trophic-level) represents top consumers as well as scavengers.

3.4.5 Sea-ice concentration data

Average of sea-ice concentration (SIC) was derived from satellite Nimbus-7 SMMR and DMSP SSM / I-SSMIS passive microwave at a grid cell size of 25 x 25 km (Cavalieri et al., 1996). The dataset was downloaded from the National Snow and Ice Data Center (https://nsidc.org/data/NSIDC-0051/versions/1). For each station, we calculated the average SIC (%) of two months: the month before the sampling and the month of the sampling date. This average was considered relevant in this study because the isotopic turnover rate in tissues of some marine invertebrates with Arctic distribution (e.g., *Onisimus litoralis*, *Mytilus edulis*, and *Macoma calcarea*) can vary between 1 and 3 months, affecting dynamics in consumers' isotopic composition (e.g., McMahon et al. 2006, Kaufman et al. 2008). In addition, consumers' isotopic composition may vary over time due to environmental conditions such as seasonal sea-ice cover dynamics (Kaufman et al., 2008).

3.4.6 Statistical analyses

All statistical analyses were performed using R Studio version 1.4.1106 (R Core Team, 2019) and graphical procedures with Ocean Data View version 5.1.7 (https://odv.awi.de). Homogeneity of variance and normality of residuals were verified using the Shapiro-Wilk test on residuals. Linear models were employed to simultaneously evaluate the effect of environmental variables (i.e., depth and SIC) and their interactions on $\delta^{13}C$ and $\delta^{15}N$ values found in sediment and the ophiuroids' samples. A Kruskal-Wallis test was conducted to examine the differences in stable isotope ratios of carbon and nitrogen in brittle stars among species, stations, and regions. Significant effects implicating categorical factors (SIC, depth, regions and species) were further analyzed with Tukey post-hoc using the emmeans package (v2.27-61) (Lenth and Lenth, 2018). The core isotopic niche space occupied by brittle stars was calculated using the standard ellipse area in R "SIBER" package (Jackson et al., 2011). Furthermore, the probabilistic method of Jackson et al. (2011) was used to estimate the mode and the credible interval of the Bayesian-simulated Standard Ellipse Areas (SEAb). Specifically, we used the sample size-corrected standard ellipse area (SEAc), which is a more robust approach that encompasses the core (around 40 %) of the isotopic observations within each species group and, therefore, is less sensitive to sample size and isotopic outliers (Jackson et al., 2011). SEAc's credibility intervals were based on 1,000,000 iterations and a burn in of 100,000.

3.5 Results

3.5.1 Isotopic composition of sediments

Sediment organic matter δ^{13}C values covered a wide range in the CAA region (ranging from –16.5 to –23.9 ‰; mean δ^{13}C‰ ± SD = –22.0 ‰ ± 2.7, n = 6), compared with a narrower range observed in the NOW (ranging from –22.2 to –22.8 ‰; mean δ^{13}C‰ ± SD = –22.4 ‰ ± 0.3, n = 4) and BB region (ranging from –21.0 to –22.8 ‰; mean δ^{13}C‰ ± SD = –21.6 ‰ ± 0.8, n = 4). In stations on the west of the CAA region (i.e., QMG3, QMG4, and QMGM), δ^{13}C values of surface sediments were slightly depleted in carbon isotopes (≤ –23 ‰). The δ^{13}C values of surface sediments found in this study overlapped partially with those determined in previous studies. For instance, δ^{13}C values ranged from –24.2 to –20.4 ‰ in the CAA (Goñi et al., 2013), from –22.7 to –18.8 ‰ in Baffin Bay (Yunda-Guarin et al., 2020), and from –22.9 to –22.1 ‰ in the NOW (Friscourt 2016, unpublished data). δ^{15}N sediment's values covered a wide range of values among stations ranging from 5.6 to 8.6 ‰ (Table 3.1). The most ^{15}N-enriched values in sediments occurred at the deepest BB stations, whereas the most ^{15}N-depleted values were found in the NOW (Table 3.1; Figure. 3.1). Significant differences were found in δ^{15}N values of sediments among regions (ANOVA, F = 7.29, df = 2, p-value = 0.001). Linear models revealed a significant effect of depth on sediment δ^{15}N values (F = 28.59, p-value < 0.001).

Table 3.1. Surface sediment dataset derived from sediment stations collected in three different regions of the Canadian Arctic Ocean.

Stations	Region[a]	Depth (m)	Date[b]	Latitude (N)	Longitude (W)	δ^{13}C[c] (‰)	δ^{15}N[d] (‰)	SIC[e] (‰)	nChl[f]	Chl *a*[g] (μg g^{-1})
312	CAA	67	2018-08-19	69.17	–100.70	–16.5	7.3	45	3	0.07 ± 0.0
QMG1	CAA	39	2018-08-21	68.49	–99.89	–22.9	6.7	34	3	0.64 ± 0.6
QMG2	CAA	73	2018-08-21	68.31	–100.80	–22.7	6.2	43	1	0.05
QMG3	CAA	51	2018-08-22	68.33	–102.94	–23.9	6.0	32	3	0.06 ± 0.1
QMG4	CAA	70	2018-08-22	68.48	–103.43	–23.0	7.9	36	2	0.02 ± 0.0
QMGM	CAA	112	2018-08-22	68.30	–101.74	–23.2	7.0	32	1	0.01
101	NOW	373	2018-08-28	76.38	–77.41	–22.8	5.6	0	2	0.16 ± 0.1
108	NOW	447	2019-07-22	76.26	–74.60	–22.3	5.9	1	10	0.48 ± 0.3
115	NOW	663	2019-07-20	76.31	–71.24	–22.3	5.5	0	3	0.19 ± 0.1
d5	BB	1838	2019-08-26	69.00	–61.41	–21.0	8.6	0	3	0.01 ± 0.0
d4	BB	1809	2019-08-25	68.62	–62.01	–21.0	7.8	1	4	0.02 ± 0.0
d3	BB	1570	2019-08-25	68.24	–62.59	–21.5	7.9	1	3	0.02 ± 0.0
d2	BB	266	2019-08-25	67.86	–63.15	–22.8	6.0	3	3	0.06 ± 0.0

[a] Regions of sampling collection: Canadian Arctic Archipelago (CAA), North Water polynya (NOW), and Baffin Bay (BB),

[b] Sampling date (year/month/day).

[c] Carbon isotope values of sediment (n=1).

[d] Nitrogen isotope values of sediment (n=1).

[e] Sea-ice concentration.

[f] Number of total samples per station used for Chlorophyll *a* analysis.

[g] Mean values ± standard deviation of Chlorophyll *a* (Chl *a*) in surface sediments.

3.5.2 Trophic position and isotopic composition of brittle stars

Trophic positions of brittle stars ranged between the second and the fifth trophic level. *O. bidentata* had the highest modal TP (mean TP = 4.33), while *O. sericeum* showed the lowest modal TP (mean TP = 2.63) in the CAA region (Figure 3.2). The greatest modal TP of *O. sericeum* (mean TP = 3.99) was evidenced mainly in the NOW region where all brittle stars predominantly occupied high trophic positions compared to BB region. Whereas, the greatest modal TP of *O. borealis* (mean TP = 4.05) was found in the CAA region. The greatest ranges of trophic positions were observed for all three species of brittle stars in the BB region (Figure 3.2).

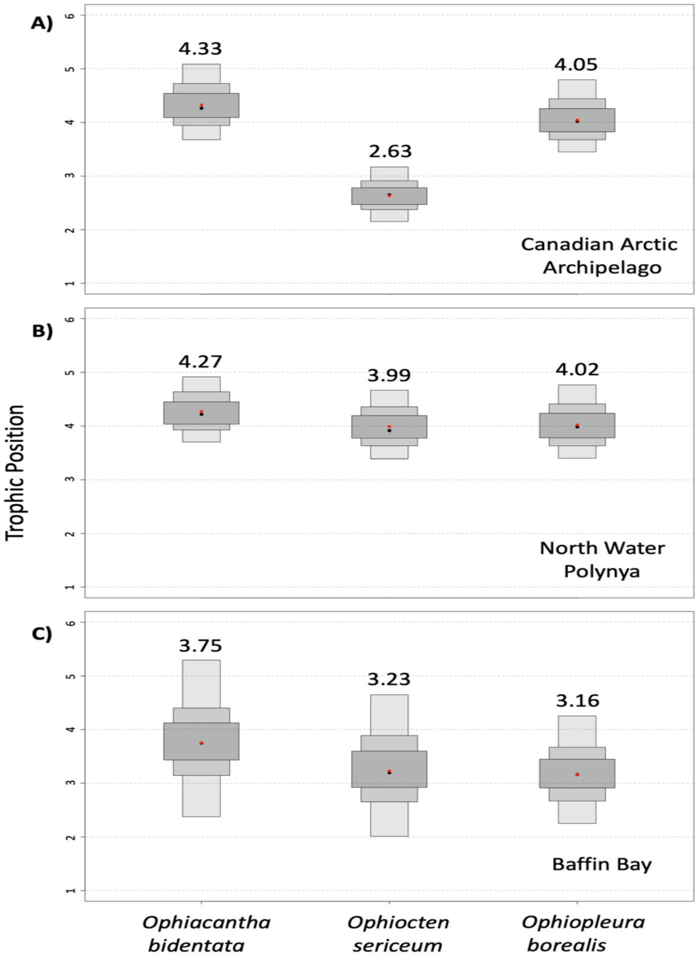

Figure 3.2. Density plots of the estimated trophic position of brittle stars. Density box plots represent the modal Trophic Position (TP) occupied by different brittle star species (mean TP values given above; black numbers). Shaded boxes represent, from light to dark grey, 50, 75, and 95% Bayesian credibility intervals. Estimates were made using the tRophicPosition model across the Arctic regions: **(A)** Canadian Arctic Archipelago, (**B)** North Water Polynya, and **(C)** Baffin Bay.

Brittle stars displayed a wide range of isotopic compositions among stations and regions (Table 3.2, Figure 3.3). Linear models revealed a significant effect of SIC and depth on δ^{13}C values of brittle stars species among regions (p-value < 0.001; Table S3.2) and also an interactive effect of SIC and depth on δ^{13}C values of ophiuroids (p-value = 0.03; Table S3.2). In addition, linear models showed an interactive effect of SIC and Chl *a* concentration on δ^{13}C values of ophiuroids (p-value < 0.001). However, Chl *a* content alone was not shown to be an environmental variable that significantly affected the δ^{13}C values of ophiuroids (p-value = 0.33). Significant differences in δ^{13}C values across species (Kruskal-Wallis, Chi square = 41.94, df = 2, p-value < 0.001) and regions (Kruskal-Wallis, Chi square = 21.36, df = 2, p-value < 0.001) were found in this study. Among species, the most ^{13}C-enriched value (δ^{13}C = –18.2 ‰) was found in *O. bidentata* in the NOW region, while the most ^{13}C-depleted value (δ^{13}C = –24.9 ‰) corresponded to the species *O. sericeum* in the CAA region (Table S3.1). Average δ^{13}C values ranged from –24.5 ‰ ± 0.2 (*O. sericeum*) to –19.0 ‰ ± 0.4 (*O. bidentata*) in the CAA region, from –20.2 ‰ ± 0.4 (*O. sericeum*) to –19.1 ‰ ± 1.5 (*O. bidentata*) in the NOW, and from –20.5 ‰ ± 0.5 (*O. sericeum*) to –19.3 ‰ ± 0.4 (*O. bidentata*) in the BB (Table 3.2).

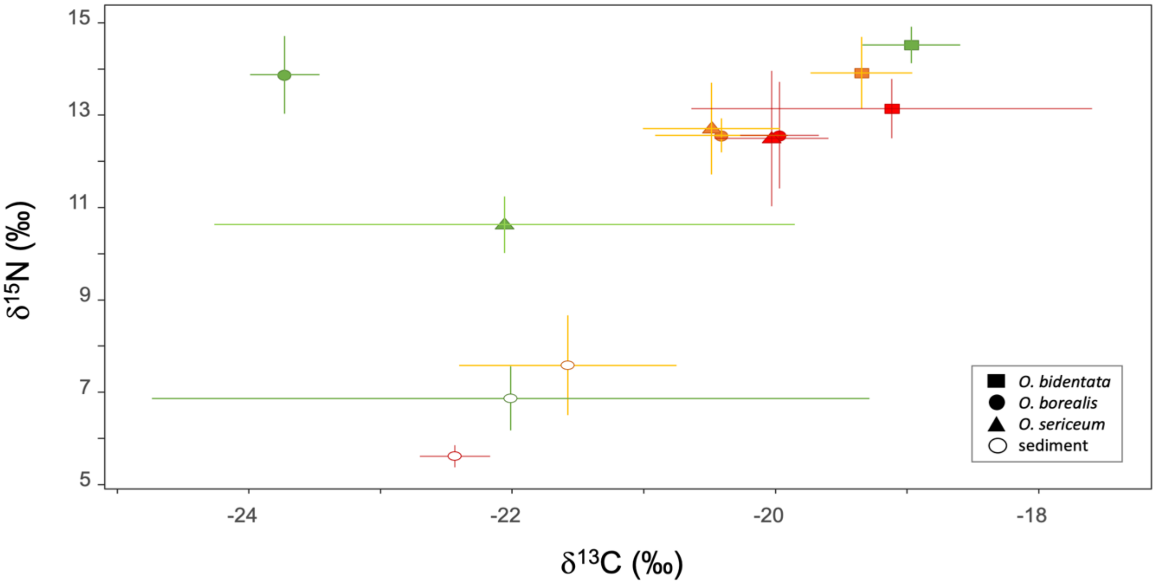

Figure 3.3. Carbon and nitrogen isotopic composition of sediment and ophiuroids. Stable isotope bi-plots illustrating the isotopic composition of the brittle stars species *Ophiacantha bidentata (square)*, *Ophiocten sericeum (triangle)*, and *Ophiopleura borealis (circle)* across the Arctic Ocean regions: the Canadian Arctic Archipelago (green), the North Water Polynya (red), and the Baffin Bay (yellow) regions. The isotopic composition of sediments is represented by a full symbol (line). Ophiuroid data points are group means with error bars representing ± SE. Sample sizes are presented in Tables 3.1 and 3.2.

Linear models revealed an effect of depth on δ^{15}N values of brittle stars species among regions (p-value < 0.01) and an interaction effect of SIC and depth on δ^{15}N values of ophiuroids (< 0.001; Table S3.3). Likewise, significant differences in δ^{15}N values among stations were found (Chi square = 24.15, df = 8, p-value = 0.002). However, δ^{15}N values showed no significant differences across regions (Chi square = 0.32, df = 2, p-value = 0.85). δ^{15}N varied across species (Chi square = 26.41, df = 2, p-value < 0.001). The most ^{15}N-depleted values were found in *O. sericeum* (10.1 ‰) in the CAA, and the most ^{15}N-enriched value in *O. bidentata* (15.2 ‰) in the BB region (Table S3.1). Average δ^{15}N values ranged from 10.2 ‰ ± 0.1 (*O. sericeum*) to 14.5 ‰ ± 0.4 (*O. bidentata*) in the CAA, from 11.6 ‰ ± 0.8 to 13.8 ‰ ± 1.3 (*O. sericeum*) in the NOW, and from 12.6 ‰ ± 0.4 (*O. borealis*) to 13.9 ‰ ± 0.8 4 (*O. bidentata*) in the BB (Table 3.2).

Table 3.2. Sampling details and isotopic compositions in brittle stars.

Species	**Station**	**Region**[a]	**Depth (m)**	**Sampling**[b] **date**	**Latitude (N)**	**Longitude (W)**	**n**[e]	δ^{13}**C**[c] **(‰)**	δ^{15}**N**[d] **(‰)**	**SIC**[e] **(‰)**
Ophiacantha bidentata	312	CAA	67	2018-08-19	69.17	–100.70	6	–19.0 ± 0.4	14.5 ± 0.4	45
	115	NOW	663	2018-08-29	76.33	–71.18	10	–19.1 ± 1.5	13.1 ± 0.6	0
	177	BB	694	2018-09-01	67.48	–63.68	6	–19.3 ± 0.4	13.9 ± 0.8	3
Ophiocten sericeum	312	CAA	67	2018-08-19	69.17	–100.70	5	–20.0 ± 0.3	11.4 ± 0.2	45
	QMG1	CAA	39	2018-08-21	68.49	–99.89	3	–20.6 ± 0.3	10.2 ± 0.1	34
	QMG4	CAA	70	2018-08-22	68.48	–103.43	6	–24.5 ± 0.2	10.2 ± 0.1	36
	101	NOW	373	2018-08-28	76.38	–77.41	10	–20.2 ± 0.4	11.6 ± 0.8	0
	115	NOW	662	2018-08-29	76.33	–71.18	7	–19.8 ± 0.4	13.8 ± 1.3	0
	177	BB	694	2018-09-01	67.48	–63.68	6	–20.5 ± 0.5	12.7 ± 1.0	3
Ophiopleura borealis	QMGM	CAA	112	2018-08-22	68.30	–101.74	8	–23.8 ± 0.2	13.8 ± 1.0	32
	QMG4	CAA	70	2018-08-22	68.48	–103.43	6	–23.6 ± 0.3	14.0 ± 0.6	36
	108	NOW	447	2019-07-22	76.26	–74.60	3	–20.0 ± 0.3	13.5 ± 0.5	1
	115	NOW	662	2018-08-29	76.33	–71.18	6	–20.0 ± 0.3	12.1 ± 1.1	0
	E1	BB	447	2019-08-23	68.28	–65.14	10	–20.4 ± 0.5	12.6 ± 0.4	3

[a] Regions of sampling collection: Canadian Arctic Archipelago (CAA), North Water polynya (NOW), and Baffin Bay (BB),

[b] Sampling date (year/month/day).

[b] Number of total individuals per station used for stable isotope analyses.

[c] Mean values ± standard deviation of δ^{15}N (‰).

[d] Mean values ± standard deviation of δ^{13}C (‰).

[e] Sea-ice concentration.

3.1. Isotopic niche widths and niche overlap of brittle star species

The isotopic niche width of brittle stars species, measured as the standard ellipse area (SEAc), differed by regions (Figure 3.4 and 3.5). SEAc ranged from 0.54 to 3.45 for *O. bidentata*, from 1.22 to 3.31 for *O. sericeum*, and from 0.52 to 1.21 for *O. borealis* (Figure 3.4). Based on SEAc values, the largest isotopic niche width was found for *O. bidentata* in the NOW region (SEAc = 3.45) and *O. sericeum* in the CAA region (SEAc = 3.31). In contrast, the smallest niche width was found for *O. borealis* in the CAA region (SEAc = 0.52). The isotopic niche area of the species *O. sericeum* in the CAA region pointed to two different sub-groups, one with ^{13}C-depleted values to the west (station QMG4; Table S3.1) another with more ^{13}C-enriched values to the east. Based on posterior Bayesian estimates, the probability of an increase in the amplitude of the SEAc varied within species and among regions. In the CAA region, *O. sericeum* showed the highest probability (100 %) of having a greater isotopic niche width than *O. bidentata* and *O. borealis*. However, in the NOW region, *O. bidentata* showed the highest probability (99 %) of having a wider isotopic niche width than the other two species of ophiuroids. Finally, in the BB region, *O. sericeum* had the highest probability of having a broader isotopic niche width than *O. borealis* (96 %) and *O. bidentata* (81 %).

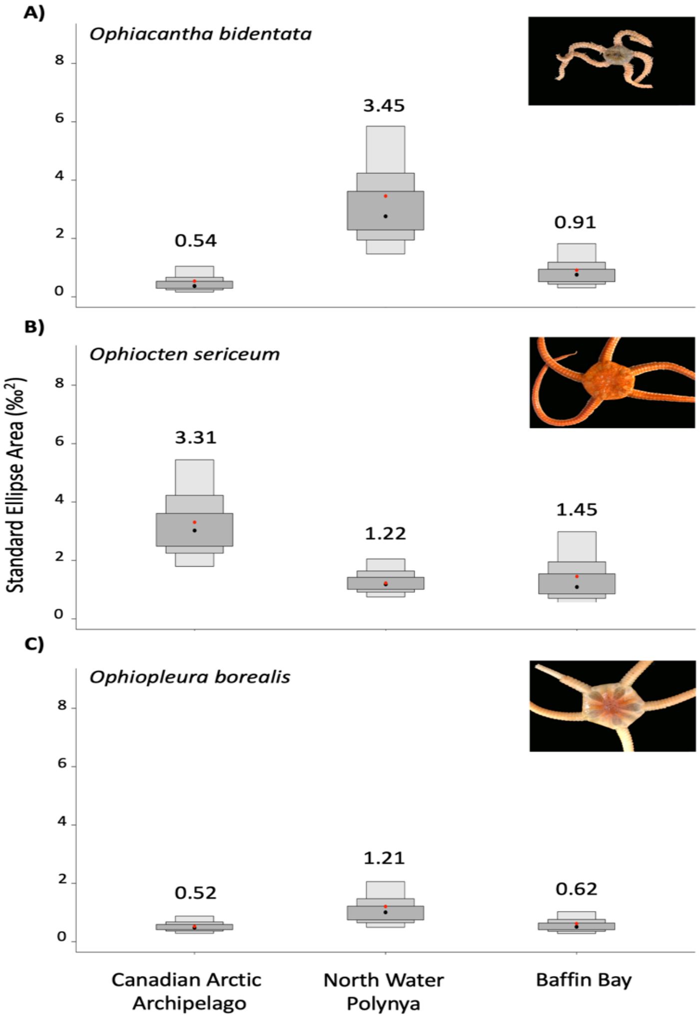

Figure 3.4. Density plots of the variation in standard ellipse areas (SEAc) for each brittle stars species using SIBER. Box plots represent the 50, 75 and 95% credible intervals from light to dark grey with the mode indicated by the black dots. The sample size-corrected standard ellipse area (SEAc, red dots; numerical value given above) of the three brittle stars: **(A)** *Ophiacantha bidentata*, **(B)** *Ophiocten sericeum*, and **(C)** *Ophiopleura borealis* for three Canadian Arctic Ocean regions.

Among regions, the isotopic niches ($\delta^{13}C$ vs. $\delta^{15}N$ biplots) revealed differences in overlap of consumers (Figure 3.5). Niche analysis showed that NOW was the only region where the three brittle star species shared the isotopic niche space. However, in other regions, our results showed marked differences in the isotopic composition and brittle stars did not share niche space (i.e., CAA) or niche overlap only occurred between two species (i.e., BB; Figure 3.5). The area of overlap comprised between 13 % and 54 % of the total isotopic niche area among all regions.

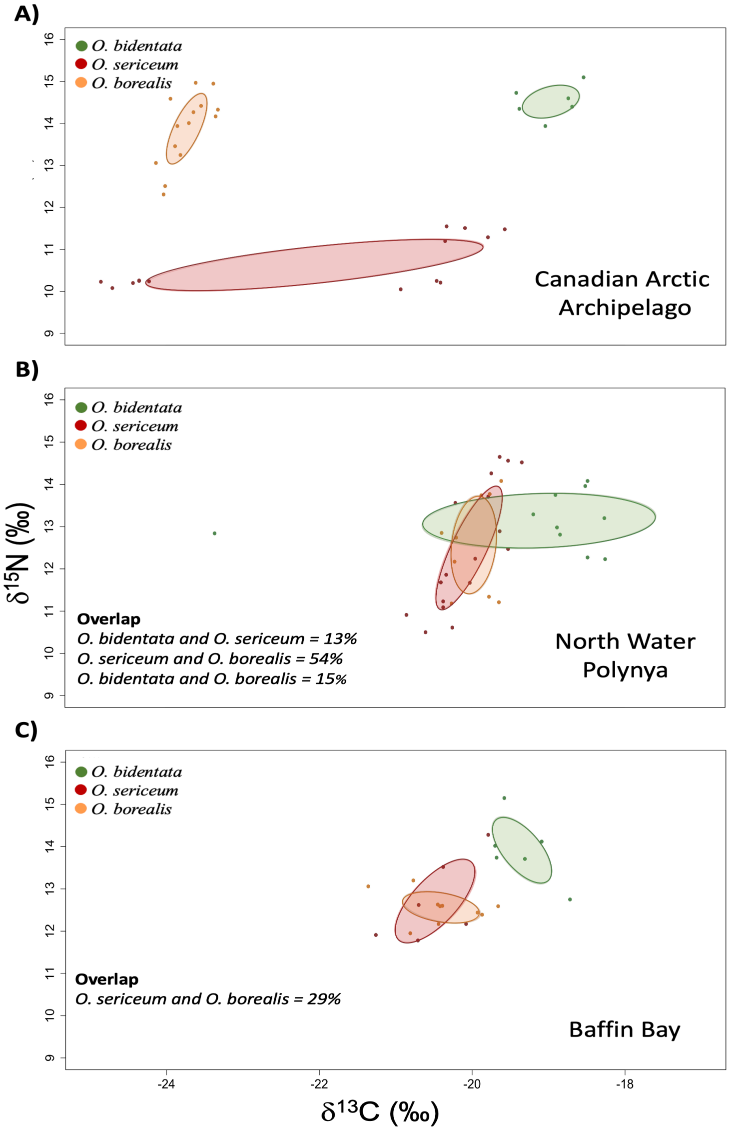

Figure 3.5. Stable isotope bi-plots for each region, illustrating the isotopic niche and overlap of the three Ophiuroidea species. Standard ellipses (solid lines) enclose the core isotopic niches of the brittle stars: *Ophiacantha bidentata* (green), *Ophiocten sericeum* (red), and *Ophiopleura borealis* (yellow) across three Arctic regions: **(A)** the Canadian Arctic Archipelago, (**B)** the North Water Polynya, and **(C)** the Baffin Bay.

The greatest niche overlaps occurred between the species *O. sericeum* and *O. borealis*, which shared at least 54 % and 29 % of the isotopic niche area in the NOW and BB regions, respectively (Figure 3.5 B-C). Moreover, biplots showed differences in resource use among species on a local and regional scale, revealing greater variability in resource use by ophiuroids in the CAA region than in the other two regions. Finally, isotopic niche and trophic position models indicated that *O. sericeum* encompassed a greater degree of isotopic variability in its prey, feeding lower in the food chain than the other ophiuroids, whereas individuals of the species *O. bidentata* fed high in the food chain.

3.6 Discussion

3.6.1 *Isotopic composition and carbon use by consumers*

Previous studies denoted a pattern in the δ^{13}C and δ^{15}N values of benthic fauna in both Arctic and Antarctic Oceans with respect to fluctuations in local oceanographic conditions such as SIC (e.g., Michel et al., 2019; Norkko et al., 2007; Yunda-Guarin et al., 2020) and depth (Stasko et al., 2018b). Together, these studies highlighted the key indirect control of environmental conditions (e.g., SIC and depth) in the isotopic composition and availability of food resources, which ultimately induced benthic food web structure shifts. For instance, seasonal changes in oceanographic conditions (e.g., depth, SIC, water temperature) and variability in the composition of food items proved to be two important factors altering the isotopic composition of Arctic amphipods by inducing changes in N and C turnover rates (Kaufman et al., 2008). Besides, isotopic values may reflect a range of varying proportions of food items assimilated by individuals over time (Bearhop et al., 2004) or similar food items with different δ^{13}C isotopic compositions. In our study, stable isotope analysis did not provide high resolution of dietary information of brittle stars according to oceanographic conditions or food availability. However, δ^{13}C values of surface sediment organic matter in this study were a useful indicator of the relative contribution of primary organic carbon sources to ophiuroids. Considering that δ^{13}C values in surface sediments in the Arctic Ocean typically range between −22 ‰ and −30 ‰ (average −26.8 ‰) for terrestrial sources and between −17 ‰ and −22 ‰ for marine sources (average −20.6 ‰) (Koziorowska et al., 2016; Kumar et al., 2016; Włodarska-Kowalczuk et al., 2019), δ^{13}C values found in surface sediments in this study suggested a mix of carbon sources available for benthic consumption (Table 3.1). In addition, the δ^{13}C values of primary sources calculated in previous studies ranged from –13.4 ‰ to –20.7 ‰ in the BB, from –7.1 ‰ to –25.3 ‰ in the CAA, and from –8.9 ‰ to –14.1 ‰ in the NOW for sympagic algae, and from –20.1 ‰ to –26.3 ‰ in the BB, from

–23.2 ‰ to –27.4 ‰ in the CAA and from –22.1 ‰ to –27.6 ‰ in the NOW for suspension particular organic matter (SPOM) (Roy 2014, Friscourt 2016, Yunda-Guarin et al. 2020, Gosselin, unpublished data). Hence, δ^{13}C values of surface sediments found in this study implied that ophiuroids' diet was influenced by carbon items from different origins. On the one hand, depleted δ^{13}C values in ophiuroids (< –23 ‰) suggested that brittle stars could use a mix of mostly marine-derived carbon sources from benthic or pelagic origin such as SPOM. On the other hand, in the NOW, the BB regions, and the east part of the CAA, δ^{13}C values suggested that brittle stars could rely on at least two food sources: marine-derived carbon and detritus enriched by microbial activity.

3.6.2 *Niche structure under local oceanographic conditions and food supply*

Bayesian estimation of the standard ellipse area (SEAc) showed differences in the isotopic niche width of brittle stars across species and regions. In this study, linear models revealed a significant effect of SIC on δ^{13}C values of ophiuroids among regions suggesting that feeding habits may differ according to changes in environmental conditions. However, a clear pattern of the influence of sea-ice condition on niche dynamics and structure could not be established, in part due to a great inter- and intraspecific variability in patterns of resource use by consumers. For example, results showed that the isotopic niche area of *O. sericeum* within the CAA region was made up of two different sub-groups of individuals, in which individuals had marked differences in δ^{13}C values between western and eastern stations. In addition, our results highlighted differences in patterns of overlap and segregation of niches according to SIC, but contrary to what we expected, an increase in the segregation of the niches was linked to regions with more SIC. In contrast, a higher overlap of niches was associated with open water regions. In other words, niches were less similar when the sea-ice concentration was greater.

Lesser et al. (2020) examined the connection between niche size and ecosystem productivity outside of the environmental influence in niche structure and found a correlation between increases in primary productivity and reductions in trophic niche size. Here, it was not possible to distinguish a clear trend of niche size reduction of brittle star species according to sediment Chl *a* concentration, a proxy of the amount of local primary production (Table 3.1) suggesting that production intensity alone is not the principal driver of isotopic variability in organisms and therefore niche characteristics. For example, our findings highlighted a greater isotopic niche width for *O. sericeum* and *O. bidentata* associated with the CAA and NOW regions where the highest concentrations of Chl *a* were recorded (Table 3.1). Meanwhile, *O. borealis* displayed the narrowest niche width in the CAA region, suggesting reliance upon a narrower range of food items or changes in dietary preferences over time (Bearhop et al., 2004). However, since sediment pigments are often considered an extremely short-term proxy of productivity due to rapid degradation processes, they are less appropriate descriptors for long-term benthic responses (Ming-Yi et al. 1993). In contrast, isotope values integrate a measure of carbon and nitrogen over longer temporal scales (Bearhop et al., 2004). Based on $\delta^{13}C$ values of individuals, the niche width of brittle stars could be influenced by differences in individual-spatial patterns of food selectivity driven by local variation in carbon items and ecological interactions (Bolnick et al., 2010). In this sense, trends towards broader niches suggest that regions with more heterogeneity of resources could support more dietary variation among consumers allowing the exploitation of preferred or more nutritive food items (Costa-Pereira et al., 2017). In contrast, a reduction of the niche size among ophiuroids could be associated with regions with more homogeneous resources due to a reduction in the number of specialist individuals. Taken together, these results suggest that the spatial variability in niche structures (niche breadth) could reflect the degrees of exposure of consumers to multiple resource pools over time and individual spatial patterns of dietary selectivity (see next section). However, given that our results correspond to a seasonal timeframe (summer), it is difficult to infer trends in niche dynamics across all seasons accurately. Therefore, further studies that monitor benthic niche dynamics in relation to environmental changes, including global warming, over a long timescale (multiyear) are necessary to more accurately predict food webs variations in areas exposed to rapid environmental changes.

3.6.3 *Species-specific dietary selectivity and population niche dynamics*

In general, brittle stars are considered generalist species and employ a large variety of foraging behaviors to access a wide diversity of resources (Pearson and Gage, 1984). These feeding attributes have led different ophiuroid species to be recognized as ecologically equivalent species that share habitat and food sources (Pearson and Gage, 1984). Nevertheless, foraging behaviors in consumers are dynamic and tend to vary over time as a response to multiple variables including prey availability, seasonality, competition, and even the consumer's physiological state (Yeakel et al., 2016). Since tendencies in generalist species towards a particular diet only exist on a short time scale, it is difficult to establish with precision the fluctuations in the isotopic composition of these individuals, especially when the isotopic composition of them probably reflects an average of different food items ingested over time (Bearhop et al., 2004). As expected, our results showed high variability in resource-use patterns (i.e., changes in the dietary niche width) among brittle star species and differences in species-specific feeding selectivity, which ultimately led to significant changes in niche width of ophiuroids.

Based on the isotopic composition of brittle stars, changes in the relative contribution of primary sources seem to have affected the interspecific characteristics of the feeding mode of ophiuroids. Interestingly and contrary to what is specified in most of the literature (see the introduction section), brittle stars showed high inter-individual variability in feeding behavior across stations in which each individual showed its own pattern of feeding. Accordingly, the species niche width varied significantly due to intraspecific variability in foraging behaviors and individual species trends in dietary selectivity linked to ecological processes such as productivity (Araújo et al., 2011; Semmens et al., 2009). For instance, consumers exhibited greater differences in resource use in the less productive regions of CAA and BB, increasing the segregation of the niches (Robinson and Strauss, 2020). Notably, in the CAA region, a broad isotopic niche (SEAc) occurred in the species *O. sericeum*, which suggested variation in its feeding selectivity at the individual level across stations, leading to an expansion of this species' trophic diversity. In contrast, in the same region, a reduction of the isotopic niche width (i.e., low trophic diversity) in the species *O. bidentata* and *O. borealis* suggested high feeding selectivity or low dietary evenness over time (Bearhop et al., 2004). This is also supported by the field experiment conducted by Mäkelä et al. (2017a) with benthic macrofauna showing differences in food utilization by polychaetes, bivalves and crustaceans were site-specific, with no taxa exclusively exhibiting higher rates of ice algal uptake, suggesting high feeding plasticity.

Variations in niche width could also be largely driven by the range of trophic levels at which individuals obtained their prey item (Bearhop et al., 2004). In connection with this assumption, an increase in brittle stars isotopic niche could also be associated with the use of a greater spectrum of trophic levels at which individuals obtained their preys. On this basis, the wide difference in $\delta^{15}N$ values among ophiuroids was interpreted as a reflection of the considerable feeding flexibility of these invertebrates. Among these, *O. sericeum* was the brittle star species that seemed to consume the widest spectrum of prey items, as shown by the important variability in both isotopic dimensions.

Trophic position estimates showed that brittle stars fed at various trophic levels. In most regions, ophiuroids occupied intermediate to high trophic levels, suggesting that ophiuroids were predominantly mobile deposit feeders and omnivorous (including carnivores/scavengers). However, brittle stars did not always show a similar range on trophic positions within the same region. For example, in the CAA region, *O. sericeum* had the most ^{15}N-depleted values of all three species, which suggested that individuals predominantly fed on lower trophic levels than the other species. In contrast, in other regions, such as the NOW, ophiuroids shared higher mean trophic levels, implying that consumers relied primarily on heterotrophic prey or reworked organic matter typically ^{15}N-enriched by microbial activity (Mäkelä et al., 2017a). Finally, brittle stars in the BB region showed the broadest range in trophic positions, indicating that individuals adopted a predominantly omnivorous behavior to exploit a broad spectrum of trophic resources (i.e., trophic generalists or intermediate feeding specialists). Based on our results, it seems likely that individuals within each species do not always share similar diets and have varied preferences towards different food items. The inter-individual dietary flexibility observed in brittle stars would suggest that ophiuroids play an important role in benthic food webs from the point of view of increasing the number of trophic links and energy flow pathways from one trophic level to the next. Considering the high densities that ophiuroids represent in benthic ecosystems of the Arctic, for example >400 ind. m^{-2} in Young Sound, Greenland and the Barents Sea (Blicher and Sejr, 2011; Piepenburg and Schmid, 1996), brittle stars could be critical ecological species driving dynamics, functioning and stability of benthic food webs.

3.6.4 *Niche overlap and brittle stars co-occurrence*

The co-occurrence of ecologically similar species is founded on the partitioning of their ecological niches or in exploiting different niches driven in some part by diet shifts (English et al., 2020; Lush et al., 2017). Some studies have been conducted in the Arctic Ocean based on approaches using multiple biomarkers to assess how benthic species co-occur using common resources (Stasko et al., 2018a; Yunda-Guarin et al., 2020). However, only a few studies have been carried out to study ecological interactions of ecologically similar species, including trophic relationships and niche partitioning using the isotopic niche concept. In resource-limited environments, competition for food sources among sympatric species is likely to increase during periods of low primary production (Chase and Leibold, 2003). Therefore, seasonality and availability of resources may be the main variables driving competition and restricting species co-occurrence in space and time (MacArthur, 1969). Furthermore, species co-occurrence may also depend on changes in the diversity of the resources (Costa-Pereira et al., 2019). According to our analysis, fluctuations in spatial patterns of sediment organic matter composition and variations in species-specific food selectivity in response to prey availability and/or competition could have influenced niche partitioning. In this instance, a greater resource heterogeneity, including the availability of a high range of sources, for example in the CAA (Figure 3.3), could induce a high degree of inter-individual dietary variation among individuals avoiding isotopic niche overlap between species in our study. Whereas, it was pointed out that an increase in niche overlaps may suggest a low degree of inter-individual diet variation promoted by resource homogeneity and omnivorous feeding behaviors (Costa-Pereira et al., 2019). Therefore, without considering possible competition with other species, our results suggested that reductions in niche overlap between the three species studied were more closely related to inter-individual dietary flexibility to exploit different resources.

The greatest niche overlap among brittle stars occurred between *O. sericeum* and *O. borealis* in the NOW region, highlighting moderate levels of resource partitioning between both species. However, given that the isotopic niche overlap between these species was moderate (54 %), their co-occurrence could be viable in natural conditions when species delimited their foraging niche using flexible feeding strategies. Conversely, *O. bidentata* exhibited little niche overlap with the other two species in the NOW and complete segregation of their niches in the CAA and BB regions, suggesting limited potential competition with co-occurring species. In this case, some individuals of *O. bidentata* showed food preferences for a ^{13}C-enriched food source, increasing plasticity at the species level in foraging behavior. Our results may suggest that isotopic niche aspects might result from past competition, environmental conditions, or changes in organic carbon composition that shape individual into adopting a specific feeding strategy to satisfy its energy requirements. Finally, based on Tinker et al. (2008) and our results, food limitation could lead to behavioral diversification and dietary specialization of benthic species, including ophiuroids. Therefore, an increase in the individual level of diet specialization could be a factor driving the structure and dynamics of benthic food webs.

3.7 Conclusion

Climate change is expected to lead to shifts in the availability and abundance of food sources for benthic consumption in the future Arctic Ocean that are not yet identified and may affect the dynamics and stability of food webs (Kędra et al., 2015). Despite the ecological importance of ophiuroids as key species in benthic assemblages and trophic cascades in the Arctic Ocean (Pearson and Gage, 1984), only a few studies have been carried out to date to understand better the mechanisms that drive feeding ecology and trophic niches of Arctic brittle star species. Here, ecological niche analyses of three syntopic brittle star species using the isotopic niche approach provided insight into the mechanisms driving niche dynamics, feeding behavior, and ophiuroids co-occurrence. We found some evidence that SIC is an important driver of niche structure in ophiuroids. Greater interspecific niche segregation was indeed associated with regions with greater SIC. Additionally, changes in organic carbon composition highlighted a strong influence of species-specific degrees of dietary selectivity shaping niche structure and overlap. Since the Arctic Ocean ecosystem is experiencing strong changes in abiotic conditions due to climate change that could affect ecosystem functioning, more studies of this type are needed to understand better the role of individual species in the functioning and stability of benthic food webs. Finally, our results revealed the great ability of some individuals to adjust their dietary behaviors according to fluctuations in resources composition, highlighting the difficulty of generalizing feeding modes of benthic consumers and the lack of information about trophic interactions, diets, and habitat use by benthic species.

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General conclusion

The ultimate purposes of this thesis were to: i) determine the influence of sea-ice concentration (SIC) on trophic ecology and food web structure of the benthic community; (ii) quantify the relative contribution of sympagic carbon in benthic consumers diets and establish the role of sea-ice concentration in benthic fauna diets and food web structure; and (iii) quantify changes in isotopic niche structure of ophiuroids in response to variation in SIC, local productivity and individual feeding behaviors. These three main objectives have been successfully achieved in the present thesis. A summary of the main results obtained during this thesis is shown below in a general conceptual model (Figure 9), which was based on the key research question on how the benthic food web and organisms respond to changes in sea-ice concentration and organic carbon contribution.

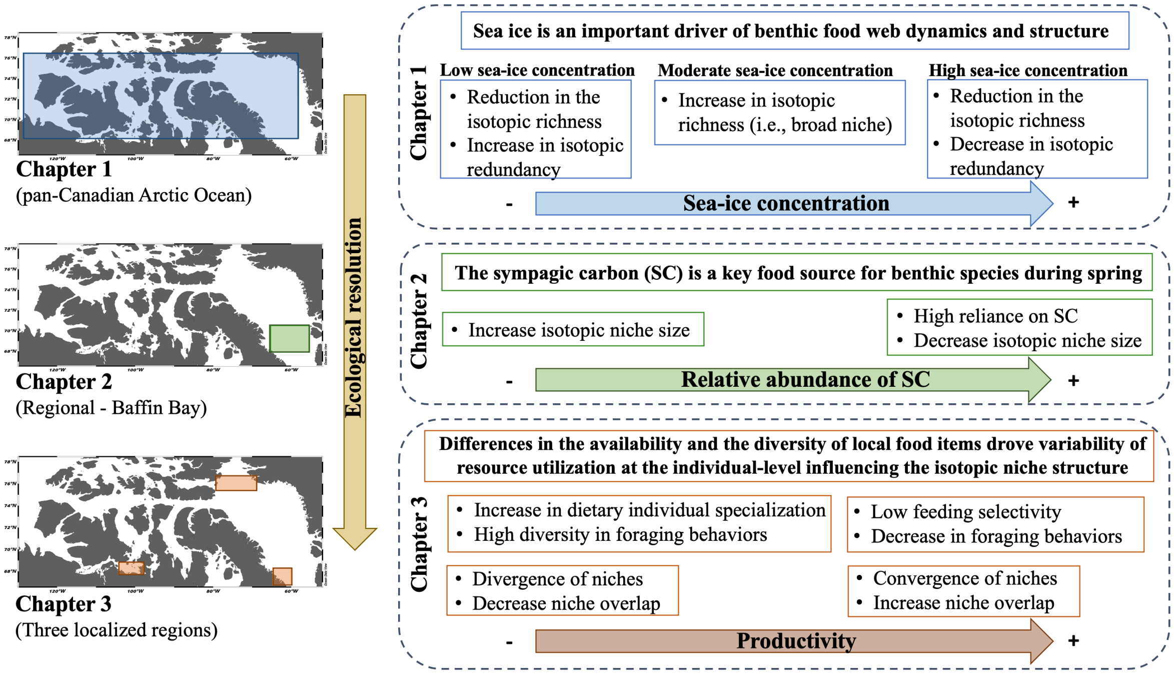

Figure 9. Conceptual model of the summary of the main results obtained from the three research chapters. The characteristics of the ecological niche at different ecological resolutions (i.e., individual, population, community) varied according to a set of extrinsic (e.g., sea-ice concentration, productivity) and intrinsic factors (e.g., individual foraging behaviors).

Study contribution

This thesis provided valuable data on the taxonomic composition of benthic communities at different depths, and provided additional data on the carbon and nitrogen isotopic composition of benthic fauna at different spatial scales in the Canadian Arctic Ocean. The results presented are based on the analysis of the isotopic composition of 1404 epibenthic individuals, among which a total of 648 individuals were processed for the extraction and quantification of HBI lipid biomarkers. Thereby, the present study is one of the most extensive research works made to date to extract and quantify lipid biomarkers and analyze the isotopic composition of the benthic fauna across the Canadian Arctic Ocean.

In Chapter 1, stable isotope analyses were used to study the biological and environmental drivers of trophic ecology of benthic communities across different regions of the Canadian Arctic Ocean. To our knowledge, the study presented in Chapter 1, was the first to use a combination of traditional community-wide metrics (i.e., convex hulls and ellipses) and recent metrics for stable isotope ecology (i.e., isotopic diversity metrics) to quantify and describe ecological niche aspects of benthic communities exposed to variations in sea-ice conditions in the Arctic. The results obtained in this chapter highlighted the role that different drivers (i.e., sea-ice conditions, resource supply, biotic pressures) play in trophic dynamics and benthic community niche structure. Moreover, our results indicated the importance of sea ice as an environmental component shaping benthic food web dynamics, reinforcing the need for further investigations of the effects of declining sea-ice cover on Arctic food web functioning.

The results obtained in Chapter 2 brought forward valuable information that elucidated the relative contribution of different HBI lipids in the diets of deep benthic consumers in the Baffin Bay in spring. Until now, HBI lipids were known to transfer through different trophic levels in the Arctic Ocean, however, only a few studies have shown the presence of these lipids in the benthic fauna. The research conducted in Chapter 2 was also the first to use a combination of lipid biomarkers (HBIs) and stable isotopes ($\delta^{13}C$, $\delta^{15}N$) to study the ecological niche structure of deep benthic communities. This novel approach increased our understanding of the relationship between the availability of carbon sources in the seafloor, and their assimilation and transfer within the benthic food web. The results obtained highlighted the importance of ice-derived algae as an important food source for deep-sea benthic fauna. Indeed, based on lipid biomarkers, most of the benthic fauna based their diet mainly on sympagic carbon during the spring.

In Chapter 3, the dietary niche width and trophic position of three coexisting species of brittle stars were studied using the Bayesian ellipses approach. This study was the first to identify and quantify trophic interactions between ophiuroid species in the Canadian Arctic Ocean. Results obtained increased our understanding on trophic interactions and individual trophic roles of coexisting brittle star species. In addition, our data analysis suggested that changes in the ecological niche structure of brittle star populations could be highly influenced by individual feeding behavior, which in turn pointed out the key role that some species play in trophic dynamics and food web structure.

In conclusion, the three chapters considered together provided additional data of the trophic ecology of benthic communities at several levels of ecological resolution and regional scale, and new data of the biological and environmental drivers influencing the trophic ecology of benthic communities. The present thesis also provided a new approach to study and quantify changes in the benthic food web structure, new records of the transfer of HBI lipids through benthic fauna, and finally, additional data of benthic trophic interactions and the role that individuals and sea ice play in benthic food web structure. In the current context of climate change, the findings of this thesis provided evidence that alterations in both sea-ice concentration and phenology of carbon supply to benthic communities could affect benthic consumers' diets, trophic interactions, feeding behaviors, and benthic food web structure and functioning.

Sea ice-derived organic carbon: a key food source for benthic consumers' diets

Sea ice-associated primary production is considered to be an important high-quality food source for a high range of wildlife from the Arctic Ocean (Brown et al., 2018; Cusset et al., 2019; Koch et al., 2020a). However, there are still very few studies that have investigated the importance of this carbon source in the diets of benthic consumers and food web dynamics, and more importantly, how sea-ice depletion could affect the quantity and quality of this resource for benthic communities. Regardless of the method used to analyze carbon assimilation and transfer through benthic consumers (i.e., HBIs and/or stable isotope analyses), our results demonstrated that ice-derived algae represented one of the most important carbon items sustaining benthic assemblages, even at deep-water depths, during the first period of the spring (Chapter 2). Indeed, the importance of this source increased in areas with a higher concentration of sea ice where benthic consumers of different taxa based their diet almost exclusively on sympagic carbon as their main source of energy. These results were consistent with recent studies that highlighted the importance of sympagic carbon in benthic consumer diets in both the Arctic (e.g., Kohlbach et al., 2019) and Antarctic Oceans (e.g., Michel et al., 2019).

Furthermore, the analysis of the isotopic composition of benthic invertebrates indicated that benthic consumers probably depended on multiple baseline items, among which ice-derived algae was an important carbon source supporting benthic food webs at different water depths. Additionally, other resources such as macroalgal detritus appeared to influence the diet of benthic consumers at different depths (Chapter 2). In Chapter 1, the ^{13}C-depleted isotopic values indicated that terrestrial organic matter was an important food source for benthic food webs in areas of Beaufort Sea. In addition, the ^{13}C-enriched values found in invertebrate tissue, commonly associated with the consumption of fresh ice algae material, would also highlight the importance of other carbon sources such as organic material originating from the microbial community (North et al., 2014).

Drivers of benthic food web structure and isotopic niche dynamics

Based on our data, benthic food web structure varied on a geographic and temporal scale due to a combination of intrinsic (e.g., interspecific feeding behavior) and extrinsic variables (e.g., sea-ice conditions, resource availability, local productivity) that influenced benthic consumers' diets, trophic dynamics and isotopic niche architecture (Costa-Pereira et al., 2017; Shipley and Matich, 2020). When the research results from this thesis are considered as a whole, several environmental and biological variables emerge as key drivers controlling the benthic food web architecture. Specifically, the present study showed that sea-ice conditions and the availability of food resources were variables that influenced changes on the ecological niche characteristics of the benthic community (i.e., isotopic niche size and overlap). Likewise, these same variables seemed to play a role in individual degrees of dietary specialization among consumers, which largely affected the structure of the ecological niche in benthic populations (see below). Interestingly, the degree of individual specialization varies widely among species according to the availability of resources (e.g., ophiuroids, Chapter 3), implying that individual specialization has potentially an important ecological role in food web dynamics.

Sea-ice conditions driving food availability and benthic food web structure

Sea ice is considered one of the most important environmental drivers influencing the Arctic Ocean primary production and the strength of the fluxes of organic particles that support benthic communities (Clark et al., 2015; Gradinger, 2009; Legendre et al., 1992; Pabi et al., 2008). In this thesis, results showed that sea ice is an important environmental variable that indirectly controls the type and availability of resources in sediments for benthic consumption at different depths. Consequently, depending on sea-ice conditions, variations in the type and quantity of the carbon sources assimilated by benthic consumers were observed, as well as changes in the ecological niche structure. Quantitative estimates of the relative proportion of sympagic carbon in both sediments and benthic fauna indicated a higher abundance of ice-derived algae associated with areas of higher sea-ice concentration. In contrast, proportions of sympagic carbon decreased in areas with less SIC (Chapter 2).

In the present thesis, changes in the ecological niche structure at the community and population scale were, in part, linked to sea-ice dynamics. For instance, a broader niche in the benthic community was associated with areas with moderate SIC, whereas a simplification of the niche structure (i.e., shorter chain length and width) was linked to areas with low and high SIC (Chapter 1; Figure 10). Indeed, a narrow niche breadth suggested homogeneity of resources, and the assimilation of analogous resources by benthic consumers, whereas a broad niche breadth suggested heterogeneity in basal food sources and/or the assimilation of sources with different isotopic compositions (Wang et al., 2020). In addition, results indicated changes in niche structure between consumers' groups. In this context, a narrow niche was associated with benthic groups that relied mostly on sympagic carbon (i.e., primary and omnivores consumers) in areas with high SIC. On the contrary, a broader niche was linked to top consumers or species with greater capacity for movement, such as fishes that relied on a wider range of resources. In addition, a longer food chain was linked to areas where consumers relied most on sympagic carbon, which suggested that the high availability of SC increased the ecological role that primary consumers play in driving a stronger transfer of this nutrient to higher trophic levels (Chapter 2). Finally, on a population scale, sea-ice conditions appeared to play an important role in patterns of convergence and divergence of the ecological niches of benthic consumers (Chapter 3). For example, results showed an increase in the divergence of the population niche associated with regions with more SIC, while a greater convergence of the niches was observed in ice-free regions.

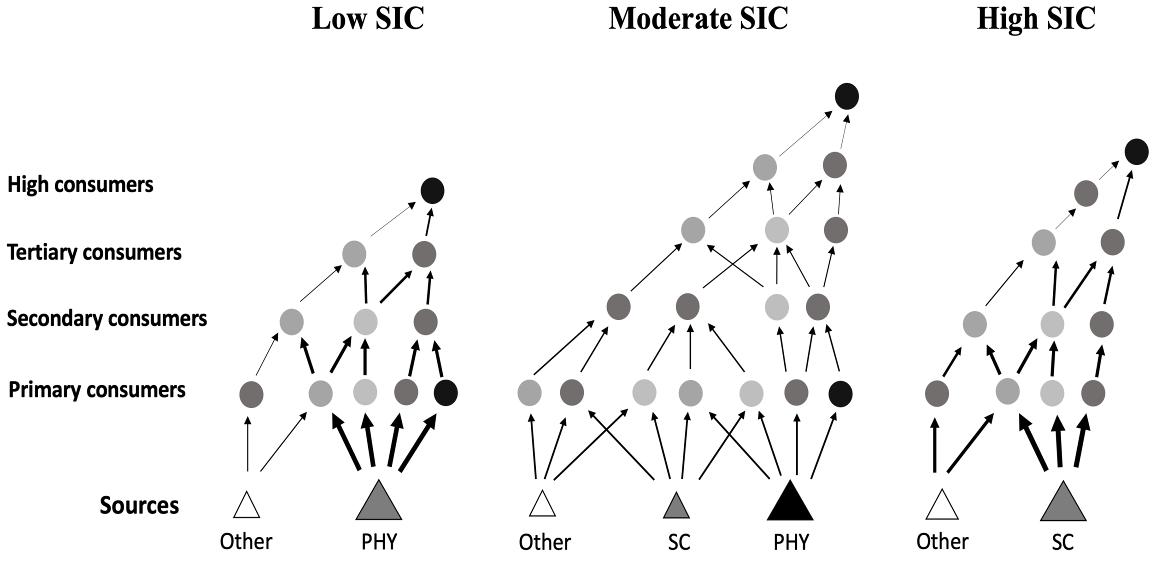

Figure 10. Illustration of the influence of sea-ice concentration on the food web structure of benthic communities. The thickness of the arrows indicates differences in the amount of contribution of each resource. The resources: ice-derived algae (sympagic carbon; SC), phytoplankton (PHY), and others are represented by triangles. The size of the triangles and their coloration represent the type and relative abundance of these resources in the sediment. Benthic consumers are represented by circles and the coloration represents different species. Depending on sea-ice concentration (SIC) the food web structure changed between ice areas. A narrow food web (i.e., shorter chain length and width) was associated with ice areas with low sea-ice concentration. A broad food web was associated to ice areas with moderate SIC.

Resource availability and ecosystem productivity shaping aspects of the trophic ecology of benthic communities

Resource availability and local primary production were important variables shaping food web structure, benthic trophic dynamics, and feeding behaviors of consumers. Specifically, we found a relationship between reductions in the ecological niche size and highly productive regions such as the North Water polynya (Chapter 1). These results were consistent with previous observations made by Lesser et al. (2020) who indicated a reduction in niche size and overlap associated with productive ecosystems. However, the findings of this thesis also denoted a reduction in niche size linked to regions with higher SIC where SC was the main carbon source for benthic consumption in spring (Chapters 1 and 2, Figure 10). On this basis, these results suggested that apart from the abundance of prey items, fluctuations in the nature and diversity of resources play an important role in the diet of consumers, interactions of species, and thus in the food web structure (Costa-Pereira et al., 2019). Accordingly, in regions with a strong input of organic carbon, the number of primary consumers (e.g., deposit feeders) would increase, while the number of omnivores (including carnivores and/or scavengers) could decrease inducing a reduction in the food chain length of the benthic community. Additionally, results highlighted that those changes in the availability of food sources could induce grades of dietary specialization of individual consumers shaping the ecological niche structure in both community and population (see next section, Chapter 3). For example, in the whole benthic community, primary and secondary consumers in systems with a high abundance of sympagic carbon sources were more selective in the consumption of this item, occupying a restricted ecological niche space and lower trophic positions in the Baffin Bay (Chapter 2). In contrast, in resource-limited environments (e.g., deep-sea environments) an increase in the ecological niche size was linked with a higher range of prey items assimilated by consumers (Figure 11).

Furthermore, we found variations in benthic food web structure associated with highly productive ecosystems (i.e., polynyas). Interestingly, results denoted niche reductions along a west-to-east gradient, exhibiting a narrow niche associated with NOW and broader niches associated with CB polynya (Chapter 1). An increase in the size of the niche in CB polynya was attributed to a significant variation in the isotopic composition of consumers in areas under the influence of terrigenous sources. These results suggested that allochthonous carbon inputs (i.e., terrestrial sources) play an important role in supporting benthic diets and food webs in the Beaufort Sea (Dunton et al., 2006; Feder et al., 2011). This result is consistent with previous studies that noticed an expansion of food web length linked to areas under the influence of terrigenous sources (e.g., Bell et al., 2016; Stasko et al., 2018a). However, the existence of such differences in niche structure may also reflect variations in seasonal productivity between the polynyas, marked by longitudinal differences in the dynamics of the ecosystems (e.g., timing of initial polynya formation and extent and persistence of open water). As a result, more studies of this type are necessary to establish more clearly how fluctuations in delivery, abundance, and nature of resources could affect the dynamics of the benthic food webs in the Arctic Ocean.

Species-specific feeding behavior shaping niche structure and niche overlap in benthic populations

In addition to environmental conditions and changes in resource availability, our results highlighted the key role that individual species play in benthic food web structure and dynamics. Based on our results, the individual feeding behavior of consumers induced by variation in abundance and nature of the resources affected trophic levels and niche structure of the benthic community (Le Bourg, 2020). These results highlighted the great adaptability of consumers to change or adapt their feeding behavior and diet, over time, in response to prey availability. For example, regardless of the identity of the benthic consumer (i.e., taxonomic group) or feeding strategy (i.e., functional group) variations in the utilization of phytoplankton or sympagic carbon sources were linked to the relative abundance of food items in the sediment in benthic communities from BB (Chapter 2, Figure 11). These results suggested that benthic communities are composed mostly of generalist species, in which foraging behaviors are dynamic and tend to vary over time in response to multiple variables including environmental conditions, prey availability, seasonality, and competition (Yeakel et al., 2016).

In the present thesis, results revealed high inter-individual variability in the feeding behavior of consumers in regions such as CAA, which suggested that within generalist populations it is also common to find specialist individuals (Araújo et al., 2011). On this note, we noticed differences in grades of dietary specialization across benthic consumers. For example, among brittle stars, the species *Ophiocten sericeum* showed greater adaptability to exploit a high range of prey items, occupying a higher number of trophic levels and positions in the $\delta^{13}C$ axe on the isotopic niche (Chapter 3). As a result of this individual level of high dietary specialization, especially in ecosystems with limited resources, a reduction or the absence of ecological niches overlap was observed between co-occurring species. These results suggested that niche size and overlap change according to individual responses of consumers to fluctuations in food availability and possibly by episodes of intra- and interspecific competition (Chapter 3). Thereby, our results highlighted the ecological importance that some species have in the transfer of energy through different trophic levels, which in turn, gave more stability to the food web and potentially reduce degrees of potential competition among species.

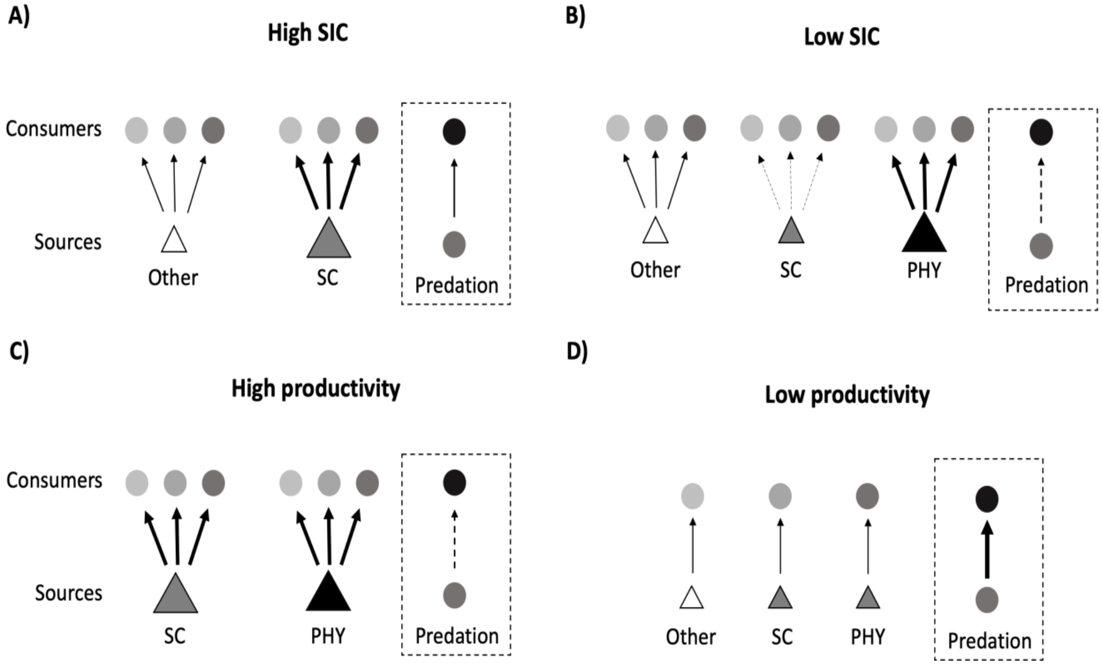

Figure 11. Illustration of the influence of sea-ice concentration and productivity on the degree of individual specialization of benthic consumers and ecological niche characteristics. The thickness of the arrows indicates differences in the amount of contribution of each resource. The resources: ice-derived algae (sympagic carbon; SC), phytoplankton (PHY), and other resources including material reworked by microbes (Other) are represented by triangles. The size of the triangles and their coloration represent the type and relative abundance of these resources in the sediment. Benthic consumers are represented by circles and the coloration represents different species. Depending on sea-ice concentrations (SIC; **A** and **B**) and availability of resources (**C** and **D**) the ecological niche size and overlap change in the benthic community. In areas with high SIC and productivity (**A** and **C**), the isotopic niche is narrow because consumers (i.e., mostly primary and secondary consumers) specialize in the consumption of the abundant food source, thus reducing dietary niches and increasing the overlap of the niches. In areas with low SIC (**B**), the ecological niche is broad because consumers used a greater diversity of food items. Finally, in low productivity areas (**D**) a narrow niche and low overlap was linked with a high inter-individual variability in the feeding behavior.

Climate change, resource availability, and benthic food web structure and stability

Decreases in sea ice due to climate warming could drive food instability in the future Arctic Ocean, affecting the transfer of matter and energy to high-level consumers including the Inuit people (Meredith et al., 2019). In addition, a mismatch in the time of formation and decay of sea ice could lead to important shifts in food supply to bottom consumers with consequences not yet totally defined on species trophic dynamics and food web functioning. For example, previous studies indicated the sensitivity of the Arctic food web and marine organisms to changes in the timing of trophic interactions due to shifts in the onset of sea-ice melt (Post, 2017). Here, results denoted a connection between sea-ice concentrations and food sources availability with changes on the degree of individual dietary specialization and ecological niche characteristics. Based on the data obtained, reductions in sea-ice cover could lead to an increase in the size of the ecological niches in benthic communities, largely driven by a higher range of trophic levels at which individuals obtained their prey items. In addition, the nature, quantity and quality of the organic sources for benthic consumption may change with a decrease in sea ice (Leu et al., 2011). In terms of food quality, ice-derived algae have a high content of essential fatty acids, which makes them of better nutritional quality than their counterpart, the phytoplankton (Søreide et al., 2010). In terms of nature and abundance, our results highlighted that ice algae constitute a crucial food source sustaining the base of the benthic food web, mostly during springtime. Consequently, results denoted a decrease in the niche size associated with areas with higher sea ice due to a major reliance of benthic consumers to sympagic primary production. Finally, results denoted changes in the feeding behavior of consumers as a result of fluctuations in the relative abundance and type of resources. Indeed, in areas with a low sea ice, an increase in the diversity of food items induced an expansion in the range of foods exploited by benthic consumers. Consequently, results highlighted increases in niche size in communities, and separation of niches in populations, which in turn, led to a decline in the redundancy of the isotopic niche in this study.

Closing perspectives

Towards a better understanding of the consequences of climate change on Arctic's communities

From region to region in the Arctic Ocean, the challenges posed by climate change will put the food security of different communities, including indigenous peoples in Canada, at risk. In the specific case of benthic communities, changes in the physicochemical drivers and in the seasonality of primary production could affect the abundance, nature and quality of the food resources on which the benthic fauna depends, affecting trophic interactions and food web complexity. Despite this, to date there are little data of the basic ecology on most Arctic benthic species to support any specific prediction of threats on food web functioning. Moreover, in the context of climate change , only a few studies have investigated the consequences of sea-ice depletion on both benthic fauna and food web dynamics in the Arctic Ocean (e.g., Kortsch et al., 2019; Pratte et al., 2019).

The present thesis provided pertinent data on the trophic ecology of a great variety of benthic species at different depths and geographic locations. However, because the results obtained here only correspond to a short window of time, results only offered a snapshot in time on consumers' diets and trophic interactions. Consequently, further long-term studies encompassing all four seasons over multiple years are necessary to establish more precisely how changes in environmental conditions may influence benthic species diets and food web functioning. In addition, in the context of the threat that climate change represents to food security, drastic mitigation measures towards the current climate emergency are urgent and must be taken collectively in a single front that brings together knowledge from both the scientific community and indigenous people in order not to pass the 1.5°C threshold in global warming in the coming decades.

Monitoring status and trends of benthic communities and food webs in a changing Arctic Ocean

Understanding the mechanisms that support trophic interactions, benthic consumers' diets, and species coexistence in regions subject to rapid environmental change is particularly important not only to predict future trends in ecosystem functioning but also to comprehend the basic ecology. Using multiple isotopic niche approaches, the three interconnected chapters of this thesis were conducted to further recognize of the responses of benthic consumers and food webs to changes in environmental and biological drivers at different ecological resolutions. Results provided new and relevant information for different benthic species of which little direct information was available on their feeding and trophic ecology. Based on the results presented in this document, it was hypothesized that changes in both sea-ice cover and phenology could affect in different ways the structure, dynamics and stability of benthic food webs. Indeed, results suggested that sea-ice dynamics was an important environmental driver shaping the timing, availability, and nature of organic carbon sources for benthic consumption, which in turn influenced trophic interactions, food web architecture, and isotopic redundancy. In addition, results highlighted that sea ice-associated carbon was a key food source in benthic consumers' diets at different water depths. Since benthic macrofauna play an essential role in key ecosystem processes in Arctic Ocean ecosystems, such as food supply and carbon cycling, further studies of the basic ecology of benthic species are essential (e.g., diets, trophic interactions) to more accurately establishing the effect of biotic and abiotic changes in the functioning of ecosystems and the services provided by benthic species. For example, such future studies could more specifically investigate changes in benthic diets throughout all four seasons with the aim of respond questions such as the relationship between environmental changes with decreases in the quality of the resources ingested by consumers. Such studies of monitoring the diet of consumers can be approached using complementary methodologies such as fatty acids (see below).

Methodological considerations and limitations

Stable isotope analyses and the lack of isotope turnover studies in benthic consumers

Stable carbon and nitrogen isotope ratio analyses are commonly used as ecological tracers in studies related to consumers' diets and trophic ecology of organisms. However, a very low number of estimates of the isotopic turnover rate in benthic consumers' tissues have been published to date. Knowledge of the turnover time of isotope incorporation in invertebrate tissues is important at the moment of interpreting $\delta^{13}C$ values because (i) these estimates could increase the insights into the relative contributions of isotopically distinct dietary components in consumers' diets (Tieszen et al., 1983), and (ii) since the Arctic Ocean has a strong seasonality in food availability and environmental conditions that may influence dynamics in biochemical turnover rates, individual turnover estimates could help better interpreting $\delta^{13}C$ values in species. In addition, the turnover time is likely to change between taxon and life cycle stage (Kaufman et al., 2008). Therefore, extreme caution must be exercised when generalizing turnover rates between benthic species. Based on this, a greater number of empirical studies are recommended to looking into the turnover time in different tissues and growth stages of benthic species in the Arctic.

Usefulness in combining multiple approaches to study the trophic ecology of benthic communities

Since climate change is causing drastic and rapid environmental changes in the Arctic Ocean, it is necessary to use or develop new methods that help us predict more accurately the implications of environmental changes in the functioning of benthic ecosystems, and thus improving the management of this important ecosystem. Arctic benthic communities are often assumed to be highly vulnerable to changes in organic carbon fluxes, therefore, due to climate change, these benthic communities are expected to experience significant changes in their structure and composition (Ruhl et al., 2008). Likewise, changes in the timing, composition, abundance, and quality of organic carbon fluxes appear to affect benthic consumers' diet composition (Chapter 2), trophic interactions and individual feeding behaviors (Chapter 3), and food web structure (Chapters 1, 2, and 3). On this basis, studies of the dietary ecology of benthic consumers are important for characterizing trophic interactions, quantifying aspects of their isotopic diversity, and predicting trends in benthic food web dynamics. However, studies related to the dietary ecology of benthic consumers are scarce in the Arctic Ocean, where most of the dietary estimates come from traditional methods such as stomach content analysis. Thus, more studies investigating the importance of different carbon sources and species feeding behaviors are critical for characterizing trophic interactions, and predicting consequences of changes in carbon supply.

In studies associated with the trophic ecology of benthic species, specific feeding behaviors of many benthic species are unknown. In Chapters 1 and 3, stable isotope analyses were used in conjunction with the Bayesian ellipse approach to study the trophic ecology of benthic consumers. However, stable isotope analyses did not provide high resolution on the feeding ecology of consumers; therefore, the complete picture of the feeding ecology was not elucidated in these chapters. To solve this gap, a novel approach that included the use of HBIs and stable isotopes was used in the second chapter of this thesis to characterize and quantify the carbon sources in benthic diets. Despite the use of this novel approach, the importance of all baseline resources was not clearly established due to some limitations in the methods used. For instance, we could not establish the importance of the organic material originating from the microbial community for consumers' diets. In this context, it seems increasingly useful to combine several methods in the study of diets and trophic ecology of consumers. For example, the Bayesian model MixSIAR, which is broadly used to obtain quantitative estimation of consumers' diets proved to be more accurate in dietary predictions when combining it with other methods such as fatty acid data (Guerrero and Rogers, 2020).

In the present thesis, the use of lipid biomarkers in the quantification of sea ice-derived carbon in combination with stable isotope analyses proved to be a valuable approach that enhanced our understanding on benthic fauna diets and food web structure. Also, the use of the relative proportions of SC assimilated by benthic macrofauna was a convenient method to separate benthic stations into "sub-regions" in areas with high temporal dynamics in sea-ice concentrations. In addition to HBI lipid biomarkers, stable isotopes in combination with multiple community-wide metrics provided relevant information of the biological and environmental drivers of niche structure, trophic ecology, and benthic food web structure. However, due to the complexity of the benthic food web and constant changes in the feeding behaviors by benthic consumers, it is difficult to obtain accurate estimates using only traditional methods. Hence, in future studies of this type, it is highly recommended to use and combine different methodologies to obtain a full picture of the importance of different sources in benthic consumers' diets year-round in the Arctic Ocean, and the implications of changes in the timing, type, and quality of carbon sources in the functioning and stability of the benthic food web. Such method combinations could involve adding fatty acid or/and DNA analyses whose added values into furthering our understanding of food webs are described below.

Recommendations of alternative/additional methods to deepen the understanding of benthic food webs

Lipids comprise a large group of chemically heterogeneous compounds that have been widely used as biochemical markers in Arctic food web and nutritional studies, due to the biochemical specificity on the synthesis of fatty acids (FAs) by organisms (e.g., Budge et al., 2007; Søreide et al., 2013). Several features make FAs excellent biomarkers, including the fact that FAs are not degraded during digestion (Iverson, 2009). In the Arctic Ocean, the use of FAs in combination with stable isotopes have been widely used as dietary tracers (e.g., Gaillard et al., 2015), and in studies of carbon flow and trophic structures (e.g., Søreide et al., 2013). Recently, the fatty acids approach and the DNA barcoding have shown to be a suitable tools to study species-specific dietary preferences for quantitative estimation of benthic consumers' diets (Chronopoulou et al., 2019). Metabarcoding allows not only the identification of prey but also provides insights into feeding modes, which permit the identification of potential species-specific food preferences (Chronopoulou et al., 2019). These approaches have the potential to bring new insights into individual feeding behaviors, helping us to increase our understanding of benthic trophic ecology. In addition, DNA barcoding seems to be an appropriate method for facilitating the identification of taxa. Finally, in researches related to food webs, the quantification of the food web flows using linear inverse models (LIM) is a valuable tool to gain additional insight in the structure of marine benthic food webs (Stukel et al., 2018), especially when new approaches can incorporate stable isotopic signatures and FAs data to these models.

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Appendix A - Chapter 1

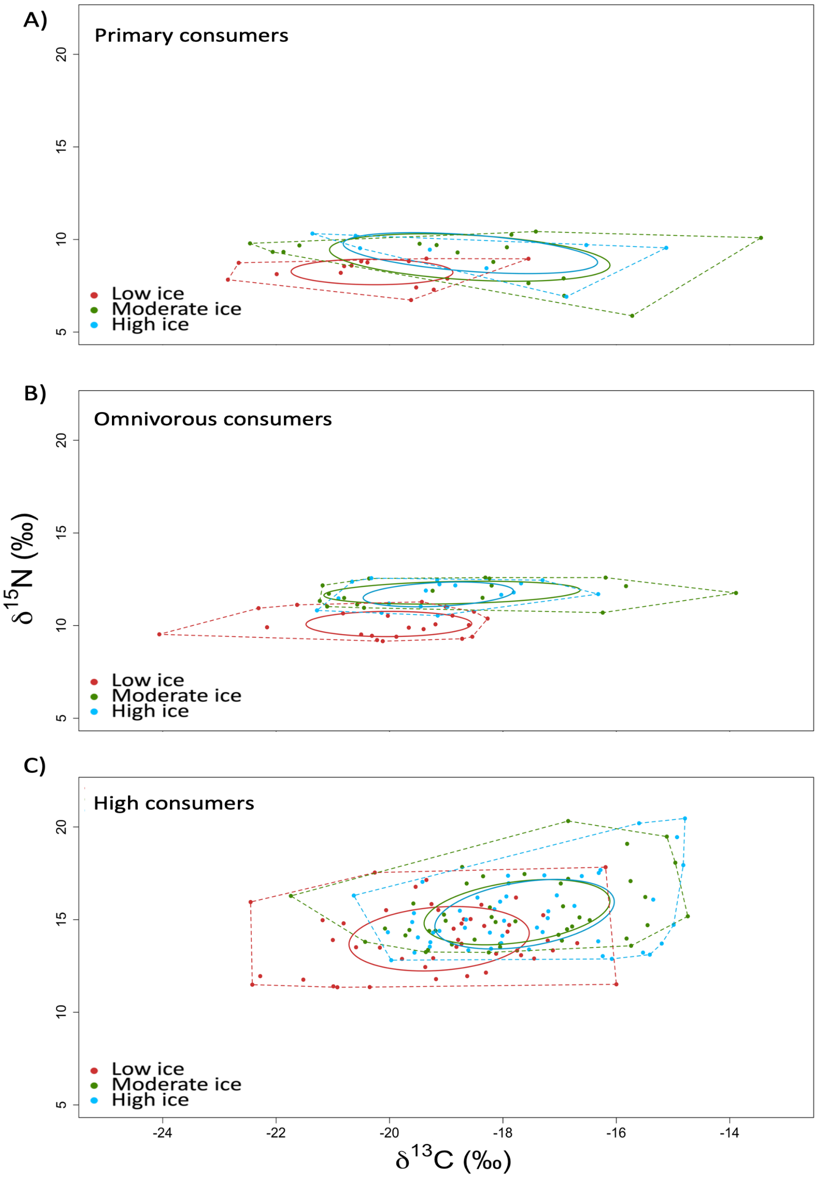

Figure S1.1. Biplots illustrating the isotopic niche structure of epibenthic groups under different ice conditions. The positions occupied by epibenthic fauna in the isotopic space are represented by dots in each δ^{13}C - δ^{15}N biplot. The representation of the convex hull area (dashed lines) encloses the isotopic richness of **A)** high consumers, **B)** omnivorous consumers, and **C)** primary consumers. Isotope data of epibenthic groups are shown in areas with different sea-ice concentrations (SIC): low ice (≤10% of SIC; red), moderate ice (>10 to 50% of SIC; green), and high ice (>50% of SIC; blue). The representation of the ellipses (solid lines) encloses the size-corrected standard ellipse area (SEAc, fits 40% of the data).

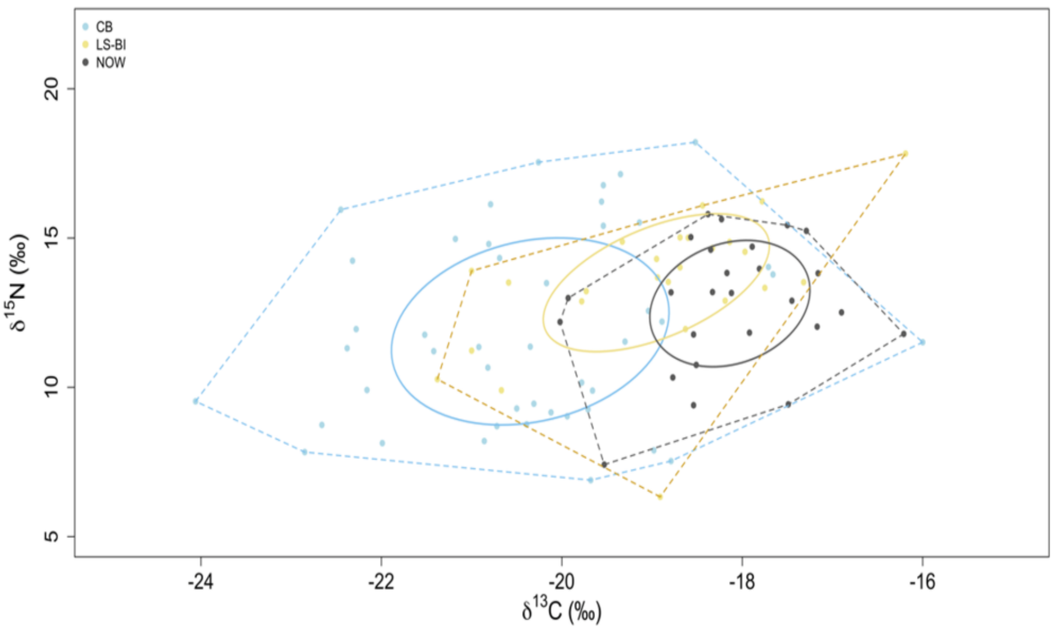

Figure S1.2. Biplot illustrating the isotopic niche structure of the epibenthic community between polynyas. The positions occupied by epibenthic fauna in the isotopic space are represented by dots in each $\delta^{13}C$ - $\delta^{15}N$ biplot. The representation of the convex hull area (dashed lines) encloses the isotopic richness of the benthic community at **A)** Cape Bathurst polynya (CB; blue dots), **B)** Viscount-Melville Sound-Lancaster Sound-Bylot Island polynya (VMS-LS-BI; yellow dots), and **C)** North Water polynya (NOW; black dots). The representation of the ellipses (solid lines) encloses the size-corrected standard ellipses area (SEAc, fits 40% of the data).

Table S1.1. Data set from stations where samples were collected across regions of the Canadian Arctic Ocean.

Station	**Region**[a]	**Sea-ice**[b] **condition**	**Water depth (m)**	**Sampling date**[c]	**Latitude**[d] **(N)**	**Longitude**[d] **(W)**	**SIC%**[e]	**Chl *a***[f] **(μg g^{-1})**
W420	CB	Low	35	2011-09-26	71.05	–128.52	0 ± 0.0	5.34
W437	CB	Low	239	2011-09-28	71.83	–126.51	0 ± 0.0	2.58
W438	CB	Low	94	2011-09-29	70.59	–127.61	0 ± 0.0	5.26
W407	CB	Low	408	2011-10-02	71.07	–126.18	0 ± 0.0	2.87
407	CB	Low	392	2014-08-18	71.11	–126.07	0 ± 0.0	1.20
437	CB	Low	318	2014-08-19	71.83	–126.76	0 ± 0.0	0.90
C307	VMS	Low	368	2011-10-08	74.021	–103.062	0 ± 0.0	1.75
E301	LS-BI	Low	665	2011-10-14	74.09	–83.42	2 ± 0.1	36.43
E323	LS-BI	Low	789	2011-10-15	74.15	–80.45	4 ± 0.1	21.31
E115	NOW	Low	647	2011-10-17	76.33	–71.15	3 ± 0.1	12.39
115	NOW	Low	656	2014-07-30	76.58	–71.17	4 ± 0.0	53.00
111	NOW	Low	594	2014-07-31	76.40	–73.26	0 ± 0.0	23.10
101	NOW	Low	360	2014-08-01	76.43	–77.61	9 ± 0.1	2.30
105	NOW	Low	343	2014-08-01	76.47	–75.83	0 ± 0.0	6.50
108	NOW	Low	447	2014-08-01	76.34	–74.72	0 ± 0.0	11.10
C331	CAA	Moderate	113	2011-08-03	74.64	–97.73	40 ± 0.1	4.47
C332	CAA	Moderate	143	2011-08-04	74.60	–96.12	20 ± 0.1	23.32

C310F	CAA	Moderate	165	2011-08-08	71.30	–97.60	43 ± 0.2	2.76
C312A	CAA	Moderate	70	2011-08-09	69.17	–100.76	45 ± 0.2	8.72
C314B	CAA	Moderate	119	2011-10-06	69.00	–106.56	47 ± 0.0	12.40
312	CAA	Moderate	66	2014-08-11	69.24	–100.86	44 ± 0.2	12.80
G418	BB	Moderate	384	2016-06-28	68.11	–57.77	31 ± 0.3	N/A[g]
G503	BB	Moderate	301	2016-06-29	70.00	–57.76	18 ± 0.2	N/A
G615	BB	Moderate	615	2016-07-05	70.50	–59.52	44 ± 0.3	N/A
G703	BB	Moderate	520	2016-07-07	69.50	–58.72	29 ± 0.3	N/A
E150	BB	High	130	2011-08-01	72.74	–79.92	75 ± 0.1	2.13
E160	BB	High	726	2011-08-01	72.67	–78.58	73 ± 0.1	12.83
C314A	CAA	High	109	2011-08-10	69.00	–106.62	58 ± 0.1	7.89
309	CAA	High	335	2014-08-10	73.10	–96.18	73 ± 0.0	2.30
314	CAA	High	84	2014-08-12	69.03	–105.54	54 ± 0.2	7.30
G107	BB	High	403	2016-06-11	68.50	–59.18	82 ± 0.1	N/A
G204	BB	High	445	2016-06-15	68.71	–59.26	79 ± 0.1	N/A
G306b	BB	High	309	2016-06-18	68.99	–58.15	60 ± 0.2	N/A
G309	BB	High	360	2016-06-18	69.00	–58.74	60 ± 0.2	N/A
G507	BB	High	294	2016-06-30	70.01	–59.12	60 ± 0.3	N/A
G512	BB	High	605	2016-07-01	70.00	–60.36	84 ± 0.2	N/A

[a] Regions of sampling collection: Baffin Bay (BB), Canadian Arctic Archipelago (CAA), Cape Bathurst polynya (CB), Viscount-Melville Sound-Lancaster Sound-Bylot Island polynya (VMS-LS-BI), and North Water polynya (NOW).
[b] Sea-ice condition in ice areas: low ice (≤10% of SIC), moderate ice (>10 to 50% of SIC), and high ice (>50% of SIC).
[c] Sampling date (day/month/year).
[d] Geographic coordinates.
[e] Mean value ± standard deviation (SD) percentage of sea-ice concentration (SIC) for a period of 30 days prior to sampling.
[f] Chl *a* = Chlorophyll *a* in surface sediments.
[g] N/A indicates data not available.

Table S1.2. Summary of the main effects of environmental variables on $\delta^{13}C$ and $\delta^{15}N$ values of baseline food sources from samples collected at different locations of the Canadian Arctic Ocean in the years 2011, 2014, and 2016.

	Model $\delta^{13}C$				**Model $\delta^{15}N$**			
Main effects and significant interaction effects	**Degree of freedom**	**F-value**	**p-value**	**Effect size (slope)**	**Degree of freedom**	**F-value**	**p-value**	**Effect size (slope)**
SCM-POM[a]					**SCM-POM**			
Depth	1	1.09	0.301		1	0.18	0.670	
SIC[b]	1	1.07	0.307		1	0.65	0.425	
Depth × SIC	1	6.85	**0.012***		1	<0.01	0.976	
Bot-POM[a]					**Bot-POM**			
Depth	1	<0.01	0.970		1	1.52	0.228	
SIC	1	1.31	0.262		1	<0.01	0.973	
Depth × SIC	1	1.26	0.272		1	<0.01	0.924	
Sed-POM[a]					**Sed-POM**			
Depth	1	82.02	**<0.001*****	0.006	1	17.09	**<0.001*****	0.004
SIC	1	3.03	0.087	– 0.173	1	8.96	**0.004****	4.937
Depth × SIC	1	15.01	**<0.001*****		1	8.12	**0.006****	

[a] The baseline food sources: subsurface chlorophyll maximum particulate organic matter (SCM-POM), bottom water particulate organic matter (Bot-POM), and surface sediment particulate organic matter (Sed-POM).
[b] Sea-ice concentration (SIC).
The level of statistical significance: ****p* <0.001***p* <0.01, **p* <0.05.

Table S1.3. Summary of main effects and significant two-way interaction effects on $\delta^{13}C$ values.

Model					Post-hoc		
Main effects and significant interaction effects	**Degrees of freedom**	**F-value**	**p-value**	**Effect size (slope)**	**Significant effect**	**p-value**	**Effect size**
Depth	1	0.65	0.421				
SIC[a]	1	11.20	<0.001***	2.525			
Ice areas[b]	2	5.63	0.004**		Moderate > High	0.024*	1.597
GC[c]	2	23.84	<0.001***		High consumers > Primary consumers	0.013*	0.591
					Primary consumers > Omnivorous	0.019*	0.648
					High consumers > Omnivorous	<0.001***	1.239
Depth × ice areas	2	5.27	0.005**		($\delta^{13}C$ ~ Depth) Moderate > High	<0.001***	0.005
					($\delta^{13}C$ ~ Depth) Moderate > Low	0.021*	0.003
Depth × GC	2	4.59	0.011*		($\delta^{13}C$ ~ Depth) High consumers > Omnivorous	0.041*	0.002
SIC × ice areas	2	8.52	<0.001***		($\delta^{13}C$ ~ SIC) High > Moderate	<0.001***	7.960
Ice areas × GC	4	3.26	0.012*		(High) High consumers > Omnivorous	<0.001***	1.467
					(Moderate) High consumers > Omnivorous	<0.001***	1.402
					(Moderate) Primary consumers > Omnivorous	0.002*	1.392

Table S1.4. Summary of main effects and significant two-way interaction effects on $\delta^{15}N$ values.

Model					Post-hoc		
Main effects and significant interaction effects	**Degrees of freedom**	**F-value**	**p-value**	**Effect size (slope)**	**Significant effect**	**p-value**	**Effect size**
Depth	1	119.02	<0.001***	0.0023			
SIC[a]	1	6.32	0.012*	0.0408			
Ice areas[b]	2	0.29	0.7476				
GC[c]	2	955.73	<0.001***		High consumers > Omnivorous	<0.001***	3.550
					Omnivorous > Primary consumers	<0.001***	3.040
					High consumers > Primary consumers	<0.001***	6.590
Depth × GC	2	16.61	<0.001***		($\delta^{15}N$ ~ Depth) High consumers > Primary consumers	<0.001***	0.003
					($\delta^{15}N$ ~ Depth) Omnivorous > Primary consumers	<0.001***	0.003

[a] Sea-ice concentration (SIC).

[b] Ice areas: low ice (≤10% of SIC), moderate ice (>10 to 50% of SIC), and high ice (>50% of SIC).

[c] Consumer group (GC): Primary consumers, omnivorous, and high consumers.

The level of statistical significance: ***p <0.001**p <0.01, *p <0.05.

Table S1.5. Benthic epifauna measurements from samples collected in different locations of the Canadian Arctic Ocean in the years 2011, 2014, and 2016.

Taxonomic classification	Ice area[a]	n[b]	$\delta^{15}N$ (‰)[c]	$\delta^{13}C$ (‰)[d]
Annelida				
Class Polychaeta				
Aglaophamus malmgreni	Low ice	9	14.4 ± 0.8	–17.9 ± 0.3
A. malmgreni	Moderate ice	1	14.5	–16.9
A. malmgreni	High ice	4	16.3 ± 0.9	–17.1 ± 1.6
Amphicteis gunneri	Low ice	1	12.0	–18.6
Chirimia biceps biceps	Low ice	4	13.9 ± 1.1	–18.8 ± 0.4
Bylgides promamme	Low ice	1	10.7	–20.8
Eunoe nodosa	Low ice	1	15.0	–18.6
E. nodosa	Moderate ice	3	12.7 ± 1.7	–19.3 ± 0.6
Harmothoe extenuata	Low ice	2	11.5 ± 0.4	–19.3 ± 0.2
Jasmineira sp.	Low ice	3	15.0 ± 0.6	–21.2 ± 0.4
Laetmonice filicornis	H High ice	1	14.9	–18.0
Maldane sp.	Low ice	1	16.8	–19.5
Melinna cristata	Low ice	1	13.5	–18.8
Nephtys incisa	Moderate ice	5	17.5 ± 0.8	–17.6 ± 0.9
N. incisa	High ice	2	17.7 ± 0.8	–16.3 ± 3.5
Nephtys longosetosa	Moderate ice	3	15.0 ± 1.3	–16.5 ± 1.6
Nereis zonata	Low ice	1	11.4	–20.3
Nicomache sp.	Low ice	2	14.7 ± 0.8	–17.9 ± 0.5
Nothria conchylega	Low ice	3	12.4 ± 0.7	–19.4 ± 0.6
Phyllodocidae	Low ice	1	11.9	–22.3
Scoletoma fragilis	Low ice	1	15.8	–18.4
S. fragilis	Moderate ice	3	13.8 ± 0.6	–20.4 ± 0.4
Spio sp.	Moderate ice	2	14.2 ± 0.6	–19.7 ± 0.1
Thelepus cincinnatus	Low ice	3	11.8 ± 0.9	–18.5 ± 0.5
Arthropoda				
Class Malacostraca				
Aega psora	High ice	1	17.0	–19.4
Aegiochus ventrosa	High ice	2	16.3 ± 0.4	–20.6 ± 0.8
Ampelisca macrocephala	Low ice	3	8.1 ± 0.6	–22.0 ± 0.3
Anonyx nugax	Low ice	4	14.8 ± 1.6	–20.8 ± 0.6
A. nugax	Moderate ice	10	15.9 ± 1.3	–19.6 ± 0.9
A. nugax	High ice	3	14.9 ± 0.9	–19.6 ± 0.4
Arctolembos arcticus	Low ice	1	8.7	–22.7
Arcturus baffini	Moderate ice	3	9.3 ± 0.5	–21.9 ± 0.1
Atlantopandalus propinqvus	Moderate ice	1	14.4	–19.7
Boreomysis nobilis	High ice	6	11.2 ± 0.4	–20.0 ± 0.1
Calathura brachiata	Low ice	1	17.5	–20.3
Diastylis rathkei	Moderate ice	2	5.9 ± 0.0	–15.7 ± 2.0
Epimeria loricata	High ice	1	15.4	–19.6
Eualus gaimardii	Low ice	2	13.5 ± 1.2	–20.2 ± 0.0
Eualus belcheri	Low ice	10	14.8 ± 1.5	–18.7 ± 0.8
Eusirus holmi	High ice	1	14.3	–18.2
Halirages qvadridentatus	Moderate ice	1	9.3	–18.8
Haploops laevis	Low ice	3	7.8 ± 0.1	–22.8 ± 0.3
Hymenodora glacialis	High ice	3	14.4 ± 0.4	–19.1 ± 0.2
Lebbeus polaris	Low ice	1	15.0	–18.7
L. polaris	Moderate ice	5	13.2 ± 0.8	–18.1 ± 0.2
L. polaris	High ice	11	14.3 ± 0.7	–17.3 ± 0.4

Leucothoe uschakovi	Moderate ice	2	14.2 ± 0.3	–17.0 ± 0.0
Pandalus borealis	Moderate ice	7	12.5 ± 0.7	–18.2 ± 0.2
P. borealis	High ice	2	13.7 ± 0.5	–18.0 ± 0.3
Pandalus montagui	High ice	1	13.8	–19.3
Pontophilus norvegicus	High ice	1	14.6	–17.4
Rhachotropis aculeata	Low ice	1	11.8	–21.5
Sabinea sarsii	High ice	2	15.1 ± 0.3	–17.2 ± 0.1
Sabinea septemcarinata	Low ice	1	15.5	–19.1
S. septemcarinata	Moderate ice	4	17.8 ± 0.9	–18.7 ± 0.2
S. septemcarinata	High ice	1	12.9	–16.1
Saduria sabini	Low ice	1	11.4	–20.9
S. sabini	Moderate ice	1	14.9	–18.1
Sclerocrangon boreas	Low ice	3	17.1 ± 0.4	–19.3 ± 0.4
S. boreas	Moderate ice	2	15.7 ± 0.9	–18.2 ± 0.4
Sclerocrangon ferox	Moderate ice	1	16.9	–17.0
Spirontocaris liljeborgii	Moderate ice	2	12.6 ± 0.2	–18.3 ± 0.3
S. liljeborgii	High ice	1	13.4	–17.5
Stegocephalus inflatus	Low ice	3	16.0 ± 1.0	–22.5 ± 0.0
Synidotea bicuspida	Low ice	3	11.3 ± 0.3	–22.4 ± 0.1
Themisto abyssorum	Moderate ice	2	11.0 ± 0.3	–20.4 ± 0.5
Class Thecostraca				
Scalpellum sp.	Low ice	1	13.5	–20.6
Bryozoa				
Class Gymnolaemata				
Alcyonidium gelatinosum anderssoni sp.A	Low ice	4	14.7 ± 1.9	–18.3 ± 0.8
A. gelatinosum anderssoni sp.A	Moderate ice	2	9.8 ± 0.2	–22.5 ± 0.8
A. gelatinosum anderssoni sp.A	High ice	1	13.0	–16.2
Alcyonidium gelatinosum anderssoni sp.B	High ice	1	15.5	–17.2
Alcyonidium sp.E	Low ice	1	13.3	–17.8
Eucratea loricata	Low ice	1	9.9	–22.2
Cnidaria				
Class Anthozoa				
Actinauge cristata	Moderate ice	4	11.7 ± 0.7	–21.1 ± 0.2
A. cristata	High ice	7	11.7 ± 1.0	–20.7 ± 0.5
Actinostola callosa	Moderate ice	1	11.1	–20.6
A. callosa	High ice	2	12.6 ± 0.2	–20.3 ± 0.5
Anemone sp.	Low ice	1	15.2	–17.3
Anemone sp.	Moderate ice	1	15.1	–18.2
Anthoptilum grandiflorum	Moderate ice	2	12.2 ± 0.2	–21.2 ± 0.5
Bolocera tuediae	Moderate ice	1	13.4	–19.3
B. tuediae	High ice	5	13.5 ± 1.0	–19.3 ± 0.2
Drifa glomerata	High ice	3	13.1 ± 1.1	–19.2 ± 0.8
Liponema multicorne	High ice	2	15.7 ± 0.2	–16.7 ± 0.1
Pitilella grandis	High ice	4	12.1 ± 1.0	–19.5 ± 1.8
Umbellula sp.	High ice	1	14.3	–20.0
Class Hydrozoa				
Hydrozoa sp.A	Moderate ice	1	9.3	–22.1
Lafoeidae	Low ice	1	13.9	–21.0
Sertulariidae	Low ice	1	9.5	–24.1
Echinodermata				
Class Asteroidea				
Bathybiaster vexillifer	Moderate ice	2	15.2 ± 0.6	–14.7 ± 0.7
Ceramaster granularis	Moderate ice	3	18.1 ± 1.1	–15.0 ± 0.7
C. granularis	High ice	3	16.1 ± 0.7	–15.3 ± 1.6
Ctenodiscus crispatus	Low ice	13	13.0 ± 1.6	–17.2 ± 1.9
C. crispatus	Moderate ice	2	12.6 ± 0.3	–16.2 ± 0.7

C. crispatus	High ice	3	13.4 ± 1.0	–16.6 ± 0.6
Henricia sp.	Moderate ice	3	19.5 ± 0.7	–15.1 ± 1.0
Henricia sp.	High ice	2	17.9 ± 0.5	–14.8 ± 1.4
Hippasteria phrygiana	Moderate ice	2	14.7 ± 0.9	–15.4 ± 0.0
Hymenaster pellucidus	Moderate ice	1	14.0	–15.8
Icasterias panopla	High ice	1	13.2	–15.5
Leilaster radians	High ice	1	20.5	–14.8
Leptychaster arcticus	Moderate ice	2	16.2 ± 1.0	–15.5 ± 0.6
Pontaster tenuispinus	Moderate ice	5	10.5 ± 0.2	–17.0 ± 1.2
Pseudarchaster parelii	Moderate ice	1	17.2	–16.8
P. parelii	High ice	1	17.5	–16.3
Psilaster andromeda	Low ice	4	17.8 ± 1.1	–16.2 ± 0.2
Pteraster militaris	High ice	1	20.2	–15.6
Stephanasterias albula	Moderate ice	2	20.3 ± 1.4	–16.8 ± 0.7
S. albula	High ice	2	14.7 ± 0.2	–15.0 ± 0.3
Tremaster mirabilis	Moderate ice	1	19.1	–15.8
Urasterias lincki	Moderate ice	1	17.3	–18.3
U. lincki	High ice	4	15.0 ± 1.2	–18.6 ± 1.0
Class Crinoidea				
Heliometra glacialis	High ice	1	13.4	–18.2
Class Echinoidea				
Strongylocentrotus sp.	Low ice	4	9.9 ± 1.1	–17.9 ± 1.5
Strongylocentrotus sp.	High ice	3	13.2 ± 1.1	–16.5 ± 2.5
Class Holothuroidea				
Molpadia sp.	Low ice	3	11.2 ± 0.2	–21.4 ± 0.4
Molpadia sp.	Moderate ice	1	17.1	–15.7
Class Ophiuroidea				
Amphiura sundevalli	Low ice	1	9.2	–20.1
Gorgonocephalus lamarckii	Moderate ice	1	12.5	–20.4
G. lamarckii	High ice	5	11.7 ± 0.8	–18.0 ± 1.2
Gorgonocephalus sp.	Low ice	5	12.9 ± 1.3	–19.2 ± 3.0
Gorgonocephalus sp.	High ice	5	15.5 ± 0.7	–18.8 ± 1.3
Ophiacantha bidentata	Low ice	19	14.5 ± 1.6	–18.9 ± 1.2
O. bidentata	Moderate ice	14	13.5 ± 1.0	–17.9 ± 2.2
O. bidentata	High ice	9	12.6 ± 0.9	–15.7 ± 1.7
Ophiacantha spectabilis	Moderate ice	4	13.9 ± 0.5	–17.0 ± 1.5
Ophiocten sericeum	Low ice	12	10.6 ± 2.9	–18.4 ± 1.2
O. sericeum	Moderate ice	12	7.6 ± 1.3	–17.5 ± 2.7
O. sericeum	High ice	5	9.9 ± 0.6	–19.2 ± 0.9
Ophiopholis aculeata	High ice	4	9.7 ± 0.2	–16.5 ± 1.2
Ophiopleura borealis	Low ice	27	13.9 ± 1.4	–17.2 ± 1.1
O. borealis	Moderate ice	2	13.2 ± 2.0	–15.3 ± 2.0
O. borealis	High ice	6	13.8 ± 1.1	–18.0 ± 0.5
Ophiopus arcticus	Moderate ice	6	10.3 ± 0.1	–17.8 ± 1.3
Ophioscolex glacialis	Low ice	2	12.9 ± 0.0	–19.8 ± 0.1
O. glacialis	High ice	1	12.2	–18.8
Ophiura robusta	Low ice	5	7.7 ± 1.3	–19.1 ± 0.8
O. robusta	Moderate ice	7	7.9 ± 1.2	–16.9 ± 2.1
O. robusta	High ice	6	6.9 ± 0.5	–16.9 ± 1.5
Ophiura sarsii	Low ice	3	12.9 ± 1.1	–17.4 ± 0.1
O. sarsii	Moderate ice	1	10.1	–13.5
O. sarsii	High ice	6	10.3 ± 0.9	–17.1 ± 2.2
Stegophiura nodosa	Low ice	3	9.3 ± 0.3	–19.7 ± 0.3
Mollusca				
Class Bivalvia				
Astarte borealis	Low ice	3	9.7 ± 0.6	–18.3 ± 1.3

Astarte crenata	Low ice	10	16.2 ± 1.0	–17.8 ± 0.6
A. crenata	Moderate ice	7	15.3 ± 1.5	–19.0 ± 1.9
A. crenata	High ice	5	17.4 ± 3.2	–17.3 ± 1.6
Astarte montagui	Low ice	16	15.2 ± 2.2	–19.4 ± 1.3
A. montagui	Moderate ice	6	13.5 ± 1.6	–19.5 ± 1.4
A. montagui	High ice	4	17.7 ± 3.6	–16.4 ± 2.9
Bathyarca glacialis	Low ice	8	13.7 ± 1.0	–18.7 ± 1.1
B. glacialis	Moderate ice	8	11.3 ± 0.5	–21.2 ± 0.6
B. glacialis	High ice	5	12.7 ± 3.0	–19.4 ± 1.3
Bathyarca sp.	Low ice	5	13.2 ± 0.3	–19.8 ± 0.7
Bathyarca sp.	Moderate ice	3	11.5 ± 0.4	–20.8 ± 0.2
Bathyarca sp.	High ice	4	14.4 ± 2.3	–18.5 ± 0.7
Ciliatocardium ciliatum	Low ice	8	9.5 ± 1.0	–19.7 ± 1.1
Cuspidaria glacialis	Low ice	6	15.5 ± 0.7	–20.1 ± 0.9
C. glacialis	Moderate ice	2	14.4 ± 0.4	–19.2 ± 0.2
Ennucula tenuis	Low ice	12	12.1 ± 2.2	–18.0 ± 1.9
E. tenuis	High ice	3	13.4 ± 0.1	–18.6 ± 0.6
Hiatella arctica	Low ice	3	9.9 ± 0.5	–19.7 ± 0.8
H. arctica	High ice	4	9.5 ± 0.3	–20.5 ± 0.4
Liocyma fluctuosa	Low ice	1	8.2	–20.9
Macoma calcarea	Low ice	2	9.0 ± 0.3	–19.9 ± 0.4
M. calcarea	Moderate ice	3	9.6 ± 0.3	–17.9 ± 0.4
Megayoldia sp.	Low ice	8	7.4 ± 0.5	–19.5 ± 0.4
Musculus discors	Low ice	2	8.8 ± 0.2	–20.4 ± 0.1
Musculus niger	Low ice	2	10.7 ± 0.8	–18.5 ± 0.6
Nuculana pernula	Low ice	3	9.5 ± 0.4	–20.3 ± 0.5
N. pernula	Moderate ice	4	11.4 ± 3.3	–20.0 ± 1.2
Similipecten greenlandicus	Moderate ice	4	10.4 ± 0.9	–21.3 ± 0.6
S. greenlandicus	High ice	4	10.7 ± 0.3	–21.3 ± 0.3
Yoldia hyperborea	Low ice	3	9.3 ± 0.4	–20.5 ± 0.3
Y. hyperborea	Moderate ice	3	9.7 ± 0.1	–19.2 ± 0.2
Yoldiella lenticula	Moderate ice	1	7.0	–16.9
Class Caudofoveata				
Chaetodermatida	Low ice	1	7.9	–19.0
Class Cephalopoda				
Bathypolypus bairdii	Moderate ice	2	14.9 ± 1.3	–19.0 ± 0.8
Rossia megaptera	Moderate ice	2	13.2 ± 0.2	–19.4 ± 0.1
R. megaptera	High ice	3	14.0 ± 0.6	–19.5 ± 0.5
Class Gastropoda				
Boreoscala sp.	Moderate ice	1	13.5	–18.1
Buccinum sp.	Low ice	1	13.2	–18.1
Buccinum sp.	Moderate ice	1	14.9	–17.8
Buccinum sp.	High ice	1	16.2	–17.9
Calliostoma occidentale	Moderate ice	2	13.7 ± 0.4	–18.9 ± 0.0
Class Polyplacophora				
Hanleya hanleyi	Moderate ice	2	13.6 ± 0.4	–15.7 ± 0.8
Stenosemus albus	High ice	2	11.8 ± 0.2	–17.8 ± 0.2
Nemertea				
Nemertina sp.	Moderate ice	1	15.1	–16.7
Porifera				
Class Demospongiae				
Geodia barretti	High ice	2	8.5 ± 0.2	–18.3 ± 0.2
Geodia macandrewii	Moderate ice	5	8.8 ± 0.8	–18.2 ± 0.3
Polymastia hemisphaerica	Moderate ice	1	16.9	–18.6
P. hemisphaerica	High ice	1	17.0	–17.9
Polymastia sp.	Moderate ice	2	15.7 ± 2.2	–16.9 ± 0.6

Polymastia sp.	High ice	1	17.4	–16.6
Porifera sp. A	High ice	3	14.6 ± 0.6	–18.7 ± 0.4
Tentorium semisuberites	High ice	1	17.4	–17.9
Thenea muricata	High ice	2	16.2 ± 0.3	–18.5 ± 0.1

[a] Sea-ice condition in ice areas: low ice (≤10% of SIC), moderate ice (>10 to 50% of SIC), and high ice (>50% of SIC).

[b] Number of total individuals per species used for stable isotope analyses.

[c] Mean values ± standard deviation of δ^{15}N (‰).

[d] Mean values ± standard deviation of δ^{13}C (‰).

Appendix B - Chapter 2

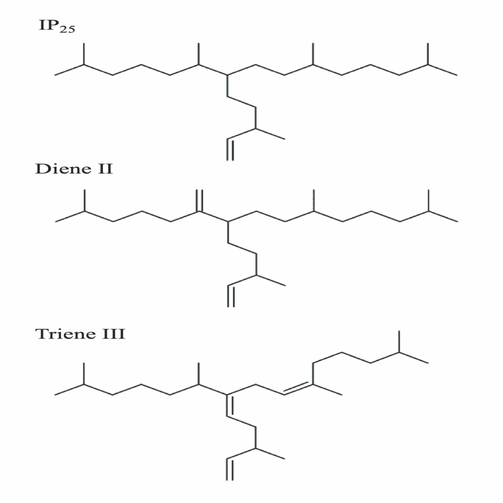

Figure S2.1. Molecular structures of highly branched isoprenoid (HBI) alkenes measured in this study. Top to bottom, sympagic (IP_{25}, Diene II) and phytoplankton-pelagic (Triene III) HBI biomarkers.

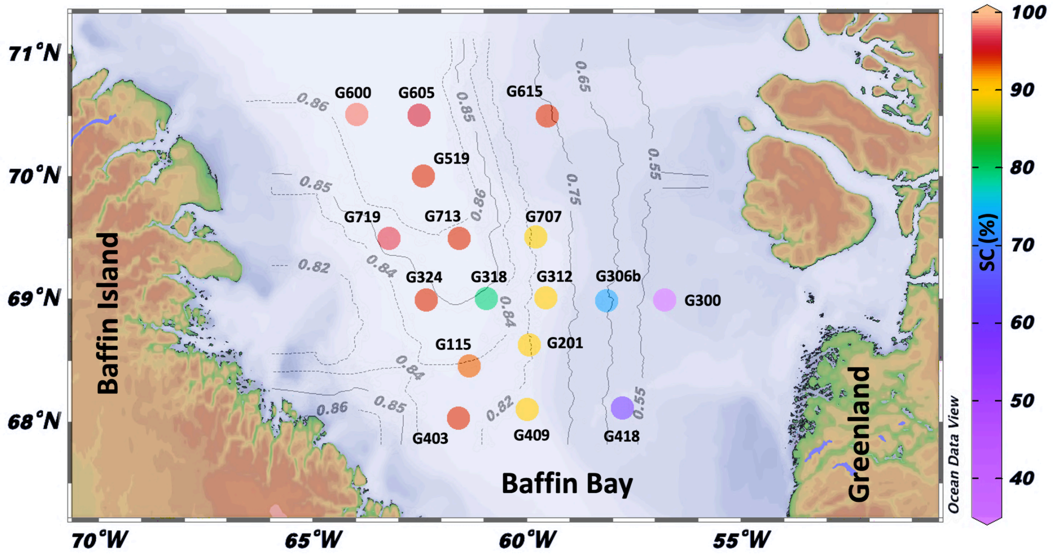

Figure S2.2. Sediment stations showing the spatial distribution and relative percentage of sympagic carbon in Baffin Bay. The percentages of sympagic carbon (SC) found in sediment are shown for each station (n = 17) according to the color bar. Average sea-ice concentrations ranging from 0 to 100% (expressed here between 0 to 1; gray lines), derived from the National Snow and Ice Data Center (https://nsidc.org/data/nsidc-0051), in spring (1 April to 30 June 30) between 1998 and 2017 in Baffin Bay, Canadian Arctic.

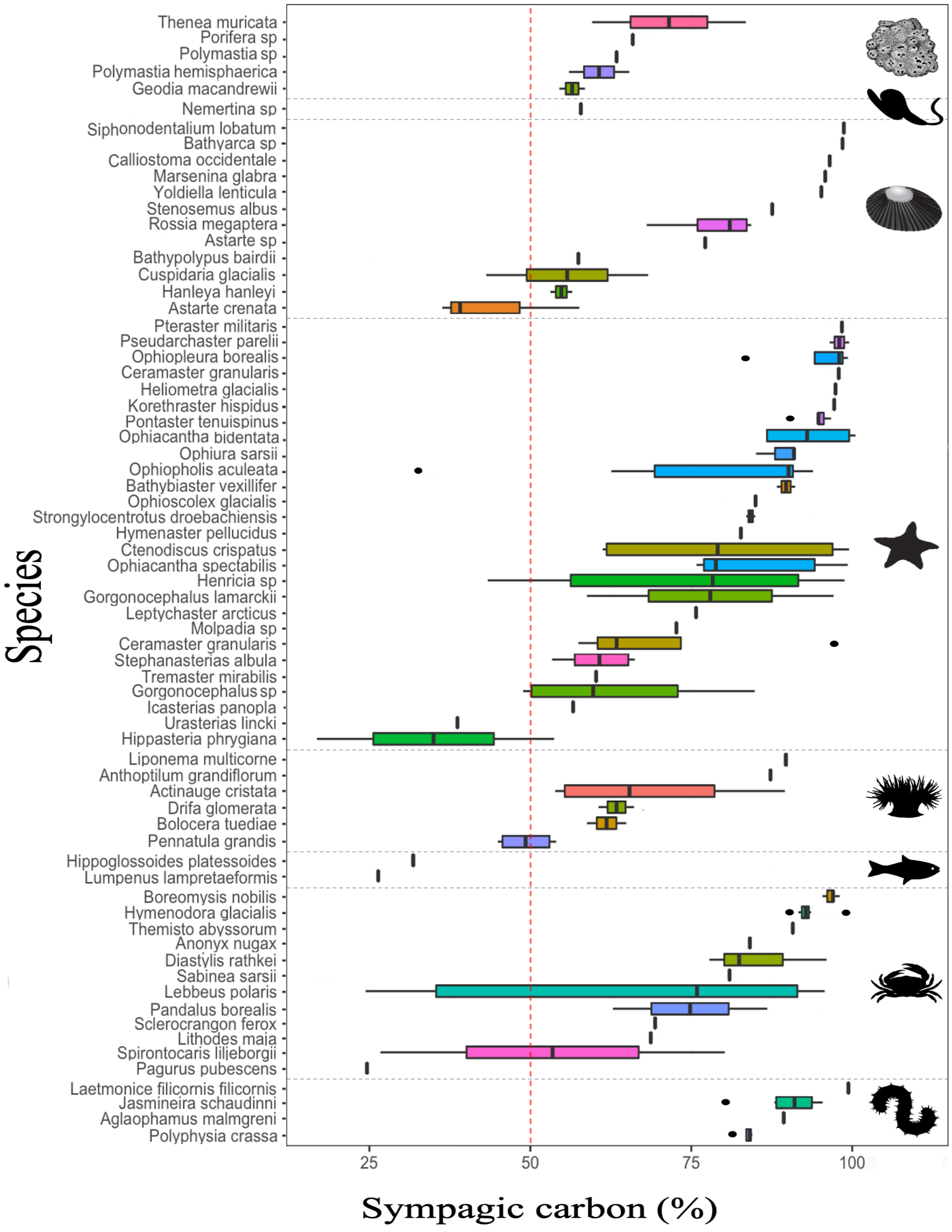

Figure S2.3. Box plot showing the relative abundance of sympagic carbon assimilated by deep benthic species among taxonomic groups. The black figures (from top to bottom) represent the taxonomic rank of the species by phylum: Porifera, Nemertea, Mollusca, Echinodermata, Cnidaria, Chordata, Arthropoda and Annelida. The middle part of the box, or the "interquartile range," represents the middle quartiles. The black line near the middle of the box represents the median (or the middle value of the data set). The minimum and maximum of the data are indicated by the lines. Points beyond the lines represent outliers in the data set.

Table S2.1. Benthic macrofauna measurements from samples collected in Baffin Bay in spring 2016.

Taxonomic classification	**Zone**	**n[a]**	**n[b]**	**δ^{15}N[c] (‰)**	**δ^{13}C[c] (‰)**	**n[d]**	**SC[c] (%)**
Annelida							
Class Polychaeta							
Aglaophamus malmgreni	C	12	1	14.5	–16.9	1	89
Jasmineira schaudinni	C	16	6	14.3 ± 0.2	–19.9 ± 0.2	6	90 ± 5.7
Laetmonice filicornis	C	1	1	14.9	–18.0	1	99
Polyphysia crassa	C	5	3	17.3 ± 0.1	–15.1 ± 1.2	5	84 ± 1.3
Arthropoda							
Class Malacostraca							
Aega psora	A	2	1	17.0	–19.4	0	N/A[e]
Aegiochus ventrosa	B	2	2	16.3 ± 0.4	–20.6 ± 0.8	0	N/A
Anonyx nugax	B	5	4	15.1 ± 0.8	–19.6 ± 0.3	1	84
A. nugax	C	4	2	16.9 ± 0.7	–19.1 ± 0.2	0	N/A
Arrhis phyllonyx	C	5	1	14.0	–18.7	0	N/A
Atlantopandalus propinqvus	B	1	1	14.4	–19.7	0	N/A
Boreomysis nobilis	C	33	8	11.2 ± 0.3	–20.1 ± 0.2	8	97 ± 0.9
Caecognathia stygia	C	40	3	17.2 ± 0.1	–19.3 ± 0.1	0	N/A
Diastylis rathkei	C	51	3	6.1 ± 0.3	–15.8 ± 1.4	3	85 ± 9.4
Epimeria loricata	B	1	1	15.4	–19.6	0	N/A
Eusirus holmi	C	1	1	14.3	–18.2	0	N/A
Halirages qvadridentatus	B	3	1	9.3	–18.8	0	N/A
Hymenodora glacialis	C	14	7	15.2 ± 0.6	–19.7 ± 0.3	7	93 ± 2.7
Lebbeus polaris	A	11	5	13.4 ± 0.5	–17.6 ± 0.3	5	59 ± 33.3
L. polaris	B	15	9	13.7 ± 0.8	–17.9 ± 0.4	3	79 ± 12.9
Leucothoe uschakovi	B	18	2	14.2 ± 0.8	–17.0 ± 0.0	0	N/A
Lithodes maja	B	1	0	N/A	N/A	1	69
Pagurus pubescens	A	1	1	12.8	–17.8	1	25
Pandalus borealis	A	1	1	12.1	–19.2	0	N/A
P. borealis	B	9	9	12.7 ± 0.9	–18.2 ± 0.2	2	75 ± 17.0
Pandalus montagui	A	1	1	13.8	–19.3	0	N/A
Pontophilus norvegicus	A	3	1	14.6	–17.4	0	N/A
Sabinea sarsii	A	2	2	15.4 ± 0.2	–17.7 ± 0.0	0	N/A
S. sarsii	B	3	2	15.1 ± 0.3	–17.2 ± 0.1	1	81
Sclerocrangon ferox	B	1	1	16.9	–17.0	1	69
Spirontocaris liljeborgii	A	5	2	12.7 ± 0.0	–18.7 ± 0.2	1	27
S. liljeborgii	B	2	2	12.9 ± 0.7	–17.8 ± 0.4	1	80
Stegocephalus inflatus	C	1	1	17.9	–19.2	0	N/A
Themisto abyssorum	B	7	2	11.0 ± 0.3	–20.4 ± 0.5	1	91
Tmetonyx sp	C	14	2	14.7 ± 0.1	–17.5 ± 0.1	0	N/A
Chordata							
Class Actinopterygii							
Cottunculus microps	A	1	1	14.4	–18.3	0	N/A
Hippoglossoides platessoides	A	1	1	14.8	–19.3	1	32
Lumpenus lampretaeformis	A	1	1	14.6	–18.7	1	26
Triglops nybelini	A	2	2	12.2 ± 0.2	–20.5 ± 0.1	0	N/A
Lycenchelys paxillus	B	1	1	16.4	–19.7	0	N/A
Triglops nybelini	B	2	2	12.7 ± 0.3	–20.4 ± 0.2	0	N/A
Class Elasmobranchii							
Rajella fyllae	C	1	1	16.9	–17.9	0	N/A
Cnidaria							
Class Anthozoa							
Actinauge cristata	A	11	7	11.4 ± 0.9	–20.8 ± 0.6	3	62 ± 11.7
A. cristata	B	2	2	12.4 ± 0.5	–20.9 ± 0.2	0	N/A
A. cristata	C	2	2	12.1 ± 0.3	–21.0 ± 0.2	1	90
Actinostola callosa	A	1	1	11.1	–20.6	0	N/A
A. callosa	C	2	2	12.6 ± 0.2	–20.3 ± 0.5	0	N/A
Anthoptilum grandiflorum	C	3	2	12.2 ± 0.2	–21.2 ± 0.5	1	87
Bolocera tuediae	A	5	5	13.5 ± 1.0	–19.3 ± 0.2	2	62 ± 4.3
B. tuediae	B	1	1	13.4	–19.3	0	N/A

Drifa glomerata	B	2	2	12.5 ± 0.0	–19.2 ± 1.1	1	66
D. glomerata	C	1	1	14.3	–19.2	1	61
Liponema multicorne	C	2	2	15.7 ± 0.2	–16.7 ± 0.1	2	90 ± 0.4
Pennatula grandis	A	4	4	12.1 ± 1.0	–19.5 ± 1.8	4	49 ± 4.6
Echinodermata							
Class Asteroidea							
Bathybiaster vexillifer	C	2	2	15.2 ± 0.6	–14.7 ± 0.7	2	90 ± 2.0
Ceramaster granularis	B	6	5	17.2 ± 1.5	–15.5 ± 0.9	5	76 ± 20.0
Ctenodiscus crispatus	A	3	3	13.0 ± 0.7	–16.2 ± 0.5	3	86 ± 21.2
C. crispatus	B	1	1	12.4	–17.3	1	62
Henricia sp	B	8	4	19.2 ± 0.8	–14.8 ± 1.0	6	70 ± 20.8
Henricia sp	C	2	1	17.6	–15.8	1	99
Hippasteria phrygiana	A	2	2	15.3 ± 1.8	–16.5 ± 1.5	1	16
H. phrygiana	B	1	1	15.3	–15.4	1	54
Hymenaster pellucidus	C	3	1	14.0	–15.8	1	83
Icasterias panopla	B	2	2	16.0 ± 3.9	–14.2 ± 1.8	2	57 ± 0.6
Korethraster hispidus	C	4	1	20.5	–14.8	1	97
Leptychaster arcticus	B	3	2	16.2 ± 1.0	–15.5 ± 0.6	1	76
Pontaster tenuispinus	C	5	5	10.5 ± 0.2	–17.0 ± 1.2	5	94 ± 2.4
Pseudarchaster parelii	B	1	1	17.2	–16.8	1	99
P. parelii	C	1	1	17.5	–16.3	1	97
Pteraster militaris	C	1	1	20.2	–15.6	1	98
Stephanasterias albula	B	16	4	17.5 ± 3.3	–15.9 ± 1.1	7	61 ± 5.1
Tremaster mirabilis	B	1	1	19.1	–15.8	1	60
Urasterias lincki	A	1	1	17.9	–13.6	1	39
Class Ophiuroidea							
Gorgonocephalus lamarckii	B	7	6	11.8 ± 0.8	–18.4 ± 1.4	6	68 ± 19.4
Ophiacantha bidentata	B	12	3	13.2 ± 0.5	–16.3 ± 2.3	4	93 ± 7.6
Ophiacantha spectabilis	B	6	2	13.9 ± 0.5	–17.0 ± 1.5	6	85 ± 11.3
Ophiopholis aculeata	A	5	3	10.7 ± 0.6	–18.4 ± 0.1	3	73 ± 34.4
O. aculeata	B	10	4	9.7 ± 0.2	–16.5 ± 1.2	3	81 ± 15.9
Ophiopleura borealis	C	4	4	13.9 ± 1.6	–16.2 ± 1.7	4	95 ± 7.4
Ophioscolex glacialis	B	7	1	12.2	–18.8	1	85
Ophiura sarsii	B	5	3	11.0 ± 0.4	–19.0 ± 0.2	3	89 ± 3.4
Class Crinoidea							
Heliometra glacialis	C	1	1	13.4	–18.2	1	97
Class Holothuroidea							
Molpadia sp	C	1	1	17.1	–15.7	1	73
Class Echinoidea							
Strongylocentrotus sp	B	2	2	13.7 ± 1.1	–15.2 ± 1.5	2	84 ± 1.0
Mollusca							
Class Bivalvia							
Astarte crenata	A	26	5	13.5 ± 0.5	–17.5 ± 0.7	3	44 ± 11.6
A. crenata	C	6	1	15.0	–17.0	0	N/A
Astarte sp	A	23	3	13.2 ± 0.6	–18.6 ± 0.4	1	77
Bathyarca sp	B	34	1	11.0	–19.5	1	99
Calliostoma occidentale	A	5	2	13.7 ± 0.4	–18.9 ± 0.0	2	97 ± 0.0
Cuspidaria glacialis	A	3	1	14.1	–19.3	1	43
C. glacialis	C	6	1	14.7	–19.1	1	68
Yoldiella lenticula	C	24	1	7.0	–16.9	1	95
Class Cephalopoda							
Bathypolypus bairdii	B	1	1	15.8	–18.5	1	57
Rossia megaptera	A	2	2	14.1 ± 0.8	–19.7 ± 0.5	2	76 ± 10.8
R. megaptera	B	3	3	13.5 ± 0.4	–19.2 ± 0.2	2	82 ± 4.0
Class Polyplacophora							
Hanleya hanleyi	B	2	2	13.6 ± 0.4	–15.7 ± 0.8	2	55 ± 2.4
Stenosemus albus	B	9	2	11.8 ± 0.2	–17.8 ± 0.2	2	88 ± 0.1
Class Gastropoda							
Boreoscala greenlandica	C	4	1	13.5	–18.1	0	N/A
Marsenina glabra	A	1	1	13.8	–18.8	1	96
Class Scaphopoda							
Siphonodentalium lobatum	C	32	1	15.2	–16.9	1	99

Nemertea							
Nemertina sp	B	1	1	15.1	–16.7	1	58
Porifera							
Class Demospongiae							
Geodia barretti	B	1	1	8.3	–18.1	0	N/A
G. barretti	C	1	1	8.6	–18.4	0	N/A
Geodia macandrewii	B	5	5	8.8 ± 0.8	–18.2 ± 0.3	2	56 ± 2.8
Polymastia hemisphaerica	B	1	1	16.9	–18.6	1	65
P. hemisphaerica	A	1	1	17.0	–17.9	1	56
Polymastia sp	A	2	2	15.7 ± 2.3	–17.0 ± 0.5	1	63
Polymastia sp	C	1	1	17.3	–16.5	0	N/A
Porifera sp	A	2	2	14.2 ± 0.2	–18.5 ± 0.1	1	66
Porifera sp	B	1	1	15.3	–19.1	0	N/A
Tentorium semisuberites	A	2	1	17.4	–17.9	1	56
Thenea muricata	A	1	1	16.0	–18.5	1	59
T. muricata	B	1	1	16.4	–18.4	1	83

[a] Number of total individuals per species and zone used for both stable isotope and HBI lipid biomarkers analyses.

[b] Number of measurements per zone used in calculating mean value ± standard deviation of stable isotope ratio analyses.

[c] Mean values ± standard deviation.

[d] Number of measurements per zone used in calculating HBI biomarkers and mean value ± standard deviation of sympagic carbon.

[e] N/A indicates data not available.

Appendix C - Chapter 3

Figure S3.1. Photo of the three species of brittle stars analyzed in this study. *Ophiacantha bidentata, Ophiocten sericeum,* and *Ophiopleura borealis* (Photo: Gustavo Yunda-Guarin).

Table S3.1. Sampling details and isotopic compositions in brittle stars species.

Species	**Station**	**Region**[a]	**Depth (m)**	**Sampling date**[b]	**Latitude (N)**	**Longitude (W)**	**δ^{13}C**[c] **(‰)**	**δ^{15}N**[d] **(‰)**
Ophiacantha bidentata	312	CAA	67	19/08/2018	69.17	–100.70	–19.42	14.73
O. bidentata	312	CAA	67	19/08/2018	69.17	–100.70	–19.38	14.35
O. bidentata	312	CAA	67	19/08/2018	69.17	–100.70	–18.69	14.40
O. bidentata	312	CAA	67	19/08/2018	69.17	–100.70	–18.74	14.60
O. bidentata	312	CAA	67	19/08/2018	69.17	–100.70	–19.04	13.94
O. bidentata	312	CAA	67	19/08/2018	69.17	–100.70	–18.54	15.10
O. bidentata	115	NOW	663	29/08/2018	76.33	–71.18	–18.48	14.08
O. bidentata	115	NOW	663	29/08/2018	76.33	–71.18	–18.51	13.96
O. bidentata	115	NOW	663	29/08/2018	76.33	–71.18	–19.19	13.29
O. bidentata	115	NOW	663	29/08/2018	76.33	–71.18	–18.90	13.75
O. bidentata	115	NOW	663	29/08/2018	76.33	–71.18	–18.88	12.98
O. bidentata	115	NOW	663	29/08/2018	76.33	–71.18	–18.48	12.27
O. bidentata	115	NOW	663	29/08/2018	76.33	–71.18	–18.84	12.81
O. bidentata	115	NOW	663	29/08/2018	76.33	–71.18	–18.26	13.20
O. bidentata	115	NOW	663	29/08/2018	76.33	–71.18	–23.36	12.84
O. bidentata	115	NOW	663	29/08/2018	76.33	–71.18	–18.25	12.23
O. bidentata	177	BB	694	01/09/2018	67.48	–63.68	–19.70	14.02
O. bidentata	177	BB	694	01/09/2018	67.48	–63.68	–19.68	13.74
O. bidentata	177	BB	694	01/09/2018	67.48	–63.68	–19.09	14.12
O. bidentata	177	BB	694	01/09/2018	67.48	–63.68	–19.58	15.15
O. bidentata	177	BB	694	01/09/2018	67.48	–63.68	–19.31	13.71
O. bidentata	177	BB	694	01/09/2018	67.48	–63.68	–18.72	12.75

Ophiocten sericeum	312	CAA	67	19/08/2018	69.17	–100.70	–20.33	11.55
O. sericeum	312	CAA	67	19/08/2018	69.17	–100.70	–19.57	11.48
O. sericeum	312	CAA	67	19/08/2018	69.17	–100.70	–19.79	11.29
O. sericeum	312	CAA	67	19/08/2018	69.17	–100.70	–20.35	11.20
O. sericeum	312	CAA	67	19/08/2018	69.17	–100.70	–20.09	11.51
O. sericeum	QMG1	CAA	39	21/08/2018	68.49	–99.89	–20.41	10.21
O. sericeum	QMG1	CAA	39	21/08/2018	68.49	–99.89	–20.93	10.05
O. sericeum	QMG1	CAA	39	21/08/2018	68.49	–99.89	–20.46	10.25
O. sericeum	QMG4	CAA	70	22/08/2018	68.48	–103.43	–24.35	10.25
O. sericeum	QMG4	CAA	70	22/08/2018	68.48	–103.43	–24.22	10.24
O. sericeum	QMG4	CAA	70	22/08/2018	68.48	–103.43	–24.35	10.26
O. sericeum	QMG4	CAA	70	22/08/2018	68.48	–103.43	–24.85	10.23
O. sericeum	QMG4	CAA	70	22/08/2018	68.48	–103.43	–24.70	10.08
O. sericeum	QMG4	CAA	70	22/08/2018	68.48	–103.43	–24.43	10.20
O. sericeum	101	NOW	373	28/08/2018	76.38	–77.41	–20.60	10.50
O. sericeum	101	NOW	373	28/08/2018	76.38	–77.41	–20.85	10.91
O. sericeum	101	NOW	373	28/08/2018	76.38	–77.41	–20.40	11.68
O. sericeum	101	NOW	373	28/08/2018	76.38	–77.41	–20.33	11.86
O. sericeum	101	NOW	373	28/08/2018	76.38	–77.41	–19.52	12.47
O. sericeum	101	NOW	373	28/08/2018	76.38	–77.41	–19.63	12.89
O. sericeum	101	NOW	373	28/08/2018	76.38	–77.41	–20.37	11.23
O. sericeum	101	NOW	373	28/08/2018	76.38	–77.41	–20.02	11.67
O. sericeum	101	NOW	373	28/08/2018	76.38	–77.41	–19.95	12.24
O. sericeum	101	NOW	373	28/08/2018	76.38	–77.41	–20.25	10.61
O. sericeum	115	NOW	662	29/08/2018	76.33	–71.18	–19.63	14.65
O. sericeum	115	NOW	662	29/08/2018	76.33	–71.18	–19.34	14.52
O. sericeum	115	NOW	662	29/08/2018	76.33	–71.18	–19.52	14.56
O. sericeum	115	NOW	662	29/08/2018	76.33	–71.18	–20.37	11.09
O. sericeum	115	NOW	662	29/08/2018	76.33	–71.18	–19.74	14.26
O. sericeum	115	NOW	662	29/08/2018	76.33	–71.18	–19.78	13.71
O. sericeum	115	NOW	662	29/08/2018	76.33	–71.18	–20.21	13.56
O. sericeum	177	BB	694	01/09/2018	67.48	–63.68	–21.26	11.91
O. sericeum	177	BB	694	01/09/2018	67.48	–63.68	–20.38	13.52
O. sericeum	177	BB	694	01/09/2018	67.48	–63.68	–19.79	14.28
O. sericeum	177	BB	694	01/09/2018	67.48	–63.68	–20.70	12.62
O. sericeum	177	BB	694	01/09/2018	67.48	–63.68	–20.71	11.78
O. sericeum	177	BB	694	01/09/2018	67.48	–63.68	–20.08	12.17
Ophiopleura borealis	QMGM	CAA	112	22/08/2018	68.30	–101.74	–23.54	14.42
O. borealis	QMGM	CAA	112	22/08/2018	68.30	–101.74	–23.61	14.97
O. borealis	QMGM	CAA	112	22/08/2018	68.30	–101.74	–23.64	14.27
O. borealis	QMGM	CAA	112	22/08/2018	68.30	–101.74	–24.13	13.06
O. borealis	QMGM	CAA	112	22/08/2018	68.30	–101.74	–23.94	14.59
O. borealis	QMGM	CAA	112	22/08/2018	68.30	–101.74	–23.85	13.94
O. borealis	QMGM	CAA	112	22/08/2018	68.30	–101.74	–24.01	12.51
O. borealis	QMGM	CAA	112	22/08/2018	68.30	–101.74	–24.03	12.31
O. borealis	QMG4	CAA	70	22/08/2018	68.48	–103.43	–23.88	13.46
O. borealis	QMG4	CAA	70	22/08/2018	68.48	–103.43	–23.32	14.33
O. borealis	QMG4	CAA	70	22/08/2018	68.48	–103.43	–23.38	14.95
O. borealis	QMG4	CAA	70	22/08/2018	68.48	–103.43	–23.70	14.01
O. borealis	QMG4	CAA	70	22/08/2018	68.48	–103.43	–23.35	14.17
O. borealis	QMG4	CAA	70	22/08/2018	68.48	–103.43	–23.81	13.25
O. borealis	108	NOW	447	22/07/2019	76.26	–74.60	–19.87	13.74
O. borealis	108	NOW	447	22/07/2019	76.26	–74.60	–20.39	12.85
O. borealis	108	NOW	447	22/07/2019	76.26	–74.60	–19.76	13.77
O. borealis	115	NOW	662	29/08/2018	76.33	–71.18	–19.61	14.08
O. borealis	115	NOW	662	29/08/2018	76.33	–71.18	–19.77	11.34
O. borealis	115	NOW	662	29/08/2018	76.33	–71.18	–20.22	12.17
O. borealis	115	NOW	662	29/08/2018	76.33	–71.18	–20.20	12.74
O. borealis	115	NOW	662	29/08/2018	76.33	–71.18	–20.26	11.18
O. borealis	115	NOW	662	29/08/2018	76.33	–71.18	–19.64	11.21

O. borealis	E1	BB	447	23/08/2019	68.28	–65.14	–20.44	12.17
O. borealis	E1	BB	447	23/08/2019	68.28	–65.14	–19.66	12.59
O. borealis	E1	BB	447	23/08/2019	68.28	–65.14	–20.81	11.95
O. borealis	E1	BB	447	23/08/2019	68.28	–65.14	–20.39	12.60
O. borealis	E1	BB	447	23/08/2019	68.28	–65.14	–20.77	13.20
O. borealis	E1	BB	447	23/08/2019	68.28	–65.14	–20.42	12.59
O. borealis	E1	BB	447	23/08/2019	68.28	–65.14	–19.87	12.39
O. borealis	E1	BB	447	23/08/2019	68.28	–65.14	–19.93	12.44
O. borealis	E1	BB	447	23/08/2019	68.28	–65.14	–20.45	12.63

[a] Regions of sampling collection: Canadian Arctic Archipelago (CAA), North Water polynya (NOW), and Baffin Bay (BB),

[b] Sampling date (day/month/year).

[b] Number of total individuals per species used for stable isotope analyses.

[c] Carbon isotope values ($\delta^{13}C$) of brittle stars, n=1.

[d] Nitrogen isotope values ($\delta^{15}N$) of brittle stars, n=1.

Table S3.2. Summary of main effects and significant two-way interaction effects on δ^{13}C values of ophiuroids.

Model					Post-hoc		
Main effects and significant interaction effects	**Degrees of freedom**	**F-value**	**p-value**	**Effect size (slope)**	**Significant effect**	**p-value**	**Effect size**
Depth	1	36.04	<0.0001	8.113e-04			
SIC	1	89.27	<0.0001	2.944e-01			
Region	2	70.61	<0.0001		NOW > CAA	<0.0001	11.580
					BB > CAA	<0.0001	11.222
Species	2	8.19	0.0006		*O. bidentata* > *O. borealis*	0.0024	1.105
					O. bidentata > *O. sericeum*	0.0005	1.108
Depth x SIC*	1	4.56	0.0356		(δ^{13}C ~ Depth) SIC 0-3 > SIC 32-45		

*Sea-ice concentration (SIC)

Table S3.3. Summary of main effects and significant two-way interaction effects on δ^{15}N values of ophiuroids.

Model					Post-hoc		
Main effects and significant interaction effects	**Degrees of freedom**	**F-value**	**p-value**	**Effect size (slope)**	**Significant effect**	**p-value**	**Effect size**
Depth	1	7.94	0.0060	0.002314			
Species	2	38.23	<0.0001		*O. bidentata* > *O. borealis*	0.0006	0.96
					O. bidentata > *O. sericeum*	<0.0001	1.97
					O. borealis > *O. sericeum*	<0.0001	1.01
Depth x SIC*	1	12.81	0.0006		(δ^{15}N ~ Depth) SIC 0-3 > SIC 32-45		
Depth x Species	2	40.57	<0.0001		(δ^{15}N ~ Depth) *O. sericeum* > *O. bidentata*	<0.0001	0.00593
					(δ^{15}N ~ Depth) *O. sericeum* > *O. borealis*	<0.0001	0.00720

*Sea-ice concentration (SIC)