https://lib.uliege.be https://matheo.uliege.be

Mémoire

Auteur : Puppin, Nora
Promoteur(s) : Michel, Loïc; Pinzone, Marianna
Faculté : Faculté des Sciences
Diplôme : Master en biologie des organismes et écologie, à finalité approfondie
Année académique : 2024-2025
URI/URL : http://hdl.handle.net/2268.2/23857

Avertissement à l'attention des usagers :

Tous les documents placés en accès ouvert sur le site le site MatheO sont protégés par le droit d'auteur. Conformément aux principes énoncés par la "Budapest Open Access Initiative"(BOAI, 2002), l'utilisateur du site peut lire, télécharger, copier, transmettre, imprimer, chercher ou faire un lien vers le texte intégral de ces documents, les disséquer pour les indexer, s'en servir de données pour un logiciel, ou s'en servir à toute autre fin légale (ou prévue par la réglementation relative au droit d'auteur). Toute utilisation du document à des fins commerciales est strictement interdite.

Par ailleurs, l'utilisateur s'engage à respecter les droits moraux de l'auteur, principalement le droit à l'intégrité de l'oeuvre et le droit de paternité et ce dans toute utilisation que l'utilisateur entreprend. Ainsi, à titre d'exemple, lorsqu'il reproduira un document par extrait ou dans son intégralité, l'utilisateur citera de manière complète les sources telles que mentionnées ci-dessus. Toute utilisation non explicitement autorisée ci-avant (telle que par exemple, la modification du document ou son résumé) nécessite l'autorisation préalable et expresse des auteurs ou de leurs ayants droit.

LIÈGE université
FOCUS

NORWEGIAN POLAR INSTITUTE

Faculté des Sciences
Département Biologie, Ecologie, Evolution
Laboratoire de systématique et diversité animale

Trophic ecology of the Arctic fjord, Kongsfjorden, Svalbard

Nora Puppin

Mémoire présenté en vue de l'obtention du diplôme de Biologie des
Organismes et Ecologie à finalité approfondie

Août 2025

Promoteur : Pr. Loïc Michel

Co-promoteur : Dr. Marianna Pinzone

Acknowledgements

Je ne pourrais pas commencer ce mémoire sans remercier toutes les personnes qui, de près ou de loin, m’ont aidé à le réaliser.

Tout d’abord, je souhaite exprimer ma profonde gratitude au Dr. Marianna Pinzone ainsi qu’au professeur Loïc Michel, sans lesquels la réalisation de ce travail n’aurait pas été possible. Merci sincèrement pour votre confiance et surtout pour votre disponibilité. Je n’imaginais pas qu’une conversation sur les statistiques puisse être à la fois aussi instructive que légère ; les références à Friends et autres GIF ont très probablement aidé. Merci d’avoir répondu à mes nombreuses questions et d’avoir consacré de votre temps à l’accompagnement et à la relecture de ce mémoire.

Je tiens également à remercier l’ensemble du personnel enseignant et administratif pour leur encadrement et leur aide précieuse. Un merci tout particulier au Dr Gilles Lepoint pour son aide lors des analyses isotopiques. Merci également à Cédric ainsi qu’à Lina et Shahidul pour leur accompagnement lors des premières étapes de ce travail.

Merci à ma famille pour leur écoute, leur soutien et leurs encouragements tout au long de mon parcours. Depuis petite, vous m’entendez parler de biologie marine ; merci de m’avoir aidé à transformer ces paroles d’enfant en un véritable projet d’adulte. J’espère vous avoir rendu fiers.

De manière plus générale, je souhaiterais remercier toutes les personnes rencontrées au cours de mes cinq années d’études. Merci à mes amis de m’avoir soutenue, merci pour les discussions parfois philosophiques, parfois beaucoup moins.

Un merci tout particulier à Pauline et Claire. On m’avait dit qu’avoir des collègues agréables était essentiel pour se sentir bien au travail : merci d’être bien plus que des collègues. Ce mémoire n’aurait pas eu la même saveur sans nos fous rires et nos discussions quotidiennes. Merci à Emilie, Hélène, Mathias, Jérôme et Pierre et à toutes les personnes avec qui j’ai pu échanger sur nos expériences respectives au fil de ce mémoire. Merci de m’avoir rassurée plus souvent que je ne pourrais le compter.

Enfin, merci à toutes les personnes qui prendront le temps de s’intéresser à mon travail. J’espère sincèrement que ce mémoire vous plaira !

Bonne lecture !

Abstract

Kongsfjorden (79°N, 12°E) is a key fjord located in the northwest of the Svalbard archipelago. This archipelago exhibits the highest rates of warming within the circumpolar Arctic. Strongly influenced by warming and Atlantification, Kongsfjorden hosts shifting biological communities and altered trophic networks (Assmy *et al.,* 2023; Hop *et al.,* 2002). This master's thesis aims to identify the prey and trophic pathways supporting high-trophic-level predators in Kongsfjorden and to evaluate potential spatial and temporal variations in their resource use. Stable isotope analyses ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) were applied to assess energy pathways and trophic interactions within the fjord food web. This work was carried out in the framework of two larger projects (HgFJORD, FNRS CR, and SEASOL, Marie Curie) led by Dr. Marianna Pinzone, which focuses on mercury pollution dynamics in Arctic coastal ecosystems.

In total, 515 samples were analyzed, spanning the entire food web from primary producers to high-trophic-level predators (three seal species: *Erignathus barbatus*, *Pusa hispida,* and *Phoca vitulina,* as well as the black-legged kittiwake, *Rissa tridactyla*). Samples were collected from Atlantic-influenced outer waters to glacier-influenced inner basins. Isotopic values covered wide ranges ($\delta^{13}C = -28.47‰$ to $-18.51‰$; $\delta^{15}N = 1.9‰$ to $15.3‰$; $\delta^{34}S = 11.6‰$ to $20.49‰$) and varied significantly between sampling sites and ecological groups ($p < 0.05$). Our results highlighted the different pathways on which the predators rely on. Kittiwakes feed on almost exclusively pelagic prey, whereas the seals and fish displayed intermediate strategies, exploiting both benthic and pelagic trophic pathways. Two fish species, *Hippoglossoides platessoides* and *Gadus morhua* also displayed high position inside the food web. Spatially, the fjord zones were relatively similar to each other but displayed a broader isotopic range compared to the head of the fjord. Temporally, variation could only be assessed in *R. tridactyla*, where both inter- and intra-annual shifts in feeding behavior were observed. As reported in previous studies, kittiwakes tended to forage more intensively near glaciers after chick hatching while exploiting broader feeding areas earlier in the breeding season.

Under ongoing climate change, understanding the trophic functioning of sentinel systems such as Kongsfjorden is essential to anticipate biodiversity responses and ecosystem resilience.

Title : 'Trophic Ecology of the Arctic fjord, Kongsfjorden, Svalbard'

Name of the student : Nora Puppin; **Promotors :** Pr. Loïc Michel and Dr. Marianna Pinzone

Academic year: 2024 – 2025; **Laboratoire:** Laboratoire de Systématique et diversité animale

Résumé

Le Kongsfjord (79°N, 12°E), un fjord situé au nord-ouest de l'archipel du Svalbard. Cet archipel présente les taux de réchauffement les plus élevés de l'Arctique circumpolaire. Fortement influencé par le réchauffement et l'Atlantification, le Kongsfjord est un site clé où l'on retrouve des communautés biologiques et des réseaux trophiques fortement impactés par le changement climatique (Assmy et al., 2023 ; Hop et al., 2002).

L'objectif de ce mémoire était d'identifier les proies et les voies trophiques soutenant les prédateurs vivant dans le Kongsfjord, ainsi que d'évaluer les éventuelles variations spatiales et temporelles. Pour ce faire, des analyses d'isotopes stables (δ^{13}C, δ^{15}N, δ^{34}S) ont été réalisées afin de retracer le réseau alimentaire. Ce travail s'inscrit dans le cadre de deux projets (HgFJORD, FNRS CR, et SEASOL, Marie Curie), dirigés par la Dr. Marianna Pinzone, portant sur la dynamique de la pollution au mercure dans les écosystèmes côtiers arctiques.

Au total, 515 échantillons ont été analysés, couvrant l'ensemble du réseau trophique, des producteurs primaires aux prédateurs supérieurs étudiés (trois espèces de phoques : *Erignathus barbatus, Pusa hispida* et *Phoca vitulina*, ainsi que la mouette tridactyle, *Rissa tridactyla*). Les échantillons ont été collectés depuis les eaux externes, influencées par l'Atlantique, jusqu'aux eaux internes, influencés par les glaciers. Les valeurs isotopiques couvraient de larges gammes (δ^{13}C = –28,47‰ à –18,51‰ ; δ^{15}N = 1,9‰ à 15,3‰ ; δ^{34}S = 11,6‰ à 20,49‰) et variaient significativement entre les sites d'échantillonnage et les groupes écologiques ($p < 0{,}05$).

Nos résultats ont mis en évidence des comportements différents pour les prédateurs étudiés. Les mouettes dépendaient presque exclusivement de proies pélagiques, tandis que les phoques et les poissons adoptaient des stratégies intermédiaires, exploitant à la fois les voies trophiques benthiques et pélagiques. Deux espèces de poissons, *Hippoglossoides platessoides* et *Gadus morhua* avaient également des positions trophiques élevées. Sur le plan spatial, les différentes zones du fjord étaient relativement similaires entre elles, mais les zones internes du fjord présentait des enveloppes convexes isotopiques plus large. Sur le plan temporel, des variations n'ont pu être évaluées que chez *R. tridactyla*, où des changements interannuels et intra-annuels de comportement alimentaire ont été observés.

Face aux changements climatiques, comprendre le fonctionnement trophique de systèmes clés tels que le Kongsfjord est essentiel pour anticiper les réponses de la biodiversité et la résilience des écosystèmes.

Abbreviations and acronyms

- ArW: Arctic water
- AW: Atlantic water
- C: Carbon
- $\delta^{13}C$: Stable isotope ratios of carbon
- ESC: East Spitsbergen Current
- N: Nitrogen
- $\delta^{15}N$: Stable isotope ratios of nitrogen
- OAS: Optically Active Substances
- POM: Particulate Organic Matter
- S: Sulfur
- $\delta^{34}S$: Stable isotope ratios of sulfur
- SD: Standard Deviation
- SEA: Standard Ellipse Area
- SEA_B: Bayesian estimation of the Standard Ellipse Area
- SEA_C: Sample-size corrected Standard Ellipse Area
- SIA: Stable Isotope Analysis
- SIBER: Stable Isotope Bayesian Ellipses in R
- TA: Total Area of the convex hull
- TAW: Transformed Atlantic Water
- WSC: West Spitsbergen Current

Table of Contents

1. Introduction

1.1. Context

1.1.1. The Svalbard archipelago

The Svalbard archipelago, a Norwegian territory, is located within the Arctic Ocean (Hop & Wiencke, 2019) (Fig. 1A). It is bordered to the south and east by the Barents Sea, to the north by the Arctic Ocean and by the Greenland Sea to the west (Hop & Wiencke, 2019). The archipelago is the northernmost land in Norway. It spans latitudes 74° to 81°N and longitudes 10° to 35°E (Fig. 1A) and has an area of 61 022km² (Halbach *et al.,* 2019; Hjelle, 1993). It is a region with harsh and inhospitable conditions for humans; however, it hosts a diverse array of emblematic Arctic species able to thrive in this extreme environment. Approximately 60% of the archipelago is covered by glaciers, and the islands are characterized by numerous mountains and fjords (Hjelle, 1993; Lydersen *et al.,* 2014; Nuth *et al.,* 2013).

Fjord waters are generally classified as brackish, resulting from the mixing of seawater with freshwater inputs from rivers and glaciers (Syvitski *et al.,* 2012). Fjords therefore act as a continuum, linking oceanic and terrestrial domains where exchanges between these two systems lead to highly variable ecosystem dynamics (Choudhary *et al.*, 2020; Cottier *et al.*, 2005). Fjords and coastal waters are among the most productive ecosystems in the Arctic (Assmy *et al.,* 2023). The samples used in this study come from Kongsfjorden, considered to be an important Arctic monitoring site (Hop *et al.,* 2002), located in the northwest of Spitsbergen, the largest island of the Svalbard archipelago.

1.1.2. Kongsfjorden

Kongsfjorden is one of the best-studied marine systems in the Arctic (Assmy *et al.,* 2023). It extends approximately 26 km in length, with a width ranging between 6 and 14 km (78° 58′ 51″ N, 11° 53′ 56″ E) (Fig. 1B) (Assmy *et al.,* 2023; Cottier *et al.,* 2005). It lacks a sill at its mouth, making it open to the advection of water masses from the adjacent shelf area (Assmy *et al.,* 2023; Hop *et al.,* 2023). It is oriented from southeast to northwest and forms a glacial fjord system with Krossfjorden, which is about 30 km long, with a width that varies from 3 to 6 km (Fig. 1B) (Svendsen et al. 2002). The total volume of Kongsfjorden is estimated as 29.4km³ (Ito & Kudoh, 1997). According to Howe *et al.* (2003), the deepest point of Kongsfjorden is approximately 394 m in the outer fjord basin (Howe *et al.,* 2003; Maclachlan *et al.,* 2010).

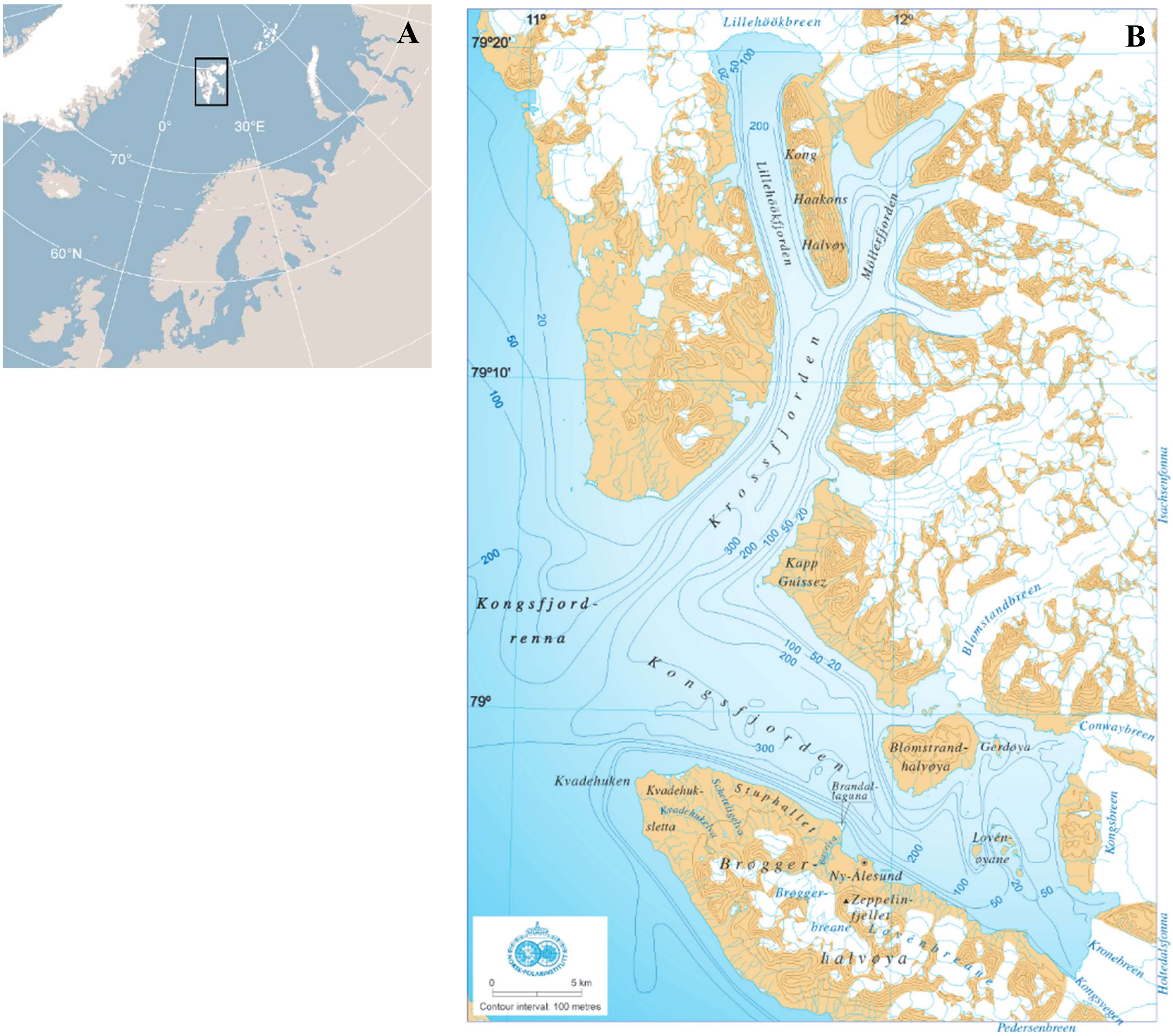


Figure 1 : **(A)** The location of the study area, the Svalbard Archipelago, is indicated with a black rectangle. Light blue is the ocean, white represents glaciers, and the ice-free land is brown (Kovacs *et al.,* 2024). **(B)** Map of the Kongsfjorden-Krossfjorden system (Svendsen *et al.,* 2002).

Arctic fjords exhibit some specific features, especially concerning the supply of freshwater. Indeed, freshwater is mostly supplied by surface meltwater and icebergs calved from glaciers (Cottier *et al.,* 2005; Svendsen *et al.,* 2002) rather than from lakes or rivers.

This fjord system is, though, strongly influenced by substantial freshwater inputs from adjacent glaciers (Choudhary *et al.*, 2020; Cottier *et al.,* 2005). Different tidewater glaciers are situated near the system formed by Kongsfjorden and Krossfjorden and influence the hydrodynamic regime (Fig. 1, 4). Lilliehöökbreen is situated at the head of Krossfjorden, whereas five other calving glaciers are located along the coast of the system (Cottier *et al.,* 2005; Svendsen *et al.,* 2002). Samples used in this study were gathered close to Kongsvegen, Conwaybreen, and Kronebreen (Fig. 1, 4). Kongsvegen, Kongsbreen, and Kronebreen glaciers overlook the Kongsfjord channel (Assmy *et al.,* 2023; Halbach *et al.,* 2019). Finally, Conwaybreen and Blomstrandbreen, situated on the northern coast of Kongsfjorden, also contribute to the hydrological regime (Halbach *et al.,* 2019; Maclachlan *et al.,* 2010) (Fig. 1, 4). Glacial ablation and ice calving, along with terrestrial runoff and snowmelt, contribute to the freshwater supply of the fjord (Assmy *et al.,* 2023; Svendsen *et al.,* 2002). The main freshwater input occurs in the summer; however, due to climate change, increased precipitation and accelerated melting rates are expected, which would lead to a rise in freshwater input to the fjord system (Svendsen *et al.,* 2002).

In the opposite direction of the freshwater input, Atlantic water and the Arctic Ocean meet and also influence the hydrography of the fjord. The warm and salty West Spitsbergen Current (WSC) from Atlantic water (AW; >3°C; S>34.65) meets the cold water masses of the East Spitsbergen Current (ESC) coming from the Arctic Ocean (ArW; -1.5-1.0°C; S=34.30-34.80) (Descamps *et al.,* 2017; Svendsen *et al.,* 2002; Assmy *et al.,* 2023; Hop *et al.,* 2023) (Fig. 2). These two bodies of water mix, forming Transformed Atlantic Water (TAW; 1.0-3.0°C; S>34.65), on the shelf, which is advected into Kongsfjorden (Svendsen *et al.,* 2002; Cottier *et al.,* 2005; Assmy *et al.,* 2023; Hop *et al.,* 2023) (Fig. 2). Despite the high latitude, the inner fjord remains ice-free during summer due to the relatively mild climate influenced by the warm Atlantic waters transported by the Spitsbergen Current (Hanelt *et al.,* 2001; Ito & Kudoh, 1997).

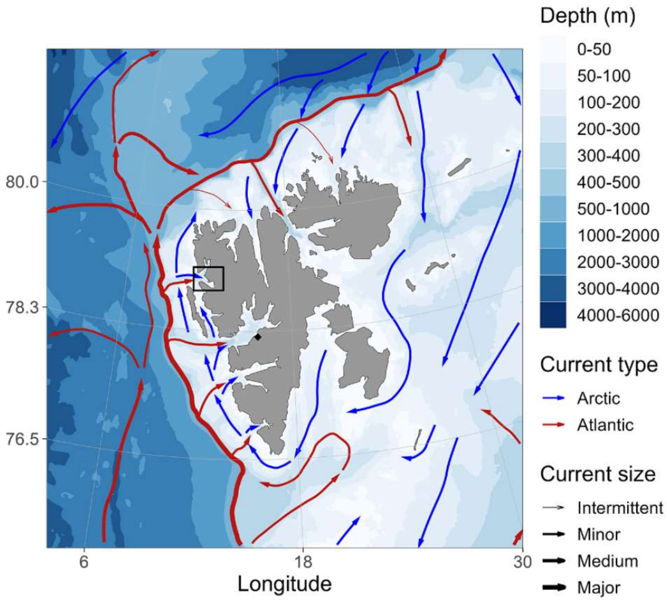


Figure 2: Map of the Svalbard archipelago showing the major currents. The black rectangle indicates the Kongsfjorden-Krossfjorden system. Atlantic water currents are shown in red, and Arctic water currents in blue. The black diamond indicates the position of Longyearbyen, the capital of Svalbard. (Assmy *et al.,* 2023)

In summary, Kongsfjorden is a glacial fjord influenced by both Atlantic and Arctic water masses, as well as significant freshwater input from glacial runoff (Fig. 1B, 2). It hosts a diverse assemblage of both boreal and Arctic flora and fauna, which must endure strong seasonal variations in physicochemical conditions driven by changes in water mass dominance, ice cover, and freshwater discharge (Hop & Wiencke, 2019).

Light represents one of the major drivers of the entire marine ecosystem. Since Kongsfjorden is located at high latitudes, there is a pronounced seasonality in light regime, changing from polar night in winter to midnight sun in summer (Hop *et al.,* 2019). The polar night lasts for about four months, from the end of October to mid-February (Karsten *et al.,* 2019). In the inner part of Kongsfjorden, the already long winter darkness is prolonged by sea ice formation, which typically breaks up between April and July (Svendsen *et al.,* 2002). Indeed, when present, snow and sea ice also strongly attenuate the transmission of solar radiation into the waters of Kongsfjorden (Hamre *et al.,* 2004, Pavlov *et al.,* 2019).

Turbidity changes drastically throughout the year (Hanelt *et al.,* 2001; Svendsen *et al.,* 2002). During spring, there is no input of meltwater, so the water body remains clear. In the beginning of summer, meltwater runoff creates a thin (~1 m) surface layer of turbid, brackish water, which significantly reduces light penetration. Below this layer, the water remains relatively clear until later in summer, when increased mixing with sediment-rich meltwater causes turbidity to extend several meters deep. The introduction of large volumes of meltwater plumes into the marine system during the summer melt season can reduce the euphotic zone to 0.3 m near the glacier front (Keck *et al.,* 1999). As snow around the fjord melts and freshwater input decreases, water transparency gradually improves. Therefore, seasonal variations in freshwater input result in strong water column stratification during summer and weak stratification in winter (Svendsen *et al.,* 2002).

Furthermore, the spring phytoplankton bloom contributes to light attenuation in the upper water column, as dense concentrations of algal cells enhance both absorption and scattering of solar radiation (Hegseth *et al.,* 2019). In general, optically active substances (OAS), such as particulate matter and phytoplankton, affect light absorption and scattering (Pavlov *et al.,* 2019).

In conclusion, Kongsfjorden exhibits pronounced spatial and temporal gradients in light availability, temperature, and salinity, mainly driven by the interaction between freshwater input and marine water inflow (Halbach *et al.,* 2019; Hop & Wiencke, 2019). Freshwater runoff introduces cold, low-salinity water at the surface, particularly in the inner fjord during the summer months (Torsvik *et al.,* 2019). In contrast, warmer and more saline Atlantic waters enter the fjord from the outer shelf, often at deeper layers (Hop & Wiencke, 2019; Svendsen *et al.,* 2002). This creates a distinct stratification, with strong horizontal and vertical gradients. Light availability also varies throughout the year, controlled by solar angle, sea ice cover, turbidity from meltwater inputs, and seasonal phytoplankton blooms, leading to significant heterogeneity in environmental conditions across the fjord (Hanelt *et al.,* 2001). These gradients shape the structure and functioning of both pelagic and benthic ecosystems.

1.2. The marine ecosystem of Kongsfjorden

As mentioned previously, Kongsfjorden is a glacial fjord that is influenced by both Atlantic and Arctic water masses (Fig. 2). Consequently, the fjord harbors a mixture of Atlantic and Arctic fauna, the composition of which varies among years depending on the advection of Transformed Atlantic Water (TAW) (Vihtakari *et al.,* 2018).

Like other marine ecosystems, the Kongsfjorden marine food web only possesses a few trophic levels (Fry, 1988; Iken *et al.,* 2005). Iken *et al.* (2005) demonstrated that the high Arctic food web is structured into four trophic levels, while Hobson & Welch (1992) and Hop *et al.* (2002) suggested the presence of five. Duarte *et al.* (2019) proposed a trophic web with up to six trophic levels. Regardless, ecosystem functioning and services are ultimately dependent on pelagic primary (phytoplankton) and secondary (zooplankton) production (Assmy *et al.,* 2023) (Fig. 3).

1.2.1. Primary producers: food web baseline

Svalbard hosts a wide diversity of marine organisms, all of which rely on primary producers (Smola *et al.,* 2017). The two main sources of marine primary production in the high Arctic are sea-ice algae and phytoplankton (Iken *et al.,* 2005; Yunda-Guarin *et al.,* 2022). Macroalgae are not included in this study; however, they are important not only as primary producers but also because they provide a substrate for benthic organisms (Smola *et al.,* 2017).

Of the 148 phytoplankton taxa identified in Kongsfjorden waters (Hop *et al.,* 2002), most are of Atlantic or cosmopolitan origin, with only 31 (21%) classified as Arctic or boreal–Arctic species (Hop *et al.,* 2006; Keck, 1999; Smola *et al.,* 2017). Phytoplankton communities inhabiting West Spitsbergen fjords show greater taxonomic diversity compared to those in adjacent open waters, although their primary production remains lower than in highly productive regions, such as the Barents Sea (Smola *et al.,* 2017) (Fig. 3).

In the Arctic Ocean, seasonal variations in sea-ice cover and light availability generate short pulses of ice-associated and pelagic primary production that form the base of the marine food web and sustain sympagic, pelagic, and benthic organisms (Iken *et al.,* 2005). Arctic fjords are characterized by a single, short, and pronounced spring phytoplankton bloom and two blooms of sea-ice algae at the beginning and end of the productive season (Ardyna & Arrigo, 2020; Renaud *et al.,* 2014; Søreide *et al.,* 2006). The nutrients depleted during the spring bloom and summer are restored during the dark period through intensive vertical mixing and upwelling (Hop *et al.,* 2006).

This bloom leads to a peak of zooplankton density and biomass at least one month later (Ardyna & Arrigo, 2020; Assmy *et al.,* 2023; Renaud *et al.,* 2024).

1.2.2. Zooplankton

Herbivorous zooplankton populations are usually seasonally coupled with pelagic primary producers (Renaud *et al.,* 2014). Zooplankton biomass in Kongsfjorden is relatively high compared to other Arctic regions, despite significant predation pressure from planktivorous fish and seabirds (Basedow *et al.,* 2004; Hop *et al.,* 2002). The zooplankton community reflects the mixture of water masses of Arctic and Atlantic origin, as the advection of Atlantic water can be a dominating factor in the shaping of the zooplankton community (Basedow *et al.,* 2004; Renaud *et al.,* 2024; Walkusz *et al.,* 2009).

A total of 84 zooplankton taxa have been identified in Kongsfjorden (Hop *et al.,* 2002, 2006). The community is dominated by *Calanus* sp., followed by amphipods (*Themisto* sp.) and euphausiids (*Thysanoessa* sp.), with ctenophores, chaetognaths, and other taxa also present but in lower abundance (Arendt *et al.,* 2013; Assmy *et al.,* 2023; Daase *et al.,* 2013; Walkusz *et al.,* 2009). *Calanus* sp. is considered to be a key species of the Arctic marine food web, as various predators rely on these copepods (Hop *et al.,* 2005, 2019; Ingvaldsen *et al.,* 2025; Renaud *et al.,* 2024) (Fig. 3). *Calanus* sp. and *Themisto libellula* are highly abundant pelagic grazers that function as key first-order consumers (Hop *et al.,* 2002; Søreide *et al.,* 2006; Wassmann *et al.,* 2006); although primarily herbivorous, evidence from Iken *et al.* (2005) indicates they may also ingest small pelagic prey alongside phytoplankton. However, *T. libellula* is also considered to have a more carnivorous diet, feeding mainly on *Calanus* sp. (Hop *et al.,* 2006).

Limacina helicina, a pelagic pteropod, has been variously classified in the literature; some studies suggest a predominantly herbivorous diet (Iken *et al.,* 2005), whereas others identify it as a carnivore (Gilmer & Harbison, 1991).

Ctenophores, siphonophores, and other gelatinous predators are important regulators of zooplankton, as they feed partly on the lower pelagic food web (Hop *et al.,* 2019; Hobson & Welch, 1992; Purcell, 1991). In general, ctenophores are preyed upon by higher trophic levels, such as cod and seabirds (Hop *et al.,* 2019) (Fig. 3).

Chaetognaths represent one of the most abundant carnivorous zooplankton taxa (Hop *et al.,* 2019). They feed on copepods and other zooplankton species and are predated by larger zooplankton, fish, and seabirds (Hop *et al.,* 2019; Terazaki, 2004) (Fig. 3).

Large populations of fish, seabirds and marine mammals feed on the lipid-rich zooplankton that can occur in large swarms (Wassmann *et al.,* 2006) (Fig. 3). Therefore, changes in zooplankton abundance, body size, and energy content alter the flow of energy through the pelagic food web, with cascading consequences for the growth and survival of seabirds and marine mammals (Hop *et al.,* 2006). Early-season availability of zooplankton prey is also critical for the survival and growth of both juvenile and adult planktivorous fish (Renaud *et al.,* 2024).

1.2.3. Fish

Due to its transitional location between polar and Atlantic water masses, Kongsfjorden supports a diverse ichthyofauna, with species representative of both Arctic and boreal ecosystems (Hop *et al.,* 2002). Some pelagic fishes are considered second-order consumers, like chaetognaths or ctenophores, whereas others occupy higher trophic levels (Hop *et al.,* 2002).

The polar cod (*Boreogadus saida*), a typical Arctic species, is one of the most common fish in Kongsfjorden (Hop *et al.,* 2002). It is the only fish species living in close association with sea ice, where it primarily consumes larger zooplankton forms as well as ice-associated fauna (Wassmann *et al.,* 2006). Together with capelin (*Mallotus villosus*), it occupies the third trophic level and constitutes a key forage resource for seabirds, marine mammals, and piscivorous fish, including commercially important Atlantic species such as haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) (Hop *et al.,* 2002; Hop & Gjøsæter, 2013; Renaud *et al.,* 2024). In contrast, demersal fish such as haddock and long rough dab (*Hippoglossoides* *platessoides*) feed mainly on benthic organisms and generally occupy slightly higher trophic levels than pelagic species (Wassmann et al., 2006).

Numerous secondary-level predators, including fish species such as capelin and polar cod, rely indirectly on a diet primarily composed of ice-associated invertebrates (Pinzone, 2021). Ice biota encompasses not only ice-associated flora and microorganisms but also a diverse ice fauna, including microbes, meiofauna, amphipods, and even fish (*B. saida*) (Hop *et al.,* 2006). The sympagic fauna plays a crucial ecological role, acting both as a trophic bridge between the sympagic and pelagic systems and as a foundational component of food chains that ultimately support top predators such as seabirds and seals (Hop *et al.,* 2006; Pinzone, 2021; Wassmann *et al.,* 2006) (Fig. 3).

1.2.4. Top predators

Svalbard hosts more marine mammal species than any other region in the High Arctic (Descamps *et al.,* 2017). Among the species familiar to the public are the emblematic polar bear (*Ursus maritimus*), several seal species such as the ringed seal (*Pusa hispida*) and the harbor seal (*Phoca vitulina*), as well as terrestrial mammals like the Arctic fox (*Vulpes lagopus*) (Hop *et al.,* 2002; Pinzone, 2021) (Fig. 3). Numerous seabird species also inhabit this region, either permanently or seasonally (Hop *et al.,* 2002; Lønne & Gabrielsen, 1992). The seabird community of Svalbard is dominated by gulls and auks (Lønne & Gabrielsen, 1992). The common eider (*Somateria mollissima*) is the largest contributor to the total bird biomass, followed by the black-legged kittiwake (*Rissa tridactyla*) and Brünnich's guillemot (*Uria lomvia*) (Isaksen *et al.,* 1995). This study focused on the black-legged kittiwake, a surface-feeder generalist that feeds on both fish and marine invertebrates (Descamps *et al.,* 2019; Hop & Gjøsæter, 2013; Vihtakari *et al.,* 2018) (Fig. 3). It breeds in colonies ranging in size from a few dozen to several thousand individuals in bird cliffs along the coast (Descamps *et al.,* 2019; Isaksen *et al.,* 1995). It is a migratory species that arrives approximately in April and leaves the Svalbard area in September for wintering areas in the North Atlantic (Hatch & Hatch, 1990; Isaksen *et al.,* 1995).

Four species of pinnipeds, the ringed seals (*Pusa hispida)*, the bearded seals (*Erignathus barbatus)*, the harbor seal (*Phoca vitulina*), and the walruses (*Odobenus rosmarus*), can also be observed in Svalbard (Hop *et al.,* 2002). The ringed seal, bearded seal, and walruse are three circumpolar pinnipeds, while the harbor seal is more widely distributed (Fig. 3). Their presence in this location can be explained by the influence of the West

Spitsbergen Current and its warm Atlantic water. On the other hand, walruses, harp seals (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) are seasonal residents along with many migratory cetaceans (Hop *et al.,* 2002). In this study, we selected three seal species as bioindicators: the harbor seal, the ringed seal and the bearded seal. These species differ in their ecological niches. The harbor seal is a pelagic species (Descamps *et al*., 2017; Hobson & Welch, 1992; Kovacs *et al*., 2024), the ringed seal is considered both sympagic and ice-associated, and the bearded seal is primarily benthic and prefers a coastal environment (Hobson & Welch, 1992; Hop *et al*., 2002).

Marine mammals and seabirds dominate the higher trophic level (Hop *et al.,* 2002). The top predators of this food web are polar bears (*U. maritimus*), killer whales (*Orcinus orca*) and Greenland sharks (*Somniosus microcephalus*) (Descamps et al., 2017). They are known to be able to feed on various other trophic levels (Fig. 3). The highest trophic level considered in this study is represented by seals and seabirds.

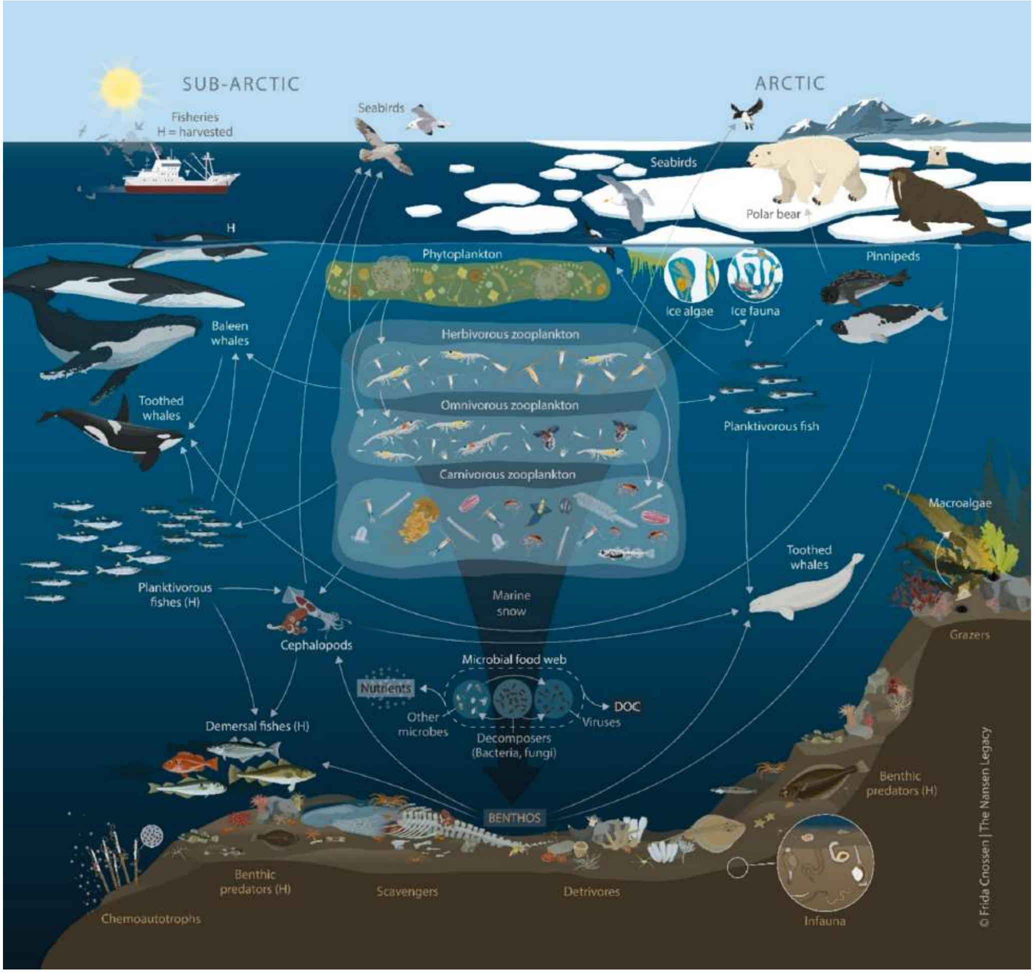


Figure 3: Schematic of the Barents Sea food web with representatives of all trophic levels. The dominant trophic linkages (who eats whom) are represented by white arrows. Primary producers are shown in green and in brown (seaweeds). Figure from Reigstad et al. (2025, in press) and (Ingvaldsen et al., 2025).

1.2.5. Pelagic-benthic coupling

The Arctic benthic system is tightly linked to pelagic and ice-associated production through the vertical flux of organic material, including phytoplankton cells, fecal pellets, zooplankton carcasses, molts, and marine snow (Iken *et al.,* 2004; Hop *et al.,* 2019) (Fig. 3).

During sinking, this phytodetritus may undergo bacterial degradation, which alters its isotopic composition before deposition on the seafloor (Iken *et al.,* 2004). In turn, benthic communities remineralize organic matter, recycling nutrients back to the water column and providing an important food source for higher trophic levels (Wassmann *et al.,* 2006).

The strength of pelagic–benthic coupling varies spatially and depends on nutrient availability, primary production, water mass distribution, stratification, and midwater grazing pressure (Iken *et al.,* 2004; Tamelander *et al.,* 2006). In regions of high productivity and low zooplankton grazing, fresh phytodetritus reaches the seabed and is efficiently exploited by the benthos, indicating a strong coupling (Tamelander *et al.,* 2006).

The seafloor hosts a rich epifauna, including hyperbenthic species such as the shrimp *Pandalus borealis*, which acts both as a predator and prey within Arctic food webs (Hop *et al.,* 2002; Wassmann *et al.,* 2006). Polychaetes are a dominant component of the benthic ecosystem, followed by mollusks (mostly bivalves), crustaceans, and echinoderms (Voronkov *et al.,* 2013; Wassmann *et al.,* 2006) (Fig. 3).

The seasonal freshwater input to Kongsfjorden, predominantly occurring during summer and autumn, significantly alters the oceanographic conditions of the inner basin and extends its influence to the central fjord (Hop *et al.,* 2006). Near glacier fronts, zooplankton exposed to low-salinity waters (<9 psu) may experience osmotic shock, resulting in significant mortality (Hop *et al.,* 2006; Lydersen *et al.,* 2013). Part of this biomass becomes readily available to surface-feeding predators such as kittiwakes (Lydersen *et al.,* 2013), while the remainder sinks to the seafloor. Hop *et al.* (2006) pointed out that this phenomenon, sustained over the 100-day melting season, can result in the removal of up to 85 tons of zooplankton from the water column, representing approximately 15% of the fjord's total zooplankton biomass. Consequently, glacial runoff plays a key role in strengthening pelagic–benthic coupling in the inner fjord by enhancing the downward flux of organic matter, both through flocculated particles and the deposition of dead zooplankton (Hop *et al.,* 2006).

1.2.6. The impact of climate change on the Kongsfjorden marine ecosystem

Svalbard is a complex and delicately balanced Arctic ecosystem, supported by fragile ecological foundations that are highly susceptible to environmental change. This archipelago is also known to be among the regions experiencing the most rapid temperature increase globally (Assmy et al., 2023; Karlsen et al., 2024; Rantanen et al., 2022). Indeed, the Arctic has warmed nearly four times faster than the global average over the past five decades, a phenomenon referred to as Arctic Amplification (Rantanen et al., 2022).

Due to their connection with both the terrestrial and the marine ecosystems, it is likely that climate change influences the fjord system from two different directions: the inner ends adjacent to the glaciers and the ends opening out into the sea (Svendsen *et al.,* 2002). At the local scale of Kongsfjorden, tidewater glacier melting and retreat is also important (Torsvik *et al.,* 2019). For instance, the glacier Kronebreen has retreated about 11 km during the last 150 years, and approximately one-third of this retreat has occurred in the last 20 years (Torsvik *et al.,* 2019). Glacial retreat and the associated decline in meltwater discharge are expected to reduce the upwelling of nutrient-rich waters, thereby lowering primary productivity in glacial fjords (Meire et al., 2017). This could also affect the foraging areas for seabirds and marine mammals in the glacial bays (Hop *et al.,* 2023).

One of the most visible effects of climate change in this region is the significant reduction of sea ice, which has seen its global extent and thickness drastically decrease over recent decades (Descamps *et al.,* 2017; Rantanen *et al.,* 2022). Beyond serving as an indicator of Arctic warming, sea-ice loss is also a major driver of Arctic amplification. Through feedback mechanisms associated with the decreasing surface albedo, the reduction in sea-ice extent accelerates the regional warming process (Post *et al.,* 2013). In addition, sea ice in polar waters is essential for the development of ice algal communities, which contribute to primary production in these ecosystems (Pavlova *et al.,* 2019), and for some obligatory sea ice species, such as the ringed seal or the polar bear (Descamps *et al.,* 2017) (Fig. 3).

Climate change is expected to cause an earlier onset of phytoplankton bloom, likely leading to a mismatch in timing between primary production and the availability of key consumers, such as the copepod *Calanus* sp., in the food web (Assmy *et al.,* 2023; Ingvaldsen *et al.,* 2025; Renaud *et al.,* 2024). This ‘mismatch’ between a phytoplanktonic bloom and high grazer density can undergo several issues (Renaud *et al.,* 2024). Another concern is that increasing meltwater input during summer is expected to enhance water column stratification. This process tends to promote the dominance of smaller phytoplankton species (<3-20 µm), which are generally a less nutritive and less accessible food source for larger zooplankton grazers (Assmy *et al.,* 2023; Li *et al.,* 2009). Li *et al.* (2009) report that ecosystems where picoplankton is dominant tend not to support large exports of biogenic carbon, either for sequestration or for extraction (food web). Indeed, grazing zooplankton migrate from overwintering depths to exploit the phytoplankton bloom (Wassmann *et al.,* 2006). This feeding period supports their reproduction and allows them to build up substantial lipid reserves essential for growth, development, and future overwintering. Through this process, they play a key role in transferring bloom-derived organic carbon to higher trophic levels (Wassmann *et al.,* 2006) (Fig. 3). Variations in zooplankton abundance, size, and energy content modify the flow of energy through the pelagic food web, ultimately impacting the growth and survival of seabirds and marine mammals (Hop *et al.,* 2006; Kovacs *et al.,* 2024).

These unprecedented transformations will induce profound ecological shifts, disrupting oceanic circulation and the global climate system (Kaleschke & Spreen, 2010). Such modifications will substantially impact Arctic marine food webs and key biological processes. The ecosystem responses to these changes include increased production, a reduction of the ice-associated ecosystem compartment, and a northward expansion of boreal species, a process commonly referred to as borealization (Ingvaldsen *et al.,* 2021; 2025) (Fig. 3).

1.2.7. The borealization of the Arctic

Also known as ‘Atlantification’, this phenomenon describes the progressive northward expansion and growing influence of boreal species in Arctic ecosystems, a process largely attributed to ongoing climate warming (Kortsch *et al.,* 2015; Ingvaldsen *et al.,* 2021). This shift alters community structure, biodiversity, and ecosystem functioning in polar regions (Fossheim *et al.,* 2015; Kortsch *et al.,* 2015), with impacts observed at all trophic levels, and is particularly noticeable in shelf waters and fjords (Bengtsson *et al.,* 2024; Bischof *et al.,* 2019).

In recent years, increased inflow of Atlantic Water has transported nutrients, algae, and fauna from the Norwegian Sea into Arctic fjords, further enhancing Atlantification (Renaud *et al.,* 2024). Such changes have been linked to earlier phytoplankton blooms and occasional mismatches with zooplankton grazing in the Barents Sea, particularly when early sea-ice retreat accelerates water column stratification (Bischof *et al.,* 2019; Renaud *et al.,* 2024). More frequent mismatches, together with altered community composition, are likely to restructure pelagic food webs (Descamps *et al.,* 2019; Renaud *et al.,* 2024).

Another consequence is that key Arctic species such as polar cod (*B. saida*) and the amphipod *T. libellula* are expected to be partly replaced by sub-Arctic and Atlantic taxa including capelin (*M. villosus*), Atlantic herring (*C. harengus*), Atlantic cod (*G. morhua*), and haddock (*M. aeglefinus*) (Hop *et al.,* 2002; Vihtakari *et al.,* 2018). The arrival of large predators may further trigger cascading effects and novel interactions with resident top predators, while new predator–parasite or pathogen relationships could intensify ecological disturbances (Bischof *et al.,* 2019).

1.3. Objectives

The overall objective of this master's thesis is to understand the ecological dynamics of Kongsfjorden marine predators and the food webs they rely upon. This study aims to investigate seasonal and spatial trophic dynamics in the fjord using stable isotope analysis to trace food-web pathways and assess ecosystem responses to environmental change. Knowledge of food-web structure, including the length, connectivity, and primary sources of trophic pathways, is important for our understanding of ecosystem function (McGovern *et al.,* 2018). We focus on four key predator species: the harbor seal (*Phoca vitulina*), the ringed (*Pusa hispida*) and the bearded seals (*Erignathus barbatus*), and the kittiwakes (*Rissa tridactyla*). Other predators such as polar bears and toothed whales pass through Kongsfjorden only occasionally and are therefore not included.

We measured $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values (in per mil, ‰) in 515 samples from 31 taxa and particulate organic matter (POM), covering the entire food web of Kongsfjorden (Table 1; Annex 1, 2). Samples were collected across four distinct zones from the Atlantic-influenced mouth of the fjord to the glacial-influenced inner fjord over a 9-month sampling period covering June to September 2023 and May to September 2024 (Fig. 4).

Specifically, this master's thesis seeks to investigate the following research questions:

What are the main trophic pathways and connections shaping the Kongsfjorden marine food web?

From this, three specific research questions arise:

1) **How does the trophic structure vary spatially between the glacial-influenced inner fjord and the Atlantic-influenced mouth?**

Given that Kongsfjorden is strongly influenced by both Atlantic and Arctic water masses, as well as by large tidal glaciers generating steep environmental gradients, distinct patterns among communities can be expected. Unfortunately, the temporal effect will not be analyzed due to insufficient sampling in several months.

2) **Which prey types and trophic pathways do Kongsfjorden high-trophic-level predators rely on most?**

The seal species do not seem to rely on the same prey, as *P. vitulina* is described to be an Atlantic pelagic feeder (Hop *et al*., 2002) whereas *P. hispida* and *E. barbatus* are more endemic ice-associated species. *E. barbatus* is known to be the most important mammal feeding on benthos of Kongsfjorden (Hobson & Welch, 1992; Hop *et al*., 2002). On the other hand, *P. hispida* is considered to be an opportunistic generalist predator (Descamps *et al*., 2017; Hobson & Welch, 1992; Kovacs *et al*., 2024). Kittiwakes are generalist surface-feeders that migrate to Svalbard for the breeding season (Descamps & Ramirez, 2021; Hop *et al*., 2002; Hop & Gjøsæter, 2013). Therefore, the top predators included in this study are expected to show distinct feeding patterns according to their ecological niches.

3) **How does the trophic position and resource use of black-legged kittiwakes (*Rissa tridactyla*) change over two consecutive breeding seasons?**

As a generalist surface-feeder, the species is constrained to a two-dimensional foraging environment (Suryan *et al.,* 2000), so its diet may vary with prey availability, affecting isotopic signatures (Descamps & Ramirez, 2021; Hop *et al.,* 2002; Mehlum & Giertz, 1984).

As food webs can help distinguish pathways of biogeochemical and contaminant cycling, the empirical knowledge gained in this study will be used in the framework of two larger projects (HgFJORD, FNRS CR and SEASOL, Marie Curie) aiming at assessing mercury pollution dynamics in Arctic coastal ecosystems.

1.4. Study of the trophic ecology using the stable isotopes

Hop *et al.* (2002) have described Kongsfjorden as an established Arctic reference site for marine ecological studies and monitoring (Hop *et al.,* 2002; Hop & Wiencke, 2019). Studying the trophic web in such a key system is therefore highly valuable for understanding ecosystem functioning and detecting responses to environmental change.

Stable isotope analysis (SIA) is a widely applied technique in ecological and environmental research, providing valuable insights into various questions, such as dietary reconstruction, animal migration patterns, and trophic interactions (Boecklen *et al.,* 2011). This method can be combined with other techniques, such as stomach content analysis or fatty acid analysis, to enhance understanding of dietary patterns.

The most compelling advantage of stable isotope analyses over other methods is that it provides a time-integrated measure of feeding habits (Nielsen *et al.,* 2017; Vander Zanden & Rasmussen, 1999). Furthermore, stable isotope ratios can be assessed in a wide range of organisms, as well as in organic particles in water and sediment, offering insights into the baseline components of food webs (Jaschinski *et al.,* 2008).

Stable isotope ratios can be used to define a geometric space, known as an 'isotopic niche', that can act as a proxy for the ecological niche of a population or species (Newsome *et al.,* 2007). In this master's thesis, three ecological tracers were employed: the stable isotopes of carbon, nitrogen and sulfur. Stable isotopes of carbon and nitrogen are the most frequently evaluated in trophic ecology studies. Carbon isotopic composition ($^{13}C/^{12}C$) is primarily employed to identify the prey consumed by the organism being studied (DeNiro & Epstein, 1978; Peterson & Fry, 1987). Indeed, carbon isotopic ratios undergo minimal alteration during transfer up the food web, but the animal is, on average, enriched in $\delta^{13}C$ by approximately 1‰ relative to its diet (DeNiro & Epstein, 1978). Therefore, $\delta^{13}C$ of aquatic consumers can provide information about the sources of energy to higher consumers. The nitrogen isotope ratio ($^{15}N/^{14}N$) provides information about the trophic position of the organism (DeNiro & Epstein, 1981). Indeed, consumers become enriched in $\delta^{15}N$ relative to their food by 3-4‰. In this master's thesis, the sulfur isotope ratio ($^{34}S/^{32}S$), less commonly used, was also analyzed. It provides information on the prey consumed, similar to the carbon isotope ratio (Peterson & Fry, 1987). A combined analysis of the carbon and sulfur isotope ratios allows for insights into the distribution of individuals within a given geographic area (Gajdzik *et al.,* 2016).

2. Materials and methods

2.1. Sampling

2.1.1. Research area

This study focuses on the marine food webs of Kongsfjorden (78° 58′ 51″ N, 11° 53′ 56″ E). Samples were collected during multiple scientific expeditions conducted from May 2023 to September 2024.

A total of 20 sampling sites were established, both inside and outside Kongsfjorden, and these were subsequently grouped into four main areas: Outer Zone (OZ); Central Zone (CZ); Northern Glacial Zone (NGZ) and Southern Glacial Zone (SGZ) (Fig. 4). In the Southern Glacial Zone there were 8 different sites: Kongsvegen, St. 960, St. 959, St. 1310, Kronebreen, Kb8, Raudvika and Kb5. In the Northern Glacial Zone, 3 sites were sampled: Kb6, Løven Islands, and Kb7. The Central Zone included 6 sampling sites: Krykkjefjellet, Bayelva, Kb4, Kb3, Thiisbukta and Old pier. Finally, the sites ExFOBB Outer, Kb1 and St.1332 are part of the Outer Zone. A total of 275 samples were collected in the Central Zone, 116 in the Outer Zone, 32 in the Northern Glacial Zone and 91 in the Southern Glacial Zone (Table 1, Annex1).

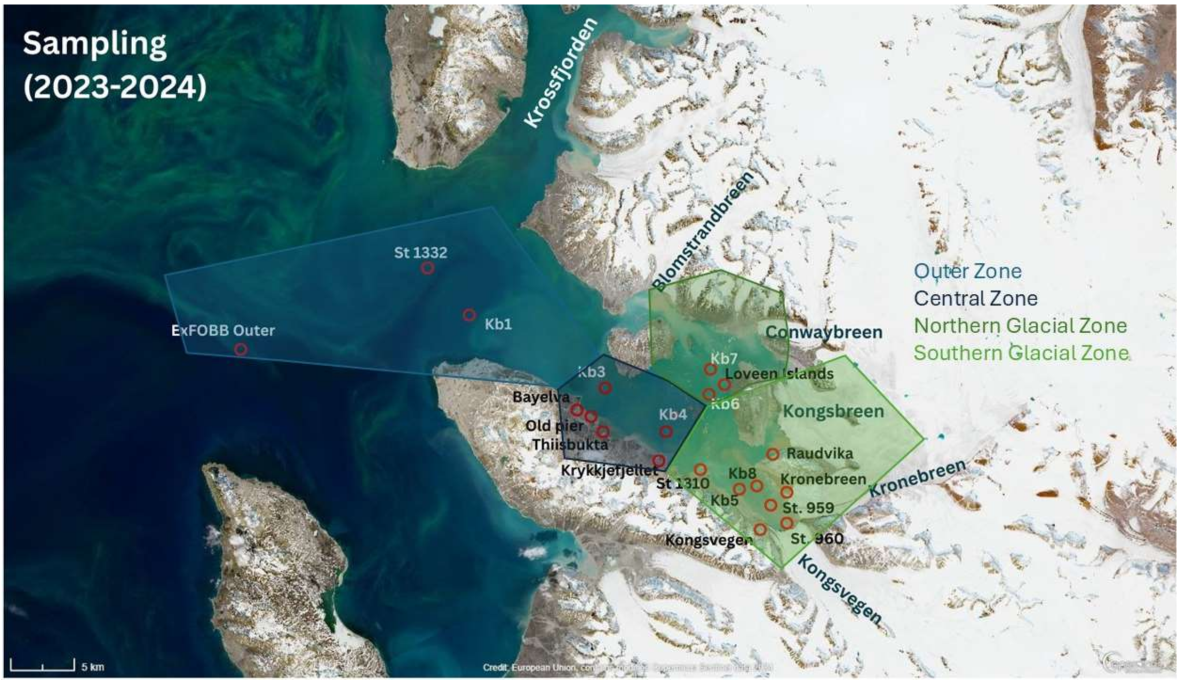


Figure 4: Sample sites by zone in Kongsfjorden, Svalbard. Zones are color-coded, and glaciers are identified in dark blue. Red dots indicate individual sampling stations, distributed across the study area.

Several campaigns have been carried out by different teams of collaborators (Table 1). The HgFJORD fieldwork targeted the fjord's inner zones, while the OpKROP cruise sampled stations outside the fjord and deployed trawling gear. An additional expedition, the UNIS-led cruise, allowed the collection of sediment, benthic invertebrates, and fish both inside and outside the fjord (Kb1, Kb4, Kb8, St1310, and St1332). During the OpKROP campaign and the UNIS-led cruise, they used the research vessel RV Helmer Hanssen. The MS Teisten, a smaller boat, was used during HgFJORD fieldwork.

2.1.2. Fjord sampling

Sea ice sampling

Six sea-ice cores were collected at two locations, Station 1 (north of the Løveen Islands, NGZ) and Station 4 (Raudvika, SGZ), during April-May 2023 and 2024. Cores were taken from fast ice just before the onset of sea-ice melt. In both sites, they cored the sea ice using a 9 cm diameter Kovacs Corer (Kovacs Ice Auger Drills, USA). The samples were stored at -20°C, sectioned, and thawed overnight at 4°C, then filtered to collect sea-ice algae (Table 1; Annex 1).

POM sampling

Particulate organic matter (POM) and plankton samples were obtained using hand nets hauled vertically from a depth of 20 m to the surface and collected directly into 1L brown plastic bottles (3 replicates per site) (Table 1; Annex 1). For each sampling, vertical profiles of salinity, temperature, chlorophyll a (Chl a) fluorescence, and turbidity were measured using an STD profiler (MiniSTD model SD-204, SAIV A/S, Bergen, Norway).

Benthic sampling

Benthic fauna were collected using a 1000 cm^2 Van Veen metal grab (15 L, KC Denmark) between two and five deployments per site, depending on weather conditions. Grab contents were sieved over a 1000 µm metal sieve, and benthic organisms were picked with ceramic tweezers and placed in Nalgene containers before categorization at the semi-wet terrestrial laboratory in Ny-Ålesund (Table 1; Annex 1).

Zooplankton sampling

Mesozooplankton were collected by vertical hauls with a WP-2 net (0.255 m opening, 200 µm mesh), and macrozooplankton with a WP-3 net (1 m^2 opening, 1000 µm mesh), covering the water column from bottom (50–300 m depth) to surface. Samples were rinsed and stored in 1 L Nalgene bottles (Table 1; Annex 1).

Macrozooplankton and fish sampling

During the OpKROP cruise, macrozooplankton and fish were sampled using pelagic and tucker trawls. Collected organisms included various fish species and macroinvertebrates (Table 1; Annex 1). During the UNIS-led cruise, fish and invertebrates were caught with a Campelen 1600 shrimp trawl with rockhopper gear (17-20 m x 4 m opening). Invertebrates were stored in plastic containers, whereas fish were dissected onboard for muscle sampling, measurement, and weighing.

Bird sampling

Adult black-legged kittiwakes were sampled at the Krykkjefjellet colony (78°54′N, 12°13′E, 7km southeast of Ny Ålesund) during pre-laying (late June) and chick rearing (early July) (Table 1; Annex 1). Birds were caught on their nests using a noose on a 5 m fishing rod. A blood sample (~1 mL) was collected from the alar vein with heparinized syringe. Birds were weighed, and their skull and tarsus length were measured. Each bird was marked with metal rings and PVC plastic bands engraved with a three-digit code and fixed to the bird's tarsus for identification from a distance.

Seal sampling

Finally, individuals from three seal species (*Erignathus barbatus, Phoca vitulina, Pusa hispida*) were captured (Table 1; Annex 1). Large-meshed monofilament nets (100 m length, 8 m depth) were set from shore, monitored continuously, and seals were removed upon entanglement. Captured animals were restrained in hoop or A-frame nets. Harbor seals were lightly anesthetized with Telazol whereas ringed and bearded seals were handled without chemical restraint. The seals were weighed to nearest 0.5 kg, the sex was determined, and a flipper tag was attached for future identification (Jumbo Roto-Tag, Dalton UK). Biopsies were collected from the seals using a custom-designed tissue corer (5 mm diameter) that takes a sample from the skin, through the whole of the blubber column. The entire handling lasted about 40 minutes. Sample collection from live animals was approved by the Norwegian Animal Care Authority and the Governor of Svalbard.

Table 1 : Summary of the number of samples for each taxon used in this master's thesis. A more detailed table, broken down by month and zone, is provided in the annex (Annex 1).

Taxon	**2023**	**2024**	**Total**
Mammals			
Erignathus barbatus	2	/	2
Phoca vitulina	15	/	15
Pusa hispida	5	/	5
Bird			
Rissa tridactyla	69	15	84
Fish			
Boreogadus saida	/	19	19
Clupea harengus	/	1	1
Gadus morhua	12	34	46
Hippoglossoides platessoides	4	12	16
Leptoclinus maculatus	3	22	25
Mallotus villosus	/	4	4
Melanogrammus aeglefinus	/	1	1
Pollachius sp.	5	/	5
Juvenile fish	1	16	17
Invertebrates			
Bivalve	/	5	5
Brittle star	/	8	8
Calanus sp.	/	46	46
Chaetognaths	/	15	15
Chlamys islandica	/	6	6
Ctenophore	/	6	6
Edwardsia sp.	/	1	1
Jellyfish	/	19	19
Juvenile crabs	/	8	8
Juvenile shrimps	/	9	9
Limacina helicina	/	1	1
Nephtys sp.	/	5	5
Pandalus borealis	10	34	44
Polynoidae	/	14	14
Sabinea septemcarinata	/	7	7
Themisto libellula	/	21	21
Thysanoessa sp.	/	27	27
Zooplankton	3	10	13
POM			
Ice-POM	/	6	6
Pelagic-POM	/	14	14
Total	**129**	**386**	**515**

Since the sampling was conducted by collaborators teams, the descriptions above are based on information from the 'SEASOL_Sampling Report' document and discussions with Dr. Marianna Pinzone, the project manager.

2.2. Stable isotope analysis

2.2.1. Samples preparation

Dried samples were homogenized using an agate mortar and pestle to avoid metal contamination, as those samples were also used for other analyses. All equipment was cleaned using 3% hydrochloric acid (HCl) and then Milli-Q water between each manipulation. Given the samples are being used for further analyses, subsamples were taken and stored in glass containers, with careful attention paid to avoid any contamination.

Echinoderms, krill, juvenile shrimps and crabs were acidified to remove carbonates. Indeed, those carbonates are more enriched in ^{13}C than other tissue components, and their composition is not directly related to diet (Schlacher & Connolly, 2014). Thus, it is necessary to remove them. Subsamples were exposed to 37% hydrochloric acid (HCl) vapor for 48 h to remove carbonates (Hedges & Stern, 1984). After 2 days, the presence of remaining carbonates was tested with ‘Champagne tests’ (Jaschinski *et al.,* 2008), where a small amount of the acidified sample is dropped in HCl to verify if the acidification was successful. The absence of effervescence resulting from the reaction of carbonates with HCl indicates sufficient carbonate removal (Jaschinski *et al.,* 2008). Acidified subsamples were then kept at 50°C for 24h before further sample preparation.

2.2.2. Isotopic analysis

Isotopic analysis involves the measurement of the isotopic composition of samples using an elemental analyzer (EA; Vario Microcube, Elementar) coupled to an isotope ratio mass spectrometer (IRMS; Isoprime precision, Elementar). The analyses were performed at the University of Liège. The capsules undergo combustion in the analyzer which allows us to know the relative elemental concentration of the sample as a percentage of dry mass (%C, %N, %S). The analyzer is continuously coupled to a mass spectrometer, which gives the stable isotope composition of the analyzed sample.

The isotopic ratios are expressed in δX (‰) notation, which reflects the deviation between the isotopic ratio of a sample and that of a standard (Coplen, 2011), calculated using the following equation :

$$\delta_x = \left(\frac{R_{sample}}{R_{standard}} - 1\right) X\ 1000$$

Where X represents either ^{13}C, ^{15}N or ^{34}S and R is the ratio of the heavy isotope to the corresponding light isotope ($^{13}C/^{12}C$, $^{15}N/^{14}N$ or $^{34}S/^{32}S$) in the sample (R_{sample}) and standard ($R_{standard}$). The international standards of carbon, nitrogen and sulfur correspond respectively to the Vienna Pee Dee Belemnite (vPDB), atmospheric nitrogen and Canon Diablo troilite (CTD).

All dried and homogenized sample materials were weighed using a precision analytical balance (Mettler Toledo AX105 Delta Range, precision 0.01g). An adequate amount of material (depending on sample nature) was packed into tin capsules for subsequent isotopic analyses. The same amount of tungsten oxide (WO_3) was added to facilitate sample combustion.

The analytical sequence, in addition to the actual samples, included three types of reference materials. Firstly, the calibration of the elemental analysis is guaranteed by sulfanilic acid (Sigma-Aldrich, Overijse, Belgium). This organic compound has known proportions of carbon, nitrogen, and sulfur ($\delta^{13}C$ = –25.6 ± 0.4‰; $\delta^{15}N$ = –0.1 ± 0.4‰; $\delta^{34}S$ = 5.9 ± 0.5‰; means ± SD). Moreover, isotopic measurements were calibrated against certified reference materials (CRM, *certified reference materials*) from the International Agency for Nuclear Energy (IAEA): IAEA-Caffeine for carbon and nitrogen ($\delta^{13}C$ = − 27.771 ± 0.043‰; $\delta^{15}N$ = 1.0 ± 0.2‰) and IAEA-SO5 for sulfur ($\delta^{34}S$ = 0.5 ± 0.2‰). Finally, in-house lab standards (seabass muscle) were used as secondary analytical standards. These reference materials have been distributed regularly between the samples (approximately every 12 samples) to ensure accurate analysis and, when needed, correct for instrument drift.

2.3. Statistical analysis

All statistical analyses were performed using the R software (v4.3.2.; R Core Team 2024) and Microsoft Excel.

Tests for normality and homoscedasticity were conducted to determine the appropriate use of either parametric or non-parametric methods for the analysis of carbon ($\delta^{13}C$), azote ($\delta^{15}N$) and sulfur ($\delta^{34}S$) isotopic ratios. In most cases, the hypotheses were not respected; therefore, to ensure consistency and comparability across all statistical analyses, only non-parametric Kruskal-Wallis tests were applied throughout the study. Post-hoc Dunn tests were then performed to identify significant pairwise differences. P-values were adjusted for multiple comparisons using the Benjamini–Hochberg (BH) correction, and the significance level was set at $p = 0.05$. All p-values used are reported in Annex 3.

Isotopic niche analysis was computed using the SIBER package version 2.1.3. (Jackson *et al.,* 2011). Boxplots and biplots generated with ggplot2 were used to visualize the overall structure of the food web. Isotopic convex hulls and standard ellipses were constructed to compare trophic niches among taxa, providing a quantitative representation of niche breadth and overlap. Niche distributions in $\delta^{13}C$–$\delta^{15}N$ and $\delta^{13}C$–$\delta^{34}S$ space were used as proxies for realized ecological niches. Bayesian analyses were performed to estimate standard ellipse areas (SEA_B), with small-sample corrections applied (SEAc; Jackson et al., 2011). SEAc values were compared to assess the probability that one niche was larger than another, with a 95% threshold chosen as the criterion for significance. Overlap among standard ellipses and 40% ellipses was used to estimate the proportion of trophic and habitat resources shared between taxa (Layman & Allgeier, 2012).

To study the ecosystem from a community perspective, convex hulls were used to encompass the isotopic variability within each zone, providing a comparative view of the extent and overlap of isotopic niche space among regions. While sampling effort varied among zones, convex hull comparisons still provided meaningful insights into spatial patterns.

3. Results

Overall, 515 samples from 31 taxa and particulate organic matter (POM) were analyzed. They were collected across four distinct zones (Central Zone: n = 275; Outer Zone: n = 117; Northern Glacial Zone: n = 32; Southern Glacial Zone: n = 91) over a 9-month sampling period spanning June to September 2023 and May to September 2024. The isotopic ratios of studied taxa ranged from *Thysanoessa* sp. (–28.47‰) to Polynoidae (–18.51‰) for the δ^{13}C, from POM (1.9‰) to *Phoca vitulina* (15.33‰) for the δ^{15}N, and from *Sabinea septemcarinata* (11.6‰) to jellyfish (20.49‰) for δ^{34}S (Fig. 6A; B).

The three stable isotope ratios measured in this study varied across taxa (Kruskal-Wallis: $p < 0.0001$ in each case) (Fig. 6A, B). Dunn's post-hoc tests were subsequently performed to identify pairwise differences; all p-values are provided in the Annex 3.

Table 2 : Mean of δ^{13}C, δ^{15}N and δ^{34}S values for each taxon and the particular organic matter analyzed in this study

Taxon	**δ^{13}C (‰) (mean ± sd)**	**δ^{15}N (‰) (mean ± sd)**	**δ^{34}S (‰) (mean ± sd)**
Mammals			
Erignathus barbatus	-20.02 ± 0.11	14.29 ± 0.08	17.55 ± 0.11
Phoca vitulina	-20.07 ± 0.25	14.78 ± 0.19	17.41 ± 0.44
Pusa hispida	-20.56 ± 0.11	14.08 ± 0.17	17.77 ± 0.09
Bird			
Rissa tridactyla	-21.18 ± 0.32	13.45 ± 0.49	18.02 ± 0.78
Fish			
Boreogadus saida	-21.45 ± 0.38	11.11 ± 0.72	19.24 ± 0.23
Clupea harengus	-21.98	10.8	18.92
Gadus morhua	-20.80 ± 0.51	12.90 ± 0.71	17.88 ± 0.75
Hippoglossoides platessoides	-20.18 ± 0.72	13.36 ± 0.54	17.29 ± 0.72
Leptoclinus maculatus	-22.08 ± 1.27	10.47 ± 0.89	18.18 ± 1.12
Mallotus villosus	-22.09 ± 0.49	10.18 ± 0.21	18.61 ± 0.10
Melanogrammus aeglefinus	-20.96	12.03	18.4
Pollachius sp.	-21.84 ± 0.20	9.91 ± 0.12	18.42 ± 0.59
Juvenile fish	-22.11 ± 0.65	9.19 ± 0.76	18.97 ± 0.64
Invertebrates			
Bivalve	-19.34 ± 1.33	6.83 ± 0.76	18.22 ± 0.96
Brittle star	-21.04 ± 0.31	8.45 ± 0.65	19.51 ± 0.42
Calanus sp.	-24.36 ± 0.73	7.01 ± 0.57	18.94 ± 0.83
Chaetognaths	-22.67 ± 0.75	8.23 ± 1.36	19.02 ± 0.94
Chlamys islandica	-20.37 ± 1.34	6.54 ± 0.85	19.19 ± 0.25
Ctenophore	-23.41 ± 1.50	6.47 ± 1.27	19.73 ± 0.89
Edwardsia sp.	-19.96	6.37	19.2
Jellyfish	-22.59 ± 0.72	6.69 ± 0.94	20.28 ± 0.11

Juvenile crabs	-22.36 ± 0.15	7.93 ± 0.19	19.49 ± 0.20
Juvenile shrimps	-22.25 ± 0.26	7.93 ± 0.42	19.54 ± 0.17
Limacina helicina	-20.51	5.28	19.3
Nephtys sp.	-18.88 ± 0.77	9.34 ± 0.33	13.87 ± 1.07
Pandalus borealis	-19.15 ± 0.33	10.77 ± 0.65	16.66 ± 1.22
Polynoidae	-19.29 ± 1.01	8.93 ± 1.49	13.88 ± 1.40
Sabinea septemcarinata	-18.87 ± 0.43	11.79 ± 0.28	14.10 ± 0.64
Themisto libellula	-22.67 ± 0.82	7.65 ± 0.27	19.50 ± 0.24
Thysanoessa sp.	-22.94 ± 1.71	8.32 ± 0.33	19.36 ± 0.30
Zooplankton	-22.89 ± 0.80	6.15 ± 1.24	19.38 ± 0.65
POM			
Ice-POM	-24.01 ± 0.67	NA	20.09 ± 0.15
Pelagic-POM	-22.75 ± 0.42	3.35 ± 1.12	20.12 ± 0.15

The $\delta^{13}C$ values of Ice-POM and Pelagic-POM differed significantly ($p = 0.002$), whereas no significant difference was found in their $\delta^{34}S$ values ($p = 0.342$) (Table 2). Unfortunately, $\delta^{15}N$ data were unavailable for Ice-POM (Table 2).

All the samples analyzed for this master's thesis were summarized by date and zone in the annex (Annex 1). Separate boxplots for the three isotopes across the four sampling zones analyzed in this study were provided in the annex (Annex 2).

3.1. Spatial variation from head to mouth of the Kongsfjorden

First, the $\delta^{13}C$– $\delta^{15}N$ isotopic hull plot illustrated that three of the four sampling zones (Central Zone, Northern and Southern Glacial Zone) had similarly sized isotopic niches, which were nearly three times larger than the remaining zone (Outer Zone) (Fig. 5A; Table 3). Indeed, the Total Area (TA) values for the Outer Zone was 10.73, whereas the TA values for the Central Zone, as well as the Northern and Southern Glacial Zones, ranged from 26.79 to 35.14, reflecting substantial differences in isotopic niche width (Table 3). All the isotopic hulls appeared to overlap, but the hull representing the Outer Zone was considerably narrower (Fig. 5A). The Southern Glacial Zone had the largest $\delta^{15}N$ range (11.84), while the Outer Zone showed the smallest $\delta^{15}N$ range (4.69). The Northern Glacial Zone displayed the widest $\delta^{13}C$ range among all zones (6.02), whereas the Outer Zone presented the narrowest range (5.22) (Fig. 5A; Table 3).

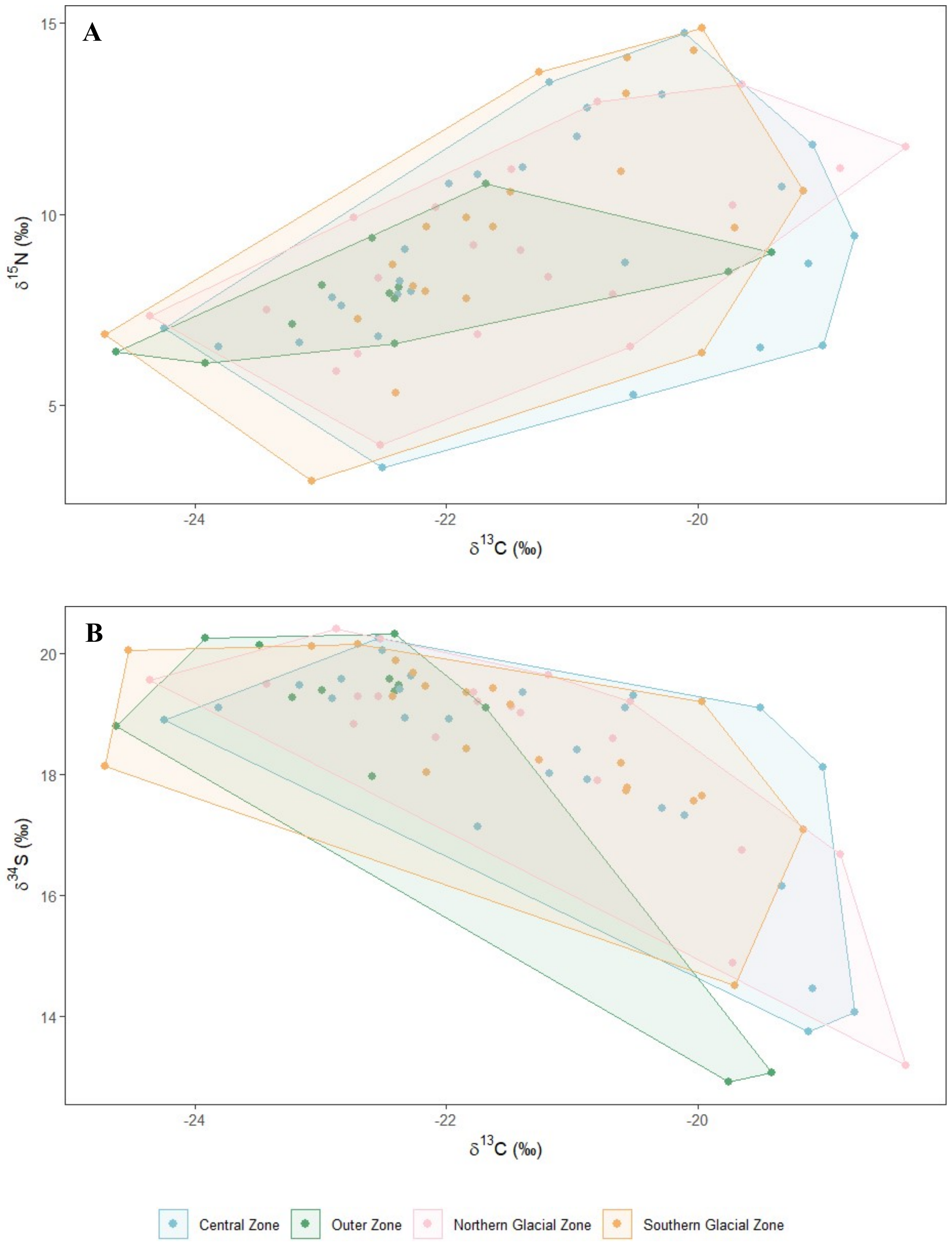


Figure 5 :**(A)** Isotopic hulls representing the niche space of marine organisms and particulate organic matter (POM) in $\delta^{15}N$ vs. $\delta^{13}C$ (‰) bi-plot space. Each point corresponds to the mean $\delta^{15}N$ and $\delta^{13}C$ value of a taxon or organic matter sources within a given zone. **(B)** Isotopic hulls representing the niche space of marine organisms and particulate organic matter (POM) in $\delta^{34}S$ vs. $\delta^{13}C$ (‰) biplot space. Each point corresponds to the mean $\delta^{34}S$ and $\delta^{13}C$ value of a taxon or functional group within a given zone.

Table 3 : Summary of three Layman (2007) metrics based on $\delta^{13}C$ and $\delta^{15}N$ values across the four oceanographic zones determined for this master's thesis. These metrics were calculated following the framework proposed by Layman et al. (2007) to assess trophic diversity and structure within each zone (Layman *et al.,* 2007).

C - N	Central Zone (CZ)	Outer Zone (OZ)	Northern Glacial Zone (NGZ)	Southern Glacial Zone (SGZ)
dY_range	11.37	4.69	9.43	11.84
dX_range	5.49	5.22	6.02	5.56
TA	35.14	10.73	26.79	34.79

The $\delta^{13}C$– $\delta^{34}S$ isotopic hull plot illustrated that the four zones had overlapping hulls of similar size (Fig. 5B), as corroborated by similar $\delta^{15}N$, $\delta^{13}C$ range, and Total Area (TA) values (Table 4). The Outer Zone and the Northern Glacial Zone exhibited the highest variability in sulfur isotopic values (Table 4).

Table 4 : Summary of three Layman (2007) metrics based on $\delta^{13}C$ and $\delta^{34}S$ values across the four oceanographic zones determined for this master's thesis. These metrics were calculated following the framework proposed by Layman et al. (2007) to assess trophic diversity and structure within each zone (Layman *et al.,* 2007).

C - S	Central Zone (CZ)	Outer Zone (OZ)	Northern Glacial Zone (NGZ)	Southern Glacial Zone (SGZ)
dY_range	6.51	7.39	7.22	5.65
dX_range	5.49	5.22	6.02	5.58
TA	17.72	13.56	15.40	17.44

3.2. Trophic analysis of the food web via the stable isotopes

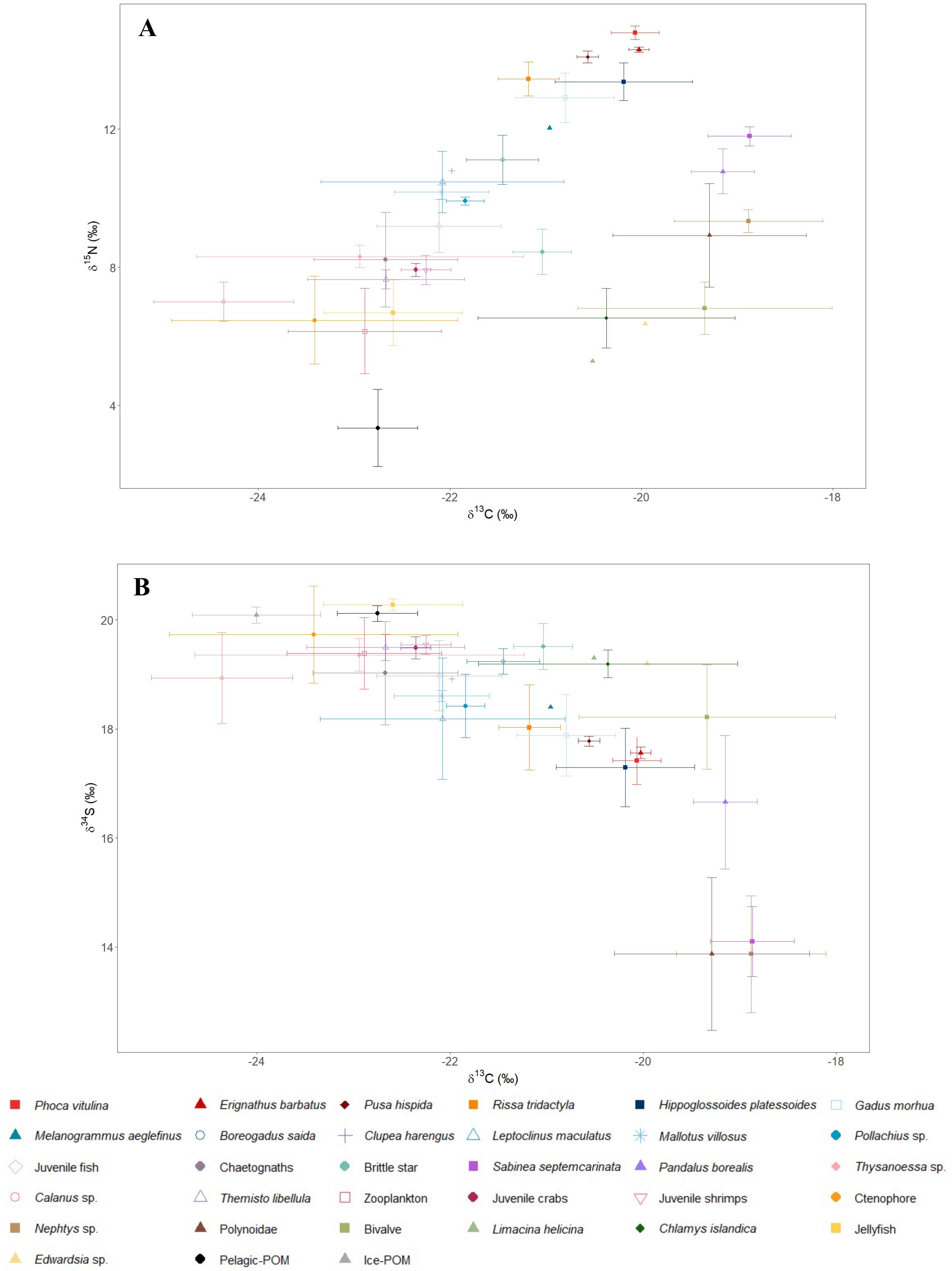


Figure 6 : Biplot of stable isotope ratios for various marine organisms and POM from the study area. Each symbol represents a taxon or organic matter sources, color-coded and shaped as indicated in the legend. **(A)** Biplot of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic composition (‰). Error bars indicate standard deviations for $\delta^{13}C$ (horizontal) and $\delta^{15}N$ (vertical), reflecting variability in isotopic values. **(B)** Biplot of stable carbon ($\delta^{13}C$) and sulfur ($\delta^{34}S$) isotopic composition (‰) for various marine organisms and POM from the study area. Error bars indicate standard deviations for $\delta^{13}C$ (horizontal) and $\delta^{34}S$ (vertical), reflecting variability in isotopic values.

The species with the highest $\delta^{15}N$ values were the three seal species (*Phoca vitulina*, *Erignathus barbatus* and *Pusa hispida*), along with the black-legged kittiwake (*Rissa tridactyla*) (Fig. 6A; Table 2). Some fish species, such as *Hippoglossoides platessoides, Gadus morhua* and *Melanogrammus aeglefinus* ($n = 1$), showed $\delta^{15}N$ values similar to those of the seals and the kittiwake. The other fish species tended to have lower $\delta^{15}N$ values (Fig. 6A; Table 2; Annex 3).

The $\delta^{13}C$–$\delta^{15}N$ biplot (Fig. 6A) suggested the presence of two relatively distinct clusters. Indeed, the two annelid taxa sampled in this study (Polynoidae and *Nephtys* sp.), the anemone *Edwardsia* sp., the two mollusk species (*Limacina helicina* and *Chlamys islandica*) and the taxon classified as 'Bivalve' exhibited less negative $\delta^{13}C$ values compared to the other taxa (Fig. 6A; Table 2). For example, $\delta^{13}C$ values of *C. islandica* and jellyfish were significantly different ($p = 0.022$). Similarly, the shrimp species, *Sabinea septemcarinata* and *Pandalus borealis*, showed relatively high $\delta^{13}C$ values compared to other crustaceans (Fig. 6A; Table 2). Both exhibited significant differences in $\delta^{13}C$ values when compared to *Thysanoessa* sp. ($p < 0.001$ for each case). A table containing the mean values for each taxon and for the three isotopes analyzed in this study is provided in the annex (Annex 3).

Most taxa exhibited $\delta^{34}S$ values ranging from approximately 16 to 21‰ (Fig. 6B; Annex 3). The $\delta^{34}S$ values of the fish species analyzed did not show any statistically significant differences (Annex 3). However, the two polychaete genera and *Sabinea septemcarinata* tended to show significantly lower $\delta^{34}S$ values compared to the other taxa (Fig. 6B). These species were clearly separated from *Pandalus borealis*, which contrasted with the pattern observed in the previous graph (Fig. 6A; Annex 3).

3.3. Temporal shifts in kittiwakes (Rissa tridactyla) isotopic niches

$\delta^{13}C$ values ranged between -22.04 and -20.6‰, whereas $\delta^{15}N$ values varied from 11.96 to 14.46‰ (Fig. 7A) and $\delta^{34}S$ from 13.92 to 19.35‰ (Fig. 7B).

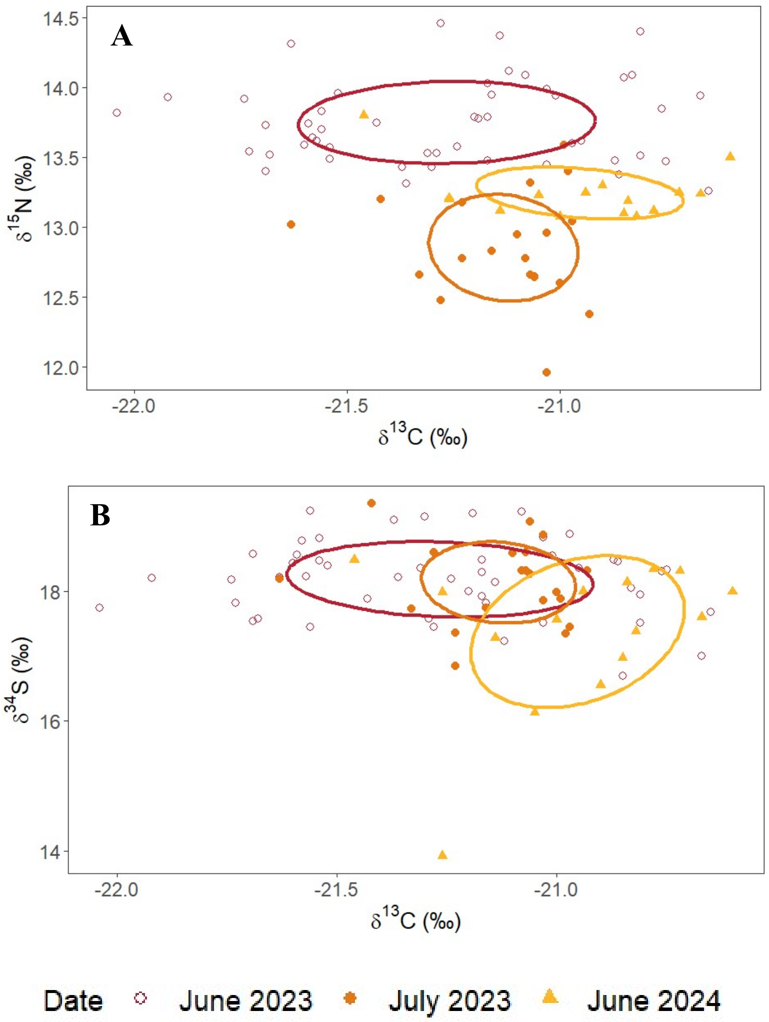


Figure 7 : Individual stable isotope values and resulting isotopic niches computed with **(A)** $\delta^{13}C$ and $\delta^{15}N$ values **(B)** $\delta^{13}C$ and $\delta^{34}S$ values of *Rissa tridactyla* at different periods. Each symbol represents a sampling period, color-coded and shaped as indicated in the legend.

First, the Kruskal-Wallis test confirmed significant variation in isotopic values across sampling dates ($\delta^{13}C$ $p = 0.0028$ and $\delta^{15}N$ $p < 0.0001$) (Fig. 7A). The Dunn post-hoc test revealed a significant difference in $\delta^{13}C$ values between kittiwakes sampled in June 2023 and those collected the following year ($p_{(2023\text{-}2024)} = 0.002$). Regarding $\delta^{15}N$, individuals from June 2023 differed significantly from both July 2023 ($p_{(\text{June 2023 - July 2023})} < 0.0001$) and June 2024 ($p_{(2023\text{-}2024)} < 0.0001$). Isotopic ellipses were non-overlapping, except between July 2023 and June 2024, where a negligible overlap of 5.5‰² was observed (representing 7.27% of the July 2023 ellipse area and 19.05% of the June 2024 ellipse area) (Fig. 7A). The June 2024 population exhibited a much narrower and smaller ellipse compared to the other time periods, as reflected by SEAc values (June 2023: 0.32‰²; July 2023: 0.22‰²; June 2024: 0.08‰²) (Fig. 8A). Model simulations further supported this pattern: the isotopic niche of June 2024 kittiwakes was smaller than that of July 2023 and June 2023 in 99.7% and 99.99% of model runs, respectively (Fig. 8A).

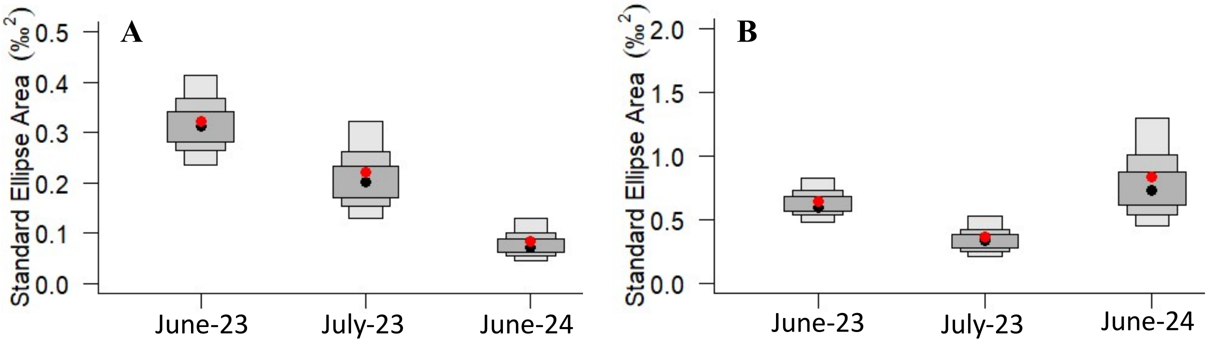


Figure 8 : SIBER density plots depicting the standard ellipse areas for *Rissa tridactyla* from the different sampling dates and computed with **(A)** δ13C and δ15N values and **(B)** δ13C and δ34S values. Black dots represent the modes. Shaded boxes represent the 50 %, 75 %, and 95 % confidence intervals from dark to light grey. Red dots are standard ellipse areas corrected for sample size (SEAc).

The biplot of $\delta^{13}C$–$\delta^{34}S$ (Fig. 7B) illustrated the kittiwakes' isotopic ellipses for the same sampling periods as those shown in the $\delta^{13}C$–$\delta^{15}N$ biplot (Fig. 7A). The majority of $\delta^{34}S$ values ranged from 16.13‰ to 19.35‰, except for one kittiwake sampled in June 2024 that displayed a value of 13.92‰ (Fig. 7B).

A Kruskal–Wallis test revealed a significant difference in $\delta^{34}S$ values among groups ($p = 0.01$). However, the Dunn post-hoc test between the July 2023 and June 2024 populations was not significant ($p = 0.064$). All isotopic ellipses overlapped to varying degrees. An overlap was observed between the ellipses of June 2023 and July 2023, with an overlapping area of 47.44‰², corresponding to 50.23% of the June 2023 ellipse and 89.18% of the July 2023 ellipse (Fig. 7B). The ellipse representing July 2023 also overlapped with that of June 2024, with an overlapping area of 9.04‰², representing 37.3% of the July 2023 ellipse and 14.66% of the June 2024 ellipse (Fig. 7B). Finally, the ellipses of June 2023 and June 2024 shared an overlapping area of 47.16‰² (June 2023: 14.07% of the ellipse area; June 2024: 20.18% of the ellipse area) (Fig. 7B). Among the three time periods, the July 2023 population showed the smallest isotopic niche, based on SEAc values (June 2023: 0.65‰²; July 2023: 0.36‰²; June 2024: 0.83‰²), which was further supported by comparisons of SEA_B values (Fig. 8B). Indeed, the July 2023 population had a smaller niche than the June 2023 and June 2024 populations in 98.8% and 99.4% of simulation runs, respectively (Fig. 8B).

3.4. Inter-zone differences between Kongsfjorden and offshore

In order to study the spatial variation and the food web on which predators relied, five fish taxa along with representatives from the zooplankton and the benthic community were used to calculate the SIBER ellipses. In addition, *Rissa tridactyla* and the three seal species (*Erignathus barbatus*, *Pusa hispida* and *Phoca vitulina*) were included. Kittiwakes and seals were sampled exclusively within the fjord, but birds were sampled in either June 2023, 2024, or July 2023 to investigate their temporal distribution. δ^{13}C values ranged between -25.47 and -18.03‰, whereas δ^{15}N values varied from 4.43 to 15.33‰ (Fig. 9). As previous analyses indicated no significant differences within the fjord, the NGZ, SGZ, and CZ were grouped together into a single "Fjord" zone, whereas the outer zone (OZ) remained distinct.

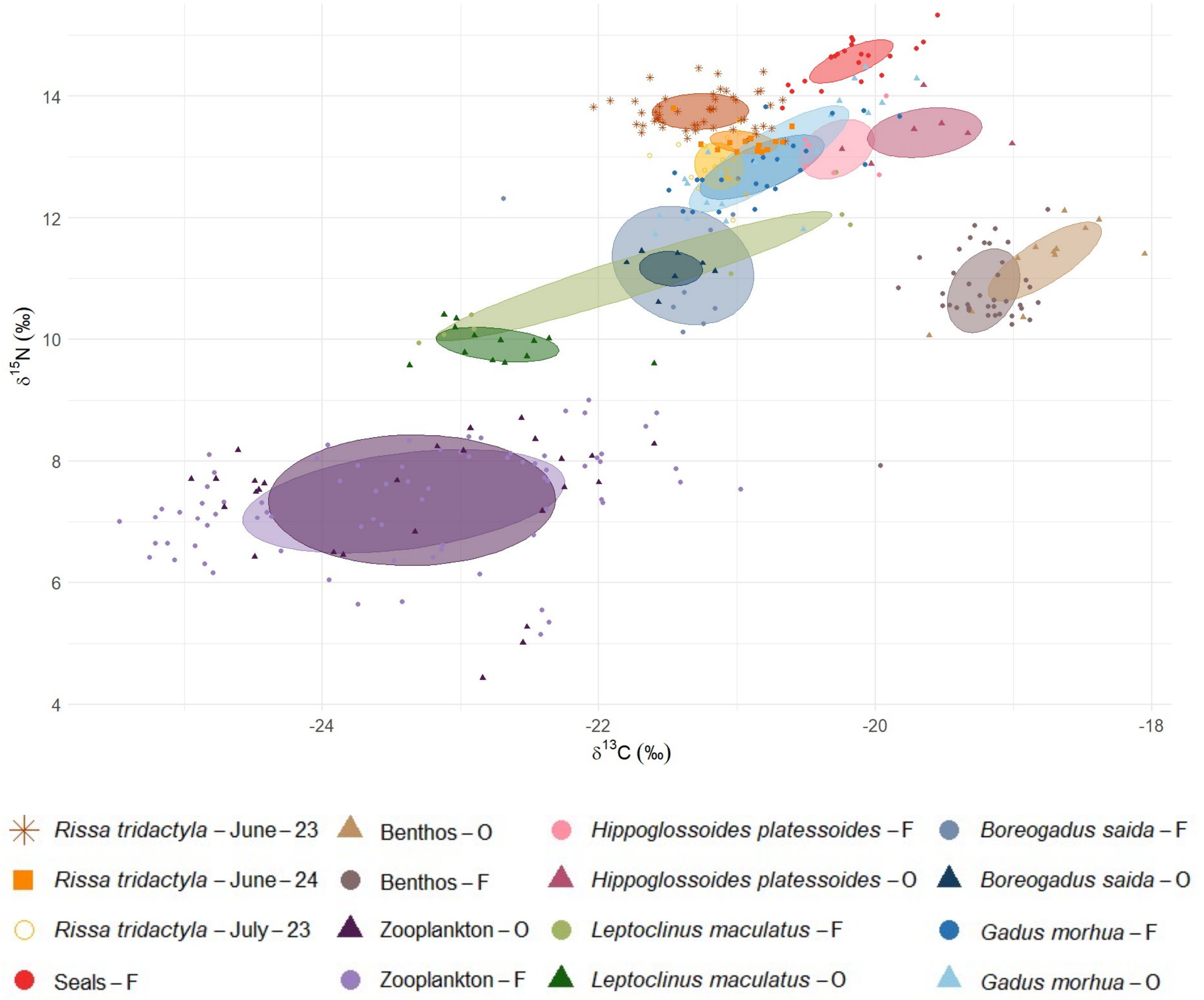


Figure 9 : Individual stable isotope values and resulting isotopic niches computed with δ^{13}C and δ^{15}N values of different taxa sampled from the head to the mouth of Kongsfjorden. Each symbol represents a taxon color-coded and shaped as indicated in the legend (F = Fjord; O = Outer zone). "Fjord" refers to samples from Central, Northern Glacial and Southern Glacial Zones. Ellipses represent 40% confidence intervals of isotopic niches and were generated using the ggplot function in R.

First, as observed previously, the benthic and the zooplankton community exhibited distinct isotopic values (Fig. 9; Table 2). Indeed, in the $\delta^{13}C$ vs. $\delta^{15}N$ biplot, the zooplankton isotopic ellipses were clearly separated from those of the benthos. There was minimal overlap in isotopic space between offshore and fjord benthic communities (9.1‰²), representing 22.03% of the Offshore ellipse area and 23.21% of the Fjord ellipse area (Fig. 9). In contrast, the niche overlap was considerably higher for zooplankton, reaching 52.1‰² of overlapping area, representing 74.52% of the Offshore ellipse area and 92.2% of the Fjord ellipse area (Fig. 9). The SEAc values revealed that the isotopic niche of Offshore benthic communities was broader than that of Fjord communities in 63.16% of model runs (Fig. 10). In contrast, the Fjord zooplankton community had a larger niche than the Offshore population in 19.56% of model runs (Fig. 10).

When considering $\delta^{13}C$ vs. $\delta^{15}N$ isotopic niches, *L. maculatus* displayed distinct isotopic ellipses depending on the zone studied, as supported by SEAc values (Fjord: 1.76‰²; Offshore: 0.40 ‰², Fig. 10). Model outputs suggested a larger niche for the Fjord population compared to the Offshore in 99.9% of model runs (Fig. 10). The *L. maculatus* populations from the two regions studied here shared an overlap area of 5.35‰², representing 27.5% of the Offshore ellipse area and 6.25% of the Fjord ellipse area (Fig. 9).

For *H. platessoides*, SEAc values were relatively similar across the two zones (Offshore: 0.62‰²; Fjord: 0.49‰²; Fig. 10). The Offshore population had a larger niche than the Fjord population in 67% of runs, indicating less certainty in this comparison (Fig. 10). The isotopic niche overlap between the two populations was minimal, with an overlapping area of 3.71‰² (Offshore: 6.49% of ellipse area; Fjord: 8.11% of ellipse area, Fig. 9).

Between the two available zones, the Fjord *Boreogadus saida* population displayed a smaller isotopic niche than the Outer Zone population in 99.9% of model runs (Fig. 10). The isotopic niche of the Offshore was fully encompassed by that of the Fjord, resulting in a 100% overlap for the Offshore. However, this corresponded to only 13.99‰² of the total overlapping area between the two niches (Fig. 9).

The isotopic ellipses of *G. morhua* displayed relatively similar values in the $\delta^{13}C$ vs $\delta^{15}N$ isospace. In fact, there was a substantial overlap between the Offshore and Fjord populations, with an overlapping area of approximately 59.77‰² (Fig. 9). This corresponded to 60.99% of the Offshore ellipse area and 96.86% of the Fjord ellipse (Fig. 9). *G. morhua* displayed distinct isotopic ellipses depending on the zone studied, as supported by SEAc values (Fjord: 0.60‰²;

Offshore: 0.83 ‰^{2}, Fig. 10). Indeed, the isotopic ellipse from the Offshore was smaller than that of the Fjord in 96.1% of model iterations (Fig. 10).

The isotopic niche of *G. morhua* also overlapped with that of kittiwakes from all sampling periods except for the June 2023 population (Fig. 9). Specifically, 54.54% of the July kittiwake population overlapped with 13.19% of the offshore *G. morhua* population, corresponding to an area of 11.9‰^{2} of overlapping area. The inshore fish population showed an even stronger overlap, with 50% of the July kittiwake population, representing 19.2% of the inshore fish niche (16.47‰^{2} of their total overlapping area) (Fig. 9). For the June 2024 kittiwake population, 7.14% of the offshore *G. morhua* isotopic niche overlapped with 48.64% of the kittiwakes, corresponding to 6.58‰^{2}. In the fjord, 5.52‰^{2} of the overlapping area was shared between *G. morhua* and June 2024 kittiwakes, representing 6.63% of the fjord *G. morhua* niche and 26.03% of the kittiwake niche (Fig. 9).

Kittiwakes were exclusively sampled within the fjord as their colony was located at Krykkjefjellet (78°54' N, 12°13' E), neither were the seals as they were sampled either in Raudvika (SGZ) or Thiisbukta (CZ). The isotopic ellipse of the seals and the kittiwakes did not overlap (Fig. 9).

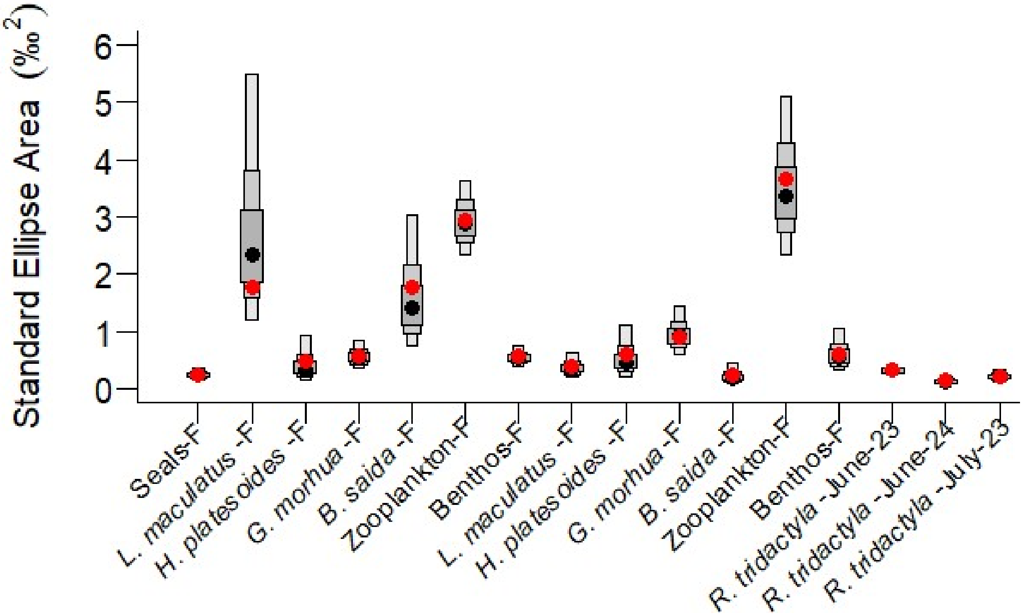


Figure 10 : SIBER density plots depicting the standard ellipse areas for the different taxa from the head to the mouth of Kongsfjorden and computed with δ^{13}C and δ^{15}N values (F = Fjord; O = Outer zone). "Fjord" refers to samples from Central, Northern Glacial and Southern Glacial Zones. Black dots represent the modes. Shaded boxes represent the 50 %, 75 %, and 95 % confidence intervals from dark to light grey. Red dots are standard ellipse areas corrected for sample size (SEAc).

4. Discussion

Hop *et al.* (2002) have described Kongsfjorden as an well-established Arctic reference site for marine ecological studies and monitoring (Hop *et al.,* 2002; Hop & Wiencke, 2019). The main objective of this master's thesis was to understand the ecological dynamics of Kongsfjorden marine predators and the food webs they rely upon using isotopic ratios. The analysis of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$) isotopic ratios provides valuable insights into a species' trophic ecology by encompassing data on prey type, trophic position, and the spatial origin of prey capture (Gajdzik *et al.,* 2016; Peterson & Fry, 1987).

4.1. Homogeneity within, variability beyond: species assemblages in Kongsfjorden

As Kongsfjorden was divided into four distinct zones for this study, it is interesting to wonder if there are isotopic differences between those "species assemblages" (Fig. 4, 5A, 5B). Because the samples were not collected consistently throughout the study period, potential temporal variations in trophic structure could not be fully assessed.

First, the isotopic hulls from the three fjord zones, Central Zone (CZ), Northern Glacial Zone (NGZ), and Southern Glacial Zone (SGZ), displayed comparable isotopic ranges (Fig. 5A, B; Table 3, 4). In contrast, the isotopic hull from the Outer Zone (OZ) exhibited narrower isotopic ranges (Fig. 5A, B; Table 3, 4). The "Outer Zone" values fell entirely within the isotopic range encompassed by the three fjord zones (Fig. 5A, B; Table 3, 4).

There appears to be no substantial differences within the fjord zones, with communities being relatively heterogenous, resulting in broader isotopic ranges compared to the mouth of the fjord (Fig. 5A, B; Table 3, 4). This pattern could be related to the inherent characteristics of this fjord, as the absence of a prominent sill makes Kongsfjorden a particularly dynamic system, which could explain the homogeneous trophic diversity within the fjord (Hop *et al.,* 2002; Renaud *et al.,* 2011; Svendsen *et al.,* 2002). A similar pattern was reported by Arendt *et al.* (2010) in a Greenland fjord, where they observed a shift between the zones inside and outside the fjord. They documented variations in physical and chemical conditions, along with changes in the water column structure at the fjord entrance, which coincided with changes in plankton community composition and biomass.

It seems that trophic pathways are more diverse within the fjord, whereas the mouth of the fjord relies primarily on a single dominant pathway. Indeed, the Outer Zone seems to display lower isotopic variability, as indicated by the narrower isotopic ranges of its community

(Fig. 5A, B; Table 3, 4). This outcome is somewhat unexpected, since fjords are often considered non-steady systems, and their communities can be viewed as subsets of the adjacent marine communities (Włodarska-Kowalczuk *et al.,* 2012). In fact, Włodarska-Kowalczuk *et al.* (2012) showed that inner fjords, outer fjords, and the open shelf host significantly different communities in terms of species composition and diversity, with the inner basins in particular exhibiting a marked decrease in species richness. This contrasts with our results, as the three fjord zones displayed broader isotopic hulls. More specifically, the head of the fjord (SGZ) exhibited one of the largest total areas, as well as the widest ranges of $\delta^{13}C$ and $\delta^{15}N$ (Fig. 5A, B; Table 3, 4).

The differences observed may be due to the sampling protocol. Indeed, sampling was not conducted in the same way across the different zones, which could lead to variation in community composition. Only a few taxa were sampled in all zones (Annex 1), either because they were absent from certain areas or because they were present but not collected. For instance, the three seal species included in this study were sampled exclusively in the SGZ or the CZ, whereas the species *Mallotus villosus* was collected only in the Outer Zone (Annex 1).

In conclusion, these results suggest that trophic pathways in Kongsfjorden are broader and more variable than at the mouth of the fjord. However, it does not seem to be a significant difference between the species assemblages within the three fjord zones. The fjord being a dynamic system, the species assemblages seem quite heterogenous (Cottier *et al.*, 2005; Hobson *et al.*, 1994; Sherwood & Rose, 2005; Włodarska-Kowalczuk *et al.*, 2012).

4.2. The main trophic pathways and connections shaping the marine food web

First, the $\delta^{13}C$–$\delta^{15}N$ biplot (Fig. 6A) revealed the presence of two relatively distinct trophic pathways within the studied ecosystem. These 2 components seem to exist along a division in pelagic versus benthic food resources (Fig. 11). Indeed, a clear separation appears between certain invertebrates that likely rely more on benthic sources, thus, characterized by less negative $\delta^{13}C$ values, and most taxa, which seem to depend predominantly on pelagic food sources (Hobson *et al.,* 1995; McGovern *et al.,* 2018; Sherwood & Rose, 2005). In summary, benthic organisms (mollusks, sea anemones, annelids and shrimps) showed less negative $\delta^{13}C$ values (and relatively higher $\delta^{15}N$ for shrimps), indicating a stronger association with the benthic producers (Fig. 6A; Table 2) whereas zooplankton (*e.g.,* Calanus *sp.*, jellyfish, and ctenophores) were characterized by lower $\delta^{13}C$ values, aligning with pelagic production (Fig. 6A; Table 2).

4.2.1. Particulate organic matter POM

Pelagic-POM and Ice-POM $\delta^{13}C$ values were significantly different ($p = 0.002$). Although Ice-POM has been reported to be more enriched in ^{13}C than Pelagic-POM (Søreide *et al.*, 2006; Tamelander *et al.*, 2006), the values obtained in this study fall within the range documented in previous works. For example, Wing *et al.* (2012) reported Ice-POM $\delta^{13}C$ values between –27‰ and –16.5‰, with most of the variability attributed to differences in sea ice thickness (Iken *et al.,* 2004; Søreide *et al.,* 2006; Wing *et al.*, 2012). The relatively low $\delta^{13}C$ values observed here were consistently transmitted throughout the food web, including to fish and benthic invertebrates, supporting the role of POM as a major basal food source in the ecosystem (Hobson *et al.*, 1995) (Fig. 6A; Table 2).

4.2.2. Benthic invertebrates

The two polychaete taxa studied here (*Nephtys* sp. and Polynoidae) are logically associated with the benthic compartment (Wlodarska-Kowalczuk *et al.,* 2007). No significant isotopic differences were observed between the two taxa (Fig. 6A, B; Table 2). Both *Nephtys* sp. and several polynoid species have previously been described as predators and scavengers (Iken *et al.,* 2005; Renaud *et al.,* 2011), which may explain their position in the $\delta^{13}C$–$\delta^{15}N$ biplot. They were both relatively enriched in ^{13}C and exhibited high $\delta^{15}N$ values, consistent with a higher trophic position and benthic feeding habits (Fig. 6A; Table 2). Along with *S. septemcarinata* they are the only taxa that appear to be closely associated with the benthic compartment as indicated by their lower $\delta^{34}S$ values (Fry *et al.,* 2008; Peterson, 1999; Nielsen *et al.,* 2018; Raoult *et al.,* 2024) compared to organisms linked to the pelagic compartment (Fig. 6B, 11; Table 2).

The intermediate isotopic signature of the brittle star ($\delta^{13}C = -21.04 \pm 0.31$‰ and $\delta^{15}N = 8.45 \pm 0.65$‰) was somewhat unexpected (Fig. 6A, 11). Given their benthic lifestyle, a stronger reliance on benthic food sources could have been anticipated (Gibson & Barnes, 2003; Hop *et al*., 2002). However, some brittle stars are highly flexible omnivores, capable of switching feeding strategies depending on resource availability (Tamelander *et al*., 2006; Yunda-Guarin *et al.,* 2022). Species-level identification was not completed, so dietary preferences could not be verified, but their relatively enriched $\delta^{13}C$ signatures suggest that brittle stars sampled for this study may exploit a different mix of food sources, and this has already been observed by Tamelander *et al.* (2006). For instance, consumption of isotopically heavier ice-derived POM reaching the seabed early in the season could increase their $\delta^{13}C$ values (Tamelander *et al.*, 2006).

P. borealis is described as a hyperbenthic shrimp that plays a central role in Arctic food chains, functioning as both an active predator and scavenger, as well as an important prey item for higher trophic-level consumers (McGovern *et al.,* 2018; Urban *et al.,* 2022; Wassmann *et al.,* 2006). According to Urban *et al.* (2022), the northern shrimp feeds on zooplankton, such as chaetognaths and jellyfish, but has also been reported to consume polychaetes, euphausiids, mollusks, and echinoderms. As a result, *P. borealis* is expected to occupy a relatively high trophic position compared to other benthic species, which is what has been observed in this study ($\delta^{15}N$ value = 10.77 ± 0.65‰) (McGovern *et al.,* 2018; Urban *et al.,* 2022; Sherwood & Rose, 2005). *S. septemcarinata* also exhibited higher $\delta^{15}N$ values than most invertebrates ($\delta^{15}N$ value = 11.79 ± 0.28‰), a finding consistent with McGovern *et al.* (2018), who suggested that this shrimp species primarily relies on detritus of phytoplanktonic origin. Unlike *P. borealis, S. septemcarinata* has been relatively understudied, making its dietary habits difficult to verify. According to Renaud *et al.* (2011), both shrimps are predators and scavengers. So, based on the present results, it can be assumed that its feeding ecology is similar to that of *P. borealis,* and they both rely more on benthic resources (Fig. 6A, 11; Table 2).

4.2.3. Zooplankton

Among the zooplankton species, the copepods (mostly represented by *Calanus* sp.) exhibited more negative $\delta^{13}C$ values than *P. borealis* and *S. septemcarinata* (Fig. 6A, 11; Table 2). This difference likely reflects their pelagic feeding habits and reliance on phytoplankton-derived carbon sources, in contrast to the more benthic or omnivorous diets of the shrimp species (McGovern *et al.,* 2018). Indeed, *Calanus* sp. grazed mainly on pelagic-POM but can also utilize ice-associated POM as a food source, especially in the early season, before phytoplankton become abundant (Hop & Gjøsæter, 2013; Søreide *et al.,* 2008; Tamelander *et al.,* 2006). These feeding habits suggest that *Calanus* sp. relies minimally on benthic carbon sources (Søreide *et al.,* 2008). Both *Calanus* sp. and *Thysanoessa* sp. (commonly referred to as krill) are extremely abundant first-order consumers within the pelagic food web (Hop *et al.,* 2002; Søreide *et al.,* 2006; Wassman *et al.,* 2006), which explains their position in the $\delta^{13}C$–$\delta^{15}N$ biplot (Fig. 6A, 11; Table 2). As those taxa were identified only to the genus level, interspecific dietary differences could not be assessed. However, both genera are generally considered to be predominantly herbivorous (Søreide *et al.,* 2006).

The pelagic amphipod *Themisto libellula* exhibited significantly higher $\delta^{13}C$ values than *Calanus* sp. ($p = 0.002$) and significantly higher $\delta^{15}N$ values (p-value = 0.013) (Fig. 6A; Table 2). These findings partially contrast with those of Tamelander *et al.* (2006), who reported significantly lower $\delta^{13}C$ values for *T. libellula* compared to *Calanus* sp. and *Thysanoessa* sp., while also observing generally higher $\delta^{15}N$ values in *T. libellula* relative to copepods (Tamelander *et al.,* 2006). In our study, *T. libellula* and krill did not differ significantly in $\delta^{13}C$ values ($p = 0.929$), but *T. libellula* did show significantly higher $\delta^{15}N$ values ($p = 0.011$) (Fig. 6A; Table 2). However, it is important to point out that in this study, no lipid extraction was performed for any of the samples, whereas Tamelander *et al.* (2006) removed lipids (Tamelander *et al.,* 2006). The extreme $\delta^{13}C$ values observed for *Calanus* sp. and some *Thysanoessa* sp. may, at least partly, be explained by their well-documented lipid-rich composition (Fig. 6A, B; Table 2). Indeed, lipids are depleted in $\delta^{13}C$, so variations in tissue lipid content will strongly influence $\delta^{13}C$ values (Bodin *et al.,* 2006; De Niro & Epstein, 1978; Griffiths, 1991; Hobson & Welch, 1992; McConnaughey& McRoy, 1979). Dunton *et al.* (1989) did not remove lipids either, and their $\delta^{13}C$ values ranged from -25 to -27‰, similarly to the results of this master's thesis. Finally, in all previously cited studies, as well as in the present one, *T. libellula* appears to rely primarily on pelagic resources.

In this study, the dominant chaetognath species was identified as *Parasagitta elegans,* which is described as a hyperbenthic carnivore preying primarily on copepods (McGovern *et al.,* 2018). Chaetognaths are among the most abundant and consistently present strictly carnivorous zooplankton species (Hop *et al.,* 2019; Søreide *et al.,* 2006), which seems to be coherent with the results found in this analysis, as the $\delta^{15}N$ values differed significantly between *Calanus* sp. and chaetognaths ($p = 0.009$) (Fig. 6A, 6B, 11; Table 2).

Except for the two annelid taxa and *S. septemcarinata,* all invertebrates sampled in this study exhibited relatively high $\delta^{34}S$ values (> 16‰) (Fig. 6B), suggesting taxon-specific levels of association with the pelagic compartment (Fry *et al.,* 2008; Peterson, 1999; Raoult *et al.,* 2024). *P. borealis* showed intermediate values ($\delta^{34}S = 16.66 \pm 1.22$‰) which is consistent with its classification as a hyperbenthic shrimp, suggesting that it may rely on both benthic and pelagic resources (McGovern *et al.,* 2018; Wassmann *et al.,* 2006) (Fig. 6B, 11).

4.2.4. Fish

The fish taxa sampled in this study illustrate a broad range of isotopic niches (Fig. 6A, 6B, 9, 11), reflecting their diverse trophic roles and habitat associations within Kongsfjorden. According to Eriksen *et al.* (2021), the ichthyofaunal community of the Barents Sea is composed mainly of generalist species. The fjord hosts a mixture of Arctic and boreal species, most of which are demersal or benthic (Hop *et al.,* 2002). However, some key species, such as the capelin (*Mallotus villosus*) are among the few that occupy the pelagic realm (Hop *et al.,* 2002).

Indeed, two species, capelin (*M. villosus*) and herring (*Clupea harengus*), are primarily pelagic and planktivorous. According to Eriksen *et al.* (2021) both feed predominantly on zooplankton such as *Calanus* sp. and euphausiids (mostly *Thysanoessa* sp.), while *C. harengus* also preys on amphipods, particularly *Themisto* sp. (Eriksen *et al.,* 2021; Hop & Gjøsæter, 2013; Renaud *et al.,* 2024; Wassman *et al.,* 2006). Herring can also be an important predator of capelin larvae (Wassman *et al.,* 2006). In this study, *M. villosus* and *C. harengus* showed low $\delta^{13}C$ values compared to other fish taxa (–22.09‰ ± 0.49 and –21.98‰, respectively), consistent with pelagic feeding (Sherwood & Rose, 2005), and intermediate $\delta^{15}N$ values (10.18‰ ± 0.21 and 10.8‰), placing them at mid-trophic levels (Fig. 6A; Table 2). In the study conducted by Eriksen *et al.* (2021), capelin was found in the stomachs of 15 fish species, which confirm its central role as a forage fish for higher predators, including Atlantic cod (*Gadus morhua*) and marine mammals. Even though there is only one sample representing herring in this study, the values found here seem coherent with the literature (Table 2) (Eriksen *et al.,* 2021; Hop & Gjøsæter, 2013).

The Atlantic cod (*G. morhua*) is a benthopelagic generalist predator with a broad omnivorous diet that predominantly includes fish, mainly capelin and polar cod (*Boreogadus saida)* (Bengtsson *et al.,* 2024). It can also prey on other species and large benthic invertebrates, such as *P. borealis* and zooplankton, for example, *Themisto* spp. and krill (Bengtsson *et al.,* 2024; Hedeholm *et al.,* 2017; Hop & Gjøsæter, 2013; Eriksen *et al.,* 2021; Wassman *et al.,* 2006). The high $\delta^{15}N$ values (12.90‰ ± 0.71), indicating a high trophic level, and intermediate $\delta^{13}C$ values (–20.80‰ ± 0.51), seem to confirm that hypothesis, suggesting reliance on both benthic and pelagic prey (McGovern *et al.,* 2018; Sherwood & Rose, 2005). Therefore, these results seem to support its role in coupling benthic and pelagic food webs and the idea that this species occupies a broad trophic niche, ranging from primary consumers to predatory fish (Hedeholm *et al.,* 2017; Eriksen *et al.,* 2021) (Fig. 6A, 6B, 9, 11).

Polar cod (*B. saida*) is the main fish species living in close association with sea ice (Hop *et al.,* 2006). This species is considered sympagic, at least in its early life stages (Eriksen *et al.,* 2021; Skjoldal *et al.,* 2025; Wassman *et al.,* 2006). It is an opportunistic planktivorous species, as smaller individuals mainly consume copepods (*Calanus* spp.), while larger ones feed on amphipods (*Themisto* spp.), krill, and juvenile fish (Bengtsson *et al.,* 2024; Hop & Gjøsæter, 2013). The dominance of pelagic prey in its diet is reflected in the negative $\delta^{13}C$ values found in this study. Polar cod and capelin are both considered key species in the Arctic marine food web (Hobson & Welch, 1992; Hop *et al.,* 2002; Hop & Gjøsæter, 2013). Their diets show considerable overlap, as both predominantly feed on zooplankton (Fig. 6A, 6B, 9, 11). Juvenile stages of fish are known to also prey heavily on pelagic prey, such as copepods (Eriksen *et al.,* 2021) which is coherent with their relatively depleted $\delta^{13}C$ and moderate $\delta^{15}N$ values observed in this study (Fig. 6A, 6B; Table 2).

Several species studied here are strictly demersal and feed predominantly on benthic prey. Firstly, long rough dab (*Hippoglossoides platessoides*) is a flatfish that preys mainly on brittle star, *P. borealis*, polychaetes, and small fish (mainly *Melanogrammus aeglefinus* and *Micromesistius poutassou*) (Eriksen *et al.,* 2021; González-Iglesias *et al.,* 2003; Tamelander *et al.,* 2006). Its diet is coherent with more ^{13}C enriched (–20.18‰ ± 0.72), reflecting a benthic feeding strategy. The elevated $\delta^{15}N$ values (13.36‰ ± 0.54) observed in this species are consistent with a carnivorous diet (Eriksen *et al.,* 2021; González-Iglesias *et al.,* 2003). According to Tamelander *et al.* (2006), demersal fishes generally have higher δ13C values than herring and capelin, which primarily feed on zooplankton. Demersal fishes also tended to occupy slightly higher trophic levels than pelagic species, although the $\delta^{15}N$ values of Tamelander *et al.* (2006) did not differ significantly between these groups, while in this study, some species do (Fig. 6A, 11; Annex 3).

Pollock (*Pollachius* sp.) exhibited isotopic values similar to those of *Leptoclinus maculatus* and *M. villosus* (Fig. 6A; Table 2). Although this genus is generally considered piscivorous, it can also feed on zooplankton, particularly euphausiids (Eriksen *et al.,* 2021). The relatively low $\delta^{15}N$ values observed here suggest that fish did not constitute a major part of its diet in Kongsfjorden, contrasting with the findings of Eriksen *et al.* (2021) but the $\delta^{13}C$ values are consistent with a predominant reliance on pelagic prey (Fig. 6A, 11; Table 2).

Overall, isotopic values from this study seem to align well with known feeding strategies and habitat use. Demersal species exhibited higher $\delta^{13}C$ values compared to pelagic species, consistent with benthic resource use (Tamelander *et al.,* 2006). $\delta^{15}N$ values helped discriminate between trophic positions, with higher values in high-trophic-level predators such as *G. morhua* and *H. platessoides* and lower values in planktivores like *M. villosus* and *L. maculatus* (Eriksen *et al.,* 2021). The presence of benthopelagic generalists such as *G. morhua* and *B. saida* underlines the importance of vertical trophic coupling in Arctic fjord systems, linking pelagic production to benthic consumers and supporting higher trophic levels, including seabirds and marine mammals (Hop *et al.*, 2002; Hop & Gjøsæter, 2013).

4.3. The seals and kittiwakes rely on different trophic pathways

The highest $\delta^{15}N$ values in this study correspond to high-trophic-level predators, namely the three seal species (*Erignathus barbatus*, *Pusa hispida,* and *Phoca vitulina*) and the black-legged kittiwake (*Rissa tridactyla*) (Fig. 6A; Table 2). These values are consistent with their trophic positions and known feeding strategies (Hjelset *et al.,* 1999; Hop *et al.,* 2002; Hop & Gjøsæter, 2013; Kovacs *et al.,* 2024; Wassmann *et al.,* 2006).

4.3.1. Seals

The three seal species studied here appear to have broadly similar diets, as none of them show significantly different values for $\delta^{13}C$, $\delta^{15}N$, or $\delta^{34}S$ (Fig. 6A, B; Table 2; Annex 3). However, all seals exhibit less negative $\delta^{13}C$ values than kittiwakes, and, except for *E. barbatus*, they have significantly higher $\delta^{15}N$ values (Fig. 6A, 6B, 11; Table 2; Annex 3). These results suggest that all seal species likely exploit both benthic and pelagic food sources, whereas kittiwakes seem to forage exclusively on pelagic prey. Moreover, *P. hispida* and *P. vitulina* appear to consume prey at higher trophic levels. These findings are consistent with previous studies (Hjelset *et al.,* 1999; Hop *et al.,* 2002; Kovacs *et al.,* 2024).

Indeed, the ringed seal (*P. hispida*), the most abundant Arctic seal in the fjord (Hop *et al.,* 2002), is described as a generalist predator feeding on sympagic, pelagic, and benthic organisms (Descamps *et al.,* 2017; Hobson & Welch, 1992; Hop & Gjøsæter, 2013; Kovacs *et al.,* 2024; Pinzone, 2021). The diet of ringed seals is dominated by fish, such as polar cod, and medium-sized crustaceans, such as *T. libellula* and *P. borealis*, relying on both pelagic and benthic food webs (Fig. 11) (Hop *et al.,* 2006; Weslawski *et al.,* 1994; Pinzone, 2021). A hypothesis proposed by Weslawski *et al.* (1994) suggests that ringed seals rely more on benthic prey during winter, whereas they shift to pelagic prey during the ice break-up and open-water periods.

A population of harbor seals (*P. vitulina*) resides year-round in Svalbard, their northernmost distribution area (Gjertz *et al.,* 2001). They feed mainly on gadoid species, with Atlantic cod and polar cod being dominant in their diet, and invertebrates playing a minor role (Hop *et al.,* 2002; Blanchet *et al.,* 2014). According to Blanchet *et al.* (2014), their dietary overlap with ringed seals further supports the generalist feeding strategy of these Arctic pinnipeds (Fig. 11). This observation is supported here, as Dunn's post-hoc tests showed no significant difference between the two seal species (Fig. 6A, B; Annex 3).

Bearded seals (*E. barbatus*) are considered to be the most important mammals feeding on benthos in Kongsfjorden (Hop *et al.,* 2002). They are primarily benthic feeders, consuming mostly fish, especially polar and Atlantic cod and long rough dab, but they can also feed on invertebrates such as crustaceans, bivalves, and polychaetes (Hjelset *et al.,* 1999; Hop *et al.,* 2002). Moreover, some overlap exists with the diets of ringed seals and walruses (Hjelset *et al.,* 1999). Its isotopic values appear consistent with its high trophic position ($\delta^{15}N$ = 14.29‰ ± 0.08), and the relatively high $\delta^{13}C$ values suggest that it relies more on benthic prey (Fig. 6A, 11; Table 2) (McConnaughey & McRoy, 1979).

It seems that all seal species rely on both pelagic and benthic food webs. But what about kittiwakes? In addition to studying their diet from a general point of view, it is possible to look for potential inter- and intra-annual shifts in their diet as they were sampled during three periods: June 2023, July 2023, and June 2024 (Fig. 7A, 7B, 9). Unfortunately, the number of seals collected was insufficient to allow for a similar temporal-scale analysis.

4.3.2. Kittiwakes

In this study, the seabirds are represented by the black-legged kittiwake (*R. tridactyla*), a surface feeder that exhibits high $\delta^{15}N$ values consistent with its predator diet, while its more depleted $\delta^{13}C$ values suggest that it does not rely much on benthic prey (Fig. 6A, 11; Table 2). This isotopic composition aligns with previous findings, which describe the kittiwakes as primarily feeding on zooplankton (such as *Thysanoessa* spp. and *T. libellula*) and pelagic fish such as capelin and polar cod (Descamps & Ramirez, 2021; Hop *et al.,* 2002; Lønne & Gabrielsen, 1992; Mehlum & Giertz, 1984). According to Descamps *et al.* (2019), due to the Atlantification, the kittiwake diet has shifted in recent years from being dominated by Arctic species (*e.g.*, polar cod) to a more mixed diet with a higher contribution from Atlantic species (*e.g.,* capelin and herring) (Descamps *et al.,* 2019; Vihtakari *et al.,* 2018). Being a migratory species, the kittiwakes show a seasonal presence in the fjord, peaking during spring and summer for breeding season (Hop *et al.,* 2002) and leaving the Svalbard area in September for wintering areas in the North Atlantic (Isaksen & Bakken, 1995). More precisely, *R. tridactyla* are colonial cliff-breeders that arrive in Spitsbergen in April and usually lay 1 or 2 eggs in mid-June (Goutte *et al.,* 2014; Hatch & Hatch, 1990; Lundgren *et al.,* 2024).

Individuals of *Rissa tridactyla* were studied over different time periods to investigate a potential temporal variation in their isotopic niche and foraging strategies. Although overall isotopic ranges were narrow, distinct separations between sampling periods were observed, with only the isotopic ellipses of July 2023 and June 2024 showing a small overlap (Fig. 7A, 9). $\delta^{13}C$ values ranged from -22.04 to -20.1‰ and $\delta^{15}N$ values varied between 11.96 and 14.46‰ (Fig. 7A, B). Most individuals exhibited $\delta^{34}S$ values between 16.1 and 18.9‰, although one bird displayed a lower value of 13.9‰ (Fig. 7B). As $\delta^{34}S$ values exhibited only minor variations, indicating a predominantly pelagic feeding mode across years (Fig. 7B). This dietary preference likely explains the limited differences in $\delta^{13}C$ values between sampling periods (Fig. 7A, B).

Kittiwakes sampled in June 2024 exhibited a markedly smaller trophic niche compared to June and July 2023, suggesting a reliance on less diverse food items and/or more comparable ecophysiology during this period (Fig. 7A). Kittiwakes sampled in June 2023 and June 2024 had $\delta^{15}N$ values significantly higher than those in July 2023 ($p_{\text{June 2023 - July 2023}} < 0.0001$ and $p_{2023\text{-}2024} < 0.0001$) (Fig. 7A). There could be two potential hypotheses to explain this pattern: seasonal shifts associated with breeding, and/or by migration-related effects, with individuals still carrying isotopic signatures from their wintering grounds (Isaksen & Bakken, 1995).

The first hypothesis for the observed difference in $\delta^{15}N$ values is that the diet of *R. tridactyla* during migration is still reflected in the isotopic signatures of individuals sampled in June, as they typically arrive in the area in April-May, lay their eggs in mid-June, with hatching occurring about 27 days later, around mid-July (Goutte *et al.,* 2014; Hatch & Hatch, 1990; Lundgren *et al.,* 2024). Finally, the chicks generally fledge by late August or early September (Hatch & Hatch, 1990).

Since blood is a metabolically active tissue with a rapid turnover rate, the samples collected provide information on diet over a relatively short time window, ranging from a few days to weeks prior to sampling (Lourenço *et al.,* 2015). It is therefore plausible that, during migration, kittiwakes consume a higher proportion of pelagic fish and higher-trophic level prey before shifting their diet upon arrival in Kongsfjorden to more crustaceans and other lower-trophic-level prey, a pattern that could still be detectable in the samples (Lundgren *et al.,* 2024; Suryan *et al.,* 2000).

The second hypothesis, which proposes that breeding is the main factor driving the temporal variations between the June and July populations, can be supported by Lundgren *et al,* (2024) findings. They explained that kittiwakes tend to consume more crustaceans during the breeding season, especially males, resulting in a lower trophic level for the individuals sampled in July (Lundgren *et al.,* 2024), which is consistent with our results (Fig. 7A).

An alternative explanation is a spatial shift in their foraging areas. Indeed, prior to chick hatching, kittiwakes typically forage outside the fjord (Schlener, 2022; Vihtakari *et al.,* 2018). Once chicks hatch, usually in mid-July, adults shift to foraging closer to tidewater glacier fronts within the fjord (Lydersen *et al.,* 2013; Schlener, 2022; Vihtakari *et al.,* 2018) (Fig. 7A, B). At this stage, birds reduce their foraging range and concentrate in “brown zones” near glaciers, which are known to be highly productive (Arendt *et al.,* 2010; Hop *et al.,* 2002; Schlener, 2022). These areas are enriched by glacial meltwater, which enhances zooplankton availability through upwelling processes and osmotic stress effects on taxa such as *Calanus* sp. (Hop *et al.,* 2002). Foraging near glacier fronts is also typically associated with lower $\delta^{15}N$ values (Heaton *et al.,* 2004; Santos-Garcia *et al.,* 2022; Vega *et al.,* 2015), so this shift in foraging grounds therefore explains the lower $\delta^{15}N$ values observed in July (Fig. 7A, 9).

As a result, the isotopic niche of July individuals would reflect feeding near glacier fronts, while the June niche is more variable. The relatively low $\delta^{15}N$ values observed in June 2024 may indicate that birds exploited prey near glacier-associated habitats earlier in the season, whereas those sampled in June 2023 likely foraged mainly outside the fjord.

While our results reveal clear temporal patterns in kittiwake isotopic values, the underlying cause, whether seasonal breeding shifts or migration carry-over effects, cannot be determined with certainty. Both hypotheses remain plausible and are not mutually exclusive. Nevertheless, the consistently narrow $\delta^{13}C$ ranges and the limited variation in $\delta^{34}S$ values strongly suggest that black-legged kittiwakes in Kongsfjorden rely predominantly on pelagic resources throughout the breeding season, regardless of temporal differences in trophic niche width or $\delta^{15}N$ values (Fig. 6A, 6B, 7A, 7B, 9, 11).

The different feeding strategies and habitat use of these predators highlight the ecological flexibility of Arctic top consumers and their key role in coupling pelagic and benthic food webs. In addition to the seals and the bird, *Hippoglossoides platessoides* and *Gadus morhua* can also be considered as high-trophic-level species as those fish exhibited similar $\delta^{15}N$ values. The isotopic values support that the three seal species, along with the two fish species, seem to rely on both benthic and pelagic food webs whereas the black-legged kittiwakes appear to be more strictly associated with the pelagic food web (Fig. 6A, 6B, 9, 11; Table 2).

4.4. Spatial differences in several taxa isotopic niches from the head to the mouth of Kongsfjorden

As previously observed, no clear spatial differences were detectable within the fjord at the community level. However, some taxa were collected both inside and at the mouth of Kongsfjorden (Annex 1). Given the objective of this thesis to explore the spatial-temporal drivers potentially shaping the Kongsfjorden food web, it seems relevant to investigate whether isotopic ellipses differ among taxa sampled in both regions and how such differences may influence the diet of high-trophic-level predators (Fig. 9).

As suggested by Arendt et al. (2010), a distinction can be made between the mouth and the rest of the fjord system, a pattern also observed in this study. Accordingly, the inner basins (CZ, NGZ, and SGZ) were therefore grouped into a single "Fjord" zone, while the outer zone (OZ) remained distinct. Even though kittiwakes were sampled only inside the fjord at the Krykkjefjellet colony (78°54' N, 12°13' E), a temporal aspect can be considered, as samples were collected in June 2023, July 2023, and June 2024. Therefore, the isotopic niches were analyzed to test whether their diet was more dependent on offshore or in-fjord prey and whether it shifted over the course of their stay (Fig. 9). Unfortunately, seals were collected only within the fjord and in insufficient numbers to allow for an assessment of temporal variation.

A consistent pattern emerges for certain taxa. Indeed, taxa linked to the pelagic food web maintained relatively stable isotopic signatures across the study area. By contrast, components of the benthic food web, as well as predators that rely on them at least partially, exhibited marked isotopic differences between zones (Fig. 9).

For instance, *Hippoglossoides platessoides* and the benthic assemblages from the head of the fjord exhibited less negative $\delta^{13}C$ values compared to those sampled within the fjord, with only limited overlap between the two zones (Fig. 9). This suggests that taxa associated with benthic pathways are strongly influenced by local environmental processes, leading to a clearer distinction between offshore and inshore habitats (McGovern *et al.,* 2018; Sherwood & Rose, 2005; Włodarska-Kowalczuk *et al.,* 2012).

In contrast, *Gadus morhua*, *Boreogadus saida*, zooplankton, and kittiwakes displayed little variation in $\delta^{13}C$ values across sampling zones, as their isotopic niches overlapped regardless of whether they were sampled inside the fjord or offshore (Fig. 9). These taxa rely more on pelagic resources, which may explain the absence of clear spatial differentiation. One possible explanation is the high mobility of these species, allowing them to integrate resources across habitats. Another factor could be the highly dynamic nature of the water column in Kongsfjorden (Cottier *et al.,* 2005; Hop *et al.,* 2002; Hopwood *et al.,* 2020). Mixing processes and temporal variability in primary producers likely obscure spatial contrasts at higher trophic levels, contributing to the observed homogeneity. In contrast, in systems with a stronger physical separation, greater differences are typically observed between pelagic organisms from offshore waters and those within the fjord (Arendt *et al.,* 2010).

No clear tendency is apparent in $\delta^{15}N$ values for most taxa (Fig. 9), except for kittiwakes (see Section 4.3.2). This contrasts with the findings of Sherwood & Rose (2005) for the Newfoundland and Labrador continental shelf, where significant $\delta^{15}N$ differences were observed for most taxa between the head and the mouth of the fjords. In their study, $\delta^{15}N$ values were consistently higher in nearshore communities, with the difference being more pronounced in invertebrates than in fish. This was attributed to the greater mobility and dietary mixing of fish, which can move across the fjord (Sherwood & Rose, 2005). One plausible explanation for the discrepancy between our results and those of Sherwood and Rose (2005) lies in the source of nitrogen enrichment. In their study, elevated $\delta^{15}N$ values in nearshore zones were hypothesized to be linked to anthropogenic inputs (Sherwood & Rose, 2005). In Kongsfjorden, such sources are much less significant; terrestrial and freshwater inputs are present but occur without substantial anthropogenic influence.

As previously observed, kittiwakes exhibited a temporal shift, as individuals sampled in June 2023 displayed higher $\delta^{15}N$ values than June 2024, which also displayed higher $\delta^{15}N$ values than July 2023 (Fig. 7A, 9). While the June 2023 did not overlap with either isotopic niche, the July 2023 and June 2024 niches overlapped with that of *G. morhua* (Fig. 9). This suggests that birds sampled in July and June 2024 may have relied on prey similar to those consumed by this fish species, whereas birds sampled in June 2023 fed on different, though still pelagic, prey.

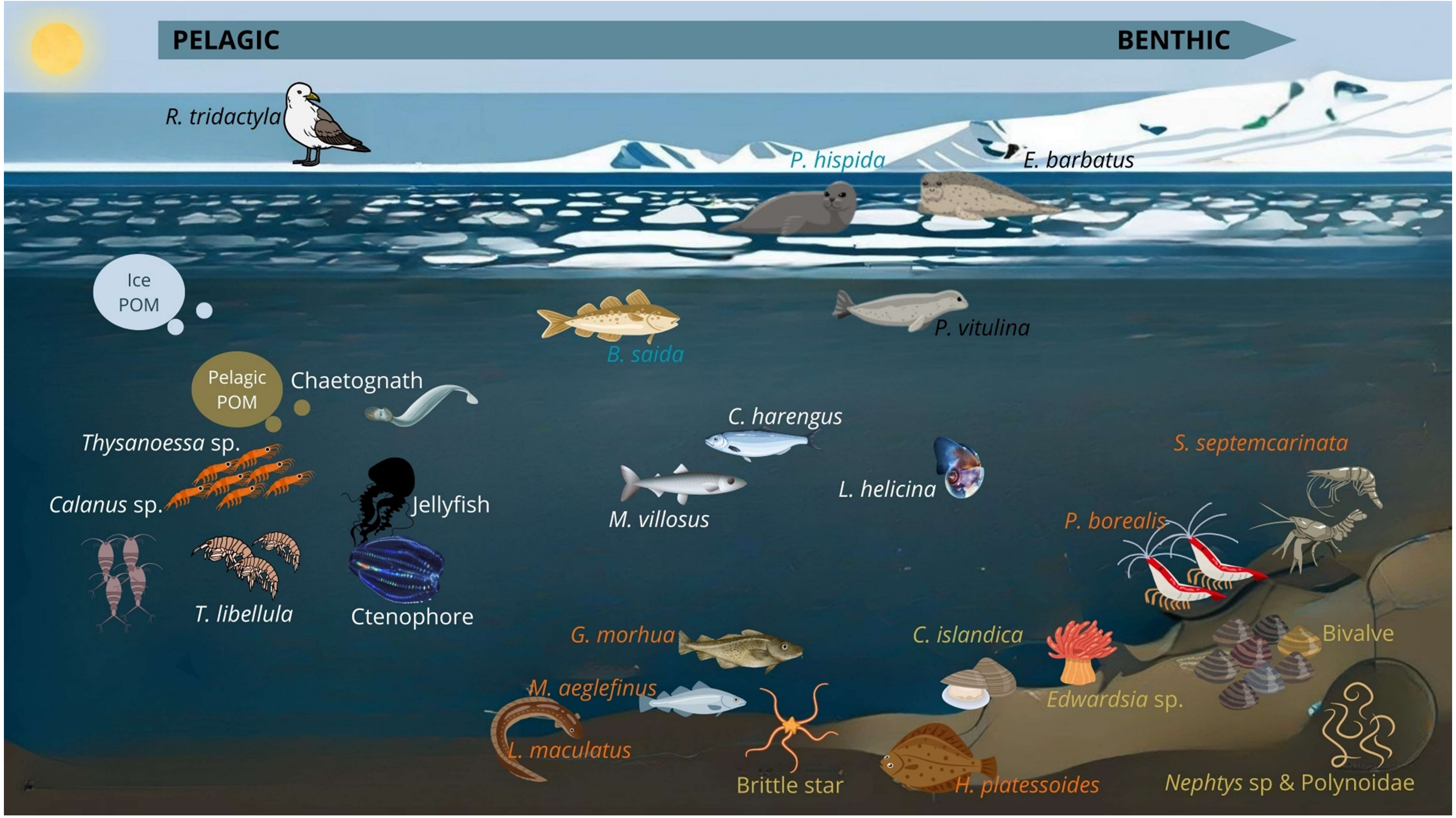


Figure 11: Schematic representation of the Kongsfjorden food web showing the distribution of organisms along the pelagic–benthic continuum. Organisms are positioned according to their dependence on pelagic, benthic, or mixed trophic pathways. The color of each taxon name indicates its typical habitat or position in the water column: black = terrestrial, white = pelagic, blue = sympagic, yellow = benthic, and orange = bentho-pelagic.

5. Conclusion

The main objective of this master’s thesis was to determine the prey and trophic pathways on which the high-trophic-level predators rely in Kongsfjorden and to assess whether these relationships vary across space and time using stable isotope analyses of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and sulfur ($\delta^{34}S$).

The study focused on three seal species (*Erignathus barbatus*, *Pusa hispida,* and *Phoca vitulina*) as well as the black-legged kittiwake (*Rissa tridactyla*). Our results highlighted the elevated position of two fish species, *Hippoglossoides platessoides* and *Gadus morhua*. Kittiwakes appeared to rely almost exclusively on the pelagic food web, while the seals and fish displayed intermediate strategies, exploiting both benthic and pelagic trophic pathways. These isotopic patterns emphasize the trophic diversity of fish species in Kongsfjorden and their role in linking benthic and pelagic energy pathways.

Spatially, the fjord zones were relatively similar to each other but displayed a broader isotopic range compared to the head of the fjord. This suggests that the organisms sampled within the fjord rely on both pelagic and benthic pathways, whereas the organisms offshore appear to rely primarily on a dominant pelagic pathway. The benthic community appeared to be more affected by the inshore–offshore gradient, in contrast, the pelagic community showed a relatively consistent isotopic composition across sampling locations.

Temporally, variation could only be assessed in *R. tridactyla*, where both inter- and intra-annual shifts in feeding behavior were observed. As reported in previous studies, kittiwakes tended to forage more intensively near glaciers after chick hatching, while exploiting broader feeding areas earlier in the breeding season.

Beyond these findings, this work also contributes to a broader understanding of Arctic food-web functioning in a rapidly changing environment. Over the past decade, the pelagic ecosystem of Kongsfjorden has shifted from a cold, Arctic-dominated system to a warmer, more Atlantic-influenced one (Vihtakari *et al.,* 2018). Most of the physical models predict that by 2050, the Arctic Ocean will no longer be frozen in summer, a first in over five million years (Polyak *et al.,* 2010; Holland & Kay, 2024). Such changes will inevitably reshape trophic interactions, prey availability, and predator foraging strategies in Arctic fjords. Therefore, it is crucial to improve our knowledge to better anticipate the ecological consequences of these inevitable shifts.

6. Bibliography

Ardyna, M., & Arrigo, K. R. (2020). Phytoplankton dynamics in a changing Arctic Ocean. *Nature Climate Change*, *10*(10), 892-903. https://doi.org/10.1038/s41558-020-0905-y

Arendt, K. E., Nielsen, T. G., Rysgaard, S., & Tönnesson, K. (2010). Differences in plankton community structure along the Godthåbsfjord, from the Greenland Ice Sheet to offshore waters. *Marine Ecology Progress Series*, *401*, 49-62. https://doi.org/10.3354/meps08480

Arendt, K. E., Juul-Pedersen, T., Mortensen, J., Blicher, M. E., & Rysgaard, S. (2013). A 5-year study of seasonal patterns in mesozooplankton community structure in a sub-Arctic fjord reveals dominance of *Microsetella norvegica* (Crustacea, Copepoda). *Journal of Plankton Research*, *35*(1), 105-120. https://doi.org/10.1093/plankt/fbs087

Assmy, P., Kvernvik, A. C., Hop, H., Hoppe, C. J., Chierici, M., Divya, D.T., Duarte, P., Fransson, A., García, L. M., Patuła, W., Kwaśniewski S., Maturilli, M., Pavlova, O., Tatarek, A., Wiktor, J. M., Wold, Anette, Wolf, K.K.E. & Bailey, A. (2023). Seasonal plankton dynamics in Kongsfjorden during two years of contrasting environmental conditions. *Progress in Oceanography*, *213*, 102996. https://doi.org/10.1016/j.pocean.2022.102996

Basedow, S. L., Eiane, K., Tverberg, V., & Spindler, M. (2004). Advection of zooplankton in an Arctic fjord (Kongsfjorden, Svalbard). *Estuarine, Coastal and Shelf Science*, *60*(1), 113-124. https://doi.org/10.1016/j.ecss.2003.11.027

Bengtsson, O., Lydersen, C., Węsławski, J. M., Berge, J., & Kovacs, K. M. (2024). Summer and polar night diets of polar cod *Boreogadus saida* and Atlantic cod *Gadus morhua* in Kongsfjorden, Svalbard, Norway. *Marine Ecology Progress Series*, *747*, 117-132. https://doi.org/10.3354/meps15405

Bischof, K., Convey, P., Duarte, P., Gattuso, J. P., Granberg, M., Hop, H., Hoppe, C., Jiménez, C., Lisitsyn, L., Martinez, B., Roleda, M.Y., Thor, P., Wiktor, J.M., & Gabrielsen, G. W. (2019). Kongsfjorden as harbinger of the future Arctic: Knowns, unknowns and research priorities. In *The ecosystem of Kongsfjorden, Svalbard* (pp. 537-562). Springer. https://doi.org/10.1007/978-3-319-46425-1_15

Blanchet, M. A., Lydersen, C., Ims, R. A., Lowther, A. D., & Kovacs, K. M. (2014). Harbour seal *Phoca vitulina* movement patterns in the high-Arctic archipelago of Svalbard, Norway. *Aquatic Biology*, 21(3), 167-181. https://doi.org/10.3354/ab00580

Bodin, N., Le Loc'h, F., & Hily, C. (2007). Effect of lipid removal on carbon and nitrogen stable isotope ratios in crustacean tissues. *Journal of Experimental Marine Biology and Ecology*, *341*(2), 168-175. https://doi.org/10.1016/j.jembe.2006.10.006

Boecklen, W. J., Yarnes, C. T., Cook, B. A., & James, A. C. (2011). On the use of stable isotopes in trophic ecology. *Annual Review of Ecology, Evolution, and Systematics*, *42*(1), 411-440. https://doi.org/10.1146/annurev-ecolsys-102209-144726

Choudhary, S., Nayak, G. N., & Khare, N. (2020). Source, mobility, and bioavailability of metals in fjord sediments of Krossfjord-Kongsfjord system, Arctic, Svalbard. *Environmental Science and Pollution Research International*, *27*(13), 15130–15148. https://doi.org/10.1007/s11356-020-07879-1

Cottier, F., Tverberg, V., Inall, M., Svendsen, H., Nilsen, F., & Griffiths, C. (2005). Water mass modification in an Arctic fjord through cross-shelf exchange: The seasonal hydrography of Kongsfjorden, Svalbard. *Journal of Geophysical Research: Oceans*, *110*(C12). https://doi.org/10.1029/2004JC002757

Daase, M., Falk-Petersen, S., Varpe, Ø., Darnis, G., Søreide, J. E., Wold, A., Leu, E., Jørgen, B., Benoit, Phillippe & Fortier, L. (2013). Timing of reproductive events in the marine copepod Calanus glacialis: a pan-Arctic perspective. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*(6), 871-884. https://doi.org/10.1139/cjfas-2012-0401

Dalpadado, P., Prokopchuk, I. P., Bogstad, B., Skaret, G., Ingvaldsen, R. B., Dolgov, A. V., Orlova, E. L., Stige, L. C., Johannesen, E., & Huse, G. (2024). Zooplankton link climate to capelin and polar cod in the Barents Sea. *Progress in Oceanography*, 226, Article 103302.

DeNiro, M. J., & Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, *42*(5), 495-506. https://doi.org/10.1016/0016-7037(78)90199-0

DeNiro, M. J., & Epstein, S. (1981). Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta*, *45*(3), 341-351. https://doi.org/10.1016/0016-7037(81)90244-1

Descamps, S., Aars, J., Fuglei, E., Kovacs, K. M., Lydersen, C., Pavlova, O., Pedersen, Å. Ø., Ravolainen, V., & Strøm, H. (2017). Climate change impacts on wildlife in a High Arctic archipelago – Svalbard, Norway. *Global Change Biology*, *23*(2), 490–502. https://doi.org/10.1111/gcb.13381

Descamps, S., Bertrand, P., Strøm, H., Steen, H., Kohler, J., & Chastel, O. (2019). *Atlantification consequences on Svalbard seabirds: Final report.* Svalbard Miljøvernfond.

Descamps, S., & Ramírez, F. (2021). Species and spatial variation in the effects of sea ice on Arctic seabird populations. *Diversity and Distributions*, *27*(11), 2204-2217. https://doi.org/10.1111/ddi.13391

Duarte, P., Weslawski, J. M., & Hop, H. (2019). Outline of an Arctic fjord ecosystem model for Kongsfjorden-Krossfjorden, Svalbard. *The Ecosystem of Kongsfjorden, Svalbard*, (pp. 485-514). Springer. https://doi.org/10.1007/978-3-319-46425-1_13

Dunton, K. H., Saupe, S. M., Golikov, A. N., Schell, D. M., & Schonberg, S. V. (1989). Trophic relationships and isotopic gradients among arctic and subarctic marine fauna. *Marine Ecology Progress Series*, *56*, 89-97. https://doi.org/10.3354/meps056089

Eriksen, E., Skjoldal, H. R., Dolgov, A. V., Strand, E., Keulder-Stenevik, F., Prokopchuk, I. P., Orlova, E. L., Trofimov, A., Prozorkevich, D. V., Sokolov, K. M., Smirnov, O., Yaragina, N. A., Rolskiy, A. Y., & Benzik, A. N. (2021). Diet and trophic structure of fishes in the Barents Sea: Seasonal and spatial variations. *Progress in Oceanography*, *197*, 102663. https://doi.org/10.1016/j.pocean.2021.102663

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., & Dolgov, A. V. (2015). Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change*, *5*(7), 673-677. https://doi.org/10.1038/nclimate2647

Fry, B. (1988). Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnology and Oceanography*, *33(5),* 1182-1190. https://doi.org/10.4319/lo.1988.33.5.1182

Fry, B., Cieri, M., Hughes, J., Tobias, C., Deegan, L. A., & Peterson, B. (2008). Stable isotope monitoring of benthic–planktonic coupling using salt marsh fish. *Marine Ecology Progress Series*, *369*, 193-204. https://doi.org/10.3354/meps07612

Gajdzik, L., Parmentier, E., Sturaro, N., & Frédérich, B. (2016). Trophic specializations of damselfishes are tightly associated with reef habitats and social behaviours. *Marine Biology*, *163*(1), 1-15. https://doi.org/10.1007/s00227-015-2809-8

Gibson, R. N., & Barnes, M. (2003). Arctic brittle stars (Echinodermata: Ophiuroidea). In R. N. Gibson & M. Barnes (Eds.), *Oceanography and marine biology: An annual review* (Vol. 38, pp. 189-256). CRC Press.

Gilmer, R. W., & Harbison, G. R. (1991). Diet of *Limacina helicina* (Gastropoda: Thecosomata) in Arctic waters in midsummer. *Marine Ecology Progress Series*, *77*, 125-134. https://doi.org/10.3354/meps077125

Gjertz, I., Lydersen, C., & Wiig, Ø. (2001). Distribution and diving of harbour seals (*Phoca vitulina*) in Svalbard. *Polar Biology*, *24*(3), 209-214. https://doi.org/10.1007/s003000000196

González-Iglesias, M. D. L. C., Román-Marcote, E., & Paz, X. (2003). *Food and feeding chronology of American plaice (Hippoglossoides platessoides) in the North Atlantic*. Instituto Español de Oceanografía, Centro Oceanográfico de Vigo.

Goutte, A., Angelier, F., Bech, C., Clément-Chastel, C., Dell'Omo, G., Gabrielsen, G. W., Moe, B., & Chastel, O. (2014). Annual variation in the timing of breeding, pre-breeding foraging areas and corticosterone levels in an Arctic population of black-legged kittiwakes. *Marine Ecology Progress Series*, *496*, 233-247. https://doi.org/10.3354/meps10567

Griffiths, H. (1991). Applications of stable isotope technology in physiological ecology. *Functional Ecology*, *5*(2), 254-269. https://doi.org/10.2307/2389263

Ito, H., & Kudoh, S. (1997). Characteristics of water in Kongsfjorden, Svalbard. *Proceedings of the NIPR Symposium on Polar Meteorology and Glaciology, 11,* 211–32.

Halbach, L., Vihtakari, M., Duarte, P., Everett, A., Granskog, M. A., Hop, H., Cottier, F., Høygård, I. K., Falk-Petersen, S., Wold, A., Sundfjord, A., & Assmy, P. (2019). Tidewater glaciers and bedrock characteristics control the phytoplankton growth environment in a fjord in the Arctic. *Frontiers in Marine Science*, *6*, 254. https://doi.org/10.3389/fmars.2019.00254

Hamre, B., Winther, J. G., Gerland, S., Stamnes, J. J., & Stamnes, K. (2004). Modeled and measured optical transmittance of snow-covered first-year sea ice in Kongsfjorden, Svalbard. *Journal of Geophysical Research: Oceans*, *109*(C10), C10006. https://doi.org/10.1029/2003JC001926

Hanelt, D., Tüg, H., Bischof, K., Groß, C., Lippert, H., Sawall, T., & Wiencke, C. (2001). Light regime in an Arctic fjord: A study related to stratospheric ozone depletion as a basis for determination of UV effects on algal growth. *Marine Biology, 138*(3), 649-658. https://doi.org/10.1007/s002270000484

Hatch, S. A., & Hatch, M. A. (1990). Breeding seasons of oceanic birds in a subarctic colony. *Canadian Journal of Zoology*, *68*(8), 1664-1679. https://doi.org/10.1139/z90-246

Heaton, T. H., Wynn, P., & Tye, A. M. (2004). Low $^{15}N/^{14}N$ ratios for nitrate in snow in the High Arctic (79° N). *Atmospheric Environment*, *38*(33), 5611-5621. https://doi.org/10.1016/j.atmosenv.2004.06.028

Hedeholm, R. B., Mikkelsen, J. H., Svendsen, S. M., Carl, J., & Jensen, K. T. (2017). Atlantic cod (*Gadus morhua*) diet and the interaction with northern shrimp (*Pandalus borealis*) in Greenland waters. *Polar Biology, 40*(7), 1335-1346. https://doi.org/10.1007/s00300-016-2059-1

Hedges, J. I., & Stern, J. H. (1984). Carbon and nitrogen determinations of carbonate-containing solids 1. *Limnology and oceanography*, *29*(3), 657-663. https://doi.org/10.4319/lo.1984.29.3.0657

Hegseth, E. N., Assmy, P., Wiktor, J. M., Wiktor, J., Kristiansen, S., Leu, E., Tverberg, V., Dahl, T. M., & Cottier, F. (2019). Phytoplankton seasonal dynamics in Kongsfjorden, Svalbard and the adjacent shelf. *The Ecosystem of Kongsfjorden, Svalbard* (pp. 173–227). Springer. https://doi.org/10.1007/978-3-319-46425-1_6

Hjelle, A. (1993). *Geology of Svalbard*. Norsk Polarinstitutt.

Hjelset, A. M., Andersen, M., Gjertz, I., Lydersen, C., & Gulliksen, B. (1999). Feeding habits of bearded seals (*Erignathus barbatus*) from the Svalbard area, Norway. *Polar Biology*, *21*(3), 186-193. https://doi.org/10.1007/s003000050349

Hobson, K. A., & Welch, H. E. (1992). Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. *Marine Ecology Progress Series, 84,* 9-18. https://doi.org/10.3354/meps084009

Hobson, K. A., Ambrose Jr, W. G., & Renaud, P. E. (1995). Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: Insights from $\delta^{13}C$ and $\delta^{15}N$ analysis. *Marine Ecology Progress Series, 128,* 1-10. https://doi.org/10.3354/meps128001

Hodal, H., Falk-Petersen, S., Hop, H., Kristiansen, S., & Reigstad, M. (2012). Spring bloom dynamics in Kongsfjorden, Svalbard: Nutrients, phytoplankton, protozoans and primary production. *Polar Biology, 35,* 191-203. https://doi.org/10.1007/s00300-011-1053-7

Hop, H., Pearson, T., Hegseth, E. N., Kovacs, K. M., Wiencke, C., Kwasniewski, S., Eiane, K., Mehlum, F., Gulliksen, B., Wlodarska-Kowalczuk, M., Lydersen, C., Weslawski, J. M., Cochrane, S., Gabrielsen, G. W., Leakey, R. J. G., Lønne, O. J., Zajaczkowski, M., Falk-Petersen, S., Kendall, M., ... & Er Gerland, S. (2002). The marine ecosystem of Kongsfjorden, Svalbard. *Polar Research, 21*(1), 167–208. https://doi.org/10.1111/j.1751-8369.2002.tb00073.x

Hop, H., Falk-Petersen, S., Svendsen, H., Kwasniewski, S., Pavlov, V., Pavlova, O., & Søreide, J. E. (2006). Physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden. *Progress in Oceanography*, *71*(2-4), 182-231. https://doi.org/10.1016/j.pocean.2006.09.007

Hop, H., & Gjøsæter, H. (2013). Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. *Marine biology research*, *9*(9), 878-894. https://doi.org/10.1080/17451000.2013.775458

Hop, H., & Wiencke, C. (2019). The ecosystem of Kongsfjorden, Svalbard (pp. 1–20). In H. Hop & C. Wiencke (Eds.), *The ecosystem of Kongsfjorden, Svalbard* (pp. 1–20). Springer. https://doi.org/10.1007/978-3-319-46425-1_1

Hop, H., Wold, A., Vihtakari, M., Daase, M., Kwasniewski, S., Gluchowska, M., Promińska, A., & Falk-Petersen, S. (2019). Zooplankton in Kongsfjorden (1996–2016) in relation to climate change. In H. Hop & C. Wiencke (Eds.), *The ecosystem of Kongsfjorden, Svalbard* (pp. 229–300). Springer. https://doi.org/10.1007/978-3-319-46425-1_7

Hop, H., Wold, A., Vihtakari, M., Assmy, P., Kuklinski, P., Kwasniewski, S., Gluchowska, M., Promińska, A., & Steen, H. (2023). Tidewater glaciers as "climate refugia" for zooplankton-dependent food web in Kongsfjorden, Svalbard. *Frontiers in Marine Science*, *10*, 1161912. https://doi.org/10.3389/fmars.2023.1161912

Hopwood, M. J., Carroll, D., Dunse, T., Hodson, A., Holding, J. M., Iriarte, J. L., Ribeiro, S., & Meire, L. (2020). How does glacier discharge affect marine biogeochemistry and primary production in the Arctic?. *The Cryosphere*, *14*(4), 1347-1383. https://doi.org/10.5194/tc-14-1347-2020

Howe, J. A., Moreton, S. G., Morri, C., & Morris, P. (2003). Multibeam bathymetry and the depositional environments of Kongsfjorden and Krossfjorden, western Spitsbergen, Svalbard. *Polar Research*, *22*(2), 301-316. https://doi.org/10.3402/polar.v22i2.6450

Hunt Jr, G. L., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R. D., Napp, J. M., & Bond, N. A. (2002). Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep Sea Research Part II: Topical Studies in Oceanography*, *49*(26), 5821-5853. https://doi.org/10.1016/S0967-0645(02)00321-1

Iken, K., Bluhm, B. A., & Gradinger, R. (2005). Food web structure in the high Arctic Canada Basin: evidence from $\delta^{13}C$ and $\delta^{15}N$ analysis. *Polar Biology*, *28*(3), 238-249. https://doi.org/10.1007/s00300-004-0669-2

Ingvaldsen, R. B., Assmann, K. M., Primicerio, R., Fossheim, M., Polyakov, I. V., & Dolgov, A. V. (2021). Physical manifestations and ecological implications of Arctic Atlantification. *Nature Reviews Earth & Environment*, *2*(12), 874-889. https://doi.org/10.1038/s43017-021-00228-x

Ingvaldsen, R. B., Bratbak, G., Planque, B., & Søreide, J. E. (2025). Food web structure, functions, drivers, and dynamics in the Barents Sea and adjacent seas. *Progress in Oceanography*, *233*, 103454. https://doi.org/10.1016/j.pocean.2024.103454

Isaksen, K. J. E. L. L., & Bakken, V. I. D. A. R. (1995). Breeding populations of seabirds in Svalbard. *Seabird Populations in the Northern Barents Sea. Source Data for the Impact Assessment of the Effect of Oil Drilling Activity.* (Norsk Polarinstitutte Meddelelser, No. 135, pp. 11-35). Norsk Polarinstitutte.

Ito, H. & KuooH, S. (1997). Characteristics of water in Kongsfjorden, Svalbard. In *Proceedings of the NIPR symposium on polar meteorology and glaciology* (Vol. 11, pp. 211-232). National Institute of Polar Research.

Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, *80*(3), 595-602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jahn, A., Holland, M. M., & Kay, J. E. (2024). Projections of an ice-free Arctic Ocean. *Nature Reviews Earth & Environment*, *5*(3), 164-176. https://doi.org/10.1038/s43017-023-00515-9

Jaschinski, S., Hansen, T., & Sommer, U. (2008). Effects of acidification in multiple stable isotope analyses. *Limnology and Oceanography: Methods*, *6*(1), 12-15. https://doi.org/10.4319/lom.2008.6.12

Karlsen, S. R., Elvebakk, A., Stendardi, L., Høgda, K. A., & Macias-Fauria, M. (2024). Greening of Svalbard. *Science of the Total Environment*, *945*, 174130. https://doi.org/10.1016/j.scitotenv.2024.174130

Karsten, U., Schaub, I., Woelfel, J., Sevilgen, D. S., Schlie, C., Becker, B., Wulff, A., Graeve, M., & Wagner, H. (2019). Living on cold substrata: New insights and approaches in the study of microphytobenthos ecophysiology and ecology in Kongsfjorden. In H. Hop & C. Wiencke (Eds.), *The Ecosystem of Kongsfjorden, Svalbard*, (pp. 303–330). Springer. https://doi.org/10.1007/978-3-319-46425-1_8

Keck, A. (1999). Phytoplankton assemblages related to physical gradients in an arctic, glacier-fed fjord in summer. *ICES Journal of Marine Science*, *56*(S1), 203-214. https://doi.org/10.1006/jmsc.1999.0622

Kern, S., Kaleschke, L., & Spreen, G. (2010). Climatology of the Nordic (Irminger, Greenland, Barents, Kara and White/Pechora) seas ice cover based on 85 GHz satellite microwave radiometry: 1992–2008. *Tellus A: Dynamic Meteorology and Oceanography*, *62*(4), 411-434. https://doi.org/10.1111/j.1600-0870.2010.00441.x

Kinnard, C., Zdanowicz, C. M., Fisher, D. A., Isaksson, E., de Vernal, A., & Thompson, L. G. (2011). Reconstructed changes in Arctic sea ice over the past 1,450 years. *Nature*, *479*(7374), 509-512. https://doi.org/10.1038/nature10581

Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V., & Aschan, M. (2015). Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1814), 20151546. https://doi.org/10.1098/rspb.2015.1546

Kovacs, K. M., Liston, G. E., Reinking, A. K., Gerland, S., & Lydersen, C. (2024). Climate warming impacts on ringed seal breeding habitat in Svalbard. *Ecological Modelling*, *495*, 110790. https://doi.org/10.1016/j.ecolmodel.2023.110790

Laudien, J., Herrmann, M., & Arntz, W. E. (1991). Soft bottom community structure and diversity in Kongsfjorden (Svalbard). In W. E. Arntz & M. Herrmann (Eds.), *The coastal ecosystem of Kongsfjorden, Svalbard. Synopsis of biological research performed at the Koldewey station in the years 1991–2003* (pp. 91–102). Alfred-Wegener-Institute.

Layman, C. A., Arrington, D. A., Montaña, C. G., & Post, D. M. (2007). Can stable isotope ratios provide for community-wide measures of trophic structure?. *Ecology, 88*(1), 42-48. https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2

Layman, C. A., & Allgeier, J. E. (2012). Characterizing trophic ecology of generalist consumers: a case study of the invasive lionfish in The Bahamas. *Marine Ecology Progress Series*, *448*, 131-141. https://doi.org/10.3354/meps09511

Leu, E., Falk-Petersen, S., Kwaśniewski, S., Wulff, A., Edvardsen, K., & Hessen, D. O. (2006). Fatty acid dynamics during the spring bloom in a High Arctic fjord: importance of abiotic factors versus community changes. Canadian Journal of Fisheries and Aquatic Sciences, 63(12), 2760-2779. https://doi.org/10.1139/f06-159

Li, W. K., McLaughlin, F. A., Lovejoy, C., & Carmack, E. C. (2009). Smallest algae thrive as the Arctic Ocean freshens. *Science*, *326*(5952), 539. https://doi.org/10.1126/science.1179798

Lønne, O. J., & Gabrielsen, G. W. (1992). Summer diet of seabirds feeding in sea-ice-covered waters near Svalbard. *Polar Biology*, *12*(8), 685-692. https://doi.org/10.1007/BF00238868

Lourenço, P. M., Granadeiro, J. P., Guilherme, J. L., & Catry, T. (2015). Turnover rates of stable isotopes in avian blood and toenails: Implications for dietary and migration studies. *Journal of Experimental Marine Biology and Ecology*, *472*, 89-96. https://doi.org/10.1016/j.jembe.2015.07.016

Lundgren, S. S., Abbasi, N. A., Waugh, C. A., Lee, M. M., Ciesielski, T. M., Gabrielsen, G. W., Descamps, S., & Jaspers, V. L. (2024). Metals and other trace elements in plasma and feathers of seabirds breeding in Svalbard. *Science of the Total Environment*, *952*, 175895. https://doi.org/10.1016/j.scitotenv.2024.175895

Lydersen, C., Assmy, P., Falk-Petersen, S., Kohler, J., Kovacs, K. M., Reigstad, M., Steen, H., Strøm, H., Sundfjord, A., Varpe, O., Walczowski, W., Weslawski, J.M., & Zajaczkowski, M. (2014). The importance of tidewater glaciers for marine mammals and seabirds in Svalbard, Norway. *Journal of Marine Systems*, *129*, 452-471. https://doi.org/10.1016/j.jmarsys.2013.09.006

MacLachlan, S. E., Howe, J. A., & Vardy, M. E. (2010). Morphodynamic evolution of Kongsfjorden–Krossfjorden, Svalbard, during the Late Weichselian and Holocene. *Geological Society Special Publications*, *344*, 185–199. https://doi.org/10.1144/SP344.13

Mattlin, R. H., Reynolds III, J. E., Huntington, H. P., & Pungowiyi, C. (2000). Impacts of changes in sea ice and other environmental parameters in the arctic. In *Marine Mammals and the Arctic Environment* (pp. 45–60). U.S. Marine Mammal Commission.

McConnaughey, T., & McRoy, C. P. (1979). Food-web structure and the fractionation of carbon isotopes in the Bering Sea. *Marine biology*, *53*(3), 257-262. https://doi.org/10.1007/BF00952434

McGovern, M., Berge, J., Szymczycha, B., Węsławski, J. M., & Renaud, P. E. (2018). Hyperbenthic food-web structure in an Arctic fjord. *Marine Ecology Progress Series*, *603*, 29-46. https://doi.org/10.3354/meps12713

Mehlum, F., & Gjertz, I. (1984). Feeding ecology of seabirds in the Svalbard area: A preliminary report. *16,* 1–41. *Norsk Polarinstitutt.*

Newsome, S. D., Martínez del Rio, C., Bearhop, S., & Phillips, D. L. (2007). A niche for isotopic ecology. *Frontiers in Ecology and the Environment, 5*(8), 429-436. https://doi.org/10.1890/060150.01

Nielsen, J. M., Clare, E. L., Hayden, B., Brett, M. T., & Kratina, P. (2018). Diet tracing in ecology: Method comparison and selection. *Methods in Ecology and Evolution*, *9*(2), 278-291. https://doi.org/10.1111/2041-210X.12869

Nuth, C., Kohler, J., König, M., von Deschwanden, A., Hagen, J. O., Kääb, A., Moholdt, G., & Pettersson, R. (2013). Decadal changes from a multi-temporal glacier inventory of Svalbard. *The Cryosphere*, *7*(5), 1603-1621. https://doi.org/10.5194/tc-7-1603-2013

Pavlov, A. K., Tverberg, V., Ivanov, B. V., Nilsen, F., Falk-Petersen, S., & Granskog, M. A. (2013). Warming of Atlantic Water in two west Spitsbergen fjords over the last century (1912-2009). *Polar Research*, *32*(1), 11206. https://doi.org/10.3402/polar.v32i0.11206

Pavlov, A. K., Leu, E., Hanelt, D., Bartsch, I., Karsten, U., Hudson, S. R., Gallet, J.-C., Cottier, F., Cohen, J. H., Berge, J., Johnsen, G., Maturilli, M., Kowalczuk, P., Sagan, J., Meler, J., & Granskog, M. A. (2019). The underwater light climate in Kongsfjorden and its ecological implications. In H. Hop & C. Wiencke (Eds.), *The ecosystem of Kongsfjorden, Svalbard* (pp. 137–170). Springer. https://doi.org/10.1007/978-3-319-46425-1_5

Pavlova, O., Gerland, S., & Hop, H. (2019). Changes in sea-ice extent and thickness in Kongsfjorden, Svalbard (2003–2016). In H. Hop & C. Wiencke (Eds.), *The ecosystem of Kongsfjorden, Svalbard* (pp. 105–136). Springer. https://doi.org/10.1007/978-3-319-46425-1_4

Peterson, B. J., & Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics, 18,* 293-320. https://doi.org/10.1146/annurev.ecolsys.18.1.293

Peterson, B. J. (1999). Stable isotopes as tracers of organic matter input and transfer in benthic food webs: A review. *Acta Oecologica*, *20*(4), 479-487. https://doi.org/10.1016/S1146-609X(99)00124-7

Pinzone, M. (2021). *Sourcing and dynamics of mercury in Arctic true seals*. (Doctoral dissertation, Université de Liège, Belgium). ORBi. https://orbi.uliege.be/handle/2268/263365

Polyak, L., Alley, R. B., Andrews, J. T., Brigham-Grette, J., Cronin, T. M., Darby, D. A., Dyke, A. S., Fitzpatrick, J. J., Funder, S., Holland, M., Jennings, A. E., Miller, G. H., O'Regan, M., Savelle, J., Serreze, M., St. John, K., White, J. W. C., & Wolff, E. (2010). History of sea ice in the Arctic. *Quaternary Science Reviews*, *29*(15-16), 1757-1778. https://doi.org/10.1016/j.quascirev.2010.02.010

Post, E., Bhatt, U. S., Bitz, C. M., Brodie, J. F., Fulton, T. L., Hebblewhite, M., Kerby, J., Kutz, S. J., Stirling, I., & Walker, D. A. (2013). Ecological consequences of sea-ice decline. *Science*, *341*(6145), 519-524. https://doi.org/10.1126/science.1235225

Purcell, J. E. (1991). A review of cnidarians and ctenophores feeding on competitors in the plankton. In R. B. Williams, P. F. S. Cornelius, R. G. Hughes, & E. A. Robson (Eds.), *Coelenterate Biology: Recent Research on Cnidaria and Ctenophora: Proceedings of the Fifth International Conference on Coelenterate Biology, 1989* (pp. 335-342). Springer. https://doi.org/10.1007/BF00026483

Raoult, V., Phillips, A. A., Nelson, J., Niella, Y., Skinner, C., Tilcock, M. B., Burke, P. J., Szpak, P., James, W. R., & Harrod, C. (2024). Why aquatic scientists should use sulfur stable isotope ratios (δ34S) more often. *Chemosphere,355*, 141816. https://doi.org/10.1016/j.chemosphere.2024.141816

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment*, *3*(1), 168. https://doi.org/10.1038/s43247-022-00498-3

Renaud, P. E., Daase, M., Leu, E., Geoffroy, M., Basedow, S., Inall, M., Campbell, K., Trudnowska, E., Sandbank, E., Cnossen, F., Dunn, M., Camus, L., Porter, M., Aune, M., & Gradinger, R. (2024). Extreme mismatch between phytoplankton and grazers during Arctic spring blooms and consequences for the pelagic food-web. *Progress in Oceanography*, 229, 103365. https://doi.org/10.1016/j.pocean.2024.103365

Renaud, P. E., Tessmann, M., Evenset, A., & Christensen, G. N. (2011). Benthic food-web structure of an Arctic fjord (Kongsfjorden, Svalbard). *Marine Biology Research, 7*(1), 13-26. https://doi.org/10.1080/17451001003671597

Santos-Garcia, M., Ganeshram, R. S., Tuerena, R. E., Debyser, M. C., Husum, K., Assmy, P., & Hop, H. (2022). Nitrate isotope investigations reveal future impacts of climate change on nitrogen inputs and cycling in Arctic fjords: Kongsfjorden and Rijpfjorden (Svalbard). *Biogeosciences*, *19*(24), 5973-6002. https://doi.org/10.5194/bg-19-5973-2022

Schlacher, T. A., & Connolly, R. M. (2014). Effects of acid treatment on carbon and nitrogen stable isotope ratios in ecological samples: a review and synthesis. *Methods in Ecology and Evolution*, *5*(6), 541-550. https://doi.org/10.1111/2041-210X.12183

Schlener, J. (2022). *Consequences of Individual Variation in Foraging Behaviour in Black-Legged Kittiwakes (Rissa Tridactyla)* [Master's thesis, McGill University]. McGill eScholarship. https://escholarship.mcgill.ca/downloads/1c18dm853

Sherwood, G. D., & Rose, G. A. (2005). Stable isotope analysis of some representative fish and invertebrates of the Newfoundland and Labrador continental shelf food web. *Estuarine, Coastal and Shelf Science*, *63*(4), 537-549. https://doi.org/10.1016/j.ecss.2004.12.010

Skjoldal, H. R., Eriksen, E., Ono, K., & Dolgov, A. (2025). Diet and trophic structure of fishes in the Barents Sea: between empty and full stomachs–large individual variability follows a common pattern. *Journal of Fish Biology.* https://doi.org/10.1111/jfb.16058

Smoła, Z. T., Tatarek, A., Wiktor, J. M., Wiktor, J. M., Kubiszyn, A., & Węsławski, J. M. (2017). Primary producers and production in Hornsund and Kongsfjorden–comparison of two fjord systems. *Polish Polar Research, 38*(3), 351-373. https://doi.org/10.1515/popore-2017-0013

Søreide, J. E., Hop, H., Carroll, M. L., Falk-Petersen, S., & Hegseth, E. N. (2006). Seasonal food web structures and sympagic–pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. *Progress in Oceanography, 71*(1), 59-87. https://doi.org/10.1016/j.pocean.2006.06.001

Søreide, J. E., Falk-Petersen, S., Hegseth, E. N., Hop, H., Carroll, M. L., Hobson, K. A., & Blachowiak-Samolyk, K. (2008). Seasonal feeding strategies of Calanus in the high-

Arctic Svalbard region. *Deep Sea Research Part II: Topical Studies in Oceanography*, *55*(20-21), 2225-2244. https://doi.org/10.1016/j.dsr2.2008.06.015

Suryan, R. M., Irons, D. B., & Benson, J. (2000). Prey switching and variable foraging strategies of black-legged kittiwakes and the effect on reproductive success. *The Condor*, *102*(2), 374-384. https://doi.org/10.1650/0010-5422(2000)102[0374:PSAVFS]2.0.CO;2

Svendsen, H., Beszczynska-Møller, A., Hagen, J. O., Lefauconnier, B., Tverberg, V., Gerland, S., Ørbæk, J. B., Bischof, K., Papucci, C., Zajaczkowski, M., Azzolini, R., Bruland, O., Wiencke, C., Winther, J.-G., & Dallmann, W. (2002). The physical environment of Kongsfjorden–Krossfjorden, an Arctic fjord system in Svalbard. *Polar research*, *21*(1), 133-166. https://doi.org/10.3402/polar.v21i1.6479

Syvitski, J. P., Burrell, D. C., & Skei, J. M. (2012). *Fjords: Processes and products.* Springer Science & Business Media. https://doi.org/10.1007/978-94-015-8658-0

Tamelander, T., Renaud, P. E., Hop, H., Carroll, M. L., Ambrose Jr, W. G., & Hobson, K. A. (2006). Trophic relationships and pelagic–benthic coupling during summer in the Barents Sea Marginal Ice Zone, revealed by stable carbon and nitrogen isotope measurements. *Marine Ecology Progress Series, 310,* 33-46. https://doi.org/10.3354/meps310033

Terazaki, M. (2004). Life history strategy of the chaetognath *Sagitta elegans* in the World Oceans. *Coastal Marine Science*, *29*, 1-12.

Torsvik, T., Albretsen, J., Sundfjord, A., Kohler, J., Sandvik, A. D., Skarðhamar, J., ... & Everett, A. (2019). Impact of tidewater glacier retreat on the fjord system: Modeling present and future circulation in Kongsfjorden, Svalbard. *Estuarine, Coastal and Shelf Science*, *220*, 152-165. https://doi.org/10.1016/j.ecss.2019.02.011

Urban, P., Præbel, K., Bhat, S., Dierking, J., & Wangensteen, O. S. (2022). DNA metabarcoding reveals the importance of gelatinous zooplankton in the diet of *Pandalus borealis*, a keystone species in the Arctic. *Molecular Ecology*, *31*(5), 1562-1576. https://doi.org/10.1111/mec.16370

Vander Zanden, M. J., & Rasmussen, J. B. (1999). Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. *Ecology*, 80(4), 1395–1404. https://doi.org/10.1890/0012-9658(1999)080[1395:PCCAND]2.0.CO;2

Vega, C. P., Björkman, M. P., Pohjola, V. A., Isaksson, E., Pettersson, R., Martma, T., Marca, A., & Kaiser, J. (2015). Nitrate stable isotopes and major ions in snow and ice samples from four Svalbard sites. *Polar Research*, *34*(1), 23246. https://doi.org/10.3402/polar.v34.23246

Vihtakari, M., Welcker, J., Moe, B., Chastel, O., Tartu, S., Hop, H., Bech, C., Descamps, S., & Gabrielsen, G. W. (2018). *Black-legged kittiwakes as messengers of Atlantification in the Arctic. Sci Rep 8: 1178*. https://doi.org/10.1038/s41598-017-19118-8

Voronkov, A., Hop, H., & Gulliksen, B. (2013). Diversity of hard-bottom fauna relative to environmental gradients in Kongsfjorden, Svalbard. *Polar Research*, *32*(1), 11208. https://doi.org/10.3402/polar.v32i0.11208

Walkusz, W., Kwasniewski, S., Petersen, S. F., Hop, H., Tverberg, V., Wieczorek, P., & Weslawski, J. M. (2009). Seasonal and spatial changes in the zooplankton community of Kongsfjorden, Svalbard. *Polar Research*, *28*(2), 254-281. https://doi.org/10.1111/j.1751-8369.2009.00105.x

Wassmann, P., Reigstad, M., Haug, T., Rudels, B., Carroll, M. L., Hop, H., Gabrielsen, G.W., Falk-Petersen, S., Denisenko, S.G., Arashkevich, E., Slagstad, D., & Pavlova, O. (2006). Food webs and carbon flux in the Barents Sea. *Progress in Oceanography*, *71*(2-4), 232-287. https://doi.org/10.1016/j.pocean.2006.10.003

Weslawski, J. M., Ryg, M., Smith, T. G., & Oritsland, N. A. (1994). Diet of ringed seals (*Phoca hispida*) in a fjord of West Svalbard. *Arctic*, *47*(2), 109-114. https://doi.org/10.14430/arctic1358

Wing, S. R., McLeod, R. J., Leichter, J. J., Frew, R. D., & Lamare, M. D. (2012). Sea ice microbial production supports Ross Sea benthic communities: influence of a small but stable subsidy. *Ecology*, *93*(2), 314-323. https://doi.org/10.1890/11-0475.1

Wlodarska-Kowalczuk, M., Sicinski, J., Gromisz, S., Kendall, M. A., & Dahle, S. (2007). Similar soft-bottom polychaete diversity in Arctic and Antarctic marine inlets. *Marine Biology, 151*(2), 607-616. https://doi.org/10.1007/s00227-006-0542-0

Włodarska-Kowalczuk, M., Renaud, P. E., Węsławski, J. M., Cochrane, S. K., & Denisenko, S. G. (2012). Species diversity, functional complexity and rarity in Arctic fjordic versus open shelf benthic systems. *Marine Ecology Progress Series*, *463*, 73-87. https://doi.org/10.3354/meps09835

Yunda-Guarin, G., Michel, L., Nozais, C., & Archambault, P. (2022). Interspecific differences in feeding selectivity shape isotopic niche structure of three ophiuroids in the Arctic Ocean. *Marine Ecology Progress Series*, *683*, 81-95. https://doi.org/10.3354/meps13908

Zhuravskiy, D., Ivanov, B., & Pavlov, A. (2012). Ice conditions at Gronfjorden Bay, Svalbard, from 1974 to 2008. *Polar Geography*, *35*(2), 169-176. https://doi.org/10.1080/1088937X.2012.687370

Front page pictures :

© *Rissa tridactyla*: Oleg Nabroven

© Kongfsjorden: Goncalo Diniz

© *Phoca vitulina*: A. Weith

© *Boreogadus saida*: Institute of Marine Research

Annex

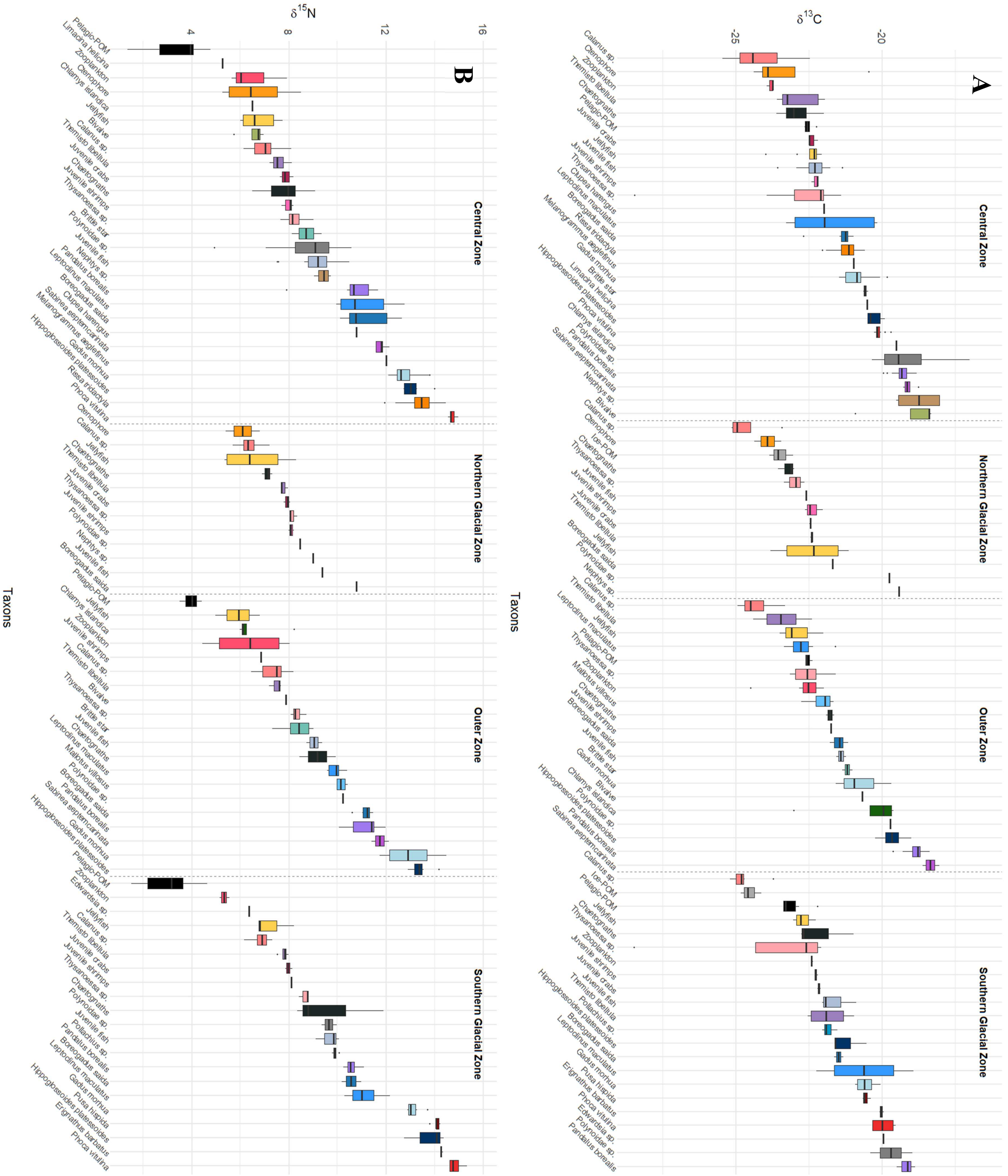
Annex 1. All the samples used for this study were divided into the four different zones and by sampling period.

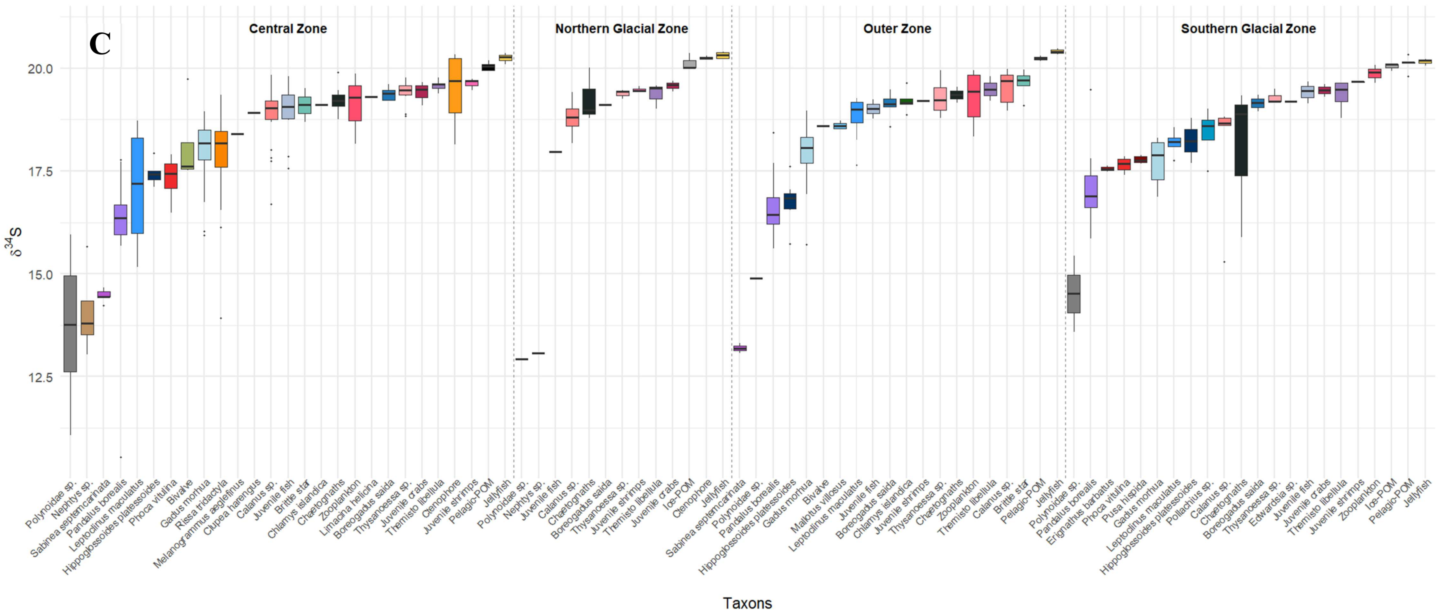
Taxon	Period	Central Zone	Outer Zone	Northern Glacial Zone	Southern Glacial Zone	Total
Cnidarian						20
Edwardsia sp.	Jun-24				1	1
Jellyfish						19
	Jun-24	5	1	3	2	11
	Jul-24	1			1	2
	Aug-24	3	2	1		6
Chaetognaths						15
	Jun-24	2			1	3
	Jul-24	1			1	2
	Aug-24	4	2	3	1	10
Ctenophore						6
	Jun-24	2		1		3
	Aug-24	2		1		3
Annelids						19
Nephtys sp.						5
	Jun-24	3		1		4
	Jul-24	1				1
Polynoidae						14
	May-24	1			1	2
	Jun-24	7	1	1	1	10
	Jul-24	2				2
Echinoderms						8
Brittle star						8
	Jun-24	1	4			5
	Jul-24	1				1
	Sep-24		2			2
Mollusks						12
Bivalve	Jun-24	4	1			5
Chlamys islandica	Sep-24	1	5			6
Limacina helicina	May-24	1				1
Arthropods						175
Calanus sp.						46
	May-24	2				2
	Jun-24	8	3	1	2	14
	Jul-24	3			2	5
	Aug-24	13	7	3	2	25
Pandalus borealis						44
	Aug-23	5				5
	Sep-23		2		3	5
	Jun-24	1			11	12

	Jul-24				1	1
	Aug-24	4	2		3	10
	Sep-24	6	5			11
Sabinea septemcarinata	Sep-24	5	2			7
Themisto libellula						21
	Jun-24	2	1		2	5
	Jul-24	2			1	3
	Aug-24	7	2	3	1	13
Thysanoessa sp.						27
	May-24	1				1
	Jun-24	3	5		2	10
	Jul-24	2			1	3
	Aug-24	7	2	3	1	13
Zooplankton						13
	Jun-23	1				1
	Aug-23	2				2
	May-24		6		3	9
	Aug-24		1			1
Juvenile crabs						8
	Jul-24	1			1	2
	Aug-24	2		3	1	6
Juvenile shrimps						9
	Jul-24	1			1	2
	Aug-24	2	1	3	1	7
Chordate						240
Boreogadus saida						19
	Jun-24	4			1	5
	Aug-24	1		1	1	3
	Sep-24	4	7			11
Clupea harengus	Jun-24	1				1
Gadus morhua						46
	Sep-23		6		6	12
	Jun-24	11	12			23
	Sep-24	6	5			11
Hippoglossoides platessoides						16
	Sep-23		1		3	4
	Jun-24	1				1
	Sep-24	5	6			11
Leptoclinus maculatus						25
	Sep-23				3	3
	Jun-24	2	10		1	13
	Sep-24	6	3			9
Mallotus villosus	Jun-24	1	4			4
Melanogrammus aeglefinus	Jun-24	1				1
Pollachius sp.	Sep-23				5	5

Juvenile fish						17
	Jun-23	1				1
	Jun-24		2			2
	Jul-24	2			1	3
	Aug-24	8		1	2	11
Erignathus barbatus						2
	Aug-23				1	1
	Sep-23				1	1
Phoca vitulina	Aug-23	11			4	15
Pusa hispida	Aug-23				5	5
Rissa tridactyla						84
	Jun-23	49				49
	Jul-23	20				20
	Jun-24	15				15
POM						**20**
Ice-POM						6
	May-24			3	3	6
Pelagic-POM						14
	May-24	5	3		6	13
	Jun-24					1
Total		**275**	**117**	**32**	**91**	**515**

Annex 2. (A) Boxplots of δ¹³C for the taxa used in this study across the 4 sampling zones. Each boxplot represents the distribution of δ¹³C values for a specific taxon within a given zone. (**B)** Boxplots of δ¹⁵N for the taxa used in this study across the 4 sampling zones. Each boxplot represents the distribution of δ¹⁵N values for a specific taxon within a given zone. (**C)** Boxplots of δ³⁴S for the taxa used in this study across the 4 sampling zones. Each boxplot represents the distribution of δ³⁴S values for a specific taxon within a given zone. The horizontal axis lists taxa names (grouped by zone), and each taxon is associated with the same colors for each graph. The vertical axis indicates the respective isotopic ratios (‰). The vertical dotted lines separate the graph according to the 5 sampling zones named at the top of the graph.




C
Central Zone
Northern Glacial Zone
Outer Zone
Southern Glacial Zone
$\delta^{34}S$
20.0
17.5
15.0
12.5
Taxons
Polynoidae sp.
Nephtys sp.
Sabinea septemcarinata
Pandalus borealis
Leptoclinus maculatus
Hippoglossoides platessoides
Phoca vitulina
Bivalve
Gadus morhua
Rissa tridactyla
Melanogrammus aeglefinus
Clupea harengus
Calanus sp.
Juvenile fish
Brittle star
Chlamys islandica
Chaetognaths
Zooplankton
Limacina helicina
Boreogadus saida
Thysanoessa sp.
Juvenile crabs
Themisto libellula
Ctenophore
Juvenile shrimps
Pelagic-POM
Jellyfish
Polynoidae sp.
Nephtys sp.
Juvenile fish
Calanus sp.
Chaetognaths
Boreogadus saida
Thysanoessa sp.
Juvenile shrimps
Themisto libellula
Juvenile crabs
Ice-POM
Ctenophore
Jellyfish
Sabinea septemcarinata
Polynoidae sp.
Pandalus borealis
Hippoglossoides platessoides
Gadus morhua
Bivalve
Mallotus villosus
Leptoclinus maculatus
Juvenile fish
Boreogadus saida
Chlamys islandica
Juvenile shrimps
Thysanoessa sp.
Chaetognaths
Zooplankton
Themisto libellula
Calanus sp.
Brittle star
Pelagic-POM
Jellyfish
Polynoidae sp.
Pandalus borealis
Erignathus barbatus
Phoca vitulina
Pusa hispida
Gadus morhua
Leptoclinus maculatus
Hippoglossoides platessoides
Pollachius sp.
Calanus sp.
Chaetognaths
Boreogadus saida
Thysanoessa sp.
Edwardsia sp.
Juvenile fish
Juvenile crabs
Themisto libellula
Juvenile shrimps
Zooplankton
Ice-POM
Pelagic-POM
Jellyfish

Annex 3. Pairwise comparisons (post-hoc Dunn test) of stable isotope values (δ^{13}C, δ^{15}N, and δ^{34}S) between marine taxa sampled. For each taxon pair, the table presents the Z-scores (Z) and associated p-values (p) for differences in isotopic composition. Z-scores indicate the standardized difference between taxa, while p-values reflect the statistical significance of these differences. Green p-values (< 0.05) denote statistically significant differences.

A) Pairwise comparisons (post-hoc Dunn test) of stable isotope values (δ^{13}C, δ^{15}N, and δ^{34}S) among the fish sampled.

Taxon 1	Taxon 2	Z δ^{13}C	Z δ^{15}N	Z δ^{34}S	p δ^{13}C	p δ^{15}N	p δ^{34}S
B. saida	*C. harengus*	0.791	0.179	0.539	0.429	0.858	0.59
B. saida	*G. morhua*	-4.43	-5.76	6.29	<0.001	<0.001	<0.001
C. harengus	*G. morhua*	-2.00	-1.74	1.15	0.069	0.124	0.375
B. saida	*H. platessoides*	-4.183	-4.813	6.877	0.004	<0.001	<0.001
C. harengus	*H. platessoides*	-2.32	-2.17	2.18	0.03	0.045	0.043
G. morhua	*H. platessoides*	-3.13	-2.41	2.99	0.05	0.048	0.08
B. saida	*L. maculatus*	1.72	2.15	3.97	0.086	0.032	<0.001
C. harengus	*L. maculatus*	-0.321	0.346	0.697	0.873	0.817	0.8
G. morhua	*L. maculatus*	4.43	6.5	-2.6	<0.001	<0.001	0.028
H. platessoides	*L. maculatus*	4.81	6.2	-2.47	<0.001	<0.001	0.013
B. saida	*M. villosus*	2.73	2.25	2.91	0.019	0.037	0.005
C. harengus	*M. villosus*	0.013	0.415	0.333	0.989	0.825	0.862
G. morhua	*M. villosus*	2.63	3.21	-2.14	0.012	0.002	0.048
H. platessoides	*M. villosus*	2.22	3.0	-2.25	0.001	<0.001	0.037
L. maculatus	*M. villosus*	-0.14	-0.024	-0.384	0.889	0.981	0.701
B. saida	*M. aeglefinus*	-1.58	-1.14	1.72	0.171	0.762	0.256
C. harengus	*M. aeglefinus*	-2.17	-1.03	0.228	0.091	0.458	0.82
G. morhua	*M. aeglefinus*	3.3	3.34	-2.62	0.003	0.002	0.026
H. platessoides	*M. aeglefinus*	0.669	1.21	-1.094	0.704	0.452	0.479
L. maculatus	*M. aeglefinus*	-1.067	-0.823	-0.003	0.471	0.605	0.997
M. villosus	*M. aeglefinus*	-1.279	-0.85	0.3	0.469	0.615	0.856
B. saida	Pollachius sp.	2.49	3.7	3.12	0.019	0.001	0.005
C. harengus	Pollachius sp.	-0.124	0.711	0.544	0.971	0.636	0.865
G. morhua	Pollachius sp.	2.976	4.437	-1.375	0.01	<0.001	0.364
H. platessoides	Pollachius sp.	3.26	3.46	-2.65	0.003	0.002	0.024
L. maculatus	Pollachius sp.	0.391	0.869	-0.236	0.847	0.634	0.876
M. villosus	Pollachius sp.	-0.372	0.924	-0.054	0.71	0.355	0.957
M. aeglefinus	Pollachius sp.	1.168	1.155	-0.102	0.453	0.463	0.953

B) Pairwise comparisons (post-hoc Dunn test) of stable isotope values ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$) among the fish and the predators sampled.

Taxon 1	Taxon 2	Z $\delta^{13}C$	Z $\delta^{15}N$	Z $\delta^{34}S$	p $\delta^{13}C$	p $\delta^{15}N$	p $\delta^{34}S$
B. saida	*E. barbatus*	-2.819	-3.33	3.198	0.013	0.002	0.008
C. harengus	*E. barbatus*	-2.51	-2.33	1.51	0.024	0.039	0.263
G. morhua	*E. barbatus*	1.433	2.08	-0.975	0.257	0.075	0.506
H. platesoides	*E. barbatus*	0.5	1.398	0.071	0.679	0.255	0.988
L. maculatus	*E. barbatus*	3.124	3.692	-1.671	0.005	0.001	0.223
M. villosus	*E. barbatus*	3.226	3.208	-2.002	0.005	0.004	0.136
M. aeglefinus	*E. barbatus*	0.899	1.848	-1.158	0.497	0.119	0.407
B. saida	*P. vitulina*	-5.828	-7.864	6.991	<0.001	<0.001	<0.001
C. harengus	*P. vitulina*	-2.71	-2.68	1.72	0.01	0.011	0.128
G. morhua	*P. vitulina*	-3.202	-5.861	2.493	0.005	<0.001	0.049
H. platesoides	*P. vitulina*	-0.813	-3.585	-0.045	0.539	0.001	0.979
L. maculatus	*P. vitulina*	-6.775	-9.044	3.874	<0.001	<0.001	0.001
M. villosus	*P. vitulina*	-4.818	-5.364	3.148	<0.001	<0.001	0.008
M. aeglefinus	*P. vitulina*	-0.986	-2.424	1.409	0.465	0.033	0.299
E. barbatus	*Pollachius* sp.	3.209	3.518	-1.658	0.005	0.001	0.221
P. vitulina	*Pollachius* sp.	5.039	6.165	-2.758	<0.001	<0.001	0.026
B. saida	*P. hispida*	-3.146	-4.596	4.018	0.005	<0.001	<0.001
C. harengus	*P. hispida*	-2.091	-2.162	1.548	0.071	0.063	0.251
G. morhua	*P. hispida*	-1.105	-2.838	0.735	0.395	0.011	0.598
H. platesoides	*P. hispida*	0.273	-1.722	-0.803	0.849	0.152	0.569
L. maculatus	*P. hispida*	-3.635	-5.2	1.776	0.001	<0.001	0.2
M. villosus	*P. hispida*	-3.398	-3.894	2.051	0.003	<0.001	0.14
M. aeglefinus	*P. hispida*	-0.535	-1.914	0.968	0.686	0.105	0.5
Pollachius sp.	*P. hispida*	-3.431	-4.392	1.627	0.003	<0.001	0.228
B. saida	*R. tridactyla*	-2.68	-7.58	6.26	0.015	<0.001	<0.001
C. harengus	*R. tridactyla*	-1.55	-2.00	1.25	0.146	0.068	0.319
G. morhua	*R. tridactyla*	3.112	-3.174	-0.884	0.005	0.004	0.529
H. platesoides	*R. tridactyla*	4.512	-0.469	-3.371	<0.001	0.781	0.001
L. maculatus	*R. tridactyla*	-3.028	-7.871	1.589	0.007	<0.001	0.238
M. villosus	*R. tridactyla*	-2.71	-3.35	1.9	0.01	0.001	0.087
M. aeglefinus	*R. tridactyla*	0.502	-1.335	0.549	0.7	0.279	0.713
Pollachius sp.	*R. tridactyla*	-2.344	-4.395	1.132	0.043	<0.001	0.415

C) Pairwise comparisons (post-hoc Dunn test) of stable isotope values (δ^{13}C, δ^{15}N, and δ^{34}S) among the seals and the kittiwakes sampled

Taxon 1	Taxon 2	Z δ^{13}C	Z δ^{15}N	Z δ^{34}S	p δ^{13}C	p δ^{15}N	p δ^{34}S
E. barbatus	*P. vitulina*	0.135	-0.54	0.107	0.893	0.707	0.915
E. barbatus	*P. hispida*	0.57	0.295	-0.535	0.683	0.768	0.712
Phoca vitulina	*P. hispida*	0.727	1.266	-1.023	0.701	0.308	0.46
E. barbatus	*R. tridactyla*	2.646	1.974	-1.403	0.016	0.097	0.482
P. vitulina	*R. tridactyla*	6.392	6.49	-3.869	<0.001	<0.001	0.001
P. hispida	*R. tridactyla*	3.077	2.531	-1.209	0.006	0.034	0.453

D) Pairwise comparisons (post-hoc Dunn test) of stable isotope values (δ^{13}C, δ^{15}N, and δ^{34}S) among some invertebrates taxa sampled.

Taxon 1	Taxon 2	Z δ^{13}C	Z δ^{15}N	Z δ^{34}S	p δ^{13}C	p δ^{15}N	p δ^{34}S
Bivalve	Brittle star	1.58	-2.66	-2.67	0.172	0.016	0.046
Bivalve	Chaetognaths	3.92	-2.24	-1.65	0.001	0.038	0.295
Brittle star	Chaetognaths	2.57	0.829	1.53	0.02	0.489	0.254
Bivalve	*C. islandica*	0.728	0.32	-0.698	0.677	0.911	0.705
Brittle star	*C. islandica*	-0.787	2.59	0.604	0.647	0.039	0.722
Chaetognaths	*C. islandica*	-3.37	2.78	-0.1	0.002	0.016	0.92
Bivalve	Ctenophore	3.75	-0.006	-2.85	0.001	0.996	0.026
Brittle star	Ctenophore	2.507	2.51	-0.797	0.042	0.042	0.66
Chaetognaths	Ctenophore	1.05	2.37	-1.99	0.295	0.036	0.093
C. islandica	Ctenophore	3.081	-0.075	-1.311	0.009	0.962	0.407
Bivalve	*Edwardsia sp.*	0.255	0.314	-0.448	0.921	0.892	0.818
Brittle star	*Edwardsia sp.*	-0.553	1.461	0.243	0.768	0.259	0.982
Chaetognaths	*Edwardsia sp.*	-1.46	1.257	-0.074	0.309	0.361	1
C. islandica	*Edwardsia sp.*	-0.149	0.139	-0.063	0.901	0.93	0.994
Ctenophore	*Edwardsia sp.*	-1.796	0.179	0.637	0.181	0.919	0.737
Bivalve	Jellyfish	3.438	0.068	-3.473	0.003	0.946	0.004
Brittle star	Jellyfish	3.35	3.69	-3.2	0.001	0.001	0.003
Chaetognaths	Jellyfish	-0.171	2.86	-3.853	0.926	0.021	0.001
C. islandica	Jellyfish	2.748	-0.341	-2.825	0.022	0.916	0.024
Ctenophore	Jellyfish	-1.05	-0.249	-1.209	0.508	0.904	0.408
Edwardsia sp.	Jellyfish	1.412	-0.302	-1.223	0.323	0.88	0.415
Bivalve	*L. helicina*	0.55	0.864	-0.605	0.749	0.601	0.743
Brittle star	*L. helicina*	-0.249	2.029	0.081	0.904	0.106	0.955
Chaetognaths	*L. helicina*	-1.147	1.84	-0.24	0.471	0.141	0.959

C. islandica	*L. helicina*	0.149	0.697	-0.222	0.922	0.705	0.951
Ctenophore	*L. helicina*	-1.497	0.737	0.478	0.302	0.692	0.813
Edwardsia sp.	*L. helicina*	0.228	0.426	-0.122	0.899	0.862	0.964
Jellyfish	*L. helicina*	-1.097	0.89	1.055	0.491	0.6	0.486
Bivalve	*Nephtys* sp.	-0.517	-2.851	1.266	0.756	0.02	0.421
Brittle star	*Nephtys* sp.	-2.093	-1.049	2.718	0.102	0.49	0.03
Chaetognaths	*Nephtys* sp.	-4.17	-2.36	3.24	<0.001	0.036	0.004
C. islandica	*Nephtys* sp.	-1.77	-2.73	2.22	0.153	0.019	0.08
Ctenophore	*Nephtys* sp.	-4.206	-3.227	3.269	<0.001	0.009	0.007
Edwardsia sp.	*Nephtys* sp.	-0.554	-1.96	1.179	0.79	0.118	0.413
Jellyfish	*Nephtys* sp.	-4.089	-3.655	5.065	<0.001	<0.001	<0.001
L. helicina	*Nephtys* sp.	-0.849	-2.51	1.336	0.615	0.045	0.43
Bivalve	Polynoidae	-0.083	-3.49	2.16	0.934	0.003	0.061
Brittle star	Polynoidae	-2.52	-1.09	4.77	0.024	0.333	<0.001
Chaetognaths	Polynoidae	-5.38	-2.11	4.51	<0.001	0.07	<0.001
C.islandica	Polynoidae	-1.033	-3.465	2.5	0.503	0.008	0.049
Ctenophore	Polynoidae	-4.679	-3.377	4.051	<0.001	0.008	0.001
Edwardsia sp.	Polynoidae	-0.331	-1.779	1.244	0.877	0.154	0.418
Jellyfish	Polynoidae	-5.085	-4.347	7.219	<0.001	0.001	<0.001
L. helicina	Polynoidae	-0.643	-2.361	1.411	0.732	0.055	0.396
Nephtys sp.	Polynoidae	0.507	0.588	-0.006	0.745	0.759	0.995

E) Pairwise comparisons (Post-hoc Dunn test) of stable isotope values (δ^{13}C, δ^{15}N, and δ^{34}S) among some zooplankton taxa sampled.

Taxon 1	Taxon 2	Z δ^{13}C	Z δ^{15}N	Z δ^{34}S	p δ^{13}C	p δ^{15}N	p δ^{34}S
Calanus sp.	Juvenile crabs	-3.136	-2.321	-1.704	0.004	0.03	0.155
Calanus sp.	Juvenile shrimps	-3.693	-2.678	-2.142	0.001	0.012	0.064
Juvenile crabs	Juvenile shrimps	-0.297	-0.179	-0.263	0.795	0.858	0.924
Calanus sp.	*P. borealis*	-11.18	-10.0	5.735	<0.001	<0.001	<0.001
Juvenile crabs	*P. borealis*	-3.008	-3.178	4.845	0.006	0.004	<0.001
Juvenile shrimps	*P. borealis*	-2.765	-3.1	5.44	0.011	0.005	<0.001
Calanus sp.	*S. septemcarinata*	-6.274	-6.366	4.337	<0.001	<0.001	<0.001
Juvenile crabs	*S. septemcarinata*	-2.597	-3.272	4.661	0.016	0.003	<0.001
Juvenile shrimps	*S. septemcarinata*	-2.38	-3.188	5.041	0.028	0.004	<0.001
Pandalus borealis	*S. septemcarinata*	-0.684	-1.64	1.93	0.494	0.101	0.054
Calanus sp.	*T. libellula*	-3.21	-2.55	-2.08	0.002	0.013	0.045
Juvenile crabs	*T. libellula*	0.435	0.853	-0.057	0.774	0.424	0.954
Juvenile shrimps	*T. libellula*	1.46	2.37	0.408	0.86	0.036	0.82
P. borealis	*T. libellula*	5.04	5.941	-7.11	<0.001	<0.001	<0.001
S. septemcarinata	*T. libellula*	3.493	4.693	-5.581	0.001	<0.001	<0.001
Calanus sp.	Chaetognaths	-3.026	-3.023	-0.306	0.009	0.009	0.901
Calanus sp.	*Thysanoessa* sp.	-3.28	-3.96	-1.73	0.001	<0.001	0.084
Juvenile crabs	*Thysanoessa* sp.	0.551	-2.59	1.25	0.698	0.029	0.425
Juvenile shrimps	*Thysanoessa* sp.	1.39	-1.93	1.93	0.492	0.08	0.162
P. borealis	*Thysanoessa* sp.	5.573	3.065	-6.391	<0.001	0.005	<0.001
S. septemcarinata	*Thysanoessa* sp.	3.656	2.899	-5.03	0.001	0.007	<0.001
T. libellula	*Thysanoessa* sp.	0.089	-2.73	0.963	0.929	0.011	0.47
Calanus sp.	Zooplankton	-2.775	0.772	-1.995	0.011	0.456	0.086
Juvenile crabs	Zooplankton	0.734	2.518	0.058	0.618	0.018	0.989
Juvenile shrimps	Zooplankton	1.093	2.81	0.356	0.427	0.009	0.879
P. borealis	Zooplankton	4.707	7.454	-5.816	<0.001	<0.001	<0.001
S. septemcarinata	Zooplankton	3.57	6.026	-5.09	0.001	<0.001	<0.001
T. libellula	Zooplankton	0.422	2.202	0.141	0.753	0.039	0.956
Thysanoessa sp.	Zooplankton	0.365	4.636	-0.688	0.77	<0.001	0.655