Investigations into food web structure in the Beaufort Sea

by

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Author's declaration

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Statement of contributions

While the research in this thesis was my own, co-authors provided valuable input and contributions to each chapter. The research was conducted in association with the Beaufort Regional Environmental Assessment Marine Fisheries Project (BREA MFP). Fisheries and Oceans Canada oversaw the design and execution of the field sampling program, led by Andrew Majewski and James Reist. A full list of field participants, including myself, can be found in Majewki et al. (2016). Over-arching research objectives and themes for the PhD were developed collaboratively by myself, Michael Power, Heidi Swanson, and James Reist in concert with priorities defined by the BREA MFP. Writing, data analysis, and specific study design ideas for each chapter were primarily developed by myself, with contributions from Michael Power and Heidi Swanson (University of Waterloo), as well as Bodil Bluhm (UiT – the Arctic University of Norway). Specific additional contributions to each chapter from co-authors are outlined below.

Chapter 2: Influences of depth and pelagic subsidies on the size-based trophic structure of Beaufort Sea fish communities. Ashley D. Stasko, Heidi Swanson, Andrew Majewski, Sheila Atchison, James Reist, and Michael Power.

Aside from the co-author contributions stated above, AM provided fish distribution data and SA provided biomass and trawl area calculations. All authors provided significant edits and helpful insights during manuscript preparation. The text presented in this thesis is a pre-copy editing version of a manuscript published as: Stasko AD, Swanson H, Majewski A, Atchison S, Reist J, Power M (2016) Influences of depth and pelagic subsidies on the size-based trophic structure of Beaufort Sea fish communities. *Marine Ecology Progress Series*, 549: 153-166, doi: 10.3354/meps11709

Chapter 3: Benthic-pelagic trophic coupling in an Arctic marine food web along gradients of water mass structure and organic matter input. Ashley D. Stasko, Bodil A. Bluhm, Heidi Swanson, Christine Michel, Philippe Archambault, Andrew Majewski, James D. Reist, and Michael Power.

Aside from the co-author contributions stated above, BAB provided significant input regarding study design and results, and acted as a primary advisor during a period of research abroad. CM provided algal biomass and primary productivity data. PA provided analyses of sediment granulometry, organic matter content, and pigment concentrations. All authors provided significant edits and helpful insights during manuscript preparation. This chapter has been submitted for publication under the same title and authorship in *Marine Ecology Progress Series* (manuscript ID 22559).

Chapter 4: Relationships between depth and δ^{15}N of Arctic benthos vary among regions and trophic functional groups. Ashley D. Stasko, Bodil A. Bluhm, James D. Reist, Heidi Swanson, and Michael Power.

Aside from the co-author contributions stated above, all authors provided significant edits and helpful insights during manuscript preparation. This manuscript has been submitted for publication under the same title and authorship in *Deep Sea Research I: Oceanographic Research Papers* (manuscript ID DSRI_2017_43).

Chapter 5: Responses of benthic functional food web structure to variable food supply in two Arctic shelf ecosystems. Ashley D. Stasko, Shannon MacPhee, Philippe

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Aside from the co-author contributions stated above, SM provided samples for epifauna and infauna. PA provided analyses of sediment granulometry, organic matter content, and pigment concentrations. JE provided oceanography data.

Abstract

The effects of climate change on marine ecosystems are most pronounced in the Arctic, where ice free summers have been predicted to occur by mid-century. Climate-related changes to sea ice phenology, oceanographic habitat characteristics, and primary production regimes will likely have strong effects on ecosystem structure that could alter energy pathways, species distributions, food web dynamics, and secondary production. Knowledge of many offshore Arctic ecosystems remains poor, undermining the ability to predict the effects of a changing climate on food web structure and function. This thesis capitalizes on the first comprehensive offshore sampling program in the Canadian Beaufort Sea and Amundsen Gulf to address substantial knowledge gaps regarding fish and invertebrate food web structure in the region. Trophic structure and benthic-pelagic linkages for biological communities on the continental shelf and slope were examined using stable isotope values measured in 127 fish and invertebrate taxa, biomass distributions, and a database of biological functional traits compiled for 166 taxa. Four empirical studies were conducted to test hypotheses regarding the responses of trophic structure to environmental gradients of depth, organic matter input regimes, water mass structure, and benthic food supply. Understanding food web structure and its link to large-scale environmental gradients will be key to assessing and predicting the effects of climate change on offshore marine communities in the Canadian Beaufort Sea and Amundsen Gulf.

In Chapter 2, benthic-pelagic coupling via active biological transport was identified as important for sustaining fish communities in the Beaufort Sea. Lower availability of benthic resources with increasing depth restricted biomass production for small size classes of fish in deep habitats. In those same fish communities, pelagic subsidies obtained by benthopelagic fishes were important for maintaining a relatively

high biomass of large-bodied fish in deep habitats. When fish and invertebrates were considered together in Chapter 3, benthic-pelagic coupling weakened eastward alongshore, across three regions. Benthic-pelagic coupling was (1) highest west of the Mackenzie River where sinking flux of pelagic particulate organic matter (POM) is known to be relatively high, (2) intermediate on the Mackenzie Shelf where riverine inputs of terrestrial organic matter dominate the sediment, and (3) lowest in the Amundsen Gulf where strong pelagic grazing is known to limit POM sinking flux to the benthos. Within all regions considered, benthic-pelagic coupling was consistently weakest in slope habitats underlying the transition between Pacific- and Atlantic-origin waters, where much of the organic carbon is transformed or intercepted in the water column. Analyses in Chapter 4 indicated that the dominance of terrestrial POM discharged from the Mackenzie River in the Beaufort Sea dampened depth-related changes in the $\delta^{15}N$ values of suspension/filter feeders, infaunal deposit feeders, and bulk sediment. In contrast, a faster rate of change in consumer and sediment $\delta^{15}N$ with depth was observed in the Amundsen Gulf. Relatively high primary production in the Amundsen Gulf likely promoted intensified biological transformation of autochthonous POM in the pelagic zone and lower downward POM flux, causing greater change in POM $\delta^{15}N$. Surprisingly, when isotopic diversity was weighted by species biomasses in Chapter 5, most benthic communities in the Canadian Beaufort Sea and Amundsen Gulf were found to rely on similarly diverse ranges of sedimentary organic matter, regardless of the sources. Trait-based functional diversity indicated that shelf edge communities maintained a relatively high diversity of biological trophic traits, presumably to exploit pulsed food inputs associated with dynamic shelf break hydrography. Several lines of evidence supported a role for episodic food inputs in structuring shelf edge trait composition. However, pairwise relationships between trophic traits and indicators of benthic food supply were not significant at the regional scale. Functional redundancy was low across most of the region, suggesting benthic food web function will be sensitive to species loss.

The research in this thesis presents the first comprehensive empirical studies of benthic food web structure for offshore fish and invertebrate communities in the Canadian Beaufort Sea and Amundsen Gulf. Each study proposes causal explanations for spatial patterns in food web structure based on data for habitat characteristics, species biomass distributions, and previously documented physical and biological properties of the regions. Three emergent properties are identified: (1) the Canadian Beaufort Sea and Amundsen Gulf should be considered separate but interconnected ecosystems, (2) organic matter pathways are key properties that define and determine trophic structure in the study systems, and (3) local habitat complexity interrupts linear associations between environmental gradients and trophic structure at the regional scale. The research represents a significant advancement in our knowledge of food webs in a rapidly changing, and understudied ecosystem. Several significant implications for ecosystem-based management are outlined in the General Conclusions section. Further study is needed to identify species-specific feeding relationships, understand how functional food web structure relates to indicators of ecosystem function, characterise winter ecology, and, ultimately, to develop an over-arching food web model that can be used to predict the impacts of a changing benthic food supply and species loss on community structure and function.

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1 General Introduction

General context of thesis

On a global scale, ecological structure and physical-biological coupling are better understood for continental shelves than for deep sea habitats (Levinton 2009). This is especially true in the Arctic Ocean, where the permanent sea ice pack has historically impeded comprehensive sampling programs in offshore habitats. With increasingly warmer annual temperatures, sea ice extent is declining at a rate of 11% per decade, and much of the central Arctic Ocean is no longer covered with multi-year ice (Polyakov et al. 2012). Such rapid change has brought our lack of knowledge regarding Arctic offshore ecosystems into sharp focus, but has also facilitated access to areas of the Arctic Ocean that were previously difficult to sample and study. The work in this thesis capitalizes on the first comprehensive biological sampling program conducted in offshore regions (> 200 m depths) of the Beaufort Sea and Amundsen Gulf to address knowledge gaps concerning demersal food web structure and trophic responses to environmental gradients. The research outlined here pairs trophic information derived from > 113 taxa with habitat characteristics, species biomass distributions, and the most recent literature on physical-biological forcings to describe regional food web patterns and propose mechanistic explanations for them. Establishing a knowledge base now is key to assessing and managing future changes in food web structure and function in the Canadian Beaufort Sea and Amundsen Gulf.

The physical setting: Bathymetry and hydrography

The southern Canadian Beaufort Sea is defined by the relatively narrow Mackenzie continental shelf, which extends approximately 120 km offshore. Past shelf break, the seafloor descends quickly to several thousand meters. The shelf is narrower in the semi-enclosed Amundsen Gulf where maximum depths are approximately 500 m. The Beaufort Sea and Amundsen Gulf have “interior shelves” that are isolated from the direct input of heat, nutrients, and biomass from the north Pacific and Atlantic oceans (Carmack et al. 2006). Circulation is therefore largely determined by wind-forcing, salinity, and the movement of deep water masses along the continental slope (Fig. 1.1; Carmack & Wassmann 2006, Williams & Carmack 2015). Open-water surface circulation in the Beaufort Sea is typically dominated by westward winds that push surface waters seaward in the anti-cyclonic Beaufort Gyre (Carmack & Macdonald 2002). Below the surface, circulation is topographically steered eastwards, bringing waters of Pacific and Atlantic origin along the slope and into the Beaufort Sea before entering the Amundsen Gulf (Carmack & Macdonald 2002, Barber et al. 2010). A narrow (< 20 km), intensified current known as the shelf break jet is confined to the upper slope around 100 to 150 m depths (Pickart 2004). Surface circulation in the Amundsen Gulf is more variable than that in the Beaufort Sea and poorly understood (reviewed in Barber et al. 2010).

Because thermal expansion coefficients for seawater are small at low temperatures, salinity rather than temperature is the most important determinant of density-driven stratification in the Arctic Ocean (Aagaard & Carmack 1989). In the Beaufort region, the result is a highly structured water column that can be simplified into four vertically stacked layers (Fig 1.2; described by McLaughlin et al. 1996, 2005, Lansard et al. 2012). At the surface, the Polar Mixed Layer comprises a low-salinity surface layer up to ~ 50 m thick, formed by wind mixing of freshwater inputs with marine water. Underneath, a cold, complex layer called the Pacific Halocline extends from ~ 50 to 200 m. Pacific-origin waters are modified by mixing and biogeochemical processes on the Chukchi Shelf before they are diverted eastwards into the Beaufort Sea (Kadko & Muench 2005, Clement et al. 2005). Consequently, these waters are nutrient-dense and carry resuspended particulate organic matter (POM), marine snow, and zooplankton into the Beaufort Sea (Ashjian et al. 2005, Kadko & Muench 2005). A strong thermohalocline around 200 m marks the relatively narrow transition between the Pacific Halocline and the warmer, saltier Atlantic Layer below (McLaughlin et al. 1996). The deeper Atlantic-origin waters enter from the East Siberian Sea before joining with the Pacific undercurrent. Finally, the Atlantic Layer transitions into the very cold and saline Arctic Deep Water, also of Atlantic origin, at ~ 750 to 800 m depths across a relatively diffuse pycnocline.

A seasonally variable freshwater plume from the Mackenzie River forms an additional layer up to ~ 10 m thick on the inner shelf (Carmack & Macdonald 2002). The Mackenzie River discharges > 330 km^3 of fresh water and between 40 and 120 x 10^6 t of sediment annually, exceeding the sediment input of any other Arctic river (Macdonald et al. 1998, Doxaran et al. 2015, Rachold et al. 2004). The small size of the Mackenzie Shelf relative to the volume of fresh water makes it the most estuarine of all Arctic interior shelves (Williams & Carmack 2015). The sediment and freshwater plume typically flows eastward along the Tuktoyaktuk Peninsula, but can be forced offshore and westward under the influence of easterly winds (Fig. 1.1; Carmack & Macdonald 2002).

The biological setting: Status of knowledge on benthic marine ecosystems

Faunal distributions

Prior to the initiation of large-scale research projects in the 1980's, Arctic benthic communities were considered depauperate relative to temperate and Antarctic systems (Piepenburg 2005). More than 30 years of intensified research across the Arctic, and especially on the shelves, have since painted a picture of vibrant benthic faunal assemblages characterised by high spatial heterogeneity (Piepenburg 2005). From these studies, it is clear that patterns in benthic community structure are affected by a large array of complex, interacting biotic and abiotic variables involving hydrography, bathymetry, nutrient regime, granulometry, ice cover, and sedimentation rates (e.g., Grebmeier & Barry 1991, Dunton et al. 2005, Conlan et al. 2008, 2013, Roy et al. 2014). However, localized habitat heterogeneity appears to interrupt spatial relationships between benthic community composition and large-scale environmental gradients, such as sedimentary characteristics or annual primary production (Conlan et al. 2008, Roy et al. 2014).

The Mackenzie Shelf is typified by muddy-bottom benthic invertebrate communities, with higher taxonomic diversity and biomass near the shelf break compared to inshore (Conlan et al. 2008, 2013). Taxonomic diversity is more spatially variable where communities experience higher temporal variation in habitat conditions, such as inshore and near the Mackenzie River (Conlan et al. 2008). Macrobenthic biomass on the Mackenzie Shelf generally declines eastward from ~ 80 g m^{-2} near Point Barrow, Alaska, to as low as 0.01 g m^{-2} near the mouth of the Mackenzie River (Dunton et al. 2005), then increases eastward to a maximum of ~ 1016 g m^{-2} near the Cape Bathurst upwelling region (Conlan et al. 2013). There are no strong differences in benthic invertebrate community characteristics between the Canadian Beaufort Sea and Amundsen Gulf aside from higher richness and beta diversity in

Amundsen Gulf, and a higher abundance of estuarine-tolerant species in the Beaufort Sea (Conlan et al. 2008, Roy et al. 2015b).

Fish community composition in the western Arctic appears to be most closely associated with the gradients of temperature, depth, and salinity associated with the circulation of water masses (Logerwell et al. 2011, Majewski et al. 2013, 2017, Norcross et al. 2013). In the Beaufort Sea, small-bodied benthic fishes dominate the nearshore shelf, whereas large-bodied predatory fishes dominate the lower slope (Majewski et al. 2013, 2017). Fish biomass peaks on the upper slope (between 200 to 350 m; Majewski et al. 2017). Arctic Cod (*Boreogadus saida* (Lepechin)) is by far the most abundant and well-studied species, and is common at all depths down to 1000 m (Majewski et al. 2013, 2017).

Basic structure of offshore food webs

Outside of shallow areas where benthic algae occur, benthic food webs typically begin in the pelagic zone where carbon is fixed by autotrophs. Here, pelagic zooplankton have a strong influence on the quantity and quality of primary production that is exported to the benthos below (Grebmeier & Barry 1991). The portion of primary production that escapes grazing at the surface is subject to microbial remineralization and degradation during sinking (Kellogg et al. 2011). Further microbial processing occurs in the sediment, and in some cases can transform refractory material into more labile food for higher trophic level benthic invertebrates (Lovvorn et al. 2005, Savvichev et al. 2007, Bell et al. 2016).

At the seafloor, resident members of benthic marine food webs are typically grouped into one of three simplified feeding types: suspension/filter feeders that exploit sinking or re-suspended particles, deposit feeders that exploit detritus and reworked organic material on the seafloor, and mobile scavenger/predators that exploit large food falls and prey on other benthic organisms (e.g., Tamelander et al. 2006, Divine et al. 2015, Bell et al. 2016). Demersal fauna can be epifaunal (live at the sediment surface), infaunal (live below the sediment surface), or benthopelagic (commonly utilise habitat some distance above the seafloor). There is evidence that highly mobile scavengers/predators in the deep basin such as fish, amphipods, and decapods can rely to a great extent on resources from the pelagic environment rather than consuming biota that are supported by benthically processed carbon (Iken et al. 2005). Consequently, deep benthic food webs can display an apparent split between a detritus- and pelagic-based food chain (Iken et al. 2005). Aside from the three resident feeding types, two additional groups act as temporary members of benthic food webs on the shelves. Vertically-migrating pelagic zooplankton and amphipods can occupy bottom waters on a seasonal or daily cycle, and can act as both predators and prey (Berge et al. 2009, Connelly et al. 2012). Diving seabirds and large benthic-feeding marine mammals (e.g., beluga whale *Delphinapterus leucas* Pallas, Pacific walrus *Odobenus rosmarus divergens* Illiger, grey whales *Eschrichtius robustus* Lilljeborg, ringed seal *Pusa hispida* Schreber 1775, and bearded seals *Erignathus barbatu* Erxleben) can act as predators in shallow areas during migratory feeding seasons (e.g., Bluhm & Gradinger 2008).

Organic matter pathways to the benthos

Climate change is significantly altering the organic matter pathways that fuel benthic marine food webs worldwide (Hoegh-Guldberg & Bruno 2010). In the Arctic, shifts in organic matter pathways are linked to sea ice loss, which has already transformed the rates and dominant sources of primary production in some areas (McLaughlin & Carmack 2010, Kortsch et al. 2012). Enhanced primary production from rising sea temperatures and longer ice-free periods is expected to favour pelagic communities on the shelves, driving a shift from benthic- to pelagic-driven food webs (Forest et al. 2010, McLaughlin et al. 2011, Wassmann & Reigstad 2011). In contrast, increased input of fresh water from melting ice in the Canada Basin has resulted in a deepened nutricline that will likely reduce primary production in the deep basin (McLaughlin & Carmack 2010). Predicting the effects of climate-driven changes in production regimes requires identifying current linkages between organic matter pathways and trophic structure.

The major sources of primary production in the Arctic Ocean are pelagic and sympagic (ice-associated) algae. Estimates of the relative importance of sympagic algal production range from 0 to 80 % of total annual primary productivity, increasing northwards with annual ice cover (Gosselin et al. 1997, Wassmann et al. 2008). Longitudinal patterns of primary production in the Beaufort Sea region are somewhat variable within and among years (Carmack et al. 2004, Morata et al. 2008, Ardyna et al. 2013). Generally, annual primary production is relatively high in the Chukchi Sea to the west (~100 g C m^{-2} yr^{-1}) and the Canadian Archipelago to the east (~ 140 g C m^{-2} yr^{-1}), and considerably lower in the Beaufort Sea (~ 62 g C m^{-2} yr^{-1}; Ardyna et al. 2013). Heterotrophic bacteria and benthic algae contribute substantially to production in nearshore areas in the Beaufort Sea, but are minor sources at the regional scale (Garneau et al. 2006, Oxtoby et al. 2016). Significant macrophyte beds or kelp forests have not been identified in the region (Cobb et al. 2008).

Pelagic primary production in the Beaufort region follows the same general annual cycle as other Arctic marginal seas (Carmack & Macdonald 2002, Sakshaug 2004). Briefly, primary production is lowest during the Arctic winter when the sea ice is extensive and daylight hours are short, allowing unused nutrients to accumulate in the upper water column. The return of light, the recession of sea ice, and the onset of stratification from melting ice and river input trigger the spring phytoplankton bloom, which begins on the shelf and follows the retreating sea ice (Carmack & Macdonald 2002, Sakshaug 2004). The export of ungrazed phytoplankton, fecal pellets, and other biogenic material can increase substantially at this time (up to 75%; Forest et al. 2007), creating a moving zone of increased carbon flux to the benthos. Nutrients in the strongly stratified euphotic zone are quickly depleted once light becomes available, resulting in lower rates of primary production during late summer (Hill & Cota 2005, Walsh et al. 2005).

Aside from the regular seasonal cycle, pelagic primary production in the Canadian Beaufort Sea and Amundsen Gulf is punctuated by upwelling events that replenish nutrients in surface layers and promote sudden, localised phytoplankton blooms (Carmack & Chapman 2003, Carmack et al. 2004). Upwelling can occur at any point along the shelf, but Cape Bathurst, Mackenzie Trough, and Kugmallit Valley are considered upwelling “hot spots” due to steep topography (Carmack & Kulikov 1998, Williams et al. 2008, Williams & Carmack 2015). In contrast, downwelling is important for the vertical mixing and resuspension of surface production on the shelves (Williams & Carmack 2015). Upwelling/downwelling in the Beaufort Sea is most frequent when the ice pack has receded north of shelf break (Carmack & Chapman 2003), but under-ice upwelling events have also been observed in the Amundsen Gulf

(Mundy et al. 2009). The frequency and importance of under-ice upwelling events remains uncertain (Mundy et al. 2009).

The delivery of pelagic production to Arctic benthos is thus characterised by pulsed food inputs, some of which are seasonal and fairly predictable (e.g., ice-edge bloom), and some of which are episodic (e.g., upwelling). Pulsed pelagic blooms are important sources of fresh phytodetritus for benthos, as more primary production is typically produced than can be grazed by pelagic communities (e.g., Forest et al. 2007). Freshly sedimented phytodetritus can be consumed quickly by benthic communities, and is thought to provide rare essential fatty acids that may be important for reproduction in some invertebrates (McMahon et al. 2006, Renaud et al. 2007b). However, benthic communities appear to be very efficient at long-term carbon processing, consuming relatively consistent fractions of sedimentary organic carbon in between pulsed food inputs (Lovvorn et al. 2005, Renaud et al. 2008, North et al. 2014).

Aside from the direct export of pelagic POM, food supply to the benthos can be augmented by various other sources. For example, sufficient food may be obtained to support rich benthic communities through lateral advection of organic matter from adjacent regions (Dunton et al. 2005, Feder et al. 2005, 2007) or even the entrainment of nutrient-poor waters long enough for POM to settle (Feder et al. 2011). Terrestrial organic matter on the Mackenzie Shelf and inshore areas is thought to be a favourable substrate for microbial communities which then fuel productivity at higher trophic levels (Dunton et al. 2006, Bell et al. 2016). Indeed, bacteria and bacterial matrices can be a direct food source for deposit-feeding invertebrates (Lovvorn et al. 2005, McTigue & Dunton 2014, North et al. 2014). On the other hand, many mobile predators and scavengers are able to seek prey through vertical or horizontal migrations (e.g., Hovde et al. 2002). The frequency of large food falls, like whales, is unquantified in the

Beaufort region but such rich food deposits in the Arctic attract scavengers from great distances at surprising speed (Klages et al. 2001). Vertically migrating phytoplankton grazers may be a particularly important source of lipids for benthic communities (Connelly et al. 2012). The result of a diverse food supply is that obvious indicators of productivity in the overlying pelagic system are not always good predictors of where benthic communities will flourish (e.g., Feder et al. 2011, Roy et al. 2014).

Knowledge gaps

Although a conceptual model of feeding linkages between mammals, fish, and invertebrates has been established for the Canadian Beaufort Sea (e.g., Cobb et al. 2008, Darnis et al. 2012), little is known about trophic niche dimensions, the proportional contributions of different energy pathways to diets, or the strength of benthic-pelagic trophic coupling for demersal food webs. Even less is known about how such food web parameters respond to large-scale habitat heterogeneity or to environmental changes. Biological traits analyses, which investigate the distribution of functional attributes that contribute to ecosystem function regardless of species identities, have not been conducted for demersal communities in the region. Process-oriented studies of organic matter pathways and benthic remineralisation exist for the Canadian Beaufort Sea and Amundsen Gulf (e.g., Renaud et al. 2007a, Darnis et al. 2012, Roy et al. 2015), but food web structure itself remains understudied. Associations between demersal food web structures and the organic matter production/input regimes that sustain them have yet to be defined across much of the study region. Moreover, significant knowledge gaps remain regarding the distributions and occurrences of offshore biota in the Canadian Beaufort Sea and Amundsen Gulf, especially for fish. The lack of baseline knowledge regarding trophic and ecosystem structure in the Canadian Beaufort Sea region inhibits effective ecosystem-based management in the face of climate change and other potential disturbances (e.g., hydrocarbon development, offshore fisheries, and increased shipping).

Stable isotope applications in trophic ecology

The work in this thesis relied largely on sampling events that could not be repeated. As such, stable isotope analysis was applied to obtain temporally-integrated indications of feeding (weeks to months; e.g., Hesslein et al. 1993, Frazer et al. 1997). Stable isotope ratios of nitrogen ($\delta^{15}N$) measured in consumer tissues exhibit stepwise enrichment between trophic levels and can be used to estimate relative trophic levels (DeNiro & Epstein 1981, Minagawa & Wada 1984, Peterson & Fry 1987). In contrast, $\delta^{13}C$ changes little between trophic levels and can trace consumer food sources when the $\delta^{13}C$ values of those sources differ (DeNiro & Epstein 1978, Rounick & Winterbourn 1986, Cabana & Rasmussen 1996). In the Arctic Ocean, differences in $\delta^{13}C$ between primary organic carbon sources are usually sufficient to discriminate between open-water phytoplankton and ice-algae in the pelagic zone (e.g., Søreide et al. 2006), and between terrestrial, fresh marine, and refractory marine sedimentary organic carbon in the benthic zone (e.g., Magen et al. 2010). Moreover, quantitative isotopic niche metrics can be calculated for populations or communities from the distributions of individuals in $\delta^{15}N$ and $\delta^{13}C$ bivariate space, which then act as proxies for trophic niche dimensions (Bearhop et al. 2004, Layman et al. 2007, Swanson et al. 2015). Stable isotope analyses were therefore well suited to the purposes of this thesis, allowing the identification of the primary energy pathways that fuelled and structured demersal marine communities.

Sampling program: The BREA Marine Fishes Project

Sample collection for this thesis was conducted by the Beaufort Regional Environmental Assessment Marine Fishes Project (BREA MFP), a multi-stakeholder research initiative established by Aboriginal Affairs and Northern Development Canada and implemented by Fisheries and Oceans Canada. The BREA MFP was designed to fill large knowledge gaps regarding diversity, distributions, and habitat associations of offshore fishes in the Canadian Beaufort Sea in support of regulatory decision making and conservation initiatives. Prior to the BREA MFP, ecological studies in the Canadian Beaufort Sea and Amundsen Gulf had been restricted to nearshore areas (< 200 m; reviewed in Majewski et al. 2016). Essentially, the primary objective of the BREA MFP was to provide an ecological baseline of ecosystem structure and function in offshore regions.

Although the BREA MFP was touted as a fish-focused research initiative, the program aimed to be a comprehensive ecosystem study that described the habitat setting and biological communities within which fishes operate. As a result, a stable isotope database that included > 4000 individual samples of 127 unique fish and invertebrate taxa was developed over the course of this thesis (Table 1.1). Food web analyses were supported by data for biomass distributions, physical oceanography, sedimentary characteristics, and primary production. Species inventories provided by the program extended the scope of research by allowing the development of a biological traits database for many taxa additional to those included in the stable isotope database (see Appendices B & C).

Ultimately, the collaborative sampling program and research network provided by the BREA MFP set the physical-biological context for analysing food web structure. Understanding the environmental setting was critical for interpreting stable isotope data (see Chapter 4) and for developing mechanistic explanations of the spatial patterns detected in food web structure (see Chapters 3 and 5).

Research objectives

Understanding the structure of Arctic benthic food webs and their responses to environmental gradients is key to predicting ecosystem functioning in future climates. To that end, this thesis aimed to **(a) build a more comprehensive understanding of trophic linkages in marine fish and invertebrate communities between nearshore and offshore environments, and between benthic and pelagic habitats, and (b) characterise food web responses to gradients in oceanography and benthic food availability.** These primary research objectives were addressed through four analytical chapters, which were conducted as related but independent studies on the trophic ecology, structure, and function of benthic fish and invertebrate communities in the Canadian Beaufort Sea and Amundsen Gulf:

In Chapter 2, size spectra were quantified for fish communities at four habitat depths along the Canadian Beaufort Sea shelf and continental slope. The objectives of the chapter were to assess whether fish food webs were strongly size structured (i.e., the largest individuals occupied the highest trophic positions), whether size structure changed with depth, and finally whether depth-related patterns in size structure were influenced by the relative use of benthic versus pelagic food sources. By examining the link between benthic-pelagic coupling and size spectra, the information in Chapter 2 may inform the development of methods to monitor changes in fish food web structure. Moreover, results contribute to the currently underdeveloped knowledge base regarding the ecology of offshore fishes.

In light of findings from Chapter 2, drivers of benthic-pelagic food web coupling for fish and invertebrates across the Canadian Beaufort Sea and Amundsen Gulf were explicitly examined in Chapter 3. The objectives of Chapter 3 were to examine how trophic structure was influenced by the vertical water mass profile and by alongshore gradients in organic matter input regimes. Stable isotope data were used to quantify trophic niche indices at the community and functional group level. Trophic niche indices were paired with algal biomass and sedimentary data to assess differences in trophic structure among four water mass assemblages, and among three longitudinal regions. Information provided by Chapter 3 identified benthic areas that will respond in different ways to predicted climate-driven changes in hydrography and surface production.

Investigations in Chapter 4 built on differences in food web structure between the Canadian Beaufort Sea and Amundsen Gulf observed in Chapter 3, which were hypothesised to be related to POM input and flux dynamics. Microbial processing of organic matter during sinking can cause an increase in the $\delta^{15}N$ of POM with water depth, which is then reflected in the tissues of some benthic functional groups (Mintenbeck et al. 2007). The objectives of this chapter were to identify which functional groups exhibited significant change in $\delta^{15}N$ with water depth, and to assess whether the rate of change differed between the Canadian Beaufort Sea and Amundsen Gulf, which are subject to different POM flux dynamics in the upper water column (e.g., Sampei et al. 2011). A mixed effects modelling approach was employed to examine and compare δ^{15}N-depth relationships among functional trophic groups and regions. The conclusions of Chapter 4 have implications for comparing isotopic trophic structure among regions and functional groups, and provide more evidence that organic matter flux regimes play an important role in structuring benthic food webs across the study region.

Following the conclusions of previous chapters, the aim of Chapter 5 was to assess linkages between benthic functional food web structure and environmental indicators of benthic food supply and bottom oceanography. Functional diversity measures based on biological species traits and stable isotope ratios were calculated and combined to examine spatial trends in trophic functional structure across the study region. Significant associations between pairwise combinations of biological traits and environmental indicators were tested with a multivariate approach. Because species with the greatest biomass are likely to have the largest impact on ecosystem functioning (Grime 1998), all analyses in Chapter 5 were weighted by relative species biomasses. The results of Chapter 5 demonstrate the utility of using traits-based and isotopic functional composition as indicators of food web responses to environmental change.

Finally, the main findings of the research are synthesized in Chapter 6 and emergent patterns in physical-biological properties that structure benthic food webs in the Canadian Beaufort Sea and Amundsen Gulf are outlined. The relevance of new knowledge to ecosystem management is discussed, and fruitful avenues for future research are suggested.

Table 1.1. Summary of the taxonomic distribution of stable isotope samples processed for food web studies contained in the thesis.

Food web component	N	Num. of taxa	Num. of genera	Phyla
Fish	1823	30	18	Chordata
Epifauna	1635	41	29	Mollusca, Cnidaria, Echinodermata, Arthropoda, Chaetognatha
Infauna	288	32	19	Mollusca, Annelida, Sipuncula, Arthropoda
Zooplankton	286	24	15	Arthropoda, Mollusca, Ctenophora, Cnidaria, Chaetognatha, Chordata
Sediment	70	NA	NA	NA
Total:	4102	127	81	10

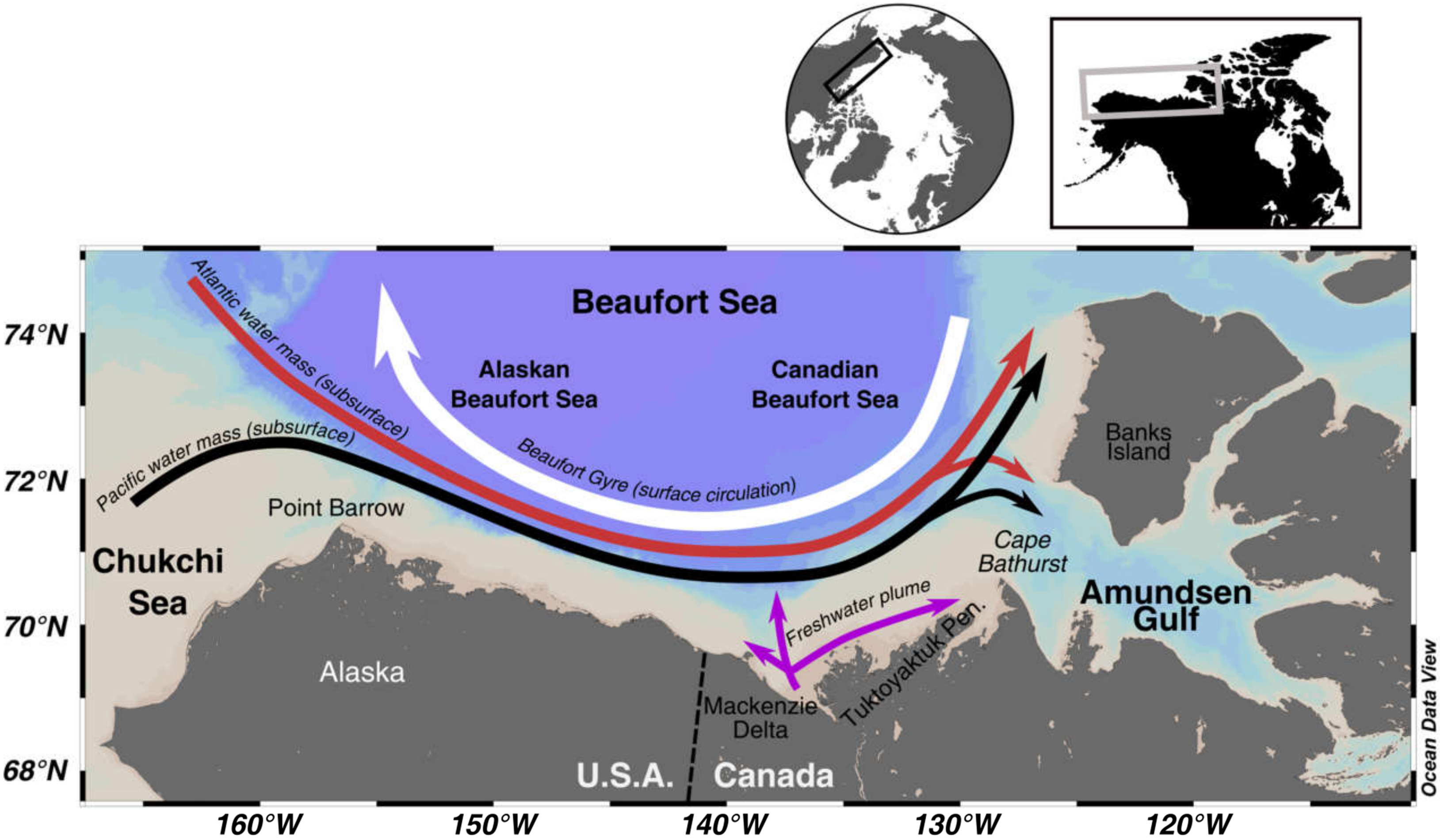
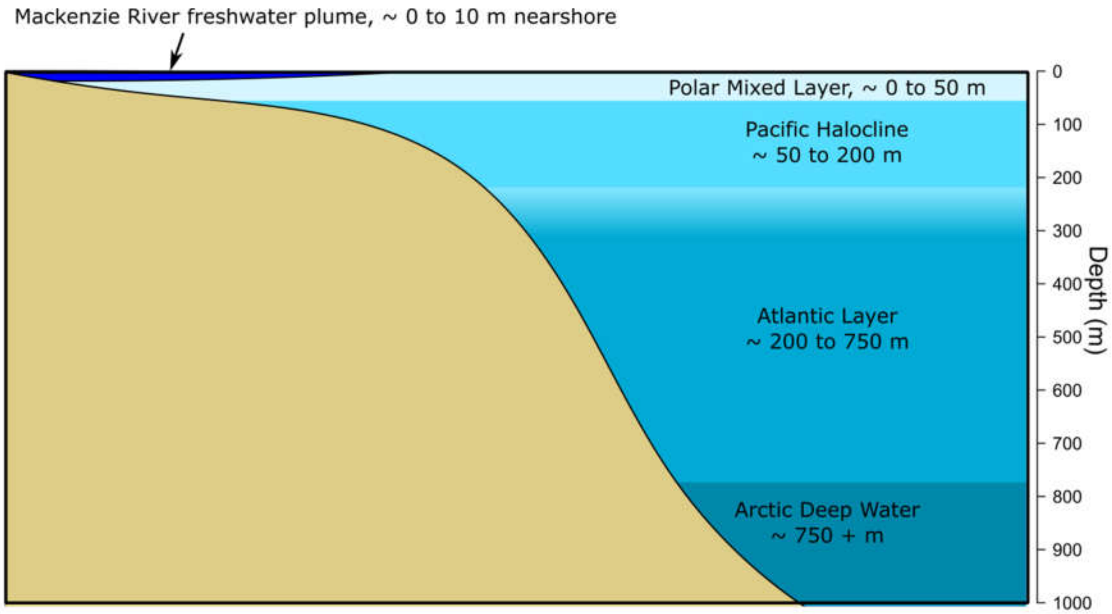


Figure 1.1. Map of the Beaufort Sea and Amundsen Gulf. Ice and surface water circulation in the Beaufort Sea is dominated by the anti-cyclonic Beaufort Gyre. Pacific-origin waters enter the Beaufort Sea and Amundsen Gulf from the Chukchi Sea, whereas Atlantic-origin waters enter from the East Siberian Sea. Subsurface circulation of Pacific- and Atlantic-origin waters flows eastward along the continental slope. The freshwater plume from the Mackenzie River is typically steered eastward along the shore by the Coriolis force, but can be drawn offshore and to the west by westward winds.



Water mass layer	Salinity range (PSU)	Mean temperature (˚C)
Freshwater plume	temporally and spatially variable, but as low as 10	temporally and spatially variable, but as high as 15
Polar Mixed Layer	30 to 33.5	~0
Pacific Halocline	33 to 34.3	0 to -1.4
Atlantic Layer	34.5 to 34.9	~ 0
Arctic Deep Water	34.9	~ -0.5

Figure 1.2. The simplified vertical water mass structure that occurs in the Canadian Beaufort Sea and Amundsen Gulf, with mean salinity and temperature for each layer (Swift et al. 1997, MacDonald et al. 2000, McLaughlin et al. 1996, 2005; Mulligan et al. 2010).

2 Influences of depth and pelagic subsidies on the size-based trophic structure of Beaufort Sea fish communities

Introduction

Demersal communities depend on energy and matter produced in the near-surface layers of the ocean. This imposes depth-related constraints on food availability by limiting the amount of carbon flux reaching the seafloor and on food quality by increasing the length of time available for organic matter to degrade during sinking (Lee et al. 2004, Smith et al. 2008). As a result, shifts in demersal (bottom-dwelling) community composition, biomass, diversity, and associated trophic strategies are commonly observed along depth gradients (e.g., Grebmeier et al. 1989, Conlan et al. 2008, Wei et al. 2010, Majewski et al. 2015). To date, most depth-related shifts in community structure have been examined from a taxonomic perspective. Taking a macroecological approach, however, can shed light on how depth influences community structure via the distribution of biomass among body sizes or trophic levels irrespective of taxonomy (e.g., Haedrich & Merrett 1992). Investigations of the relationship between biomass and body mass (known as biomass size-spectra relationships) can lend insight into energy transfer, metabolic processes, and predator-prey interactions (Dickie et al. 1987, Brown & Gillooly 2003, Jennings & Mackinson 2003). Changes in biomass size-spectra relationships can also be employed to track changes in community structure incurred from anthropogenic stress (Jennings & Blanchard 2004), but processes that contribute to natural variation in biomass size-spectra relationships must be understood before the relationships are used as a monitoring tool.

Aquatic food webs are strongly size-structured, with larger predators consuming smaller prey (e.g., Scharf et al. 2000). Size is thus often a better predictor of trophic level than species identity for individuals feeding within a hierarchal food chain, as many aquatic predators increase in size by several orders of magnitude through ontogeny (Dickie et al. 1987, Jennings et al. 2001). At the same time, the inefficient transfer of energy from prey to predators at each trophic step in the food chain constrains the amount of energy available to higher trophic levels (i.e., larger-bodied individuals), leading to predictable negative relationships between biomass and body size (Duplisea & Kerr 1995).

Not all components of the food web, however, are energy-limited in a size-dependent manner. Disaggregating communities into feeding guilds for size spectral analyses has a significant impact on the slope of size-spectra relationships and can provide insight into community dynamics (Blanchard et al. 2009). For example, benthic detritivores and filter-feeders at the seafloor share a common resource irrespective of body size and, therefore, do not commonly display strong negative size-spectra relationships when analysed separately from the remainder of the food web (e.g., Saiz-Salinas & Ramos 1999). The size-spectra slopes of disaggregated benthic invertebrate communities become steeper when they are subject to heavier predation by fish because fish tend to prey on the largest invertebrates (Blumenshine et al. 2000, Blanchard et al. 2009). Observations of steeper benthic invertebrate size-spectra relationships at greater depths (Saiz-Salinas & Ramos 1999) suggest that fish predators feed more heavily on benthic prey in deeper habitats. The effect of benthic diets on disaggregated predatory fish size spectra remains unclear (Blanchard et al. 2009). Modelling exercises performed by Blanchard et al. (2011) demonstrated that high benthic-pelagic coupling promoted steeper, truncated size-spectra relationships in predator fish communities compared to scenarios where relatively small proportions of detrital fall-out reached the seafloor. As the amount of detrital fall-out reaching the seafloor declines rapidly with depth (Lee et al. 2004, Smith et al. 2008), shallower (less negative) predator size-spectra slopes should be observed in deeper habitats for fish, indicating a weaker relationship between size and biomass production.

While surface production is the ultimate energy source for deep-sea food webs, not all predators wait for it to reach the seafloor passively. Demersal fishes commonly take advantage of active biological transport to obtain additional energy from the pelagic food web by consuming pelagic organisms that make diel vertical migrations to the seafloor (e.g., fishes, zooplankton, jellyfish, euphausiids; Trueman et al. 2014). Demersal fish may also make vertical migrations to feed in the upper reaches of the water column (Mauchline & Gordon 1991). Consequently, the biomass of strictly benthic-feeding fishes declines with depth as resources become restricted, while the biomass of benthopelagic fish that supplement their diet with pelagic prey increases (Haedrich & Merrett 1992, Trueman et al. 2014). Thus, subsidies from “external” ecosystems can sustain high biomass in upper trophic levels even if there is not enough energy available from lower trophic levels in the local food web (del Giorgio et al. 1999, Hocking et al. 2013). Inverted biomass pyramids and positive size-spectra slopes can be observed if subsidies are accessible to only a subset of the community (Polis et al. 1997, Trebilco et al. 2013). Therefore, predator size-spectra slopes could become shallower with increasing habitat depth via two potential mechanisms. Predator communities may become less trophically size-structured with depth due to greater reliance on a shared benthic invertebrate resource rather than a hierarchical food chain. Alternatively, pelagic subsidies may facilitate reduced competition in deep habitats and allow the maintenance of high biomass in upper trophic levels despite strong size-structuring within the predator community.

The present study investigated depth-related changes in the size structure of demersal predator/scavenger fish communities across an Arctic continental slope, and tested whether changes in biomass size-spectra relationships were systematically related to reliance on benthic-derived carbon sources. Specifically, the following predictions were tested: (1) predator size-spectra slopes become shallower (less negative) with increasing habitat depth; (2) the trophic structure of predator fish communities remains strongly influenced by body size (i.e., size-structured) regardless of depth; and (3) the shallowing of size-spectra slopes with increasing habitat depth, despite the presence of strong trophic size-structuring, is associated with pelagic subsidies to demersal predators rather than with reliance on shared benthic resources.

Methods

Sample collection and processing

The southern Canadian Beaufort Sea is defined by the broad, rectangular Beaufort continental shelf, which extends approximately 120 km offshore to the 200 m isobath, past which the seafloor descends quickly to several thousand meters (Cobb et al. 2008). The Beaufort Continental Shelf thus provides a wide geographic region with relatively similar bathymetry in which to test the effects of depth on size spectra (Fig. 2.1).

Sampling was conducted by the Beaufort Regional Environmental Assessment Marine Fishes Project (Fisheries and Oceans Canada) aboard the chartered commercial stern trawler F/V *Frosti* during the ice-free season from 5 August to 3 September 2012.

Samples were collected along four transects that spanned the Beaufort Shelf and associated continental slope (TBS, GRY, KUG, and DAL; Fig. 2.1), each with seven pre-defined sampling stations at depths of 18-40, 75, 200, 350, 500, 750, and 1000 m. Sampling station boundaries were defined by a radius of one nautical mile. Fish were collected with a modified Atlantic Western IIA benthic otter trawl (successive mesh sizes of 127 and 114 mm for the wings and belly, respectively, and 102 mm with a 13 mm liner in the intermediate and cod-end to retain small fish). The trawl net was attached to Thyborøn Type II, 2.72 m bottom-tending doors to ensure the net remained open laterally during trawling. Trawling was targeted at 20 min bottom-time and standardized to a target speed-over-ground of 1.49 ms^{-1} (2.9 knots; 2.7 to 3.1 kn acceptable range). Trawling was typically conducted along bathymetric contours unless local currents dictated adjustment to ensure acceptable trawl performance. Scanmar CGM-05/TE40-2 net mensuration equipment was used in conjunction with door spread and trawleye sensors to monitor net performance and bottom-contact to ensure consistent sampling efficiency across stations. A Furuno GP31 global positioning system was used to monitor bottom-contact and lift-off positions, and speed-over-ground. Average door spread, speed, and bottom-time of each net deployment were recorded and used to calculate area swept.

Fish were sorted to the lowest possible taxonomic resolution, weighed (g), measured for standard length (mm), and frozen at – 50 °C immediately after collection. Where taxonomic doubt existed, voucher specimens were preserved in formaldehyde for later examination by taxonomists. Brittle stars from the family Ophiuridae (*Ophiocten sericeum* (Forbes), and *Ophiopleura borealis* Danielssen & Koren) were also collected from trawl catches as a representative benthic primary consumer for later calculations of fish trophic levels. The zooplankter *Calanus hyperboreus* Krøyer was collected as a representative pelagic primary consumer from oblique tows of a bongo net (0.25 m^2, 500 μm mesh) through the upper 200 m of the water column.

Analyses were focused on 14 of the most abundant fish species caught, which represented a predator/scavenger food web and comprised 97% of the total catch. Species not included were considered rare (<10 individuals caught across all sites combined and never represented more than 0.01 % of numerical abundance of total catch). A subset of individuals from each species was selected for stable isotope analysis and included a wide range of sizes, with minimum n = 15 per species (Table 2.1). Samples of dorsal muscle tissue (fish) and whole body (*C. hyperboreus,* Ophiuridae) were oven-dried at 50 °C, ground to a homogenous powder, and analysed for N and C isotopic composition using a Delta Plus continuous flow isotope mass spectrometer (Thermo-Finnigan) coupled to a 4010 Elemental Analyzer (Costech Instruments) at the University of Waterloo Environmental Isotopes Laboratory. Following acidification with 1 N HCl to remove inorganic carbon, ground brittle stars were re-analysed to obtain $\delta^{13}C$ values that more accurately reflected metabolically active tissues (Søreide et al. 2006). The acidification protocol followed the drop-by-drop method, without rinsing, proposed by Jacob et al. (2005). Elemental stable isotope ratios (^{15}N:^{14}N, ^{13}C:^{12}C) were expressed in standard δ notation as parts per thousand (‰) relative to the international standards Vienna Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen (Craig 1957, Mariotti 1983). Working laboratory standards included two standards of $(NH_4)_2SO_4$ for $\delta^{15}N$ (0.77 and 20.2 ‰) and one standard of cellulose for $\delta^{13}C$ (-25.5 ‰). Analytical error for $\delta^{15}N$ and $\delta^{13}C$ during any given sample run did not exceed 0.3 and 0.2‰, respectively, based on repeated measurements of working laboratory standards cross-calibrated to the international standards (no less than 20% of all samples within a given run were replicates of laboratory standard material). Repeatability based on duplicate measurement of sample material was 0.2 and 0.1 ‰, respectively, for $\delta^{15}N$ and $\delta^{13}C$.

Lipid extraction can cause significant change in analysed isotope ratios (e.g., Logan et al. 2008). Lipid extraction was originally proposed as a procedure for removing bias from estimates of food chain length based on $\delta^{13}C$ data (McConnaughey & Roy 1979), and is now often suggested as a solution to avoid confusion between isotopic variability caused by lipids and variability caused by a habitat or dietary shift (Logan et al. 2008). The choice of lipid extraction or mathematical correction technique has implications for stable isotope values (Logan et al. 2008, Fagan et al. 2011), particularly as not all extraction methods are equally effective at removing polar and non-polar lipids (Iverson et al. 2001). Thus, choice of whether to extract and/or extraction technique has implications for comparisons among studies (Murry et al. 2006). However, decisions to use extracted or non-extracted data do not appear to affect interpretations of food web structure (Murry et al. 2006). Increasing evidence for the inconsistency among species and lack of significance in studied bulk C:N ratio and $\Delta^{13}C$ relationships (e.g., Fagan et al. 2011; Medeiros et al. 2015) has resulted in a consensus in the literature that extraction is unnecessary where C:N ratios are consistently < 4 (e.g., Jardine et al. 2013). Given the above and the consistently low C:N values observed in the fish included in this study (Table 2.2), lipids were not extracted prior to stable isotope analyses (Søreide et al. 2006).

Data analysis

Sampling sites were divided into four habitat depth categories: nearshore shelf (18 to 50 m), offshore shelf (75 to 200 m), upper slope (350 to 500 m), and lower slope

(750 to 1000 m). Cut-off points between depth categories were based on significant differences in fish community composition associated with gradients of depth, salinity, and water mass structure (Majewski et al. 2013, Majewski et al. 2015). Fish from each depth category were pooled across transects for analyses (Jennings et al. 2001, Macdonald et al. 2012).

To assess changes in biomass size-spectra relationships with depth, normalized biomass size spectra were examined for each habitat depth separately. All fish were assigned to $\log_2$ body mass classes which were the midpoints between intervals of 1 on the $\log_2$ scale from 1.5 to 10.5, representing mass intervals of 2-4, 4-8, 8 -16, 16-32, 32-64, 64-128, 128-256, 256-512, 512-1024, and 1024-2048 g (Jennings et al. 2001). Fish < 2 g (generally < 65 mm) were excluded from the analysis as a conservative measure against potential mesh size-selectivity of trawl catches. Fish that weighed > 2048 g were excluded because they represented a very small proportion of the catch (n = 4 across all sites). Cumulative biomass within each $\log_2$ body mass class was measured as biomass density in g m^{-2} and normalized by the width of the size class (Duplisea & Kerr 1995). All species within the *Lycodes* genus (*L. frigidus* Collett 1879, *L. seminudus* Reinhardt 1837, and *L. polaris* Sabine 1824) displayed negative relationships between $\delta^{15}N$ and $\log_2$ body mass, which is likely associated with feeding from ^{15}N-enriched infaunal food sources in early life (Atkinson & Percy 1992, Bjelland et al. 2000). When included in community-wide $\delta^{15}N$-body mass relationships, *Lycodes* spp. constituted a separate grouping that did not align with the remainder of the community (Fig. 2.2). *Lycodes* spp. were therefore considered uncoupled from the size-structured food web and excluded from further analyses. Size spectra were quantified using linear regressions of normalized $\log_2$ biomass density as a function of $\log_2$ body mass class.

A one-way analysis of covariance (ANCOVA) was conducted to determine if size-spectra slopes differed among habitat depth categories.

Trophic levels were calculated from δ^{15}N values for all fish using the scaled approach developed by Hussey et al. (2014). Trophic levels are commonly calculated from δ^{15}N values under the assumption that the trophic enrichment of ^{15}N between successive trophic levels (Δ^{15}N) can be treated as constant (assumed to be 3.4 ‰ in most aquatic systems, Post 2002). However, empirical evidence and meta-analyses have shown that Δ^{15}N can be negatively related to diet δ^{15}N values such that the Δ^{15}N between a predator and its prey decreases up the food chain (Hussey et al. 2014). This phenomenon leads to non-linear relationships between δ^{15}N and body mass in size-structured food webs, a trend observed in the data collected for this study. Trophic level was calculated for all individuals using model parameters taken from Hussey et al. (2014) and using brittle stars (family Ophiuridae) as the depth-specific benthic primary consumers at trophic level 2.5 (Iken et al. 2005). Ophiuridae are deposit feeders, and thus would be expected to reflect depth-related increases in δ^{15}N of sediment particulate organic matter observed along continental slopes (Mintenbeck et al. 2007)

The presence of trophic size-structuring in food webs was assessed using linear regressions between biomass-weighted trophic level and $\log_2$ body mass class for each habitat depth separately (Jennings et al. 2002). Biomass-weighted trophic level was calculated as:

$$\overline{TL} = \frac{\sum TL_{\mathrm{ij}} \cdot W_{\mathrm{ij}}}{\sum W_{\mathrm{ij}}}$$

where TL_{ij} and W_{ij} are the trophic level and mass, respectively, of individual *i* in body mass class *j* (Jennings et al. 2002). Minimum *n* per body mass class was three individuals. Data for the entire size distribution of the fish community were included in the linear regressions of trophic level against $\log_2$ body mass class so size-structure could be estimated across all size classes, including those with weights < 2 g. Where unknown, $\delta^{15}N$ values were estimated from species-specific linear regressions with $\log_2$ standard length and used to calculate trophic level to ensure biomass weighting was not biased by lack of data (Jennings et al. 2002). Analyses of covariance (ANCOVA) were used to assess if depth had a significant effect on the slope of the relationship between $\delta^{15}N$ and $\log_2$ standard length for each species. Estimates of $\delta^{15}N$ were made separately for each depth in cases where depth did have a significant effect on the slope of the relationship. Otherwise, estimates of $\delta^{15}N$ were made based on all individuals pooled across habitats. In all cases, $\delta^{15}N$ estimation was restricted to individuals within the size range for which observed $\delta^{15}N$ data were available.

A lack of strong negative scaling between biomass and body size can indicate a lack of size structure within a community (i.e., that both large and small individuals may occupy any given trophic level). Proportions of total biomass density (% g m^{-2}) observed within each trophic level were calculated for each habitat depth to assess whether shallower size-spectra slopes were associated with more uniform distributions of biomass among trophic levels.

Stable isotopes of C were used to assess whether depth-related changes in size-spectra slopes were related to greater reliance on benthic resources with increasing depth. Sinking particulate organic matter becomes enriched in ^{13}C with depth due to preferential uptake of the lighter isotope during microbial decay (Magen et al. 2010). As a result, benthic predators have higher $\delta^{13}C$ values than those feeding primarily from the epibenthic environment (Trueman et al. 2014). Delta ^{13}C was used to estimate the per-mille isotopic enrichment relative to a pelagic baseline (Δ_{pel} ; referred to as ε by Clark & Fritz 1997) for all individuals for which observed $\delta^{13}C$ data were available as

$$\Delta_{pel_{i-j}} = \left(\frac{1000 + \delta_i}{1000 + \delta_j} - 1\right) \times 10^3$$

where δ_i is the pelagic baseline $\delta^{13}C$ value, and δ_j is the consumer $\delta^{13}C$ value (Clark & Fritz 1997). *C. hyperboreus* was used as the depth-specific pelagic baseline primary consumer. The relationship between Δ_{pel} and $\log_2$ body mass was then assessed using linear regression for each habitat depth separately.

Fish species were classified as either benthic (feeding predominantly on prey at or within the sediment) or benthopelagic (feeding predominantly on prey that live above the seafloor) according to published dietary observations (Atkinson & Percy 1992, Bjelland et al. 2000, Coad & Reist 2004, Norcross et al. 2011). Differences in Δ_{pel} values were assessed between the two feeding classifications at each depth category to assess realized differences in benthic resource use (e.g., Macpherson 1981, Haedrich & Merrett 1992, Trueman et al. 2014).

All statistical and graphical procedures were performed in R (version 3.1.0, R Core Team, 2014) using the packages plyr (Wickham, 2011), gplots (Warnes et al., 2014), ggplot2 (Wickham, 2009), and Hmisc (Harrell 2015). Assumptions of linearity, homoscedasticity, and normality of errors for all linear models were evaluated using the gvlma package in R (Pena & Slate, 2014), and visually using residual plots. Tests were considered significant at $\alpha = 0.05$.

Results

In accordance with the hypothesis, biomass size-spectra slopes decreased significantly with habitat depth (ANCOVA, $F_{4,19} = 9.98$, $p < 0.001$; Fig. 2.3). Biomass density was significantly negatively related to $\log_2$ body mass class for all habitat depths except the deepest habitat, and the proportion of variance in biomass density explained by $\log_2$ body mass class decreased with depth (Table 2.3).

Maximum observed fish body masses were 35, 61, 4262, and 4597 g for the nearshore shelf, offshore shelf, upper slope, and lower slope, respectively. The increase in maximum observed body mass with depth by two orders of magnitude was due to the occurrence of large-bodied Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum); Table 2.1), which were absent from the shelf habitats. Similarly, the proportion of fish biomass in trophic levels 4 and 5, which were almost exclusively occupied by Greenland halibut, was greater for the slope compared to the shelf habitats (Fig. 2.4).

Biomass-weighted trophic level was significantly positively related to $\log_2$ body mass class for all habitat depths when individuals were considered regardless of species identity (Table 2.3, Fig. 2.5). When analysed individually, most species displayed positive linear relationships between $\delta^{15}N$ and $\log_2$ body mass, although the relationship was not significant for *Icelus* spp. ($p = 0.33$) and Greenland halibut ($p = 0.42$). Depth did not have a significant effect on the slope of the relationship between $\delta^{15}N$ and $\log_2$ standard length for any individual species except Arctic alligatorfish (*Aspidophoroides olrikii* Lütken*;* ANCOVA, $F_{1, 55} = 5.78$, $p = 0.02$). Accordingly, Arctic alligatorfish was the only species for which $\delta^{15}N$ estimates were made separately for each habitat depth.

Isotopic enrichment relative to the pelagic baseline (Δ_{pel}) was positively related to $\log_2$ body mass at all depths (Fig. 2.6). The relationship was weak for the nearshore shelf habitat ($F_{1,239} = 5.00$, $p = 0.03$, $r^2 = 0.02$) and insignificant for the offshore shelf habitat ($F_{1,175} = 0.45$, $p = 0.50$, $r^2 = 0.003$). Stronger relationships were observed in deeper habitats. The positive relationships between Δ_{pel} and $\log_2$ body mass were stronger for the upper slope ($F_{1,174} = 274$, $p < 0.001$, $r^2 = 0.61$) than the lower slope ($F_{1,98} = 41.22$, $p < 0.001$, $r^2 = 0.30$). At both shelf habitats, benthic fishes had higher Δ_{pel} values than benthopelagic fishes for any given body mass (Fig. 2.6 a,b), but this distinction was not apparent for the two deeper slope habitats (Fig. 2.6 c,d). The range of Δ_{pel} values for the entire community was also larger for the two shelf habitats (nearshore = 5.66 ‰, offshore = 5.62 ‰) than for the two slope habitats (upper slope = 4.28 ‰, lower slope = 3.82 ‰). Fish biomass peaked at the upper slope habitat for both benthic and benthopelagic species (Fig. 2.7).

Discussion

Biomass size-spectra relationships became significantly shallower (less negative) and weaker with increasing habitat depth for demersal fish communities, to the point that the relationship between biomass density and $\log_2$ body mass class was not significant at the deepest habitat. Despite depth-related effects on size spectra, fish community food webs at all habitat depths were strongly size-structured (i.e., there were significant positive relationships between $\delta^{15}N$ and body size), indicating that larger individuals consistently occupied higher positions in the food chain. Size structuring was supported by the observation that the distribution of biomass among size classes was related to the distribution of biomass among trophic levels, such that communities in deeper habitats that had shallower size-spectra slopes also had a greater proportion of biomass in upper trophic levels. Communities in deeper habitats also had lower size-specific variation in isotopic enrichment relative to the pelagic baseline (Δ_{pel}). The clear difference in Δ_{pel} values between fish species classified as benthic and those classified as benthopelagic was only evident in the two shallower shelf habitats, indicating a decline in differences between feeding guilds with depth.

The presence of size-based hierarchical food chains at all habitat depths should result in lower energy availability to larger size classes due to inefficient energy transfer through the food chain, and consequently lower relative biomass production (Trebilco et al. 2013). In other words, size-spectra slopes should be strongly negative for all depths. The maintenance of high relative biomass in large size classes at deeper habitats is likely a result of two simultaneous processes: (1) lower particulate organic carbon flux restricting resource availability for small benthic feeders with increasing depth (i.e., low resource availability for smaller fishes; Carrassón & Cartes 2002, Smith et al. 2008), while (2) pelagic subsidies facilitate competitive release for benthopelagic feeders and are most accessible to large predators (Haedrich & Merrett 1992, Trueman et al. 2014).

Significant decreases in megafaunal biomass with increasing depth is a global trend in marine ecosystems attributed to lower energy availability at great depth due to lower downward organic carbon flux (Wei et al. 2010). For demersal fishes, energy acquisition from the pelagic zone via vertical migrations of either prey or predators is also important for biomass production (Mauchline & Gordon 1991, Trueman et al. 2014). When demersal fishes are considered apart from benthic invertebrates, biomass in north-temperate oceans generally peaks at mid-slope depths between 1000 and 2000 m (Gordon & Mauchline 1990, Haedrich & Merrett 1992, Trueman et al. 2014), corresponding to the maximum distribution of the vertically migrating pelagic community (Mauchline & Gordon 1991, Trueman et al. 2014). Along the Beaufort slope, demersal fish biomass peaked at depths slightly shallower than those previously reported for other slope communities, between 350 and 500 m. Shallower biomass peaks in the Beaufort Sea may be a result of several potential mechanisms. First, the depth distributions of some fishes are generally shallower in the Arctic than in the southern limits of their range due to the availability of shallow cold water habitat (Møller et al. 2005). Second, the upper slope habitat of the Beaufort Shelf generally corresponds to the front between cold Pacific water and the relatively warm, Atlantic water below, known as the thermohalocline (200 to 300 m). Large aggregations of zooplankton and predatory fishes have been observed where these two water masses meet, creating a bathymetric band of concentrated prey and predator abundances along the Beaufort slope between 300 to 500 m. Relationships between fish biomass distributions and water mass structure have been previously demonstrated in Arctic seas, including in the Beaufort Sea (e.g., Bergstad et al. 1999, Majewski et al. 2015). Third, diel migration behaviour of pelagic fauna may be affected by the receding ice pack and its associated ice-edge bloom (Wallace et al. 2010) such that maximum migratory behaviour may occur over shallower depths than in more temperate seas.

Total biomass declined beyond 500 m depth, but there was evidence for different biomass responses to depth between large and small body size classes in the size spectra. In the two shelf habitats, the data supported the modelling results of Blanchard et al. (2011) where increased benthic-pelagic coupling characteristic of shallower waters led to steeper, truncated size spectra. In the two slope habitats of this study, declines in normalized biomass were only observed for smaller size classes of fish. Biomass estimates for the larger size classes were much less variable between the two deeper slope habitats, indicating that larger individuals were not subject to the same resource limitations with depth as smaller individuals (Polis et al. 1997). The three largest size classes were dominated by Greenland halibut, a species known to commonly undertake vertical migrations to obtain energy from the pelagic system (Jørgensen 1997). Greenland halibut collected during this study similarly had some pelagic prey in their stomachs and fatty acid signatures consistent with pelagic feeding (W. Walkusz & C. Giraldo, per. communication). Such "external" inputs can result in positive or unimodal size spectra despite evidence for hierarchical food chains if subsidies are only available to a subset of the community (e.g., Polis et al. 1997, Hocking et al. 2013). In the case of demersal fish communities, larger predators are more likely than smaller fish to consume prey outside the benthic boundary layer (Carrassón & Cartes 2002), likely due to stronger swimming abilities. Although pelagic fauna have long been recognized as an important contributor to deep-sea fish production, the findings here demonstrate the impact may be size dependent.

The change in resource availability along the depth gradient appears to facilitate a transition in community composition, whereby the number of benthic species is greater in the nearshore and offshore shelf habitats than in the upper and lower slope (although it should be noted that benthic *Lycodes* spp. were excluded from analyses; see Methods). Similar transitions have been observed in other slope communities (Haedrich & Merrett 1992, Trueman et al. 2014). At shallower depths, detrital fall-out reaches the seafloor more nutritionally intact (Smith et al. 2008), providing greater opportunity for specialization. There are generally more specialist species in the benthic than in the benthopelagic guild of demersal fishes, but feeding preferences may only be a luxury afforded to those in habitats where resources are abundant (Macpherson 1981, Carrassón & Cartes 2002). A decline in the use of benthic resources at deeper habitats is evident in this study from Δ_{pel} values, which reached lower maximums in the deeper slope habitats. The positive relationship between Δ_{pel} values and $\log_2$ body mass at all habitats is most likely indicative of the collinearity between $\delta^{15}N$, $\delta^{13}C$, and body size rather than indicative of larger individuals having more benthic diets. When viewed within body mass classes, there was a clear distinction in Δ_{pel} values between the two feeding guilds in the nearshore and offshore shelf habitats which disappeared in the upper and lower slope communities, suggesting lower inter-guild dietary variation with depth. Many of the polar species included in this study have poorly characterized, but highly varied diets (Atkinson & Percy 1992, Bjelland et al. 2000, Coad & Reist 2004, Norcross et al. 2011). It is likely that they are also opportunistic such that fish in both guilds will feed on both benthic and epibenthic prey to some degree. Isotopic distinction between feeding guilds may therefore be dampened in the deeper zones as a result of lower benthic species richness, reduced opportunity to specialize as resources become scarce, or a combination of both.

Pelagic subsidies in the Beaufort Sea may also provide an important pathway for benthic-pelagic coupling at great depth. Direct benthic-pelagic coupling through down-welled surface production is the most important source of organic matter for suspension and deposit feeding invertebrates (Smith et al. 2008, Wei et al. 2010), but demersal fish in deep-sea environments create a secondary pathway for benthic-pelagic coupling via active biological transport (Trueman et al. 2014). Benthopelagic fish may transfer energy directly between the pelagic and benthic food webs by feeding within one and being consumed in the other. Such direct energetic transfers are likely more prevalent amongst small-bodied prey fishes, and likely contribute more to benthic fish production than to benthic invertebrate production. Alternatively, vertically migrating predators that feed in the pelagic zone may transfer pelagic carbon indirectly to the benthos via faecal matter and respiration while alive (Longhurst et al. 1990), and via detritus when dead. Trueman et al. (2014) estimated that energy export from the pelagic zone by benthopelagic fishes supported an additional 50% of benthic fish biomass at depths of 1500 m in the North Atlantic.

The shallowing effect of large-bodied fish on marine size-spectra slopes is a common phenomenon, and is a useful tool for tracking the impacts of fisheries activities (i.e., the removal of large-bodied fishes) on ecosystem structure (Jennings & Blanchard 2004). Results from the current study lend support for this application of size-structure analyses in the Arctic. However, taxonomic-specific information was important for disentangling the potential causes for observed patterns, and it is argued here that size-based analyses alone lack the detail needed to understand potential anthropogenic impacts on community structure. The Beaufort Sea ecosystem has never been exploited by large-scale fisheries, such that the size spectra presented here may be considered a pre-development baseline. The role of Greenland halibut as integrators of benthic and pelagic food webs, and their impact on size-spectra relationships, suggests that size spectra could be useful indicators of change for both the benthic and pelagic environments.

In conclusion, findings support the maintenance of high relative biomass in large predators by pelagic subsidies in deeper habitats, while decreasing availability of benthic resources limited biomass in smaller size classes and the benthic guild. Both taxonomic-specific and size-based information suggested pelagic subsidies contributed to depth-related changes in size spectra in the Beaufort Sea, but it is unknown if these processes are at work in other deep-sea environments. Other investigators are encouraged to consider whether subsidies commonly play an important role in determining size-spectra relationships of deep sea fish communities, and to quantify potential cascading effects on the benthic invertebrate community.

Table 2.1. Fish species represented in this study, their affiliated habitats, the total number caught across all sampling sites (*N*), the total number submitted for stable isotope analysis (*n*), maximum standard length (SL) observed in this study, maximum weight observed in this study, and the habitat depths at which each species occurred (nearshore shelf, NS; offshore shelf, OS; upper slope, UPS, and lower slope, LWS). Fish used in this study comprised 97% of the total catch across all sampling sites.

Scientific name	**Common name**	**Feeding Type**	**Total *N* caught**	**Total biomass caught (g)**	***n* submitted for SIA**	**Habitat depth occurrences**	**Max SL (mm)**	**Max weight (g)**
Anisarchus medius	Stout Eelblenny	Benthic	83	102.9	47	NS	99.4	3.6
Boreogadus saida	Arctic Cod	Pelagic/Benthopelagic	3006	24 403.9	292	NS, OS, UPS, LWS	218.0	86.5
Gymnocanthus tricuspis	Arctic Staghorn Sculpin	Benthic	48	218.3	33	NS, OS	112.4	30.7
Icelus bicornis	Twohorn Sculpin	Benthic	26	51.6	20	NS, OS	62.4	4.6
Icelus sp.	Unknown *Icelus* sculpin	Benthic	35	14.6	18	NS, OS	38.3	0.9
Icelus spatula	Spatulate Sculpin	Benthopelagic	29	93.6	18	NS, OS, UPS	85.6	14.7
Liparis fabricii	Gelatinous Seasnail	Benthopelagic	26	1134.3	15	UPS, LWS	237.0	111.1
Liparis tunicatus	Kelp Snailfish	Benthic	95	2646.5	83	NS, OS, UPS, LWS	207.3	94.1
Lycodes adolfi	Adolf's Eelpout	Benthic	104	568.0	75	UPS, LWS	191.9	22.7
Lycodes polaris	Canadian Eelpout	Benthic	29	47.8	21	NS, OS, UPS	122.8	9.8
Lycodes seminudus	Longear Eelpout	Benthic	28	2713.1	19	UPS, LWS	473.0	716.0
Reinhardtius hippoglossoides	Greenland Halibut	Benthopelagic	110	99 244.0	103	UPS, LWS	672.0	4597.0
Triglops pingelii	Ribbed Sculpin	Benthopelagic	99	72.1	28	NS, OS, UPS	94.2	11.3
Aspidophoroides olrikii	Arctic Alligatorfish	Benthic	88	69.4	59	NS, OS	63.6	1.7

Table 2.2. Mean δ^{15}N, δ^{13}C, and C:N ratios for marine fish analysed in this study at each habitat depth, summarised by (a) species, and (b) log$_2$ body mass class.

		Nearshore Shelf			**Offshore Shelf**			**Upper Slope**			**Lower Slope**		
(a) Scientific Name	**Common Name**	**δ^{15}N**	**δ^{13}C**	**C:N**	**δ^{15}N**	**δ^{13}C**	**C:N**	**δ^{15}N**	**δ^{13}C**	**C:N**	**δ^{15}N**	**δ^{13}C**	**C:N**
Anisarchus medius	Stout Eelblenny	15.25	-23.01	3.54	15.22								
Boreogadus saida	Arctic Cod	12.57	-24.04	3.55	13.10	-23.74	3.50	14.07	-23.59	3.35	14.57	-23.41	3.35
Gymnocanthus tricuspis	Arctic Staghorn Sculpin	13.14	-22.74	3.48	14.89	-21.99	3.50						
Icelus bicornis	Twohorn Sculpin	14.95	-21.52	3.49	15.12	-22.41	3.57						
Icelus sp.	Unknown *Icelus* Sculpin	13.97	-22.00	3.57	14.47	-22.17	3.67						
Icelus spatula	Spatulate Sculpin	15.36	-22.03	3.40	15.93	-21.88	3.39	16.69					
Liparis fabricii	Gelatinous Seasnail							15.66	-23.82	3.33	16.82	-22.85	3.60
Liparis tunicatus	Kelp Snailfish	12.68	-23.29	3.47	12.95	-25.21	3.73	14.69	-23.72	3.35	15.75	-23.09	3.44
Lycodes adolfi	Adolf's Eelpout												
Lycodes polaris	Canadian Eelpout												
Lycodes seminudus	Longear Eelpout												
Reinhardtius hippoglossoides	Greenland Halibut							16.10	-22.28	3.93	15.82	-22.31	4.23
Triglops pingelii	Ribbed Sculpin	12.46	-23.72	3.49	14.12	-23.29	3.61	14.78	-23.96	3.45			
Ulcina olrikii	Arctic Alligatorfish	14.50	-21.70	3.48	15.44	-21.59	3.44						
Ophiuridae	Brittle stars	10.40	-22.16		11.73	-22.81		12.42	-20.14		12.12	-21.62	
Calanus hyperboreus		8.82	-26.63		9.22	-26.58		8.93	-27.13		9.30	-26.84	

	Nearshore Shelf			Offshore Shelf			Upper Slope			Lower Slope		
	$\delta^{15}N$	$\delta^{13}C$	C:N	$\delta^{15}N$	$\delta^{13}C$	C:N	$\delta^{15}N$	$\delta^{13}C$	C:N	$\delta^{15}N$	$\delta^{13}C$	C:N
(b) Log$_2$ Body Mass Class												
-3.5	11.13	-24.78	3.77	10.05			10.37					
-2.5	11.67	-23.76	3.46	10.93	-24.38	3.51	10.81					
-1.5	12.58	-23.18	3.53	11.93	-23.66	3.61	11.50	-24.67	3.63	12.07	-22.27	3.72
-0.5	12.95	-23.02	3.48	13.65	-22.22	3.47	11.90			12.43	-22.17	3.36
0.5	14.40	-22.57	3.53	13.99	-22.86	3.53	12.71	-24.08	3.31	13.58	-24.83	3.30
1.5	13.63	-23.13	3.57	13.54	-23.44	3.61	13.33	-24.34	3.38	14.07	-24.09	3.34
2.5	13.85	-23.00	3.45	13.79	-23.40	3.42	13.80	-23.87	3.36	14.12	-24.05	3.27
3.5	13.76	-23.07	3.48	14.42	-23.24	3.38	14.45	-23.58	3.33	14.60	-23.42	3.27
4.5	15.60	-21.89	3.40	14.90	-22.94	3.36	14.99	-23.25	3.34	15.50	-23.08	3.43
5.5				15.56	-22.33	3.34	15.83	-23.37	3.32	16.10	-23.00	3.48
6.5							15.97	-23.00	3.28	16.48	-22.98	3.49
8.5							16.50	-22.59	3.66	15.43	-22.61	3.97
9.5							16.06	-22.25	3.89	15.99	-22.26	4.15
10.5							15.79	-22.18	4.01	15.52	-22.30	4.38
11.5							16.92	-22.87	4.33	17.39	-21.89	3.75
12.5							18.15	-22.32	4.97	17.69	-22.80	4.29

Table 2.3. Linear regression statistics for fish community normalized biomass size spectra slopes, and for the relationship between biomass-weighted trophic level (TL) and $\log_2$ body mass class at four habitat depths in the Beaufort Sea. Reported 95% confidence limits (CL) are for slope estimates.

Habitat	Depth (m)	Total *n*	Slope	Intercept	*p*	r^2	F	df	95% CL
Biomass size spectra									
Nearshore shelf	18-50	177	-1.73	-6.56	0.02	0.95	38.86	1, 2	1.19
Offshore shelf	75-200	348	-1.40	-6.34	0.02	0.89	25.46	1, 3	0.88
Upper slope	350-500	2166	-0.73	-5.66	0.01	0.69	15.61	1, 9	0.47
Lower slope	750-1000	117	0.07	-13.25	0.48	0.07	0.55	1, 9	0.10
Biomass-weighted TL vs. $\log_2$ *body mass class*									
Nearshore shelf	18-50	562	0.27	3.16	0.001	0.77	23.97	1, 7	0.13
Offshore shelf	75-200	571	0.26	2.74	<0.001	0.74	22.34	1, 8	0.13
Upper slope	350-500	2228	0.17	2.65	<0.001	0.91	106.25	1, 11	0.04
Lower slope	750-1000	124	0.12	3.05	0.008	0.62	12.82	1, 8	0.08

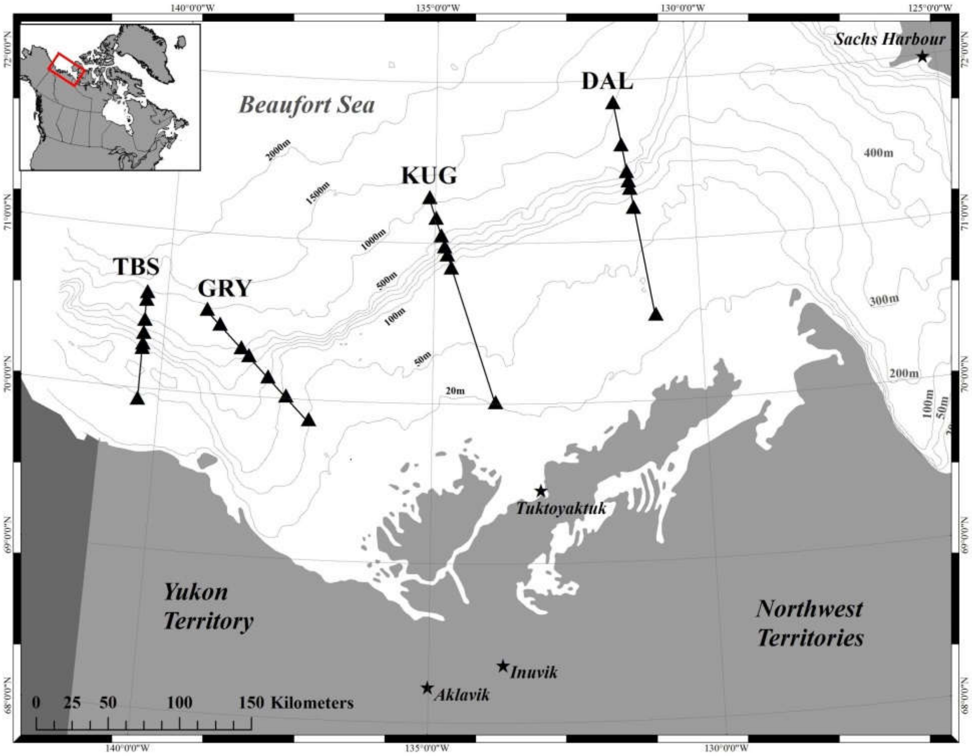


Figure 2.1. Locations of sampling stations along four transects (TBS, GRY, KUG, and DAL) spanning the Beaufort continental shelf. Sampling depths ranged from 18 to 1000m, with increasing depth offshore.

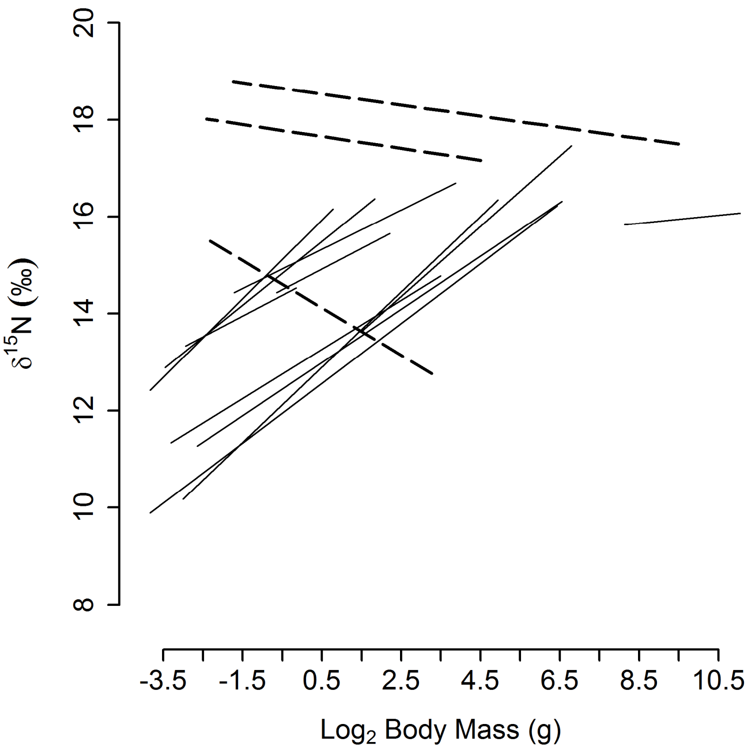


Figure 2.2. Relationships between δ^{15}N and log$_2$ body mass (g) for all species included in size spectra analyses. Fish from the *Lycodes* genus (*L. frigidus*, *L. seminudus*, and *L. polaris*; bold dashed lines) appeared decoupled from the size-structured fish community.

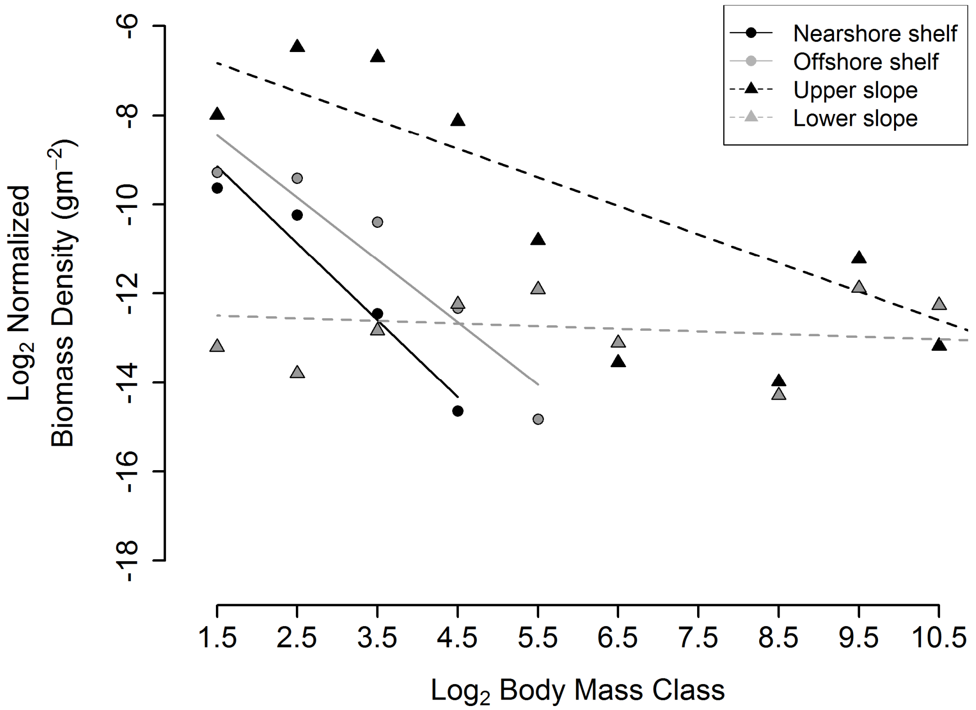


Figure 2.3. Size spectra observed for fish communities in the Beaufort Sea at four habitat depth categories: nearshore shelf (18 to 50 m), offshore shelf (75 to 200 m), upper slope (350 to 500 m), and lower slope (750 to 1000 m). Size spectra included individuals with body mass from 2 to 2048 g. Relationships were significant for all habitats except the lower slope.

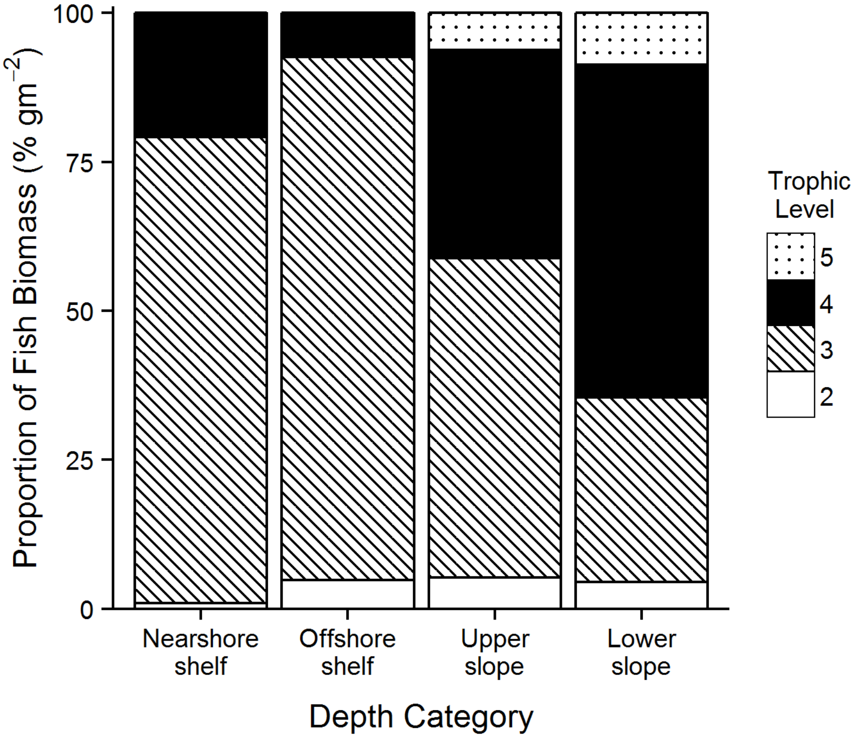


Figure 2.4. Relative distribution of fish biomass (standardized to biomass density as gm^{-2}) among trophic levels at four habitat depth categories: nearshore shelf (18 to 50 m), offshore shelf (75 to 200 m), upper slope (350 to 500 m), and lower slope (750 to 1000 m) in the Beaufort Sea.

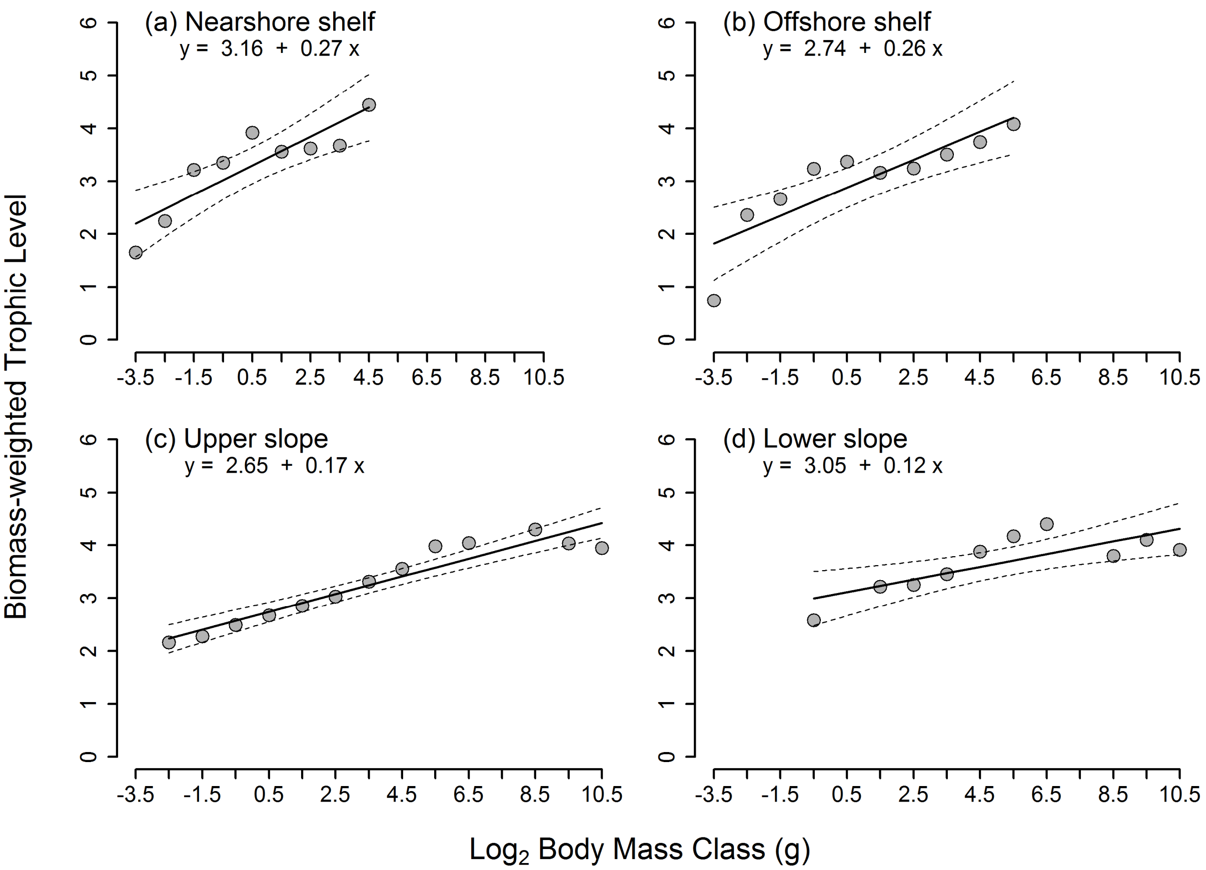


Figure 2.5. Relationship between biomass-weighted trophic level and $\log_2$ body mass class for fish communities in the Beaufort Sea at four habitat depth categories: nearshore shelf (18 to 50 m), offshore shelf (75 to 200 m), upper slope (350 to 500 m), and lower slope (750 to 1000 m). All relationships were significant. Dashed lines represent 95 % confidence limits around the slope.

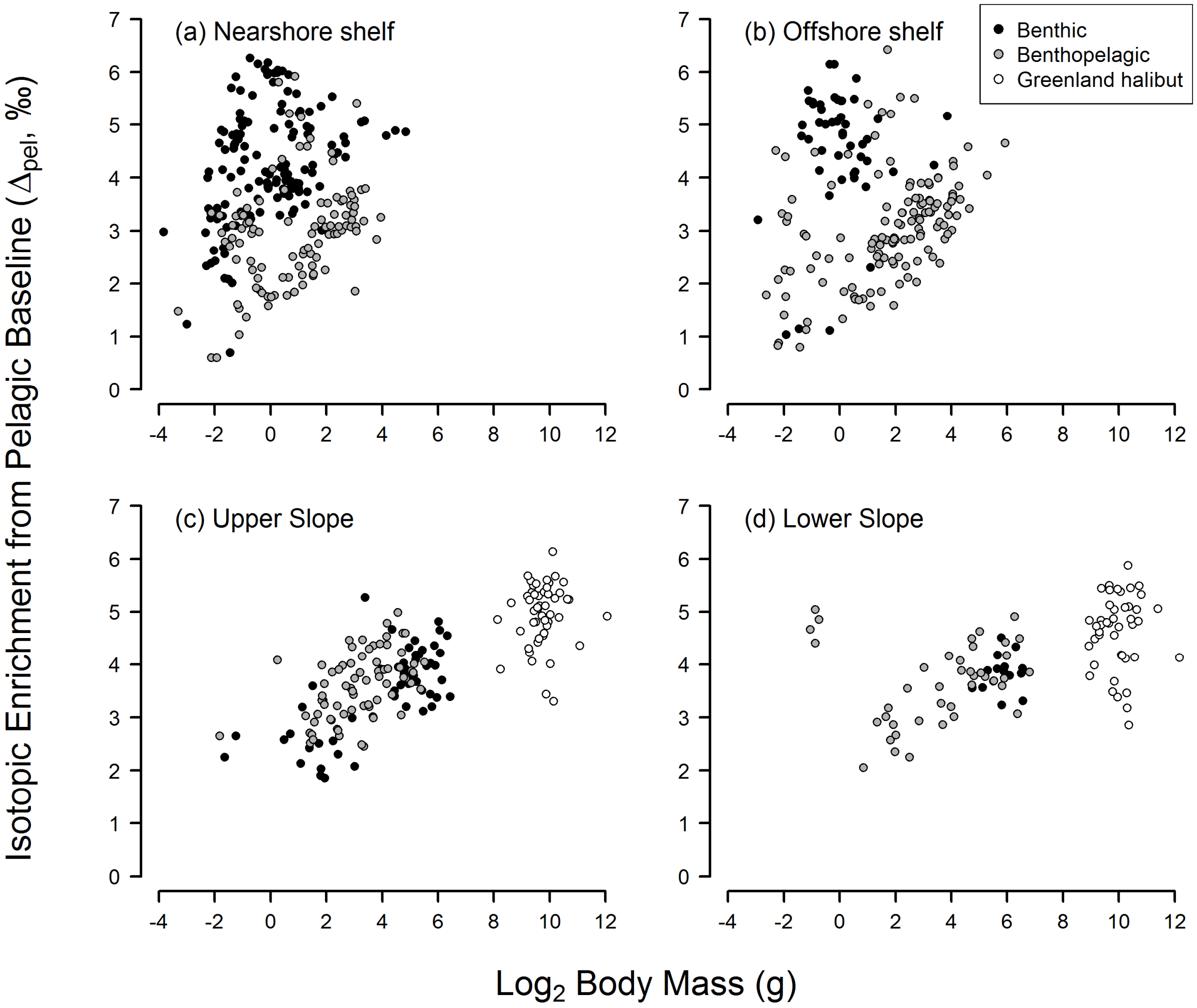


Figure 2.6. Relationships between isotopic enrichment (Δ_{pel}) from the pelagic $\delta^{13}C$ baseline (*C. hyperboreus*) and $\log_2$ body mass class for fish communities in the Beaufort Sea at four habitat depth categories: nearshore shelf (18 to 50 m), offshore shelf (75 to 200 m), upper slope (350 to 500 m), and lower slope (750 to 1000 m). Benthic species, benthopelagic species, and Greenland halibut are shown in different colours to illustrate differences in realized feeding behaviour.

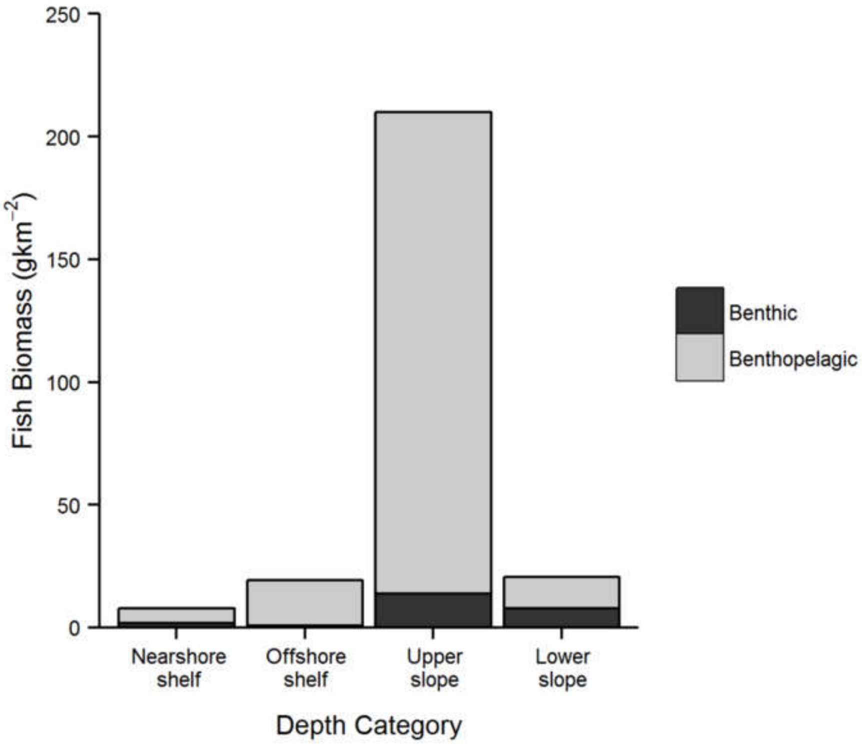


Figure 2.7. Total biomass (standardized to biomass density as g km^{-2}) of benthic and benthopelagic fishes at four habitat depth categories: nearshore shelf (18 to 50 m), offshore shelf (75 to 200 m), upper slope (350 to 500 m), and lower slope (750 to 1000 m) in the Beaufort Sea.

3 Benthic-pelagic trophic coupling in an Arctic marine food web along gradients of water mass structure and organic matter input

Introduction

Benthic communities in Arctic seas are primarily fuelled by the vertical and/or lateral flux of particulate organic carbon (POC) produced at the surface by pelagic algae, or in nearshore areas by benthic algae and macrophytes (e.g., Grebmeier et al. 2015, Renaud et al. 2015). Some Arctic shelves, such as in the Chukchi Sea, are characterized by high primary production and high sinking POC flux (e.g., Grebmeier et al. 2015). The resulting productive benthic food webs are tightly linked with surface production (i.e., strong trophic coupling between benthic and pelagic food webs). Other areas experience limited sinking flux either from low surface production or high biological interception in the upper water column (Forest et al. 2010, Iken et al. 2010). Where downward flux is low, substantial benthic secondary production may still be supported by the advection or entrainment of marine POC from nearby regions (Feder et al. 2011). In addition, terrestrial carbon from river discharge and shoreline erosion is becoming increasingly recognized as an important energy source for some Arctic benthic communities (Dunton et al. 2006, 2012, Feder et al. 2011). Understanding how spatial patterns of water movement and organic matter input influence benthic-pelagic trophic coupling is key to identifying Arctic marine ecosystems sensitive to climate-driven changes in surface production (Wassmann & Reigstad 2011).

Oceanographic conditions that regulate organic matter production and flux undergo relatively abrupt transitions where water masses meet (Belkin et al. 2009). Water mass boundaries influence faunal distributions and trophic properties at multiple scales, from zooplankton to marine birds and mammals (Bost et al. 2009, Smoot & Hopcroft 2017). Most studies in high latitude seas have compared food web structure relative to oceanic fronts arranged side-by-side at the surface (Carroll et al. 2008, Brandt et al. 2014). For example, benthic food web structure in the Chukchi Sea varies with the longitudinal distribution of nutrient-rich and nutrient-poor water masses (Iken et al. 2010). In contrast, the neighbouring Canadian Beaufort Sea (CBS) and Amundsen Gulf (AG) have narrower shelves adjacent to steep continental slopes and a relatively stable vertical water mass structure that can be simplified into four distinct layers (Fig.3.1; McLaughlin et al. 1996, 2005). Little is known of how vertical water mass structure affects Arctic benthic food webs. However, significant spatial differences in benthic fish and zooplankton community composition align with major depth-stratified water mass boundaries along the CBS continental slope (Majewski et al. 2017, Smoot & Hopcroft 2017). Water mass alignment may, therefore, also be important in structuring benthic communities at high latitudes regardless of whether alignment is primarily vertical or horizontal.

In addition, large to meso-scale alongshore patterns in organic matter inputs (Carmack & Macdonald 2002), pelagic algal production near surface (Carmack et al. 2004, Ardyna et al. 2013), and POC sinking flux (Sallon et al. 2011) affect linkages between the benthic and pelagic communities (Renaud et al. 2007a, Darnis et al. 2012, Roy et al. 2015). In areas where the water mass abutting the seafloor depends on water column depth, the hydrographic conditions experienced by the benthos can differ substantially from those that govern surface production or vertical POC flux. It remains unclear whether Arctic fish and invertebrate food web structure is more strongly influenced by hydrographic conditions at the seafloor (e.g., Feder et al. 2011), or by the gradient in overlying organic matter inputs (e.g., Iken et al. 2010).

Here, the southern CBS and AG are used to examine the effects of water mass distributions and known alongshore patterns of organic matter input on trophic structure in Arctic marine ecosystems, from 20 to 1000 m depths. The southern CBS and AG are characterized by clear vertical and alongshore habitat gradients governed by water mass assemblages, surface production, and organic matter inputs (see *Study area and hydrography*). C and N stable isotope ratios measured in marine fishes and invertebrates were paired with oceanographic profiles, pelagic algal biomass measurements, and sedimentary analyses to assess if benthic trophic structure and trophic coupling with pelagic food webs are strongly influenced by: a) bottom-water conditions and water column processes determined by the vertical water mass profile, b) by overlying regimes of organic matter inputs along a longitudinal west-to-east gradient, or c) both. Stronger benthic-pelagic trophic coupling was expected in habitats where relatively fresh marine-derived POC was more accessible at the seafloor (Tamelander et al. 2006), which was predicted to occur in communities directly under nutrient-rich water masses (Iken et al. 2010). Alongshore patterns in organic matter inputs were also expected to create stronger benthic-pelagic trophic coupling in shallow nearshore habitats, where benthos are closer to POC sinking from surface, and in regions with relatively high local primary production (Renaud et al. 2007a, Iken et al. 2010).

Methods

Study area and hydrography

The southern CBS region is defined by the relatively narrow Mackenzie continental shelf, which extends approximately 120 km offshore (Fig. 3.1a). Past shelf break, the seafloor descends quickly to several thousand meters. The shelf is much narrower in the semi-enclosed AG where maximum depths are approximately 500 m. Open-water surface circulation in the CBS is typically dominated by easterly winds that push surface waters seaward in the anti-cyclonic Beaufort Gyre (Fig. 3.1a; Carmack and Macdonald 2002). Below the surface, circulation is topographically steered eastwards, bringing waters of Pacific and Atlantic origin along the slope and into the CBS (Fig. 3.1a; Carmack and Macdonald 2002). The Mackenzie Shelf in the central CBS is strongly influenced by the Mackenzie River, which discharges > 330 km^3 of fresh water and between 40 and 120 x 10^6 t of sediment annually, exceeding the sediment input of any other Arctic river (Macdonald et al. 1998). The Mackenzie River sediment and freshwater plume typically flows eastward along the Tuktoyaktuk Peninsula, but can be forced offshore and westward under the influence of easterly winds (Fig. 3.1a; Carmack and Macdonald 2002). Circulation in the AG is more variable than that in the CBS and poorly understood, but Atlantic and Pacific waters primarily enter from the Beaufort Sea (Barber et al. 2010).

Water mass structure in the Beaufort Sea region can be simplified into four vertically stacked layers established by differences in water origin, salinity, temperature, and chemical composition (Fig. 3.1b; described by McLaughlin et al. 1996, 2005, Lansard et al. 2012). A low-salinity surface layer up to ~ 50 m thick, known as the Polar Mixed Layer, is formed by wind mixing of seasonal freshwater inputs with marine waters. Underneath, the Pacific Halocline extends from ~ 50 to 200 m depths, forming a cold, complex layer of Pacific-origin water with variable salinity. A strong thermohalocline around 200 m marks the relatively narrow transition between the Pacific Halocline and the warmer, saltier Atlantic Layer below. An important distinction between the Pacific Halocline and Atlantic Layer is that Pacific-origin waters have higher nutrient concentrations (~ 1 μmol/kg more phosphate for any given nitrate concentration; Jones et al. 1998). Finally, the Atlantic Layer transitions into the very cold and saline Arctic Deep Water, also of Atlantic origin, at ~ 750 to 800 m depths across a relatively diffuse pycnocline. Simplified vertical water mass structure in the

AG is generally similar to that in the CBS, except for the absence of Arctic Deep Water because the AG is not deep enough to receive it.

Longitudinal patterns of primary production in the Beaufort Sea region are somewhat inter- and intra-annually variable (Carmack et al. 2004, Morata et al. 2008, Ardyna et al. 2013), but recent estimates from a large database of historical chlorophyll (Chl) *a* profiles indicate that annual primary production is relatively high in the Chukchi Sea to the west (~100 g C m^{-2} yr^{-1}) and the Canadian Archipelago to the east (~ 140 g C m^{-2} yr^{-1}), and considerably lower in the Beaufort Sea (~ 62 g C m^{-2} yr^{-1}; Ardyna et al. 2013). In the AG, frequent upwelling of nutrient-laden Pacific water and a polynya near Cape Bathurst cause particularly high local spatial and inter-annual variability in primary production and downward particle flux (Sallon et al. 2011).

Sample collection and processing

Sampling was conducted by the Beaufort Regional Environmental Assessment Marine Fishes Project (Fisheries and Oceans Canada) aboard the stern trawler FV *Frosti* during the ice-free season from early August to early September of 2012 and 2013. Samples were collected along eight transects that spanned the continental shelves and slopes of the CBS and AG, each with five to eight pre-defined sampling stations at depths of 20, 40, 75, 200, 275, 300, 350, 450, 500, 750 or 1000 m (Fig. 3.1c). Fish and benthic macroinvertebrates were collected with a combination of two demersal trawl nets: a modified Atlantic Western IIA benthic otter trawl (13 mm cod end liner) and a 3 m High-Rise Benthic Beam Trawl (6.3 mm mesh cod end liner). Macrozooplankton were collected using a Bongo net (500 μm mesh) towed obliquely from 200 m to surface (or from near bottom where sampling depths were shallower).

Marine sediments were collected with a 0.25 m^2 USNEL box core. The upper 1 cm of sediment was sampled for stable isotope analysis, organic matter (OM) content, and Chl *a*. The upper 5 cm were sampled with a 60 cc truncated syringe for granulometry. Remaining sediments (~ 25 cm core) were sieved through a 1 mm stainless steel mesh to collect macroinfauna for stable isotope analysis. Sediment samples were frozen immediately at -50 ˚C. Sediment Chl *a* was analysed fluorometrically following a modified protocol by Riaux-Gobin and Klein (1993) in a Turner Design 20 fluorometer after a 24 h extraction in 90% acetone at 4 ˚C in the dark. Sediment organic matter content (% of total dry weight) was determined as loss-after-ignition following combustion for 6 hours at 550 ˚C. Sediment grain size analysis was performed on a minimum of nine replicates of wet sediment using a LS13 320 laser diffraction type granulometer (Beckman Coulter) with polarization intensity differential scattering. Prior to analysis, sediments were mixed with a 20 g L^{-1} solution of $(NaPO_3)_6$ as a dispersant and shaken for 24 h to break aggregates.

Oceanographic profiles were taken at each station with a Seabird SBE-25 conductivity, temperature and depth probe mounted to a rosette equipped with 12 Niskin bottles for water sampling. Duplicate seawater sub-samples from the chlorophyll maximum depth, which can occur as deep as 50 m below surface in the region (Carmack et al. 2004), were filtered onboard onto Whatman 25 mm GF/F filters and extracted in 90 % acetone for 18 to 24 h at 4 ˚C in the dark. Chl *a* biomass was then determined using a Turner Designs 10AU fluorometer calibrated using pure Chl *a* from *Anacystis nidulans* (Sigma Chemicals), according to Parsons et al. (1984).

A total of 113 taxa were analysed for stable isotopic composition (see Appendix B). Biota collected for stable isotope analyses were sorted to the lowest possible taxonomic resolution, rinsed with seawater and frozen immediately at -50 ˚C. Where taxonomic doubt existed, voucher specimens were preserved in a formaldehyde seawater solution for later verification by taxonomists (see Acknowledgements). Taxonomy was standardized to the currently accepted names in the World Register of Marine Species (WoRMS Editorial Board 2016). A representative subset of taxa was selected for stable isotope analysis on the basis of ubiquity, relative abundance, and taxonomic diversity as assessed during field collection. A minimum of 3 samples per taxon per water mass assemblage was targeted (see Stasko et al. 2017). All available zooplankton taxa were analysed as a single, bulk sample per station. Fish and macroinvertebrates were sampled across the observed range of body sizes to cover potential covariation between δ^{15}N and size (e.g., Romanuk et al. 2011). The index of taxonomic distinctness based on presence/absence data (Δ^{+}; Clarke and Warwick 1998) was used to determine that the species subset selected for stable isotope analysis did not deviate significantly from expectation based on the full list of observed species (observed values did not fall outside of the 90% confidence limits of expected values).

Classification of trophic functional groups

Taxa were divided into nine functional groups using information derived from published trophic marker analyses, feeding observations, and previous classifications (see Appendix C). Classification was based on systems proposed by Macdonald et al. (2010) and Jumars et al. (2015) using trophic traits relevant to the study: primary feeding habitat (benthic, pelagic, benthopelagic, sediment surface, sediment subsurface), trophic type (carnivore, herbivore), and further sub-divided into major feeding mode for the benthic omnivorous taxa (suspension feeder, deposit feeder, and facultative suspension feeders/surface deposit feeders; Table 3.1).

Fish commonly undergo ontogenetic shifts in habitat or resource use (Garrison & Link 2000 and references therein). The literature was reviewed for available stomach contents, size distribution, and length-at-age data for each fish species to identify potential ontogenetic diet shifts between benthic and pelagic prey that would affect their functional group membership (see references in Appendix C). Diet data were scarce for many species, but where available indicated no switch between pelagic and benthic feeding, except for Arctic Cod (*Boreogadus saida* (Lepechin); e.g., Matley et al. 2013) and Atlantic Poacher (*Leptagonus decagonus* (Bloch & Schneider); Källgren et al. 2015). Consequently, standard body length was used to divide Arctic Cod into pelagic (< 80 mm) and benthopelagic (> 80 mm) functional groups, and Atlantic Poacher into benthopelagic (< 85 mm) and benthic (> 85 mm) groups.

Delineation of vertical water mass structure and longitudinal regions

To assess food web structure along a longitudinal gradient of organic matter input regimes, sampling sites were divided into three regions that differ in the magnitude of published annual primary production estimates (Carmack et al. 2004, Morata et al. 2008, Ardyna et al. 2013). The *western CBS* region included transects immediately west of the Mackenzie River delta on the American Beaufort Shelf (A1 and TBS), the *central CBS* region included transects on the Mackenzie Shelf that are regularly influenced by the Mackenzie River plume (GRY, DAL, and KUG; Magen et al. 2010), and the *AG* region included transects to the east of the CBS (CBH, DAR and ULU; Fig. 3.1c).

Sites within each longitudinal region were further divided by vertical water mass structure to assess the influence of vertical water column properties on food web structure. Boundary depths between water masses were delineated using temperature, salinity and nutrient profiles taken at each sampling station, and were stable between sampling years (Eert et al. 2015, Niemi et al. 2015). Following McLaughlin et al. (1996), the term “water mass assemblage” is used to refer to the vertical package of water masses that occupy the water column in a given area. Four primary water mass assemblages were defined and named for their position along the slope: (1) the *nearshore shelf*, which contained stations with bottom sampling depths from 20 to 40 m within the Polar Mixed Layer, (2) the *offshore shelf* with sampling station depths from 75 to 200 m within the Pacific Halocline, (3) the *upper slope* with sampling station depths from 275 to 500 m within the Atlantic Layer, and (4) the *lower slope* with sampling station depths from 750 to 1000 m within Arctic Deep Water (Fig. 3.1b). A total of 11 regional faunal communities were therefore analysed for isotopic trophic structure: three regions, each of which contained four water mass assemblages, except in the AG where the lower slope assemblage was absent.

Stable isotope analysis and isotopic niche metrics

Stable isotope ratios of nitrogen (δ^{15}N) can be used to infer trophic elevation, whereas those of carbon (δ^{13}C) can be used to infer the dietary carbon sources utilized by consumers (e.g., Peterson and Fry 1987). Tissues dissected for stable isotope analysis included dorsal muscle for fish, whole body for zooplankton and small infauna, and various slow turnover tissues consistent with the literature and dissection constraints for invertebrates (e.g., Dunton et al. 2006, Stasko et al. 2017). Samples were dehydrated in a standard laboratory convection oven at 50 °C for a minimum of 48 hours until dry (fish and sediments) or a FreeZone 18 freeze-drier (Labconco; benthic invertebrates and zooplankton). Dried samples were ground to a homogenous powder and analysed for N and C isotopic composition using a Delta Plus continuous flow isotope spectrometer (Thermo-Finnigan) coupled to a 4010 Elemental Analyzer (Costech Instruments) at the University of Waterloo Environmental Isotopes Laboratory

(Waterloo, Canada). Prior to the determination of δ^{13}C, subsamples of sediment and invertebrates that contained carbonate were acidified with 1 N HCl to remove inorganic carbon following Jacob et al. (2005). Elemental isotope ratios (^{15}N:^{14}N, ^{13}C:^{12}C) were expressed in standard δ notation as parts per thousand (‰) relative to the international standards Vienna Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen (Craig 1957, Mariotti 1983). Analytical error for δ^{15}N and δ^{13}C during any given sample run did not exceed 0.3 and 0.2 ‰, respectively, based on repeated measurements of working laboratory standard material cross-calibrated to the international standards mentioned above (no less than 20 % of each run). Repeatability of duplicate measurements of sample material was 0.3 ‰ for both δ^{15}N and δ^{13}C.

Lipids were not extracted from tissues prior to analysis. Lipid extraction can cause significant change in analysed isotope ratios and is often suggested as a solution to avoid confusion between isotopic variability caused by lipids and variability caused by dietary shifts (e.g., Logan et al. 2008). Extraction is considered unnecessary for fish muscle when C:N ratios are < 4, assuming C:N is a good proxy for lipid content (e.g., Logan et al. 2008). More than 99 % of fish had C:N ratios < 4, whereas 31.3 % of invertebrates had higher C:N ratios (Stasko et al. 2017). To assess the potential for lipids to bias results, δ^{13}C was regressed by C:N for 13 widespread invertebrate taxa (total n per taxon = 30 to 145; C:N from 0.9 to 25.8). C:N did not explain substantial variation in δ^{13}C among tested invertebrates ($r^2 < 0.31$), suggesting that lipid extraction would not have significantly altered results, in agreement with other stable isotope studies on Arctic marine invertebrates (e.g., McTigue & Dunton 2014).

A representative primary consumer was used to normalize consumer stable isotope values to account for spatial heterogeneity. Consumer δ^{13}C values were converted to a measurement of isotopic enrichment (Clark & Fritz 1997) relative to a pelagic baseline ($\Delta^{13}C_{pel}$) as:

$$\Delta^{13}C_{pel_{w-c}} = \left(\frac{1000 + \delta_w}{1000 + \delta_c} - 1\right) \times 10^3$$

where δ_c is the consumer δ^{13}C value , and δ_w is the water mass- or region-specific mean δ^{13}C value of the widespread Arctic filter-feeding zooplankter *Calanus hyperboreus* Krøyer (Table 3.2). Consumer δ^{15}N values were baseline-adjusted by subtracting the water mass- or region-specific mean δ^{15}N value of *C. hyperboreus* from the consumer δ^{15}N. It must be emphasized that *C. hyperboreus* is not meant to reflect the base of the demersal food web. Rather, *C. hyperboreus* Krøyer 1838 is a representative pelagic primary consumer that marks a consistent "starting point" along the δ^{13}C continuum as dietary organic carbon is dynamically transformed during sinking, microbial processing, and integration into the benthic food web (e.g., Dunton et al. 1989).

Five metrics derived from the dispersion of stable isotope values in bivariate δ^{15}N versus δ^{13}C space were used as proxies for realized dietary niche dimensions (Fig. 3.2; Bearhop et al. 2004). Isotopic niche metrics were calculated at the community and functional group level using baseline-adjusted δ^{15}N and $\Delta^{13}C_{pel}$. *Niche region size* (a) was calculated as the smallest region in which baseline-adjusted δ^{15}N and $\Delta^{13}C_{pel}$ have a 95% probability of being found (Swanson et al. 2015). Following Layman et al. (2007), the *mean* $\Delta^{13}C_{pel}$ (b) was interpreted as the average position along the benthic-pelagic continuum, while the *carbon isotopic range* (c) was measured as the range of $\Delta^{13}C_{pel}$ values within the niche region and represents the breadth of carbon resources utilized by the sampled population. *Mean* $\delta^{15}N$ (d) was interpreted as the average baseline-adjusted trophic elevation, while *nitrogen isotopic range* (e) was measured as the range of baseline-adjusted δ^{15}N values within the niche region and is similar conceptually and computationally to isotopic food web length. All five isotopic niche metrics were calculated within a Bayesian framework using the "nicheROVER" package in R

(Swanson et al. 2015, R Core Team 2016). An uninformative normal-inverse-Wishart prior distribution was used to generate posterior distributions of the niche region centroid and covariance matrix, from which 10,000 random permutations were drawn and used to calculate posterior distributions of the niche region size and the four other associated niche metrics. The posterior modes and 95% credible intervals of the niche metrics are reported. At the functional group level, average benthic-pelagic coupling was measured as the mean isotopic separation between benthic and pelagic functional groups along the δ^{13}C continuum (‰).

Association between trophic structure and proxies for organic matter input

To relate spatial variation in trophic structure to spatial gradients of marine POC deposition, five measurements were chosen as proxies for the availability of pelagic production to the benthos (Roy et al. 2014, Roy, Iken, Gosselin, et al. 2015). Average total Chl *a* at the subsurface chlorophyll maximum depth (mg m^{-3}) was used as a proxy for pelagic primary production, assuming a linear relationship between the two (Matrai et al. 2013). Chl *a* concentrations (mg m^{-2} of dry weight) and % organic matter of surface sediments were used as proxies for marine POC input to the seafloor, where higher values usually indicate greater availability of fresh marine organic matter (Roy et al. 2014, Cooper et al. 2015). Mean grain size (μm) and C:N ratio of surface sediments were used as indicators of organic matter deposition rates, where finer sediments and lower C:N are usually associated with areas of high organic matter deposition (Cooper et al. 2015). Proxies were averaged across sites within each of the 11 regional communities (Table 3.3). Regressions were used to assess the significance of linear relationships between isotopic trophic niche metrics and each production/deposition proxy. Pearson correlation analyses between all possible pairs of proxies were used to assess whether indices of high pelagic POC deposition were significantly related to each other. Linear models met all parametric assumptions. Robust regressions with MM estimation were used to identify outliers (Rousseuw et al. 1987). Linear regressions and correlations were considered significant at $\alpha = 0.05$.

All statistical and graphical procedures were performed in R (version 3.3.1, R Core Team 2016) using the packages “ggplot2”, “gridExtra”, “nicheROVER”, “plyr”, “robustbase” and “vegan”.

Raw data reporting

Full station profiles of water temperature, salinity, oxygen, and nutrient concentrations are freely available through federal Canadian Data Reports of Hydrography and Ocean Sciences (Eert et al. 2015, Niemi et al. 2015). The $\delta^{15}N$, $\delta^{13}C$, and C:N for all individual taxa, averaged by region and water mass assemblage, are also freely available through a Canadian Data Report of Fisheries and Aquatic Sciences (Stasko et al. 2017). Data reports can be accessed via the online WAVES catalogue maintained by the Government of Canada (waves-vagues.dfo-mpo.gc.ca/waves-vagues).

Results

Influence of longitudinal gradient in organic matter inputs

When analysed across regions for any given water mass assemblage, community-level niche region size, mean $\Delta^{13}C_{pel}$, and carbon isotopic range generally increased from west to east in all but the deepest vertical water mass assemblage (Fig. 3.3a-c). When community-level niche structure was scaled down to the functional group level, the eastward increases in community-level niche region size, mean $\Delta^{13}C_{pel}$, and carbon isotopic range at the community-level were associated with increasing isotopic separation between benthic and pelagic functional groups (Table 3.4). Within each water mass assemblage, benthic functional groups shifted to higher $\Delta^{13}C_{pel}$ values in the AG relative to the western or central CBS (aside from the lower slope which is absent in the AG, Fig. 3.4). Consequently, a clear distinction between the mean $\Delta^{13}C_{pel}$ of pelagic and benthic functional groups was evident (up to 5.7 ‰) and increased from west to east (Table 3.4, Fig.3. 4). Pelagic herbivores and carnivores exhibited the lowest $\Delta^{13}C_{pel}$ values in all water mass assemblages (Fig. 3.4). Benthopelagic carnivores generally had $\Delta^{13}C_{pel}$ values lower than those of benthic carnivores, but higher than those of pelagic carnivores. These same trends of increasing $\Delta^{13}C_{pel}$ from west to east were observed for many individual benthic taxa. The most variable within- and among-region $\Delta^{13}C_{pel}$ values were exhibited by the facultative SDF/SF brittle stars *Ophiacantha bidentata* (Bruzelius) (1.3 to 14.6 ‰) and *Ophiopleura borealis* Danielssen & Koren (1.5 to 14.7 ‰), the deposit-feeding sea star *Pontaster tenuispinus* (Düben & Koren) (1.8 to 13.4 ‰), and the carnivorous gastropod *Cylichna alba* Brown (0.7 to 13.6 ‰); benthic SDF/SF and benthic SDF generally had larger niche regions and wider carbon isotopic ranges than did most other functional groups in the offshore shelf and upper slope assemblages.

Mean community-level $\delta^{15}N$ was generally highest in the central CBS, whereas nitrogen isotopic range was highest in the central CBS for the upper and lower slope assemblages only (Fig. 3.3d-e). Wide community-level nitrogen isotopic ranges in the central CBS (Fig. 3.3e) were associated with the widest ranges of mean baseline-adjusted $\delta^{15}N$ values among functional groups (Fig. 3.5). Nitrogen isotopic range for any single functional group, however, did not follow obvious regional trends.

Influence of vertical water mass structure

Water mass assemblage had an effect on community-level trophic structure. Within any given region, the upper slope assemblage exhibited the highest community-level mean $\Delta^{13}C_{pel}$, and carbon isotopic range in almost all cases, whereas the nearshore shelf assemblage exhibited the lowest values for these same niche metrics in most cases (Fig. 3.3a-c). Mean community baseline-adjusted $\delta^{15}N$ increased from the shallowest to the deepest water mass assemblage, whereas there was no consistent trend in nitrogen isotopic range across water mass assemblages (Fig. 3.3d-e).

Scaling niche metrics down to the functional group level revealed that, within any given region, the mean $\Delta^{13}C_{pel}$ of benthic functional groups generally increased from the nearshore shelf to the upper slope (Fig. 3.4). Consequently, benthic functional groups became increasingly separated from pelagic functional groups along the $\delta^{13}C$ continuum along an onshore-offshore gradient. Benthic carnivores had the highest mean $\delta^{15}N$ in almost every community, whereas pelagic herbivores almost always had the lowest (Fig. 3.5). The distance between benthic carnivore and pelagic herbivore $\delta^{15}N$ increased from the shallowest water mass assemblage to the deepest (Fig. 3.5). No clear trends emerged across water mass assemblages for functional group niche size, carbon isotopic range, or nitrogen isotopic range.

Association between trophic structure and proxies for pelagic organic matter input

Community-level mean $\Delta^{13}C_{pel}$ and carbon isotopic range were significantly positively related to % sediment organic matter content (Fig. 3.6a, $\Delta^{13}C_{pel}$: $F_{1,9} = 28.06$, $p < 0.01$, $r^2 = 0.78$; Fig. 3.6c, carbon isotopic range: $p = 0.02$, $r^2 = 0.54$, $F_{1,9} = 9.44$). Community-level mean $\Delta^{13}C_{pel}$ and carbon isotopic range were also significantly positively related to total Chl *a* at the subsurface chlorophyll maximum depth (Fig

3.6b, $\Delta^{13}C_{pel}$: $p < 0.01$, $r^2 = 0.82$, $F_{1,8} = 36.93$; Fig. 3.6d, carbon isotopic range: $p = 0.01$, $r^2 = 0.54$, $F_{1,8} = 9.55$). There were no other significant relationships between community isotopic niche metrics and proxies for availability of pelagic production to the benthos.

Sediment mean grain size was significantly positively correlated with sediment Chl *a* (Pearson correlation, $p < 0.01$, $r = 0.62$, df = 47). Sediment % organic matter content was positively, but weakly, correlated to total Chl *a* at the subsurface chlorophyll maximum depth (Pearson correlation, $p = 0.02$, $r = 0.38$, df = 37). There were no other significant associations between pairwise combinations of proxies for the availability of pelagic production to the benthos. Two nearshore sites in the central CBS (KUG 01 and DAL 02) were identified as outliers with higher than usual total Chl *a* at the subsurface chlorophyll maximum depth and were removed from analysis.

Discussion

Spatial patterns of organic matter input and water mass structure influenced trophic connectivity between benthic and pelagic functional groups in an Arctic marine system, up to 1000 m downslope, but not as expected. Benthic-pelagic trophic coupling was predicted to be highest in shallow areas with high primary production, but instead physical and biogeochemical processes controlling the availability of organic matter (OM) to the benthos established a two-dimensional regional gradient. First, benthic-pelagic trophic coupling weakened across an alongshore gradient of organic matter inputs and sinking flux regimes. Coupling was weakest in the eastern study region where pelagic grazing is known to be high, intermediate in the central study region dominated by riverine inputs of terrestrial carbon, and strongest in the western study region where carbon export to the benthos is relatively higher. Second, an onshore-offshore gradient in benthic-pelagic trophic coupling across the entire region was linked to the vertical water mass assemblage. The weakest benthic-pelagic trophic coupling consistently occurred in upper slope habitats. Here, benthos underlie the transition between Pacific- and Atlantic-origin waters, where much of the organic carbon may be transformed or intercepted by aggregations of zooplankton and fish (e.g., Crawford et al. 2012), and where intensified current velocities enhance organic matter re-suspension and heterogeneity (Forest et al. 2015).

Influence of longitudinal gradient in organic matter inputs

Amundsen Gulf – pelagic retention of autochthonous POC

At the community level, eastward increases in mean enrichment from a pelagic baseline ($\Delta^{13}C_{pel}$) and wider carbon isotopic ranges were positively related to two proxies for the availability of pelagic POC to benthos: sediment organic matter content and phytoplankton biomass at the subsurface Chl maximum depth. Both proxies were highest in the AG. If higher phytoplankton biomass resulted in a greater availability of fresh phytodetritus to the benthos, benthic suspension and deposit feeders would be expected to exhibit $\delta^{13}C$ values more similar to those of pelagic grazers (i.e., low mean $\Delta^{13}C_{pel}$; Tamelander et al. 2006). Such a phenomenon has been linked to tight benthic-pelagic coupling in other Arctic regions with high pelagic production (e.g., marginal ice zone, Tamelander et al. 2006, Chukchi Sea, McTigue & Dunton 2014). Instead, it was observed that benthic groups underlying sites with high algal biomass in the AG exhibited greater $\Delta^{13}C_{pel}$ than did their counterparts in the central and western CBS, regardless of vertical water mass assemblage. Consequently, pelagic and benthic functional groups became increasingly separated in isotopic space from west to east. Isotopic separation at the functional group level was associated with larger niche regions, higher mean $\Delta^{13}C_{pel}$, and wider carbon isotopic ranges at the whole community-level. This finding contrasts the prediction that areas with high algal biomass would have tighter linkages between benthic and pelagic food webs. However, results are consistent with sediment trap-based estimates that 70 to 90 % of autochthonous particulate organic carbon (POC) in the AG is retained in the upper 100 m of the water column (Forest et al. 2010). Sites with high POC deposition rates are often characterized by fine-grained sediment that has high organic matter content, high Chl *a*, and low C:N ratios (Cooper et al. 2015). The weak or insignificant correlations between these deposition proxies at sampling sites, along with the unusual positive association between coarse-grained sediments and high sedimentary Chl *a*, suggest benthic POC deposition is low in the region of high algal biomass. Instead, the high sediment organic matter in the AG may represent a pool of low quality food for the benthos as suggested by Magen et al. (2010) and Roy et al. (2014), or may be linked to sinking ice algae (see below).

Retention of new production by the pelagic community explains the ^{13}C enrichment of benthic relative to pelagic functional groups in the AG and the resulting wider community-level carbon isotopic ranges. Benthic consumers have to rely on a more diverse array of alternative carbon sources where fresh phytodetritus is limited (McTigue & Dunton 2014, Roy, Iken, Gosselin, et al. 2015, Bell et al. 2016), increasing the difference between benthic and pelagic $\delta^{13}C$. Arctic benthos can thrive on sinking phytodetritus when it is available (Renaud et al. 2007b, North et al. 2014, Grebmeier et al. 2015). However, benthic community structure and biomass at high latitudes are more strongly associated with long-term indices of food supply and “food banks” of accumulated organic matter than with short-term variability in primary production (Renaud et al. 2008, Smith et al. 2012). The impact of long-term changes in food supply associated with sea ice loss remains unclear. Increased primary production during a longer ice-free season may promote intensified pelagic herbivory that reduces benthic food supply in some areas (Forest et al. 2010, Wassmann & Reigstad 2011). The AG may exemplify such a scenario, and provide an opportunity to examine the carbon sources that sustain benthic communities in the absence of substantial pelagic POC inputs.

Ice algae are an addition to phytoplankton-derived POC. Ice algae can sink fast (Michel et al. 1997) and are consumed by some benthic invertebrates (McMahon et al. 2006, Renaud et al. 2007b). Benthic deposit and suspension feeders collected in the AG for this and another study were enriched in ^{13}C relative to pelagic POC by 3 to 7.5 ‰ on average (C. Michel, unpublished data, Roy et al. 2015). These data are consistent with a significant dietary contribution of ice algae, as ice algae can have $\delta^{13}C > 5$ ‰ higher than that of pelagic POC when ice algal biomass is high (Gradinger et al. 2009). Assimilation of ice algal carbon at the seafloor is a circumpolar phenomenon (e.g., Brown et al. 2012) that varies among regions and appears most significant for deposit feeders (McMahon et al. 2006, Søreide et al. 2013). Ice algae may be a source of otherwise limited essential fatty acids, especially where pelagic and terrestrial carbon inputs are minimal (McMahon et al. 2006, Sun et al. 2007). Reduced sea ice cover has already triggered regime shifts linked to changes in POC sources within some Arctic and Antarctic benthic communities (Kortsch et al. 2012, Smith et al. 2012). If ice algae are an important food source for benthic communities in areas such as the AG, changing sea ice phenology may lead to a reorganization of those communities.

Some $\Delta^{13}C_{pel}$ values observed in AG benthic consumers, however, are greater than would be expected from ice algae alone (e.g., $\Delta^{13}C_{pel}$ up to 14.7 ‰ for the deep-water brittle star *O. borealis*, with untransformed $\delta^{13}C$ values as high as -9.9 ‰; Stasko et al. 2017). Extensively decomposed organic matter that becomes enriched in ^{13}C via microbial remineralization, or the bacteria and extracellular matrices themselves, are likely additional food sources for these organisms (Lovvorn et al. 2005, McTigue & Dunton 2014, North et al. 2014). Bacterial products have higher δ^{13}C and are a more biologically accessible food than bulk sediments (Decho 1990, Lovvorn et al. 2005). Bacterial biomass and recycled organic matter may be especially important for maintaining high latitude macroinvertebrate communities when labile marine-derived POC is scarce (e.g., McTigue & Dunton 2014, Bell et al. 2016).

The central CBS - influence of terrestrial carbon

Intermediate values of community-level niche region size, mean $\Delta^{13}C_{pel}$, and carbon isotopic range observed in the central CBS can be linked to a strong terrestrial influence from the Mackenzie River. The Coriolis force usually drives the freshwater and sediment plume eastward, such that communities within the central CBS are exposed to high inputs of terrestrial organic matter (> 50 % of the bulk sediment pool as deep as 1000 m; Magen et al. 2010). Recent studies have demonstrated that terrestrial inputs can indirectly support a high relative benthic biomass (Dunton et al. 2006, 2012, Roy et al. 2015), likely by acting as favourable substrate for microbial communities that increase its lability (Bell et al. 2016). It is proposed that benthic-pelagic trophic coupling is dampened in terrestrially-dominated systems due to high benthic reliance on microbially-transformed terrestrial organic matter (Dunton et al. 2006) and lower pelagic primary production in sediment-laden waters (Carmack et al. 2004). Greater consumption of transformed terrestrial organic matter is consistent with higher mean community δ^{15}N and nitrogen isotopic range in this region compared to the western CBS and AG, as extensive microbial processing of sedimentary organic matter can lengthen Arctic benthic marine food webs (Dunton et al. 2006, Iken et al. 2010, Bell et al. 2016).

West of the Mackenzie River – lower terrestrial organic matter and grazing

The western CBS communities exhibited the smallest niche region sizes, lowest mean $\Delta^{13}C_{pel}$ values, and narrowest carbon isotopic ranges of any region examined. When niche metrics were examined at the functional group level, benthic and pelagic groups in the western CBS were closer to each other along the ^{13}C continuum than in the other two regions. Together, these findings suggest that the western study region exhibited the tightest benthic-pelagic trophic coupling. However, benthic-pelagic trophic coupling in the western CBS may still be weak compared to other Arctic areas, where most benthic fauna have $\delta^{13}C$ within 5 ‰ of *Calanus* spp. (e.g., North Water Polynya, Hobson et al. 1995, Barents Sea marginal ice zone, Tamelander et al. 2006, Chukchi Sea, McTigue & Dunton 2014). Moreover, benthic biomass on the shelf remains relatively low across most of the study region compared to, for example, the Chukchi shelf (< 50 g m^{-2} for macrobenthos; Dunton et al. 2005, Conlan et al. 2013)

Results from this study appear to be an extension of a larger gradient of weakening benthic-pelagic coupling from west to east along the entire Beaufort Sea coast (Dunton et al. 1989, Dunton et al. 2005, Bell et al. 2016). Benthic consumers west of the Colville River are under a stronger influence of nutrient-rich Pacific waters and make greater use of marine-derived POC, coincident with lower $\delta^{13}C$ and shorter food web lengths (Divine et al. 2015, Bell et al. 2016). East of the Colville River, longer benthic food webs have been attributed to the increasing influence of terrestrial organic matter (0.5 to 1.7 trophic levels longer; Bell et al. 2016). Macrobenthic biomass on the shelf also generally declines eastward from as high as ~ 80 g m^{-2} near Point Barrow, Alaska, to as low as 0.01 g m^{-2} near the mouth of the Mackenzie River (Dunton et al. 2005). Benthic-pelagic trophic coupling therefore appears to continue to weaken along an eastward, although not necessarily linear, gradient of increasing terrestrial organic matter influence and weakening Pacific influence. Since terrestrial influence is strongest in the central CBS, the weakest benthic-pelagic trophic coupling in the AG is probably a consequence of intense pelagic grazing rather than an extension of the same terrestrially-influenced gradient.

Influence of vertical water mass structure

Evidence for differing benthic food web and community structure underneath adjacent surficial water masses is mounting for high latitude systems (e.g., Carroll et al. 2008, Iken et al. 2010, Brandt et al. 2014). In contrast, studies on how vertical water mass distributions affect benthic-pelagic coupling are lacking. Findings here suggest subsurface water mass boundaries can weaken trophic connectivity between pelagic and benthic food webs where they create hotspots of biological interception and transformation of POC. Community-level niche region size and carbon-associated isotopic niche metrics increased from the nearshore shelf to the upper slope water mass assemblage, and were associated with a clear divergence between benthic and pelagic functional groups along the $\Delta^{13}C_{pel}$ continuum. These patterns suggest greater trophic diversity and lower benthic-pelagic trophic coupling in the upper slope assemblage compared to other water mass assemblages. Since the weakest trophic coupling was not observed in the deeper lower slope assemblage, the work presented here does not support depth as the only explanation. Rather, biological and physical processes linked to water profile characteristics likely interact with depth to best explain spatial trends in benthic-pelagic trophic connectivity.

Several physical and biological features of the vertically stacked water masses are unique to the study area. Following the spring phytoplankton bloom, nitrate is quickly depleted in Arctic Ocean surface waters (e.g., Carmack et al. 2004, Ardyna et al. 2013). The chlorophyll maximum layer then becomes deep, often occurring at ~ 40 to 60 m depths during summer, which is at or near bottom on much of the CBS and AG shelves. Benthos on the shelf thus have greater access to relatively fresh and untransformed marine organic matter compared to deeper communities. The consumption of fresh phytodetritus is reflected in lower mean δ^{15}N values in the shelf versus slope habitats (Divine et al. 2015, Bell et al. 2016, this study). Over deeper waters in the western Arctic, the subsurface chlorophyll maximum approximately corresponds with the transition to the Pacific Halocline and pelagic POC, therefore, has a relatively short distance to sink to reach the thermohalocline transition to Atlantic water below. A substantial proportion of sinking POC may become entrained near the thermohalocline and not reach the seafloor (Forest et al. 2015). Large aggregations of zooplankton are closely associated with the shelf break near the transition between the Pacific and Atlantic water masses (Crawford et al. 2012, Smoot & Hopcroft 2017) and in turn may explain high Arctic Cod densities in the same layer (Majewski et al. 2017). These deep zooplankton aggregations may have grazed substantial fractions of the above produced POC, limiting POC availability at the seafloor for demersal fauna. Indeed, Majewski et al. (2017) speculated that Arctic Cod may out-compete benthic fishes in the upper slope habitat where their preferred pelagic zooplankton prey are abundant and alternative benthic food sources are limited. Results from the current study support this hypothesis. High carbon interception and transformation in the upper Atlantic Layer (Crawford et al. 2012, Forest et al. 2015) may explain the largest niche size, largest carbon isotopic ranges, and high mean δ^{15}N values observed for the upper slope community. POC consumption by pelagic zooplankton and the microbial loop commonly limit benthic food supply in the global ocean, including high latitudes

(Grebmeier & Barry 1991), but biological interception by deep aggregations of higher-trophic fauna is neither well-documented nor well-understood.

The upper slope community occupies a physically dynamic habitat at the shelf break. Habitat heterogeneity associated with steep bathymetry and complex current dynamics (e.g., Forest et al. 2015) may have additionally contributed to the wider carbon isotopic ranges and larger niche sizes observed in the upper slope. In particular, high current velocities and seasonal flow reversals in the shelf break jet enhance the transport of re-suspended sediment and distinct water types between the shelf and basin (e.g., Nikolopoulos et al. 2009, Forest et al. 2015). The high carbon isotopic ranges observed for trophically flexible surface deposit and suspension feeders in the upper slope support the notion that food availability was variable (Roy, Iken, Gosselin, et al. 2015).

There is a possibility that microphytobenthos were an additional uncharacterised organic matter source for nearshore shelf communities (e.g., McTigue & Dunton 2014). The highest sediment Chl *a* measurements in this study were observed at sampling sites ≤ 40 m depths, but the data were not available to estimate the proportion of Chl *a* attributable to pelagic versus benthic algae. It is conceivable that the low δ^{13}C values of benthos in the nearshore shelf were partially attributable to the assimilation of benthic microalgal carbon (Oxtoby et al. 2016).

Regional context and conclusions

When placed in a larger regional context, findings extend the understanding of variation in benthic trophic structure and benthic-pelagic trophic coupling along the western Arctic coast of North America. The data show complex spatial patterns in benthic-pelagic coupling clearly linked to the local organic matter inputs and flux dynamics that control food supply to the benthos. Near Point Barrow, Alaska, the stable isotope values of benthic consumers on the shelf reflect strong reliance on marine-derived organic matter, despite evidence for substantial terrestrial inputs from small coastal rivers and erosion (Dunton et al. 2006, Divine et al. 2015). The influence of nutrient-laden Pacific waters that enter from the nearby Chukchi Sea and comparatively low pelagic grazing are considered responsible for the tight benthic-pelagic trophic coupling in the western American Beaufort Sea (Dunton et al. 2005, Divine et al. 2015). Further east toward the Colville River and Camden Bay, benthic consumers as deep as 1000 m have greater reliance on terrestrially-derived carbon, which is strongest near the Mackenzie River outflow (Dunton et al. 2006, Divine et al. 2015, Bell et al. 2016). Results from the current study suggest that terrestrial organic matter continues to play a role in decoupling pelagic and benthic food webs across the central CBS shelf and slope, likely because bacterially-transformed terrestrial matter is a labile and attractive benthic food source in areas with limited marine POC (Bell et al. 2016). Finally, benthic-pelagic trophic coupling is weakest in the AG, where extensive grazing by pelagic consumers limits the vertical flux of marine POC despite relatively high primary production (Forest et al. 2010, this study). In response, benthic taxa have higher ^{13}C enrichment relative to pelagic taxa (this study), benthic carbon remineralization is low (Darnis et al. 2012), epibenthic communities exhibit low biomass and high spatial heterogeneity in community composition (Roy et al. 2014), and benthic primary consumers likely rely more heavily on ice algae and transformed sedimentary organic matter (Roy et al. 2015, this study). Across the entire region, the difference in carbon use between benthic and pelagic functional groups was largest near shelf break on the upper slope, directly under the transition between Pacific- and Atlantic-origin waters. Here, benthic food supply was likely limited by biological interception but, perhaps, diversified by carbon transformation and sediment re-suspension.

Together with previous work, this study establishes that gradients in food web structure do not necessarily follow water depth or obvious indicators of pelagic productivity. Rather, Arctic benthic-pelagic trophic coupling is more closely linked to biological and physical processes in the water column that govern organic matter availability to the benthos. Arctic benthic communities that are at least partially sustained by microbially-processed terrestrial OM may be relatively less sensitive to changes in sea ice phenology than those that rely predominantly on overlying pelagic and/or ice algal production. However, the benthic response to changes at the ocean surface may be mediated by subsurface hydrography and by the food web in the upper water column that intercepts sinking POC, and is in turn influenced by water mass boundaries.

Table 3.1. Description of functional trophic groups used in this study. See Appendix C for further details and references.

Functional Group	**Description**
Pelagic herbivore	Zooplankton in the pelagic realm that feed primarily on photosynthetic, and occasionally heterotrophic, organisms.
Pelagic carnivore	Animals restricted to feeding in the upper pelagic realm on other animals. Includes predatory amphipods, molluscs, cnidarians, chaetognaths, ctenophores, and some fishes.
Benthopelagic carnivore	Highly mobile fishes and invertebrates known to feed carnivorously at and above the seafloor as predators, scavengers, or both. May consume a mix of benthic and pelagic prey. Some taxa may make substantial vertical migrations into the upper water column.
Benthic suspension feeder (SF)	Omnivorous animals known to live on the seafloor and feed on fresh or resuspended particulate organic matter (no restriction is made on particle size).
Benthic suspension and surface deposit feeder (SDF/SF)	Omnivorous animals known to live on the seafloor that can switch between the two feeding strategies depending on food availability.
Benthic surface deposit feeder (SDF)	Omnivorous animals known to live on the seafloor and feed on deposited material on the sediment surface including, but not limited to, food falls, detritus, bacteria, and bacterial products.
Benthic subsurface deposit feeder (SSDF)	Omnivorous animals known to feed below the surface of the sediment on detritus and/or bacterial products.
Benthic subsurface (SS) carnivore	Mostly predatory marine worms that feed carnivorously on animals below the surface of the sediment.
Benthic carnivore	Animals that live on the seafloor and feed carnivorously as predators, scavengers or both. May consume some portion of pelagic resources in the form of food falls or vertically migrating prey.

Table 3.2. Unadjusted δ^{15}N and δ^{13}C values for the baseline pelagic primary consumer *Calanus hyperboreus* and for sediment, by water mass assemblage and longitudinal region. Number (*n*) of samples analysed refers to bulk samples. Values are mean ± standard deviation. Stable isotope values for individual taxa can be found in Stasko et al. (2017).

		C. hyperboreus			**Sediment**		
Water mass assemblage	**Region**	***n***	**δ^{15}N**	**δ^{13}C**	***n***	**δ^{15}N**	**δ^{13}C**
Nearshore shelf							
	Western CBS	1	9.2	-26.2	1	3.8	-24.8
	Central CBS	3	8.7 ± 0.2	-26.8 ± 0.2	3	3.3 ± 0.9	-25.9 ± 0.3
	Amundsen Gulf	3	10.2 ± 0.7	-27.4 ± 0.7	3	4.7 ± 2.0	-17.1 ± 11.9
Offshore shelf							
	Western CBS	2	10.4 ± 1.0	-25.8 ± 10	3	4.7 ± 0.3	-24.8 ± 0.1
	Central CBS	6	8.8 ± 0.3	-26.8 ± 0.3	7	4.0 ± 0.8	-25.5 ± 0.3
	Amundsen Gulf	11	10.3 ± 0.5	-27.3 ± 0.5	11	4.2 ± 2.5	-14.7 ± 9.1
Upper slope							
	Western CBS	2	8.7 ± 0.1	-27.1 ± 0.1	3	5.3 ± 0.1	-24.5 ± 0.2
	Central CBS	6	9.0 ± 0.7	-27.1 ± 0.7	7	4.2 ± 0.3	-25.0 ± 0.2
	Amundsen Gulf	9	10.4 ± 0.4	-27.4 ± 0.4	9	6.7 ± 0.9	-20.7 ± 5.5
Lower slope							
	Western CBS	2	9.5 ± 0.2	-26.5 ± 0.2	3	5.1 ± 0.3	-24.3 ± 0.1
	Central CBS	6	9.2 ± 0.7	-27.0 ± 0.7	6	4.9 ± 0.5	-24.2 ± 0.4

Table 3.3. Habitat measurements used as proxies for the availability of pelagic production to the benthos, including: total chlorophyll (Chl) *a* at the subsurface chlorophyll maximum (SCM) depth (mg m^{-3}), sediment Chl *a* (mg m^{-2} of dry weight), sediment organic matter content (%), sediment mean grain size (μm), and sediment C:N ratio. Data for each proxy were averaged within regions and water mass assemblages. No data (n.d.) were available for sediment organic matter content in the lower slope assemblage of the western CBS region.

			Sedimentary characteristics			
Water mass assembly	**Region**	**Total Chl *a* at SCM depth (mg m^{-3})**	**Chl *a* (mg m^{-2})**	**% organic matter**	**Mean grain size (μm)**	**C:N**
Nearshore shelf						
	Western CBS	0.38	21.89	7.86	32.36	9.17
	Central CBS	0.73 ± 0.15	11.11 ± 13.90	8.43 ± 0.30	10.27 ± 10.51	9.35 ± 0.36
	Amundsen Gulf	0.56 ± 0	12.95 ± 0.77	10.46 ± 2.66	9.85 ± 9.43	24.32 ± 25.27
Offshore shelf						
	Western CBS	0.35 ± 0	2.67 ± 0.11	7.97 ± 1.08	12.31 ± 6.86	6.73 ± 1.37
	Central CBS	0.37 ± 0.05	2.65 ± 1.60	7.42 ± 1.86	34.57 ± 69.89	9.19 ± 0.60
	Amundsen Gulf	0.5 ± 0.14	5.68 ± 3.35	10.01 ± 2.29	12.02 ± 5.15	20.33 ± 13.89
Upper slope						
	Western CBS	0.44 ± 0.20	2.76 ± 1.64	9.40	5.88 ± 1.31	7.15 ± 0.56
	Central CBS	0.41 ± 0.08	1.88 ± 0.22	8.54 ± 0.17	5.48 ± 2.18	8.82 ± 1.30
	Amundsen Gulf	0.55 ± 0.15	2.13 ± 0.99	11.57 ± 1.87	8.82 ± 2.68	8.92 ± 5.42
Lower slope						
	Western CBS	0.39 ± 0.03	0.69 ± 0.59	*n.d.*	4.89 ± 1.58	7.81 ± 0.73
	Central CBS	0.34 ± 0.04	0.24 ± 0.16	8.79 ± 0.43	3.86 ± 0.18	7.65 ± 0.71

Table 3.4. Mean difference between $\Delta^{13}C_{pel}$ values of pelagic and benthic functional groups, showing an increasing difference from west to east, and from the nearshore shelf to the upper slope water mass assemblage.

Water mass assemblage	Region	Difference (‰)
Nearshore shelf		
	Western CBS	2.30
	Central CBS	3.01
	Amundsen Gulf	3.88
Offshore shelf		
	Western CBS	2.86
	Central CBS	4.28
	Amundsen Gulf	4.78
Upper slope		
	Western CBS	3.78
	Central CBS	4.95
	Amundsen Gulf	5.65
Lower slope		
	Western CBS	4.15
	Central CBS	3.48

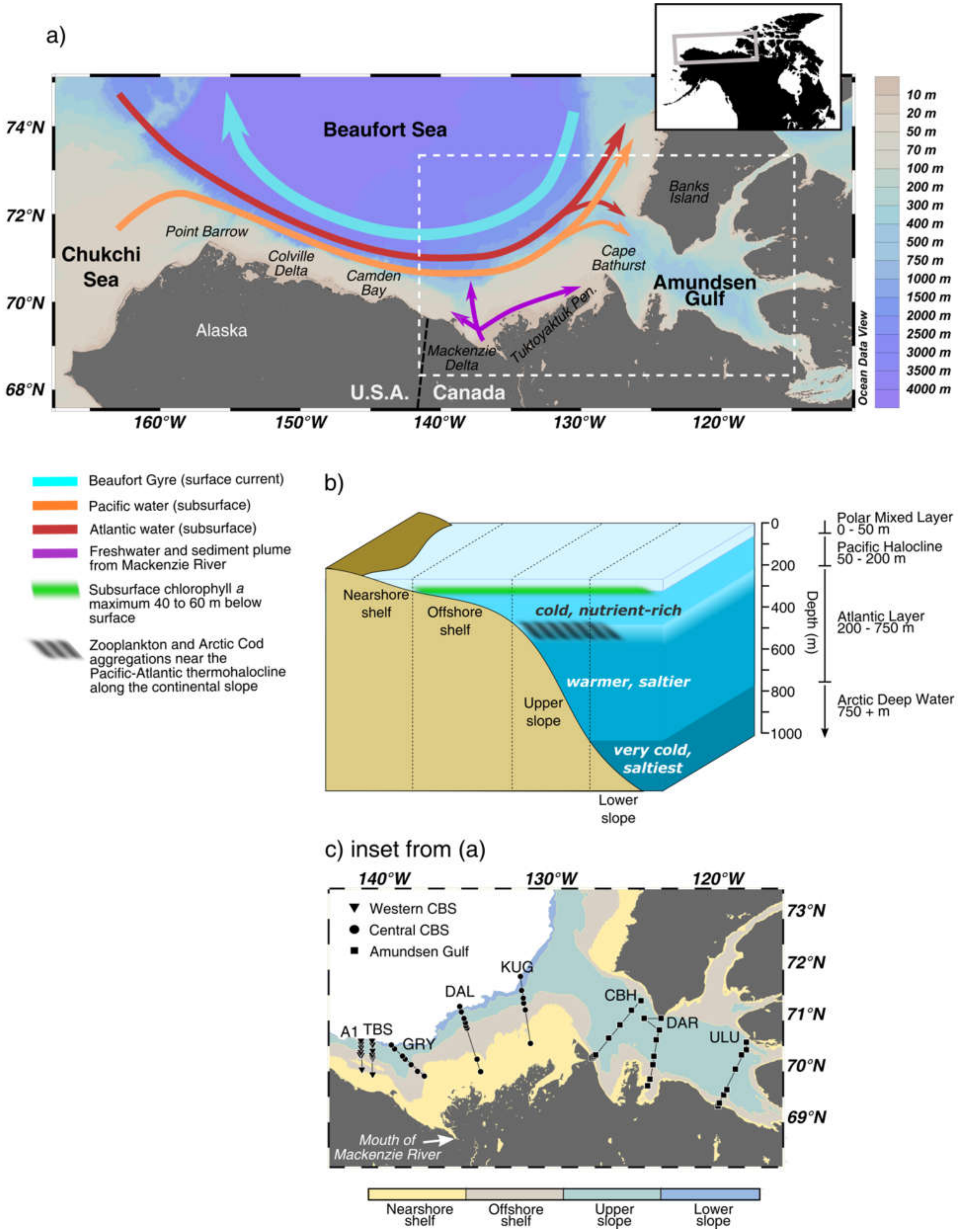


Figure 3.1. Map and oceanographic setting for the study region. a) Surface circulation in the Beaufort Sea is dominated by the anti-cyclonic, wind-driven Beaufort Gyre.

Subsurface flow is topographically steered in the opposite direction, bringing Pacific- and Atlantic-origin waters eastwards along the continental slope into the Canadian Beaufort Sea and Amundsen Gulf. The freshwater discharge from the Mackenzie River dominates the central continental shelf, typically flowing eastward along the Tuktoyaktuk Peninsula under the Coriolis force. The white dashed box delineates the area from which samples were collected. b) Schematic of the simplified, four-layer water mass structure in the Canadian Beaufort Sea and Amundsen Gulf. Water mass assemblages were delineated based on the unique combination of one to four vertically stacked water masses within the vertical profile, and are shown separated by vertical dotted lines (McLaughlin et al. 1996, 2005, Lansard et al. 2012). Water mass assemblages were named for the positions along the continental slope: the nearshore shelf, offshore shelf, upper slope, and lower slope. The chlorophyll maximum depth (green) typically occurs ~ 40 to 60 m below surface during the open water season, and large aggregations of zooplankton and Arctic Cod (dark gray hashes) have been observed near the thermohalocline transition between Pacific and Atlantic waters (Crawford et al. 2012, Majewski et al. 2017). c) Positions of sampling transects and station within three regions: the western Canadian Beaufort Sea (CBS), central CBS, and Amundsen Gulf.

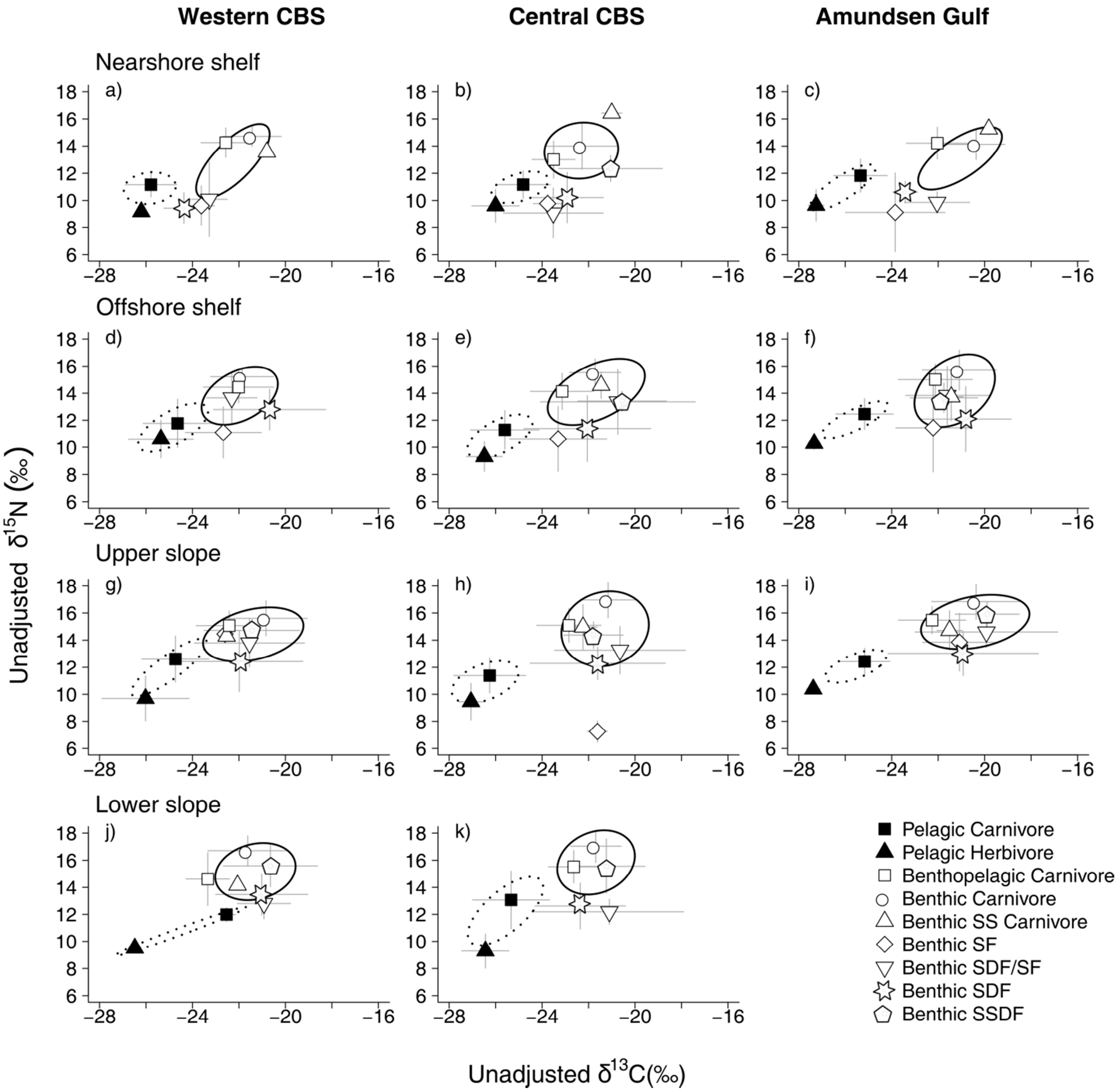


Figure 3.2. Mean δ^{15}N versus δ^{13}C for nine functional groups within each water mass assemblage, within three regions: the western Canadian Beaufort Sea (CBS), the central CBS, and Amundsen Gulf. Benthic functional groups (white) become increasingly separated from pelagic groups (black) along the δ^{13}C axis from the western CBS to the Amundsen Gulf in the east (rows), and from the shallow nearshore shelf to the upper slope water mass assemblage (columns). Isotopic niche regions are drawn for benthic (solid ellipse) and pelagic (dotted ellipse) functional groups separately to illustrate isotopic separation. Lines represent 1 standard deviation.

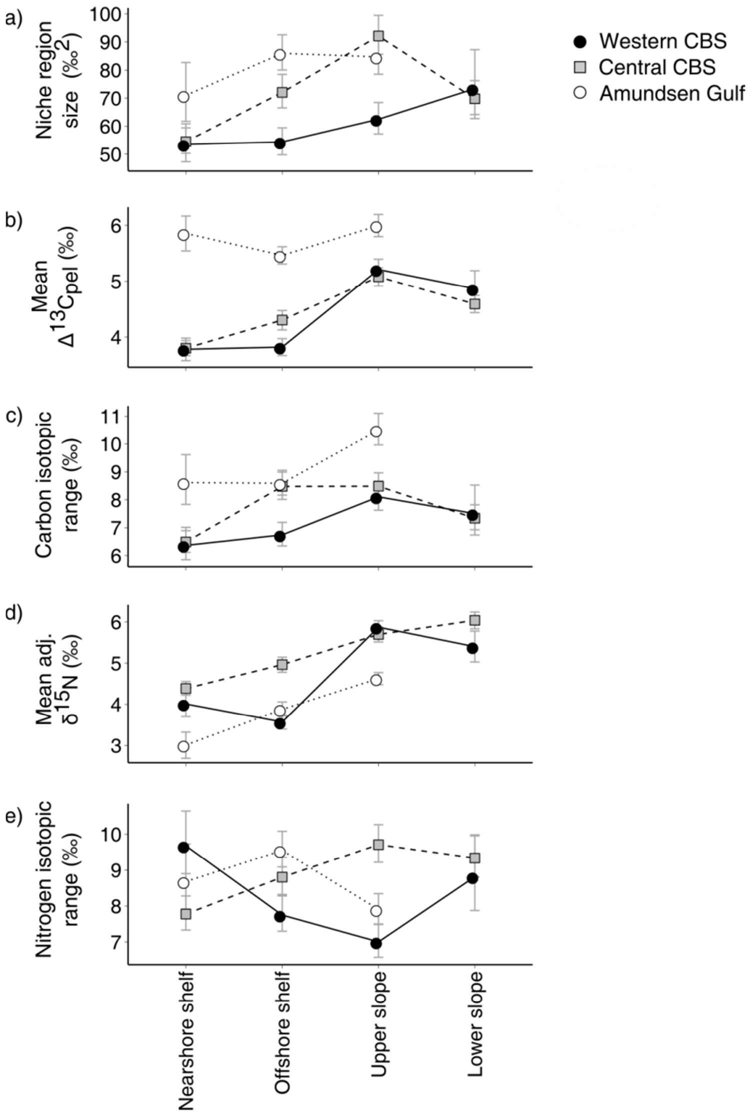


Figure 3.3. Community-level isotopic niche metrics for each longitudinal region, across vertical water mass assemblages: a) niche region size, b) mean ^{13}C enrichment from a pelagic baseline ($\Delta^{13}C_{pel}$), c) carbon range of the niche region, d) mean baseline-adjusted δ^{15}N, and e) nitrogen range of the niche region. Points represent the mode of the posterior distribution for each niche metric, created with 10,000 iterative calculations. Whiskers represent 95% credible intervals. Lines illustrate trends among discrete water mass assemblages (not a continuous scale). The lower slope assemblage does not occur in the Amundsen Gulf. Niche region size, $\Delta^{13}C_{pel,}$ and carbon isotopic range increased from west to east, and were highest in the upper slope assemblage.

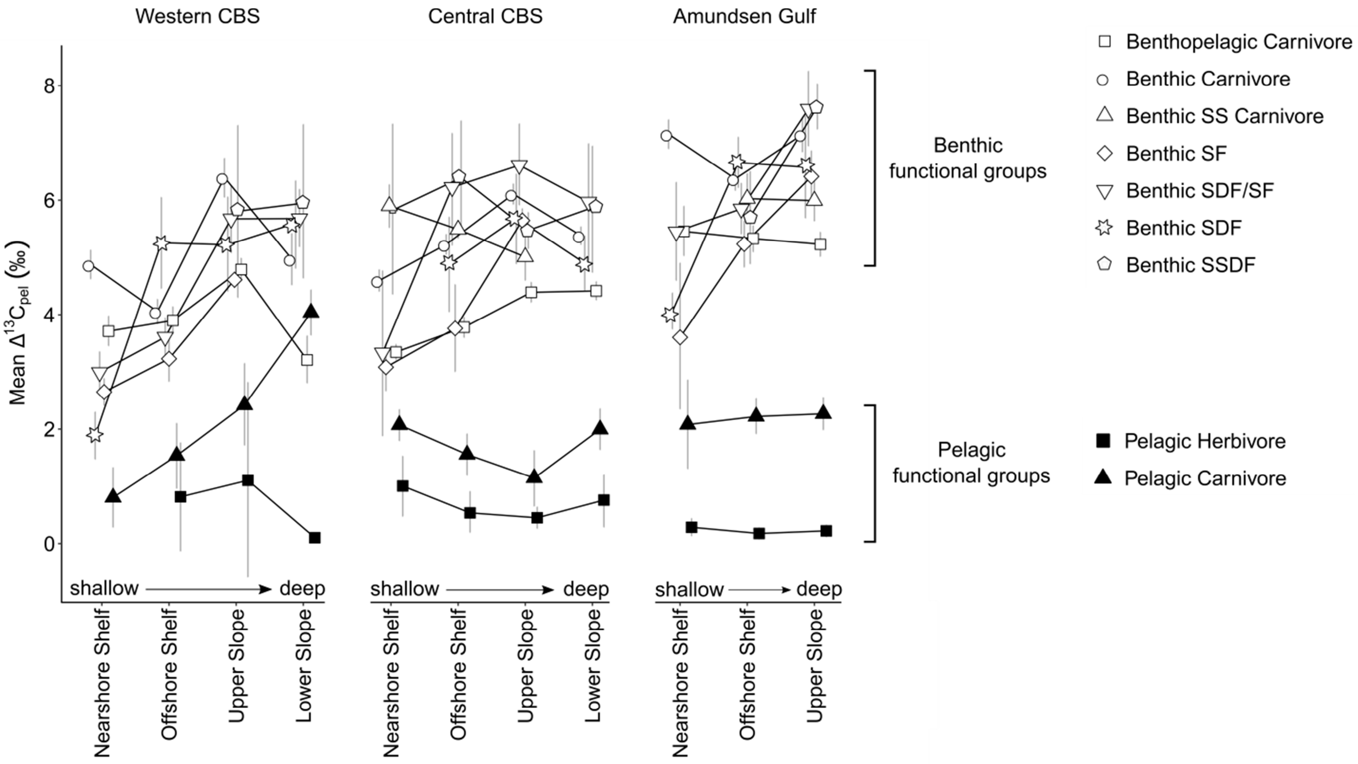


Figure 3.4. Mean enrichment from a pelagic baseline ($\Delta^{13}C_{pel}$) for functional groups across water mass assemblages, within each longitudinal region. Points represent the modes of the posterior distributions, created with 10,000 iterative calculations. Whiskers represent 95% credible intervals. Lines illustrate trends among discrete water mass assemblages (not a continuous scale). A clear and increasing divergence between benthic (white) and pelagic (black) functional groups along the $\Delta^{13}C_{pel}$ continuum suggests that benthic-pelagic coupling weakened from west to east and from the nearshore shelf to the upper slope.

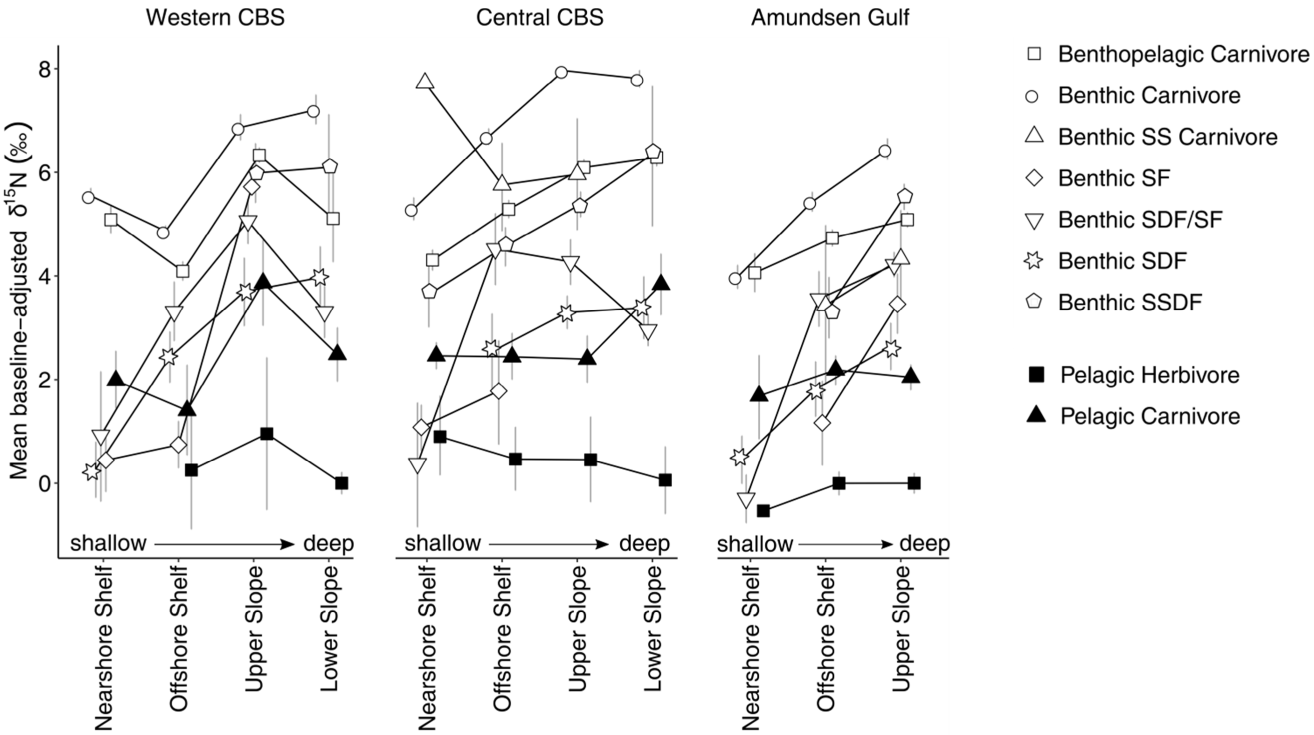


Figure 3.5. Mean baseline-adjusted δ^{15}N for functional groups across water mass assemblages, within each longitudinal region. Points represent the modes of the posterior distributions, created with 10,000 iterative calculations. Whiskers represent 95% credible intervals. Lines illustrate trends among discrete water mass assemblages (not a continuous scale). Within regions, mean δ^{15}N for most functional groups increased with depth. The central CBS generally exhibited the widest among-group spread of mean δ^{15}N values.

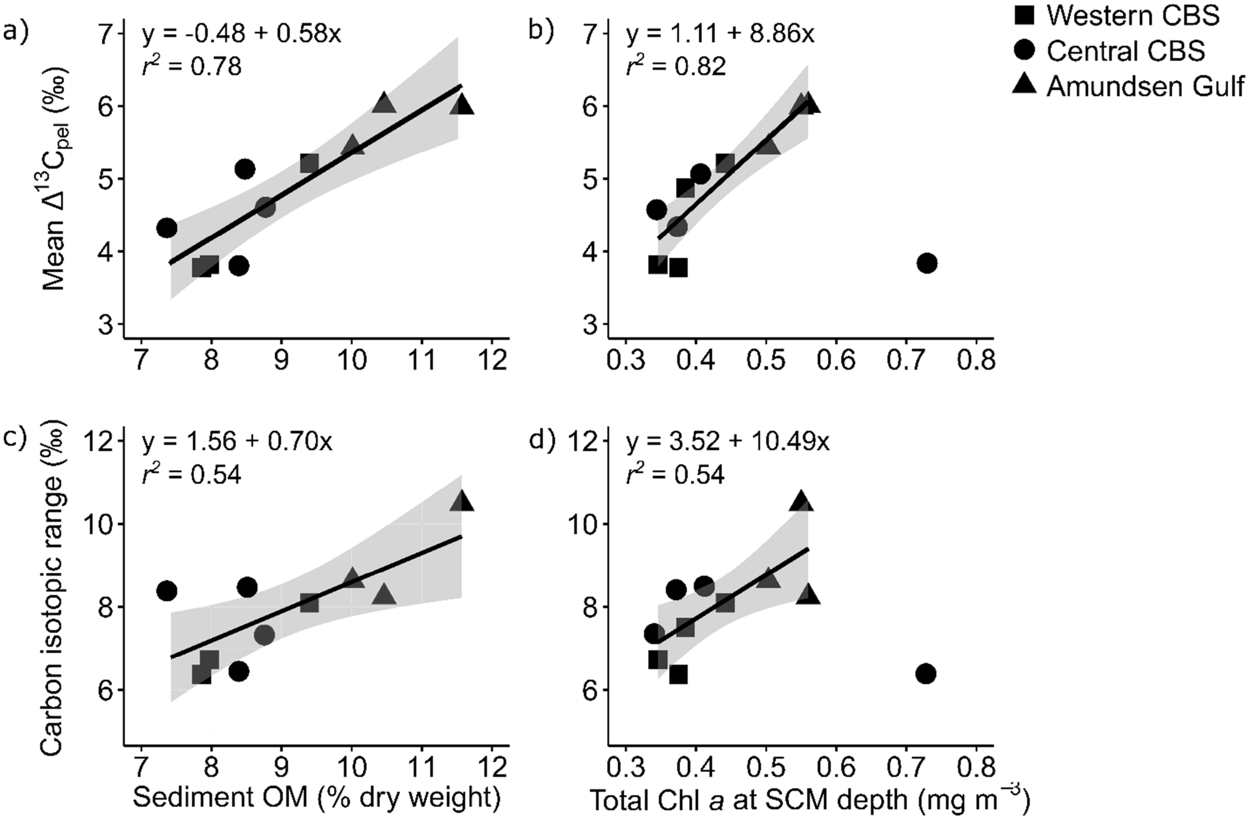


Figure 3.6. Linear regressions between mean $\Delta^{13}C_{pel}$ and (a) sediment organic matter and (b) total chlorophyll *a* at the subsurface chlorophyll maximum depth, as well as linear regressions between carbon isotopic range of the niche region and (c) sediment organic matter and (d) total chlorophyll *a* at the subsurface chlorophyll maximum depth. The isotopic niche metrics $\Delta^{13}C_{pel}$ and carbon range were calculated at the community level for longitudinal regions, within water mass assemblages (*n* = 11 communities). Results presented for (b) and (d) do not include consideration of the outlier (representing two nearshore sites in the Central CBS). All relationships were significant ($p < 0.05$).

4 Relationships between depth and $\delta^{15}N$ of Arctic benthos vary among regions and trophic functional groups

Introduction

Deep demersal food webs at high latitudes are often characterized by two interlinked trophic pathways (e.g., Iken et al. 2001, Trueman et al. 2014). These include a benthic pathway in which organic matter available at the seafloor forms the base of an obligate benthic food web, and a benthopelagic pathway in which mobile demersal species subsidize their diets with prey from the upper water column (e.g., Iken et al. 2001, Trueman et al. 2014, Stasko et al. 2016). Multiple trophic pathways can complicate interpretation of trophic structure in deep-sea food webs, especially when inferences are derived from stable isotope ratios of nitrogen ($\delta^{15}N$; e.g., Roy et al. 2015). Consumers are generally enriched in ^{15}N relative to their food, so that higher values of $\delta^{15}N$ indicate a higher relative trophic position (Minagawa & Wada 1984). However, interpreting trophic enrichment from the base of the food web is less straightforward when the basal resources that sustain benthic versus benthopelagic trophic pathways respond differently to environmental gradients, such as depth.

The $\delta^{15}N$ values of benthic suspension/filter feeders commonly increase as a function of depth in various marine systems, whereas those of mobile demersal predators/scavengers, which can access benthopelagic prey, usually do not (e.g., Catalan Sea, Polunin et al. 2001, Weddell Sea, Mintenbeck et al. 2007, Fram Strait, Bergmann et al. 2009, San Juan Archipelago, Galloway et al. 2013, Canadian Arctic Archipelago, Roy et al. 2015). Reported $\delta^{15}N$-depth relationships for other benthic consumer groups are variable, and can be negative for some deposit feeders (Bergmann et al. 2009, Roy et al. 2015, Bell et al. 2016). Mintenbeck et al. (2007) were the first to provide a detailed explanation of the depth-dependence of suspension feeder $\delta^{15}N$, linking the relationship to the microbial and biochemical transformation of fine-scale particulate organic matter (POM) in the water column (Macko and Estep 1984, Kellogg et al. 2011). Deeper water depths allow greater time for degradation, and although all POM reaching the seafloor undergoes some degree of degradation, transformation is greater for the small, slow-sinking particles that are accessible to benthic suspension/filter feeders (reviewed in Mintenbeck et al. 2007). Organisms that consume larger particle sizes and/or more intact food items tend to exhibit weaker $\delta^{15}N$-depth relationships, presumably because the food is less degraded (e.g., large-particle deposit feeders; Mintenbeck et al. 2007) or includes a mixture of benthic and benthopelagic sources (e.g., mobile predators; Bergmann et al. 2009). If particle characteristics drive $\delta^{15}N$-depth relationships in suspension feeders, regional variation in water column processes that govern particle source, size, sinking flux, cross-shelf transport and transformation should underlie variation in the strength of the relationships observed among marine regions (Bergmann et al. 2009, Roy et al. 2015, Bell et al. 2016) .

Differences in $\delta^{15}N$-depth relationships among trophic functional groups and regions have consequences for inferring relative trophic positions from isotopic data. Specifically, organisms that rely on the benthic or benthopelagic pathway may require consideration of different, pathway-specific isotopic baselines prior to comparison (Papiol et al. 2013, Roy, Iken, Gosselin, et al. 2015). Analysing $\delta^{15}N$-depth relationships by trophic functional groups in which taxa share common feeding strategies is useful, as it allows investigators to predict which taxa may have $\delta^{15}N$ influenced by depth prior to investigation (e.g., Papiol et al. 2013). To date, most studies quantifying $\delta^{15}N$-depth relationships at the functional group level have used linear regression (Mintenbeck et al. 2007, Bergmann et al. 2009, Roy et al. 2015), which is not ideal given the inherent non-independence of multi-species groups (Pinheiro and Bates 2000, Zuur et al. 2009). A modelling approach that accounts for non-independence can provide a more robust analysis of whether $\delta^{15}N$-depth relationships may be considered characteristic of a trophic functional group. Further, demersal carnivores are often considered as a single trophic functional group in $\delta^{15}N$-depth analyses despite the fact that some are primarily benthic feeders whereas others are benthopelagic feeders (e.g., Bergmann et al. 2009, Roy, Iken, Gosselin, et al. 2015). Since their primary consumer prey often exhibit significant $\delta^{15}N$-depth relationships themselves, benthic predators may have increasing $\delta^{15}N$ with depth if they are considered separately from their benthopelagic counterparts.

Here, relationships between $\delta^{15}N$ and water depth were examined for six trophic functional groups along a depth gradient from 20 to 500 m in two contiguous Arctic marine ecosystems, the Canadian Beaufort Sea and Amundsen Gulf (Fig. 4.1). POM sources and flux dynamics differ significantly between regions; the Canadian Beaufort Sea is dominated by terrestrial organic matter, whereas the Amundsen Gulf is dominated by marine-derived organic matter (see further description in *Methods*; Morata et al. 2008, Sallon et al. 2011). The objective was to identify trophic functional groups that display increasing $\delta^{15}N$ as a function of water depth in each region using a linear mixed-modelling approach that allows for taxon-level variation (Pinheiro and Bates 2000). It was predicted that (1) the slope and/or strength of relationships for all trophic functional groups would differ between the two adjacent marine regions, and (2) the relationship would be significant for benthic carnivores when analysed separately from other carnivorous groups.

Methods

Study Area

Samples were collected in the southern Canadian Beaufort Sea and Amundsen Gulf (herein collectively referred to as the Canadian Beaufort region; Fig. 4.1) aboard the stern trawler FV *Frosti* as part of the Beaufort Regional Environmental Assessment Marine Fishes Project (Fisheries and Oceans Canada, www.beaufortrea.ca). Despite being contiguous marine regions, the Beaufort Sea and Amundsen Gulf exhibit significant differences in sediment characteristics (Morata et al. 2008), primary production regimes (Ardyna et al. 2013), and vertical flux of POM (O'Brien et al. 2006, Forest et al. 2010). Primary production is higher in the Amundsen Gulf than in the Beaufort Sea (Sallon et al. 2011, Ardyna et al. 2013), but export to the benthos is lower (O'Brien et al. 2006, Sallon et al. 2011). An estimated 70 to 95 % of autochthonous particulate organic carbon in the Amundsen Gulf is retained in the upper 100 m of the water column by the pelagic community, except in the vicinity of Cape Bathurst (Forest et al. 2010, Sampei et al. 2011). The Beaufort Sea shelf is strongly influenced by the Mackenzie River, which discharges between 40 and 120 x 10^6 t of terrestrial sediment annually (Macdonald et al. 1998, Doxaran et al. 2015), exceeding that of any other Arctic River (Rachold et al. 2004). Consequently, the bulk organic matter pool in the Amundsen Gulf is dominated by marine-derived organic carbon, whereas that in the Beaufort Sea is dominated by terrigenous organic carbon (Magen et al. 2010).

Sampling and stable isotope analysis

Sampling took place from early August to late September of 2012 and 2013 along 8 transects that spanned the continental shelf and associated slope. Each sampling transect had five to eight pre-defined sampling stations at depths ranging from 20 to 500 m (Fig. 4.1). Demersal fish and epifaunal invertebrates were collected with a combination of two demersal trawl nets: a modified Atlantic Western IIA benthic otter trawl (13 mm cod end liner to retain small fish) and a 3 m High-Rise Benthic Beam Trawl (6.3 mm cod end liner). Trawling protocols are described in detail in Chapter 3 and in Majewski et al. (2013). Infaunal invertebrates were retained from the upper 30 cm of sediments collected with a 0.25 m^2 USNEL box core and sieved through a 1 mm stainless steel mesh. A sample of bulk sediment from the top 1 cm was retained for stable isotope analysis and used as a reference for the composition of the bulk sedimentary organic matter pool. Dominant biota were sorted to the lowest possible taxonomic resolution onboard with the help of taxonomists (L. De Montety, Université du Québec à Rimouski; W. Walkusz, Fisheries and Oceans Canada), rinsed with seawater, and frozen immediately along with sediment at -50 °C. Taxonomy was standardized to the currently accepted names in the World Register of Marine Species (WoRMS Editorial Board 2016). Fish and macroinvertebrates were selected for stable isotope analysis across the observed range of body sizes to capture potential covariation between $\delta^{15}N$ and size (e.g., Romanuk et al. 2011).

Bulk sediment and tissue samples dissected for stable isotope analysis were dehydrated in a standard laboratory convection oven at 50 °C (fish) or a FreeZone 18 freeze-drier (Labconco; invertebrates, sediment), then ground to a homogenous powder and analysed for N isotopic composition using a Delta Plus continuous flow isotope spectrometer (Thermo-Finnigan) coupled to a 4010 Elemental Analyzer (Costech Instruments) at the University of Waterloo Environmental Isotopes laboratory (Waterloo, Canada). C isotopic composition was additionally analysed in bulk sediment samples following acidification with 10 % HCl to remove inorganic carbon (Jacob et al.

2005). Slow-turnover tissues were targeted for analysis, consistent with the literature and dissection constraints: dorsal muscle for fish, tail muscle for large decapods, and whole body for invertebrates that could not be reliably separated from exoskeleton (e.g., Dunton et al. 2006, Stasko et al. 2017). Isotope ratios (^{15}N:^{14}N, ^{13}C:^{12}C) were expressed in δ notation as parts per thousand (‰) relative to the international standards atmospheric N_2 for nitrogen and Vienna Pee Dee Belemnite for carbon (Craig 1957, Mariotti 1983). Analytical error for $\delta^{15}N$ and $\delta^{13}C$ never exceeded 0.3 and 0.2 ‰, respectively, based on repeated measurements of working laboratory standard materials cross-calibrated to the international standards. Repeatability of duplicate measurements of sample material was 0.3 ‰ for both $\delta^{15}N$ and $\delta^{13}C$. Stable isotope values for all taxa and sediments, averaged by region and depth, can be found in Stasko et al. (2017).

Statistical analyses

To account for potential bias caused by differences in species composition, statistical analyses were restricted to those taxa that were sampled in both the Beaufort Sea and the Amundsen Gulf across the same depth range (20 to 500 m). A total of 2239 biological samples representing 38 taxa across 6 phyla, and 56 samples of marine sediment were included in analyses (Table 4.1). Analyses were repeated with the full set of taxa sampled (74 total) to ensure excluded species did not change results (i.e., taxa lists in both regions were not identical in the secondary analyses).

Taxa were delineated into six trophic functional groups based on published trophic marker data and feeding observations (see Appendix C). Trophic functional groups were defined as taxa that employ similar feeding strategies and share common resources, but do not necessarily interact strongly with each other (e.g., Bonsdorff and Pearson 1999), including: (1) benthopelagic carnivores that are highly mobile and feed both at and above the seafloor as predators, scavengers, or both; (2) epifaunal carnivores that are mostly mobile and feed at the sediment surface as predators, scavengers, or both; (3) infaunal carnivores that prey on fauna below the sediment surface (in this study, all are predatory marine worms); (4) suspension/filter feeders that live on the seafloor and feed omnivorously on fresh or resuspended POM filtered from the water; (5) epifaunal deposit feeders that feed omnivorously at the sediment surface on deposited material that can include decomposed carcasses and zooplankton molts, phytodetritus, recycled organic matter, bacteria, or bacterial products; and (6) infaunal deposit feeders that feed omnivorously below the sediment surface on detritus and/or bacteria and bacterial products (e.g., Coad and Reist 2004, Macdonald et al. 2010, Węsławski et al. 2010, Jumars et al. 2015). Facultative suspension/deposit feeders that switch between feeding modes were excluded to avoid unquantified variation.

Preliminary plotting of δ^{15}N versus depth revealed clear grouping of stable isotope data by taxon. Linear mixed effects models were thus used to investigate relationships between δ^{15}N and the fixed factor water depth for each trophic functional group, allowing the intercept and/or slope to vary randomly by taxon to account for non-independence (Pinheiro and Bates 2000). To assess whether relationships between δ^{15}N and water depth differed between the Beaufort Sea and Amundsen Gulf, an interaction term between depth and region was included in the models. Model selection between random effects structures (slope, intercept, or both) was conducted using likelihood ratio tests after model fitting with a maximum likelihood procedure (Zuur et al. 2009, Bates et al. 2015). Likelihood ratio tests were then used to assess whether the interaction between water depth and region improved fit, and if not the interaction term was dropped from the model. To more closely examine regional differences, models were fit individually for the Beaufort Sea and Amundsen Gulf for those trophic functional groups that displayed both a strong relationship between $\delta^{15}N$ and water depth, and a significant interaction between water depth and region. Finally, the best model in all cases was refit using a restricted maximum likelihood procedure for parameter reporting (Zuur et al. 2009). Goodness-of-fit was evaluated using the marginal and conditional coefficients of determination (R^2_m and R^2_c), which respectively describe the proportion of variance explained by the fixed effects alone, and the fixed and random effects combined (Nakagawa & Schielzeth 2013). Following Sullivan & Feinn (2012), an R^2_c, ≥ 0.63 was considered strong and indicative of a well-fit model. Effect size for well-fit models was considered the average change in $\delta^{15}N$ (Δ) estimated for the trophic functional group across the entire depth gradient. Relationships between sediment $\delta^{15}N$ and water depth were assessed using least-squares linear regression. In all cases, assumptions of homogeneity of variance and normality of errors were assessed with a series of residual plots, and depth was log-transformed where it improved linearity (Zuur et al. 2009). Where residual variance increased as a function of depth (epifaunal and infaunal deposit feeders), linear mixed effects models included a fixed variance structure (Zuur et al. 2009, Pinheiro et al. 2016). Linear regression and likelihood ratio tests were considered significant at $\alpha = 0.05$.

The isotopic composition of sedimentary organic matter in the Canadian Beaufort region is influenced by three primary sources: terrestrial, fresh marine, and refractory marine organic matter (Magen et al. 2010). To verify that the composition of sedimentary POM differed between the Beaufort Sea and Amundsen Gulf, as previously reported (Morata et al. 2008, Magen et al. 2010), the $\delta^{15}N$ and $\delta^{13}C$ of bulk sediments at each site were plotted relative to the $\delta^{15}N$ and $\delta^{13}C$ of representative terrestrial, fresh marine, and refractory marine source data taken from the literature. The terrestrial source data were based on organic material recovered from the Mackenzie and Colville River Deltas ($\delta^{15}N$ = 1.0 ‰, $\delta^{13}C$ = -27.0 ‰; estimated from various studies by Magen et al. 2010). The refractory marine source data were taken from Amundsen Gulf sediments, where pigment analyses indicated the presence of highly degraded marine POM ($\delta^{15}N$ = 6.7 ‰, $\delta^{13}C$ = -21.1 ‰; Morata et al. 2008). Source values for fresh marine organic matter were more difficult to assign due to high spatial and seasonal variation in the isotopic composition of primary producers (Morata et al. 2008). Consequently, the $\delta^{15}N$ and $\delta^{13}C$ measured in pelagic POM collected from the chlorophyll maximum depth in the Amundsen Gulf for this study (C. Michel, unpublished data) were averaged with $\delta^{15}N$ and $\delta^{13}C$ measured in pelagic POM from the eastern Beaufort Sea and Amundsen Gulf reported by Roy et al. (2015). The resulting fresh marine source values ($\delta^{15}N$ = 5.6 ‰, $\delta^{13}C$ = -26.5 ‰) fall within the range reported for summer across the Canadian Beaufort region by Morata et al. (2008; $\delta^{15}N$ = 1.0 to 7.0 ‰, $\delta^{13}C$ = -27.0 to -21.0 ‰). Some sites in the Amundsen Gulf were excluded as outliers due to anomalous $\delta^{13}C$ (> median + interquartile range).

All statistical and graphical procedures were performed in R (version 3.3.1, R Core Team 2016) using the packages lme4 (Bates et al. 2015), nlme (Pinheiro et al. 2016), peicewiseSEM (Lefcheck 2015), ggplot2 (Wickham 2009), ggtern (Hamilton 2016) and plyr (Wickham 2011).

Results

Linear mixed effects models indicated $\delta^{15}N$ was strongly related to depth for epifaunal carnivores, suspension/filter feeders, epifaunal deposit feeders and infaunal deposit feeders, but not for benthopelagic or infaunal carnivores (Table 4.2). The slope of the relationship was positive and steepest for suspension/filter feeders and infaunal deposit feeders, followed by epifaunal carnivores (Fig. 4.2, Table 4.2). The estimated increase in $\delta^{15}N$ for these groups between 20 and 500 m depths ranged between 0.82 and 1.44 ‰ (Table 4.2). Epifaunal deposit feeder $\delta^{15}N$ was strongly negatively related to depth, but had the shallowest slope of all trophic functional groups when both regions were considered together (Table 4.2). Benthopelagic and infaunal carnivores displayed a positive trend between $\delta^{15}N$ and water depth, but the association was weak (Table 4.2).

For those trophic functional groups that displayed a strong relationship between $\delta^{15}N$ and depth (Table 4.2), a model that included an interaction term between water depth and region (Beaufort Sea versus Amundsen Gulf) fit the data significantly better than a model with no interaction (likelihood ratio tests; $p < 0.01$ for epifaunal carnivores, suspension/filter feeders, epifaunal deposit feeders and infaunal deposit feeders). In other words, the slopes of the $\delta^{15}N$-depth relationships were significantly different between the Beaufort Sea and Amundsen Gulf. Slopes were steeper in the Amundsen Gulf for suspension/filter feeders and infaunal deposit feeders, whereas slopes were steeper in the Beaufort Sea for epifaunal carnivores and epifaunal deposit feeders (Table 4.3, Fig. 4.2). When fit for individual regions, infaunal deposit feeders displayed the largest increase in $\delta^{15}N$ of any group (Table 4.3). Including taxon as a random variable (R^2_c) explained an additional >40 % of the variance relative to depth alone (R^2_m) for all groups except infaunal deposit feeders (Tables 4.2 and 4.3). Including all available taxa in analyses (i.e., not restricting taxa assemblages to be identical in both regions) did not reveal any differences between which trophic functional groups displayed strong δ^{15}N-depth relationships, but did increase the strength of fit (data not shown).

Bulk sediment δ^{15}N was weakly, but significantly positively related to water depth in both the Beaufort Sea ($F_{1,31} = 13.12$, $p < 0.01$, $r^2 = 0.30$) and Amundsen Gulf ($F_{1,21} = 5.19$, $p = 0.03$, $r^2 = 0.20$). The slope of the relationship between δ^{15}N and water depth was significantly steeper in the Amundsen Gulf relative to the Beaufort Sea (ANCOVA, $F_{3,34} = 5.94$, $p = 0.03$; Fig. 4.3). Sediment isotopic composition was clearly more influenced by terrestrial sources in the Beaufort Sea than in the Amundsen Gulf, where sediment δ^{15}N and δ^{13}C at most sampling sites were well constrained between fresh and refractory marine end-members (with the exception of a few terrestrially-dominated nearshore sites; Fig. 4.4).

Discussion

Enrichment of ^{15}N in consumer tissues with increasing water depth is a commonly observed phenomenon among benthic marine organisms at high latitudes and elsewhere, particularly in deposit and suspension feeders (e.g., Mintenbeck et al. 2007, Bergmann et al. 2009, Roy et al. 2015). Here, results demonstrated for the first time in the Arctic that the δ^{15}N of epifaunal carnivores can also increase as a function of depth. Study results confirmed the phenomenon for suspension and infaunal deposit feeders in the Canadian Beaufort region while accounting for taxon-level variation, and revealed that the rate of change for δ^{15}N with depth differed between the two Arctic marine regions studied. It is proposed that the regional differences in δ^{15}N-depth relationships are linked to regional heterogeneity in POM input and vertical flux properties.

The significant, positive effect of water depth on the $\delta^{15}N$ values of suspension/filter and infaunal deposit feeders is likely linked to the transformation of POM during sinking, as suggested by Mintenbeck et al. (2007). Summer maximum chlorophyll *a* concentrations in the Canadian Beaufort region occur deeper than in other oceans, between ~ 40 to 60 m depths (Carmack et al. 2004, Ardyna et al. 2013), such that fresh, relatively untransformed phytodetritus is more accessible to benthos in shallow habitats than in deep habitats. In contrast, marine-derived POM received by benthos in deeper habitats is subject to greater degradation, and consequently greater enrichment in ^{15}N (Lee et al. 2004). The majority of POM synthesized in the euphotic zone during the spring bloom is consumed by heterotrophic zooplankton and bacteria in the Canadian Beaufort region (Lee et al. 2004, Sampei et al. 2011). The small fraction of POM that escapes the euphotic zone and is exported below 100 m has consequently higher $\delta^{15}N$ due to biochemical transformation processes that preferentially release the lighter ^{14}N isotope, a process that continues during sinking (Kellogg et al. 2011, Galloway et al. 2013) .

Several water column processes in the Canadian Beaufort region may additionally contribute to increased consumer $\delta^{15}N$ with increasing depth. The transition from nutrient-rich Pacific-origin water to warmer Atlantic-origin water occurs around 200 to 350 m below surface (McLaughlin et al. 1996). Here, the hyperbenthic habitat along the upper continental slope appears to be a hotspot for organic matter transformation and interception via large aggregations of zooplankton and predatory benthopelagic fish (Crawford et al. 2012, Majewski et al. 2017), which may be linked to low POM export below 200 m (Forest et al. 2015). With little fresh marine-derived POM reaching the seafloor along the upper slope, benthic primary consumers would be limited to ^{15}N-enriched POM that has either been recycled among the benthos and sedimentary bacteria (e.g., North et al. 2014, Bell et al. 2016), or resuspended and advected downslope by upwelling/downwelling events characteristic of the Beaufort Sea shelf break (Forest et al. 2007).

In contrast to suspension and infaunal deposit feeders, epifaunal deposit feeder δ^{15}N decreased slightly with depth, in agreement with observations in Fram Strait that were attributed to the lesser availability of bacterial food sources at greater depths (Bergmann et al. 2009). Opposing δ^{15}N-depth relationships between epifaunal and infaunal deposit feeding groups is unintuitive, but may be explained by differences in trophic flexibility. Epifaunal taxa that feed omnivorously at the sediment surface are more trophically flexible than infaunal taxa, both in terms of food source and particle size. Such trophic flexibility was supported by the increasing variance of δ^{15}N within individual epifaunal deposit-feeding taxa with water depth, especially for the asteroid *Pontaster tenuispinus* (Düben & Koren) (data not shown). Increased variance may be a result of highly flexible diets within suspension feeders in the face of limited primary-producer derived organic matter (e.g., North et al. 2014, and as suggested by Roy et al. 2015). Conversely, the two infaunal deposit feeding taxa examined here extract nutrition directly from ingested sediment at deeper layers (MacDonald et al., 2010). Infauna with similar feeding habits have been observed to exploit more consistent fractions of bulk sedimentary organic matter than their epifaunal counterparts (North et al., 2014). Infaunal deposit feeder δ^{15}N values would therefore be expected to reflect the of bulk sedimentary organic matter more closely than those of epifaunal deposit feeders.In this study, the change in epifaunal deposit feeder δ^{15}N between 20 and 500 m depths was so small that it is difficult to ascribe its biological significance (< 0.69 ‰), but it may have greater trophic consequences over larger depth gradients (see Bergmann et al. 2009; $\Delta^{15}N > -4.5$ ‰ from 1000 to 5000 m depths).

Water depth is thought to have a weaker influence on the $\delta^{15}N$ of mobile carnivorous predators and scavengers than on primary consumers because the former can feed on both benthic and benthopelagic prey (Bergmann et al. 2009, Roy, Iken, Gosselin, et al. 2015). However, findings suggest the relationship between $\delta^{15}N$ and depth differs among finer-scale carnivorous functional groups. In particular, the $\delta^{15}N$-depth relationship for benthic epifaunal carnivores was significant when analysed separately from benthopelagic and infaunal carnivores. It is conceivable that the positive trend between epifaunal carnivore $\delta^{15}N$ and water depth is a consequence of feeding on ^{15}N-enriched prey at depth (e.g., Birkely and Gulliksen 2003, Coad and Reist 2004). Suspension feeders are an important prey for many of the taxa in this trophic group (e.g., Birkely and Gulliksen, 2003; Coad and Reist, 2004). In addition, there is likely limited ability to feed opportunistically on pelagic prey, such as vertically migrating zooplankton, on the upper slope of the Canadian Beaufort region because those prey are intercepted by large aggregations of benthopelagic predators (Crawford et al. 2012, Majewski et al. 2017). Curiously, infaunal carnivore $\delta^{15}N$ values did not reflect those of the infaunal deposit feeders that may comprise an important prey base. The infauna are the most data-poor trophic groups in this study ($n < 100$ individuals for each group), and without additional dietary information it is difficult to estimate the importance of infaunal deposit feeders to the diets of infaunal carnivores examined in this study. Regardless, the different $\delta^{15}N$-depth relationships among carnivore groups highlight variation in their use of benthic and pelagic trophic pathways. Benthopelagic carnivores subsidize their diets with pelagic prey, especially fishes such as Arctic Cod (*Boreogadus saida* (Lepechin); Cui et al. 2012) and Greenland

Halibut (*Reinhardtius hippoglossoides* (Walbaum); Bjelland et al. 2000). Benthopelagic predators are, therefore, not restricted to trophic pathways beginning in benthic resources that have undergone depth-related ^{15}N enrichment. Findings thus suggest that carnivorous trophic groups should be considered separately in food web analyses rather than pooling them as one group.

Remineralization of organic matter by the pelagic food web, and its link to POM sources and flux dynamics (Sallon et al., 2011; Kellogg et al., 2011), may be key to steeper δ^{15}N-depth relationships for suspension/filter feeders, infaunal deposit feeders, and sediments in the Amundsen Gulf than in the Beaufort Sea. Sediment δ^{15}N and δ^{13}C data verified geographic differences previously found in the composition of bulk benthic POM between the Beaufort Sea and Amundsen Gulf (Morata et al. 2008, Magen et al. 2010). Unlike the Amundsen Gulf, the bulk sedimentary organic matter pool in the Beaufort Sea is dominated by terrigenous material from the Mackenzie River plume (Magen et al. 2010). Terrestrial organic matter from the Mackenzie River can become entrained in upper water masses upon entry into the Beaufort Sea or via frequent resuspension events on the shelf (Carmack & Macdonald 2002, Forest et al. 2007). Once suspended, terrestrial POM is typically directed eastwards and offshore by winds and the Coriolis force at the surface (Carmack & Macdonald 2002), and by eddies and the prevailing eastward-flowing Beaufort Undercurrent in deeper waters (Aagaard 1984, O'Brien et al. 2006, Forest et al. 2007). Consequently, terrestrial POM can comprise > 50 % of the bulk sediment pool as far as the eastern tip of Tuktoyaktuk Peninsula and as deep as 1000 m (Magen et al. 2010). The quantitative dominance of terrestrial POM in the benthic POM pool, even at great depths, may explain why the δ^{15}N measured in sediment, suspension/filter feeders and infaunal deposit feeders changes at a slower rate with depth in the Beaufort Sea than in the Amundsen Gulf.

The stronger and steeper δ^{15}N-depth relationships for suspension/filter and infaunal deposit feeders in the Amundsen Gulf relative to the Beaufort Sea may be linked to more heterogeneous POM inputs and low vertical sinking flux. Sediment data indicated that deep sites in the Amundsen Gulf had higher proportions of marine-derived organic matter than nearshore sites. Marine organic matter in the Amundsen Gulf may have been subject to extensive transformation in the upper water column, where the majority of autochthonous organic carbon is retained by the pelagic community (Sampei et al. 2011). Sallon et al. (2011) observed that sinking POM contained greater proportions of algal cells and exopolymeric substances when primary production was high, such as in some areas of the Amundsen Gulf. The authors did not measure the quality of material that reached the seafloor, but suggested the presence of exopolymeric coatings on algal cells likely intensified microbial activity on sinking particles by facilitating bacterial attachment (Parsmore & Costerton 2003, Sallon et al. 2011), which would consequently lead to greater ^{15}N enrichment (Macko & Estep 1984, Kellogg et al. 2011). Regional differences in the slope of the δ^{15}N-depth relationship within suspension and infaunal deposit feeders are, therefore, likely related to the dominant POM flux regimes: (1) in the Beaufort Sea, the strong influence of a single, terrestrial POM source likely dampens POM δ^{15}N heterogeneity with depth, and (2) in the Amundsen Gulf, relatively higher primary production likely promotes intensified biological transformation of POM via recycling through the pelagic community and enhanced microbial activity on sinking particles, resulting in weaker benthic-pelagic coupling (see Chapter 3) and consequently higher benthic POM δ^{15}N heterogeneity.

Conversely, the slope of the epifaunal carnivore δ^{15}N-depth relationship was slightly steeper in the Beaufort Sea compared to the Amundsen Gulf. This finding appeared to be most influenced by a few taxa, including the generalist-feeding fishes Atlantic Poacher (*Leptagonus decagonus* (Block & Schneider)), Gelatinous Eelpout (*Liparis fabricii* Krøyer), and Canadian Eelpout (*Lycodes polaris* (Sabine); Coad and Reist 2004, Giraldo et al. 2016, Whitehouse et al. 2016). Some generalist benthic fishes can switch feeding strategies to take advantage of benthopelagic prey when benthic resources are scarce (e.g., Carrassón & Cartes 2002). A switch to benthopelagic prey could explain the flatter δ^{15}N-depth relationships in the Amundsen Gulf observed for these fishes, however, there is only evidence for such a shift in Atlantic Poacher (according to δ^{13}C; see data in Stasko et al. 2017). Without further diet information, the flatter δ^{15}N-depth relationships of Gelatinous and Canadian eelpouts in the Amundsen Gulf remain difficult to explain.

Results presented here are relevant to studies that take a functional group approach to marine food web analyses, but must be applied with caution. Our dataset is limited by taxon occurrences and distributions, as well as sample availability. Many taxa occurred across a limited depth range, and some occurred along a limited number of transects (Table 1). Any trophic functional group, including suspension feeders, can include taxa that feed at substantially different trophic levels from each other (e.g., Bergmann et al. 2009), affecting how closely linked their δ^{15}N values are to POM. The importance of taxon-level variation was underscored by the fact that including taxon as a random variable in the models consistently explained an additional > 40 % of variance ($R^2_c > R^2_m$). Confidence that the results can be applied more generally to other studies should be evaluated in light of the limitations in taxa richness and distributions available in this dataset.

In conclusion, a linear mixed-effects modelling approach confirmed that δ^{15}N-depth relationships in the Beaufort Sea and Amundsen Gulf are characteristic of four benthic trophic functional groups: epifaunal carnivores, suspension/filter feeders, infaunal deposit feeders, and to a lesser degree, epifaunal deposit feeders. The results presented here agree with other studies that a depth-stratified normalization approach is necessary when making conclusions about primary consumer trophic levels from δ^{15}N across depth gradients in marine systems (e.g., Mintenbeck et al. 2007, Roy, Iken, Gosselin, et al. 2015). Such an approach may also be necessary for benthic-feeding carnivores. This work additionally highlights the need to be cognisant of differences in POM input and vertical flux regimes when comparing food webs among distinct marine systems, as such differences may alter the rate at which consumer δ^{15}N changes with depth.

Table 4.1. List of taxa used in the study, sorted by trophic functional group and Phylum. The sample sizes for each taxon are given individually for the Beaufort Sea and Amundsen Gulf. Plot ID # is indicated for those taxa shown in Fig. 4.2. Dashes indicate those taxa missing from Fig. 4.2 because they were only sampled at one water depth.

				Sample size		**Depth range**	
Functional Group	**Phylum**	**Taxon**	**Plot ID #**	**Beaufort Sea**	**Amundsen Gulf**	**Beaufort Sea**	**Amundsen Gulf**
Benthopelagic carnivore							
	Arthropoda	*Argis dentata*		49	21	40 - 200	40 - 200
	Arthropoda	*Eualus gaimardii*		92	49	20 - 500	40 - 350
	Arthropoda	*Lebbeus polaris*		6	55	500	75 - 500
	Chordata	*Boreogadus saida*		327	91	20 - 500	40 - 500
	Chordata	*Icelus spatula*		53	3	20 - 200	40 - 75
	Chordata	*Reinhardtius hippoglossoides*		67	10	350 - 500	300 - 350
	Chordata	*Triglops pingelii*		54	14	20 - 350	40 - 200
Epifaunal carnivore							
	Arthropoda	*Sabinea septemcarinata*	*1*	25	23	40 - 350	40 - 350
	Arthropoda	*Saduria sabini*	*2*	9	15	20 - 40	40 - 200
	Arthropoda	*Sclerocrangon ferox*	*3*	73	70	40 - 500	75 - 500
	Chordata	*Anisarchus medius*	*4*	53	7	40 - 200	40 - 75
	Chordata	*Aspidophoroides olrikii*	*5*	118	40	20 - 200	40 - 200
	Chordata	*Gymnocanthus tricuspis*	*6*	49	16	20 - 200	40 - 75
	Chordata	*Icelus bicornis*	*7*	64	44	40 - 200	40 - 275
	Chordata	*Leptagonus decagonus*	*8*	10	7	350 - 500	200 - 350
	Chordata	*Liparis fabricii*	*9*	14	11	40 - 500	200 - 500
	Chordata	*Lycodes pallidus*	*10*	4	21	40 - 500	200 - 350
	Chordata	*Lycodes polaris*	*11*	23	11	20 - 200	40 - 75
	Chordata	*Lycodes sagittarius*	-	7	3	350	350
	Chordata	*Lycodes seminudus*	*12*	39	7	350 - 500	350 - 500
	Cnidaria	Actiniaria sp.	-	13	4	500	200

Functional Group	Phylum	Taxon	Plot ID #	Sample size Beaufort Sea	Sample size Amundsen Gulf	Depth range Beaufort Sea	Depth range Amundsen Gulf
	Echinodermata	*Gorgonocephalus* sp.	*13*	35	19	40 - 500	75 - 300
Infaunal carnivore							
	Annelida	*Abyssoninoe* sp.		2	5	350	75 - 350
	Annelida	*Aglaophamus* sp.		5	3	350 - 500	350 - 500
	Annelida	*Eucranta* sp.		6	11	40 - 200	75 - 350
	Annelida	*Nephtys* sp.		4	3	40 - 75	40 -75
Suspension/filter feeder							
	Arthropoda	*Haploops laevis*	-	3	5	75	40
	Echinodermata	*Heliometra glacialis*	*14*	47	45	40-350	75-350
	Mollusca	*Astarte* sp.	*15*	4	15	75	40 - 350
	Mollusca	*Bathyarca* sp.	*16*	8	4	75	300 - 500
	Mollusca	*Similipecten greenlandicus*	*17*	39	10	40 - 75	75
	Mollusca	Thyasiridae sp.	*18*	13	9	75 - 500	200 - 500
Epifaunal deposit feeder							
	Annelida	Ampharetidae sp.	*19*	11	11	350 - 500	200 - 500
	Arthropoda	*Synidotea* sp.	*20*	17	23	40 - 75	40 - 300
	Echinodermata	*Ctenodiscus crispatus*	*21*	6	25	200	75 - 350
	Echinodermata	*Pontaster tenuispinus*	*22*	63	21	75 - 500	200 - 500
Infaunal deposit feeder							
	Annelida	*Maldane* sp.	*23*	34	24	75 - 500	40 - 500
	Echinodermata	*Molpadia* sp.	*24*	19	19	350 - 500	350 - 500

Table 4.2. Results of linear mixed effects models describing the relationship between δ^{15}N and water depth for six trophic functional groups in the Canadian Beaufort region. Random effects structures allowed either intercept (b), slope (m), or both to vary by taxon. Goodness-of-fit was evaluated using the marginal (R^2_m) and conditional (R^2_c) coefficients of variation, which respectively describe the proportion of variance explained by depth alone and by depth and taxon together. An $r^2 \geq 0.63$ was considered a strong fit and is indicated in bold. The estimated change in δ^{15}N (Δ) across the observed water depth range is given for well-fit models.

Trophic functional group	***n*** **individuals**	***n*** **taxa**	**Intercept (b)**	**Slope (m)**	**t**	**Goodness of fit**		**Random effects structure**	**Depth range (m)**	**Δ (‰)**
						R^2_m	R^2_c			
Benthopelagic carnivores	891	7	11.50 ± 0.36	0.67 ± 0.04	16.24	0.25	0.60	b	20 - 500	
Epifaunal carnivores	834	15	12.37 ± 0.55	0.59 ± 0.11	5.42	0.24	**0.67**	m, b	20 - 500	0.82
Infaunal carnivores*	39	4	14.77 ± 0.51						40 - 500	
Suspension/filter feeders	202	6	3.79 ± 1.43	1.30 ± 0.20	6.64	0.12	**0.83**	b	40 - 500	1.43
Epifaunal deposit feeders	177	4	12.24 ± 1.22	-0.12 ± 0.20	-0.60	0.22	**0.89**	b	40 - 500	-0.13
Infaunal deposit feeders	96	2	8.12 ± 1.48	1.03 ± 0.25	4.16	0.84	**0.84**	m, b	20 - 500	1.44

*No model fit the infaunal carnivore data better than a null model with intercept as the only term (i.e., depth had little effect)

Table 4.3. Results of linear mixed effects models describing the relationship between δ^{15}N and water depth for those trophic groups that exhibited significantly different slopes in the Beaufort Sea and Amundsen Gulf. Random effect structures allowed either intercept (b), slope (m), or both to vary by taxon. Goodness-of-fit was evaluated using the marginal (R^2_m) and conditional (R^2_c) coefficients of variation, which respectively describe the proportion of variance explained by depth alone and by depth and taxon together. An $R^2 \geq 0.63$ was considered a strong fit and is indicated in bold (Sullivan and Feinn, 2012). The estimated change in δ^{15}N (Δ) across the observed water depth range is given for well-fit models.

Functional Group	**Region**	***n***	***n* taxa**	**Intercept (b)**	**Slope (m)**	***t***	**Goodness of fit**		**Random effects structure**	**Depth range (m)**	**Δ (‰)**
							R^2_m	**R^2_c**			
Epifaunal carnivores	Beaufort Sea	536	15	11.97 ± 0.71	0.69 ± 0.15	4.67	0.20	**0.70**	m, b	20 - 500	0.96
	Amundsen Gulf	298	15	12.79 ± 0.79	0.58 ± 0.16	3.66	0.13	**0.73**	m, b	20 - 500	0.81
Suspension/filter feeders	Beaufort Sea	114	6	5.69 ± 1.11	0.84 ± 0.14	5.99	0.08	**0.89**	b	40 - 500	1.17
	Amundsen Gulf	88	6	5.62 ± 2.21	1.07 ± 0.36	2.99	0.04	**0.81**	b	40 - 500	1.50
Epifaunal deposit feeders	Beaufort Sea	97	4	15.19 ± 1.77	-0.63 ± 0.27	-2.23	0.06	**0.93**	b	40 - 500	-0.69
	Amundsen Gulf	80	4	14.42 ± 1.39	-0.26 ± 0.24	-1.10	0.02	**0.84**	b	40 - 500	-0.29
Infaunal deposit feeders	Beaufort Sea	53	2	8.13 ± 1.49	1.04 ± 0.25	4.14	0.61	0.61	b	75 - 500	1.45
	Amundsen Gulf	43	2	7.12 ± 1.24	1.37 ± 0.22	6.19	**0.80**	**0.81**	b	40 - 500	2.08

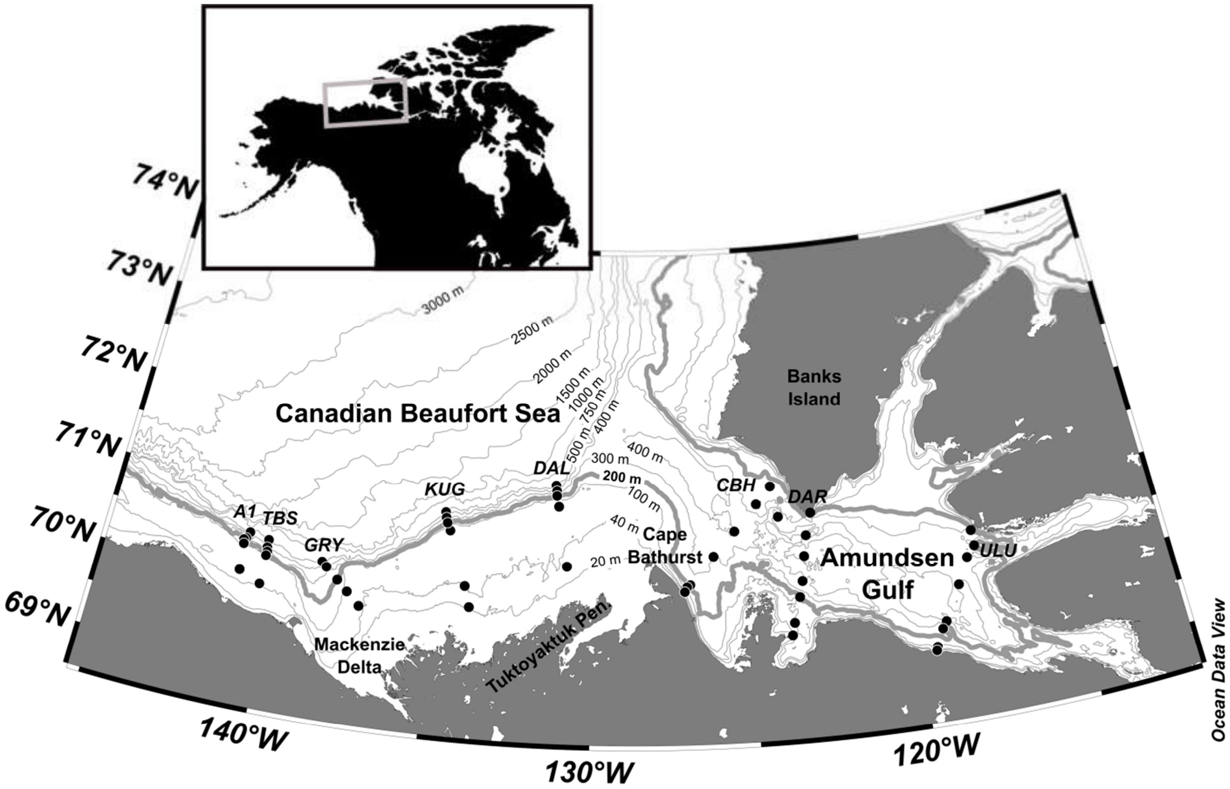


Figure. 4.1. Map of sampling station locations (black circles) along 8 transects in the Canadian Beaufort Sea (A1, TBS, GRY, KUG, DAL) and Amundsen Gulf (CBH, DAR, ULU). The 200 m isobath that defines the continental shelf break is shown bolder than other isobaths. Map was created using Ocean Data View 4.

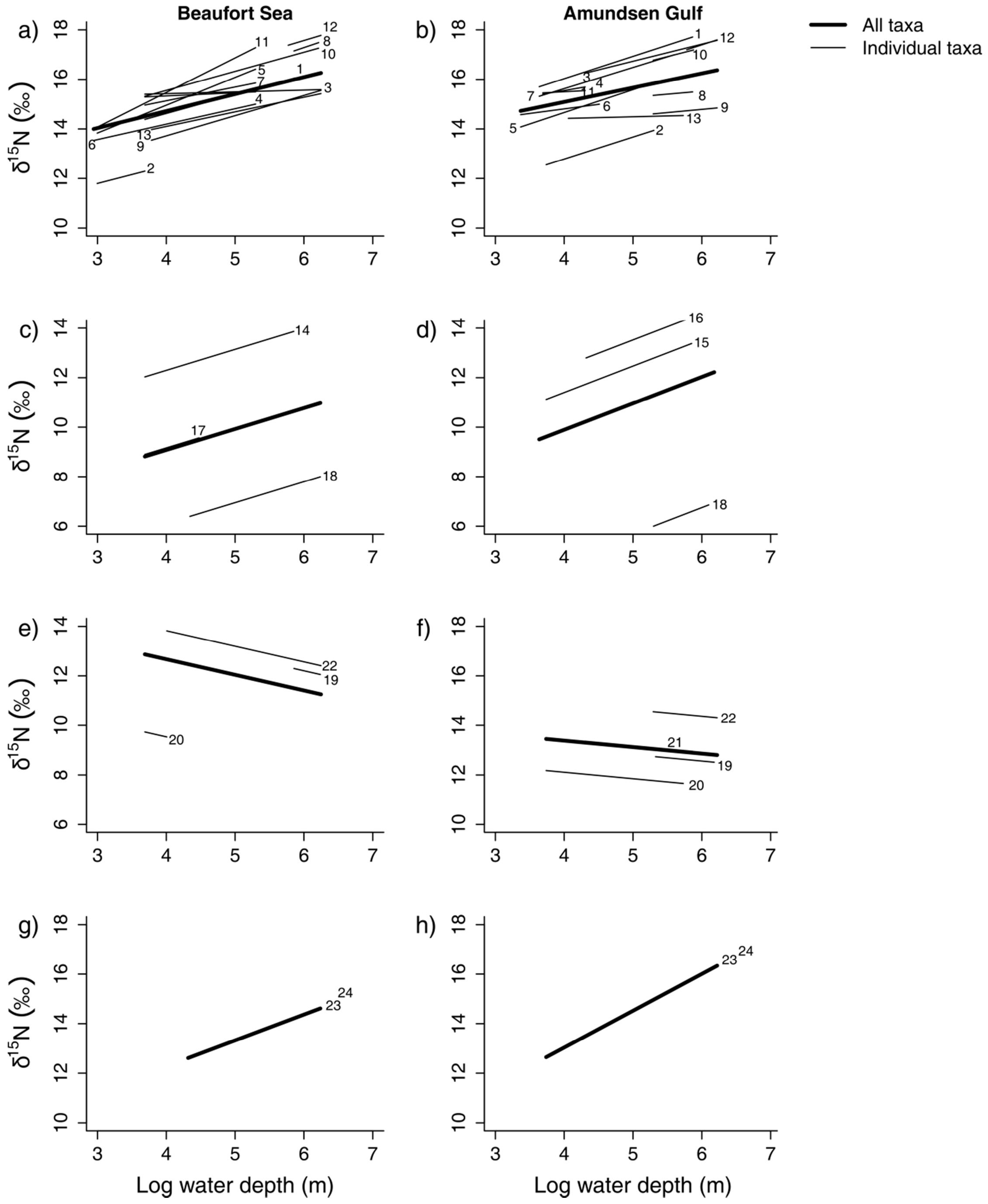


Figure. 4.2. Relationships between $\delta^{15}N$ (‰) and log water depth (m) for epifaunal carnivores (a, b), suspension/filter feeders (c, d), epifaunal deposit feeders (e, f) and infaunal deposit feeders (g, h) in the Beaufort Sea and Amundsen Gulf. Relationships estimated from linear mixed effects models for the entire functional group are shown in bold lines, whereas those for individual taxa are shown in thin lines. Separate intercepts were estimated for each taxon in all cases, but were almost identical for the two infaunal deposit feeders (g, h). Separate slopes were estimated for epifaunal carnivore taxa (a, b). Taxa are numbered according to Table 4.1 on either the leftmost or rightmost extent of the regression line, whichever provided more visual clarity.

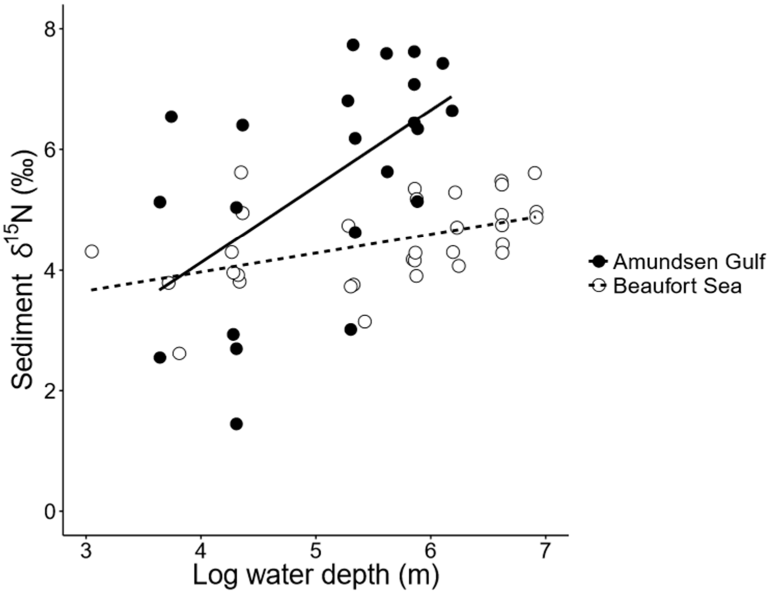


Figure. 4.3. Regressions of δ^{15}N (‰) against log water depth (m) from sediment sampled in the Beaufort Sea (white circles, dashed line; $\delta^{15}N = 2.5 + 0.35x$, $r^2 = 0.3$) and the Amundsen Gulf (black circles, solid line; $\delta^{15}N = -0.7 + 1.2x$, $r^2 = 0.2$). Sediment δ^{15}N was significantly positively related to depth in both regions, but the slope of the relationship was significantly greater in the Amundsen Gulf.

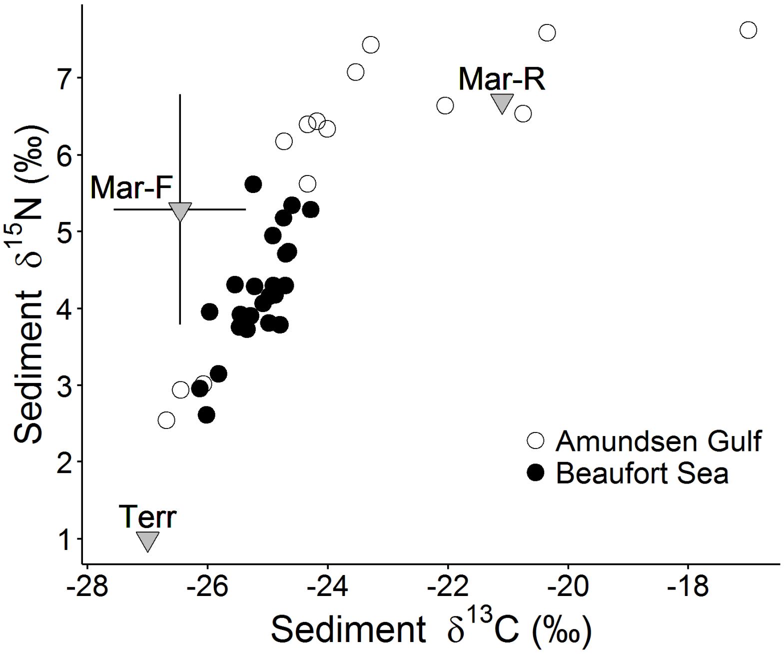


Figure. 4.4. Bulk sediment δ^{15}N and δ^{13}C from the Beaufort Sea (filled black circles) and Amundsen Gulf (open circles), relative to terrestrial (Terr), fresh marine (Mar-F), and refractory marine (Mar-R) isotopic sources (grey triangles). Terrestrial source data were estimated by Magen et al. (2010) from samples from the Colville and Mackenzie River deltas. Refractory marine source data were taken from Amundsen Gulf sediments composed of highly degraded marine POM (Morata et al. 2008). Fresh marine source data were estimated from pelagic POM collected in the Amundsen Gulf and Beaufort Shelf from the current sampling program (C. Michel, unpublished data) and from data reported by Roy et al. (2015). Error bars indicate standard deviation for the fresh marine source. Variation associated with terrestrial and refractory marine sources was not available. Sediments in the Beaufort Sea were clearly more influenced by terrestrial organic matter inputs than those in Amundsen Gulf. Bulk sediments in the Amundsen Gulf were more influenced by fresh and refractory marine organic matter (aside from a few terrestrially-dominated nearshore sites).

5 Responses of benthic functional food web structure to variable food supply in two Arctic shelf ecosystems

Introduction

Benthic food web structure and function strongly influence the broader ecological functioning of marine ecosystems (e.g., nutrient cycling, sediment resuspension; Snelgrove 1997). Benthic trophic processes can significantly affect carbon storage (e.g., Trueman et al. 2014), organic matter remineralisation and nutrient cycling (e.g., Bourgeois et al. 2017), community resilience (e.g., Blanchard et al. 2011), and the locations of important feeding grounds for migratory marine mammals (Bluhm & Gradinger 2008). Climate change is altering the organic matter pathways that fuel benthic marine food webs worldwide (Hoegh-Guldberg & Bruno 2010). In the Arctic, sea ice loss has already transformed the rates and dominant sources of primary production in some areas (McLaughlin & Carmack 2010, Kortsch et al. 2012), raising concerns over climate-change impacts on food web functioning (Wassmann & Reigstad 2011). Enhanced primary production from rising sea temperatures and longer ice-free periods on Arctic shelves is expected to be largely retained by pelagic communities, decreasing the export of labile organic matter to benthos (Wassmann & Reigstad 2011).

Monitoring the effects of shifting production regimes in Arctic marine ecosystems requires identifying aspects of benthic food web function that vary with benthic food supply. To that end, biological traits analysis is a promising approach (Bremner et al. 2003). Biological traits analysis aims to describe ecological functioning via the abundance and distribution of species' traits that confer either a response to, or an effect on, ecological processes (e.g., Bremner et al. 2003). Multivariate functional trait data can be used to calculate a variety of abundance-weighted indices that summarise the range (functional diversity) and dominance (functional composition) of functional attributes present in a community, regardless of taxonomic identities (e.g., Garnier et al. 2004, Laliberte & Legendre 2010, Villéger et al. 2008). If ecosystem functioning is determined by the traits of the most dominant species (Grime 1998), measuring community responses to environmental gradients based on the distribution of functional attributes will provide a more mechanistic understanding of community responses than will taxonomic measurements alone (Bremner et al. 2003, Mouillot et al. 2013a, Teresa & Casatti 2017). Indices of functional diversity and composition that summarize the influence of habitat filtering on community structure are thus potentially powerful ecological indicators (Beauchard et al. 2017).

Traits-based methods are well developed in plant and terrestrial ecology, where many taxa exhibit functional properties that can be measured on similar scales (e.g., Lavorel & Garnier 2002). In marine benthic communities, the variety of body forms and living habits precludes the use of easily measured quantitative traits that maintain a similar function across taxa (e.g., gape size cannot be meaningfully compared between fish, echinoderms, and polychaetes). Consequently, biological traits analysis of marine benthic communities has mostly relied on fixed, categorical traits. Fixed traits summarize important aspects of species' functional roles (e.g., Bremner et al. 2006, Frid et al. 2008, Beauchard et al. 2017); however, they do not represent the inherent, and often substantial, spatiotemporal variation in feeding strategies that are important to studies of food web function (e.g., Węsławski et al. 2010, Jumars et al. 2015). Newly proposed indices of isotopic functional diversity (Rigolet et al. 2015) have the potential to fill the gap between the "fundamental" trophic diversity summarised by fixed traits, and the "realized" trophic diversity expressed by a community. Stable isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) measured in the tissues of consumers can represent the trophic breadth of each species (Bearhop et al. 2004, Layman et al. 2007). By treating $\delta^{15}N$ and $\delta^{13}C$ as quantitative trophic traits, isotopic functional diversity can be calculated using biomass-weighted methods akin to those used for functional and taxonomic diversity (Rigolet et al. 2015). Functional food web structure can then be assessed from two sets of complementary information: (1) a set of fixed biological traits, which reflects the range of possible trophic functions a community can express, and (2) a set of $\delta^{15}N$ and $\delta^{13}C$ values measured in the quantitatively dominant organisms at each site, which integrates dietary variation expressed across spatial and/or environmental gradients.

Here, a biological traits framework with a trophic focus was applied to assess trait-environment relationships for benthic fish and epifaunal invertebrate communities in two contiguous Arctic marine ecosystems, the Canadian Beaufort Sea and Amundsen Gulf. Analyses combined diversity measures based on trophic functional traits and stable isotope ratios as complementary approaches to describe spatial patterns in functional food web structure, and used taxonomic diversity to estimate functional redundancy. In addition, the study assessed whether the spatial distribution of trophic functional traits varied with environmental gradients of sedimentary food supply and bottom oceanography. Benthic taxonomic composition in the region does not appear strongly related to indices of benthic food supply (Conlan et al. 2008, Roy et al. 2014). However, a lower sinking flux of pelagic organic matter in the Amundsen Gulf relative to the Beaufort Sea (Sallon et al. 2011, Sampei et al. 2011) has been linked to weaker benthic-pelagic coupling and the use of a wider diversity of carbon sources among benthic consumers (see Chapter 3). Thus, it was predicted that: (1) trophic functional diversity would be greater in the Amundsen Gulf where communities must rely on more diverse organic matter sources; (2) as a corollary, functional redundancy would be lower in the Amundsen Gulf; and (3) the composition of trophic functional traits in communities would be linked to gradients of organic matter delivery to the seafloor (e.g., Grebmeier et al. 1989, Link et al. 2013).

Methods

Study area

Sampling took place in the southern Canadian Beaufort Sea and Amundsen Gulf during the ice-free season from early August to mid-September of 2012 and 2013. The Beaufort continental shelf extends approximately 120 km offshore to the 200 m isobath, past which the seafloor descends quickly to several thousand meters. The Beaufort shelf is under a strong freshwater influence from the Mackenzie River, which discharges between 40 and 120 x 10^6 t of terrestrial sediment annually (Doxaran et al. 2015). The continental shelf in the Amundsen Gulf is much narrower, and maximum depths in the gulf are ~500 m. Primary production in the Amundsen Gulf generally exceeds that in the Beaufort Sea, but sinking export of pelagic production is lower, except in the vicinity of Cape Bathurst (Sallon et al. 2011, Sampei et al. 2011, Ardyna et al. 2013). Bottom oceanography in the region varies predictably with depth and water mass (reviewed in Lansard et al. 2012).

Collection of biological samples

Sampling occurred along seven transects that spanned the continental shelf and associated slope as part of the Beaufort Regional Environmental Assessment Marine Fishes Project (Fisheries and Oceans Canada; Fig. 5.1). Each transect had five to eight pre-defined sampling stations at depths ranging from 20 to 500 m. Demersal fish and epifaunal invertebrates were quantitatively sampled from the commercial stern trawler FV *Frosti* at 39 stations with a 3 m High-Rise Benthic Beam Trawl (6.3 mm mesh cod end liner; 4.27 m headrope and footrope). Trawling was targeted at a speed-over-ground of 2.0 knots (1.81 to 2.35 acceptable range) for 10 minutes bottom-contact time, and was monitored with a Scanmar CGM-05/TE40-2 trawleye sensor (Scanmar, Åsgårdstrand, Norway). Biota were sorted onboard to the lowest possible taxonomic resolution with the aid of a certified taxonomist (L. de Montety at L'Université du Québec à Rimouski). Where taxonomic doubt existed, voucher specimens were frozen or preserved in a 10% formalin solution for subsequent verification in the laboratory. Taxonomy was standardized to names currently accepted in the World Register of Marine Species (WoRMS 2016).

Collection of environmental data

Benthic community composition and food web structure in Arctic seas are influenced by large-scale environmental gradients defined by bottom oceanography, and by meso-scale environmental gradients that define sedimentary characteristics and benthic food supply (Grebmeier et al. 1989, Link et al. 2013, Roy et al. 2014, Majewski et al. 2017). Eight habitat variables were chosen to assess the influence of the environment and benthic food supply on trait distributions (Table 5.1). Benthic Chlorophyll (Chl) *a* concentrations (mg m^{-2} of dry weight), sediment organic matter content (% of total dry weight), the ratio of Chl *a* : phaeopigments (an indicator of pigment degradation), mean grain size (μm), and the proportion of sediment comprised of silt (%) were used as meso-scale descriptors of sedimentary habitat and food availability. Bottom temperature (˚C), salinity (PSU), and oxygen concentrations (ml L^{-1}) were included as large-scale environmental variables.

Marine sediments were collected at each station with a 0.25 m^2 USNEL box core. The upper 1 cm of sediment was sampled for benthic organic matter content and pigment concentrations, whereas the upper 5 cm were sampled for granulometry (Bale & Kenny 2005). Sediment samples were immediately frozen onboard at -50 ˚C. Detailed methodology for subsequent sedimentary analyses is described in Chapter 3. Oceanographic profiles were taken at each station with a Seabird SBE-25 s/n 0415 (Sea-Bird Scientific) conductivity, temperature and depth probe and oxygen sensor mounted to a rosette equipped with 12 Niskin bottles for water sampling. Detailed methods for oceanographic profiling are described elsewhere (Eert et al. 2015, Niemi et al. 2015). Bottom oceanography variables were averaged from the three bottom-most profile measurements (within 4 m above bottom).

Stable isotope analysis

Stable isotope analyses were completed following the protocols described in Stasko et al. (2017) at the University of Waterloo Environmental Isotopes Laboratory (Canada). Analytical precision for $\delta^{15}N$ and $\delta^{13}C$ did not exceed 0.3 and 0.2 ‰, respectively, based on repeated measurements of working laboratory standard material cross-calibrated to the international standards (no less than 20 % of each run). Repeatability of duplicate sample measurements was 0.3 ‰ for both $\delta^{15}N$ and $\delta^{13}C$. Raw isotopic data, summarised by species and location, is available in Stasko et al. (2017).

Compilation of taxa biomass and functional trait data

Biomass estimates for epifaunal invertebrates were calculated from wet weights measured onboard during field collection, whereas those for fish were calculated from wet weights of thawed individuals in the laboratory after field collection. Missing fish weights were estimated from species-specific regressions of total length on weight for conspecifics caught during sampling, where possible. Estimated weights were used for 4.1 % of individuals; 1.5% were removed for lack of reliable length measurements due to bodily damage or insufficient data to perform length-weight regressions. Biomass was standardized to density (g m^{-2}) using the area swept calculated for each trawl.

Prior to statistical analyses, taxa that never comprised more than 1 % of total biomass at any sampling station were removed from analyses to avoid biases created by rare taxa (Clarke & Warwick 2001). Constraining the taxa list in this way removed most infaunal species that were not sampled effectively by the beam trawl. Planktonic species likely caught during net retrieval were also removed. A total of 106 taxa representing 62 families, and 12 phyla were retained for final analyses.

Five trophically relevant functional traits, subdivided into 25 trait modalities, were used to represent trophic functionality (Table 5.2). Selected traits either directly influence how a species obtains food (e.g., feeding mechanisms), or indirectly influence food web functioning (e.g., particle transport and body size). Many of the selected trophic functional traits and trait modalities are considered fundamental to describing the ecological functioning of benthic marine communities (Bremner et al. 2006, Beauchard et al. 2017). Redundancy and correlation among traits was avoided by assessing draftsman plots of community-weighted means of trait values (see description of calculation in *Testing trait-environment linkages*). Information used to assign taxa to trophic functional trait modalities was derived from the primary literature, grey literature, taxonomic texts, and online databases (see Appendix C*)*. A fuzzy coding approach (Chevenet et al. 1994) was used to assign the affinities of taxa to each trait modality, between 0 (no affinity) and 1 (high affinity). Fuzzy coding captures trophic flexibility by allowing taxa to be assigned an affinity > 0 for multiple trait modalities when there is evidence (e.g., for species that may opportunistically act as predators or deposit feeders). Affinity scores were standardized to sum to 1 within each trait, to give the same weight to each taxon and each trophic functional trait (e.g., a taxon may score 0.25 for deposit feeder, 0.75 for predator, and 0 for all other modalities within the trait "feeding type"). In some cases, information for an individual species or genus was not available and trait affinities were based on closely related species (e.g., trait affinities for *Maldane* spp. were based on information reported for *M. calcarea* and *M. moesta*; see Appendix C). When a taxon could not be assigned an affinity due to missing information, it took on the mean trait profile for all other taxa to avoid influencing subsequent trait analyses (Statzner & Bêche 2010).

Associations between taxonomic, functional, and isotopic diversity

Taxonomic diversity at each sampling station was quantified with Shannon-Weiner's diversity index (H'). Trophic functional diversity was measured using functional dispersion (FDis), calculated as the mean distance of taxa to the community centroid in multivariate trait space, with taxa weighted by their relative biomass densities (Laliberte & Legendre 2010). FDis simultaneously quantifies trait dissimilarity and evenness, such that high values of FDis indicate an even distribution of dissimilar traits within the community. FDis was computed for each sampling station from a table containing taxa biomass densities at each station and a Gower distance matrix of the fuzzy coded trophic functional traits, using the R package FD (Laliberté et al. 2014). Biomass densities were square-root transformed prior to FDis calculations to decrease the influence of highly abundant taxa (Clarke & Warwick 2001). Functional redundancy was estimated for each station as the ratio between functional and taxonomic diversity (FDis : H'; van der Linden et al. 2012). Isotopic functional dispersion (IFDis; Rigolet et al. 2015) was calculated for each sampling station using the same method as FDis, but with the means and standard deviations of $\delta^{15}N$ and $\delta^{13}C$ for each taxon at each station acting as "traits." Because IFDis is a relative measurement (multivariate distance to biomass-weighted community centroid), there is no need to adjust $\delta^{15}N$ and $\delta^{13}C$ to account for spatial variation in isotopic baselines (e.g., Post 2002). IFDis was only calculated for sampling stations where $\delta^{15}N$ and $\delta^{13}C$ data were available for taxa that comprised at least 70 % of the total biomass of the community (range of 70.8 to 91.2 % at 24 of 39 stations; Rigolet et al. 2015).

Spearman's rank correlations between all pairwise combinations of diversity indices (FDis, IFDis, and H') were used to test whether diversity indices provided unique information, and whether communities with higher species diversity possessed a greater diversity of functional attributes. Correlations were performed using stations with available IFDis. Spatial differences between diversity indices were visualized with heat maps using Ocean Data View (Schlitzer 2017).

Testing trait-environment linkages

Trait responses to environmental gradients were assessed using the combined RLQ and fourth-corner method described by Dray et al. (2014), which is currently regarded as the most robust approach for biological traits analysis (Beauchard et al.

2017). Both RLQ and fourth-corner analysis simultaneously analyse the information contained in three tables: table **R** contains a set of environmental variables for each sampling site, table **L** contains abundances or biomass measurements for each taxon by station, and table **Q** contains information for a set of functional traits measured in each taxon (in this case, a table of fuzzy coded ordinal variables). RLQ analysis finds linear combinations of traits and environmental variables that maximize their squared cross-covariance, and provides a graphical summary of the joint structure among the three tables via multivariate ordination (Dolédec & Chessel 1994, Dolédec et al. 1996). However, RLQ does not provide a method for testing trait-environment relationships. Fourth-corner analysis tests the statistical significance of bivariate associations between each possible pair of traits and environmental variables, but does not consider covariation among traits or environmental variables (Legendre et al. 1997). The methods were used jointly to explicitly test how organism traits respond to environmental gradients, using the package “ade4” in R (Dray & Dufour 2007). Briefly, RLQ analysis was first used to test the significance of the overall link between traits and environmental variables, mediated through the distribution of taxa biomasses across stations (via correspondence analysis of the square-root transformed table **L**, principal components analysis of table **R**, and fuzzy correspondence analysis of table **Q**; see detailed methodology in Dray et al. 2014). The resultant multivariate ordination scores for environmental variables (sites) and taxa traits (species) were then used in fourth-corner analysis to evaluate the statistical significance of their relationships to the original trait and environmental variable data. To test for significant relationships between all possible pairwise combinations of traits and environmental variables, a second fourth-corner analysis was conducted using original trait and environmental data. The global significance of the RLQ analysis was evaluated using the S_{RLQ} statistic

(Dray & Legendre 2008). Bivariate fourth-corner relationships were evaluated using square correlation coefficients (Dray et al. 2014). In both cases, test statistics were generated by sequential random permutations of sites and species (Model 6; Dray & Legendre 2008). Inflated type I error rates associated with multiple testing were accounted for by using a high number of permutations (99,999) and by using the false discovery rate method to adjust *p* values (Benjamini & Hochber 1995). Environmental variables were log($x + 1$) transformed where necessary to improve normality (mean grain size and sediment Chl *a*). Two stations were removed from RLQ/fourth corner analyses because of missing (DAR_01) or outlying (DAL_02, mean grain size) environmental data.

To visualise the distribution of trophic traits among stations regardless of environment, functional composition at each station was summarized with community weighted means of trait values, wherein the traits present in a community were weighted by the relative biomass densities of the species that exhibit them (Garnier et al. 2004). Hierarchical clustering using group-average linking was performed on a Bray-Curtis dissimilarity matrix of community-weighted means of trait values to identify sampling stations that had similar functional composition, regardless of the environmental variables measured at those stations. The trait modalities "M.tubiculous" and "M.sessile" were very rare and removed prior to clustering analysis. Significant clusters were identified using approximately unbiased probability values calculated via multiscale bootstrap resampling with 99,999 iterations using the R package 'pvclust' (Suzuki & Shimodaira 2006). Non-metric multidimensional scaling of the Bray-Curtis dissimilarity matrix was then used to visualize the rank-order dissimilarities among stations in relation to traits, and to verify groupings identified by hierarchical clustering, using the R package 'vegan' '(Oksanen et al. 2017). The number of dimensions to retain in NMDS ordination was evaluated with stress, wherein stress < 0.1 indicated good interpretability with two dimensions (Clarke & Warwick 2001).

Indicator values (IndVal) were calculated from the community-weighted mean trait values to find the trophic functional traits that were most strongly associated with each station cluster (Dufrêne & Legendre 1997). An IndVal index of 100% indicates a trait that is observed at all stations of one cluster and not in any other cluster. Significant IndVal indices were determined using 9999 random permutations of stations using the 'labdsv' package in R (Roberts 2016).

All statistical and graphical procedures were performed in R version 3.3.1 (R Core Team 2016). Parametric tests were considered significant at $p \leq 0.05$. Bootstrapped tests were considered significant if the probability of obtaining the test statistic was < 0.05 based on permutated data.

Results

Associations between taxonomic, functional, and isotopic diversity

As predicted, no significant correlations existed between indices of functional, isotopic, or taxonomic diversity (Table 5.3). The relationship between FDis and H' appeared quadratic (Fig. 5.2), but a subsequent polynomial regression indicated that species richness was not significantly related to functional diversity ($F_{3,20}$=1.40, p = 0.27, r^2 = 0.17).

Values of FDis and IFDis were generally higher in the Amundsen Gulf compared to the Beaufort Sea, although relatively high FDis values also occurred along the shelf break of the Beaufort Sea (Fig 5.3a). Especially high FDis occurred along the northern margins of Amundsen Gulf, near the hamlets of Sachs Harbour and Ulukhaktok (Fig. 5.3a). IFDis values were less variable than FDis values (Fig. 5.3b). Functional redundancy was generally low across the study area, except for a few high values in the Amundsen Gulf near the hamlet of Ulukhaktok (Fig. 5.3c).

Testing trait-environment linkages

The overall joint structure between traits and environmental variables was significant ($S_{RLQ} = 2.26$, $p = 0.02$), with the first and second RLQ axes accounting for 81.21% and 9.14% of cross-covariance, respectively. Fourth-corner analysis indicated that environmental gradients on the first RLQ axis (represented by site scores) were significantly positively related to traits associated with obligatorily benthic species, including: discrete mobility, crawling, and body size ≤ 20 mm. Environmental gradients were significantly negatively related to swimming and predatory feeding type, which are generally associated with fish and large decapods (Fig. 5.4a). Overall, the variation in trait structure (species scores on the first RLQ axis) was significantly positively related to bottom oxygen concentrations and significantly negatively related to bottom temperature, indicating a depth gradient (lower temperatures and higher oxygen concentrations in shallow relative to deep habitats; Fig. 5.4b). However, there were no significant relationships between specific pairwise combinations of traits and environmental variables (data not shown).

Three significant station clusters were identified by hierarchical cluster analysis of community-weighted mean trait values and named for their distinctive characteristics (Fig. 5.5a). The first group, named the hyperbenthic communities cluster, was characterized by trophic functional traits that included predatory feeding modes, swimming, advective particle transport, and feeding on zooplankton (Table 5.4). Hyperbenthic communities were generally located on the upper continental slope (275 to 350 m depths) of the Canadian Beaufort Sea and Amundsen Gulf (Fig. 5.5b). The deposit-feeding dominated cluster included stations that were proximate to especially steep bathymetric features. This second cluster was characterized by trophic functional traits that included deposit feeding, maximum body sizes ≤ 100 mm, and bioturbation of sediment (Table 5.4). The third and most distinctive cluster (IndVal indices > 0.6) was named the Amundsen Gulf shelf break cluster for its consistent station locations within a narrow depth range corresponding to shelf break in the Amundsen Gulf (75 to 200 m depths; Fig. 5.5b). The third cluster was characterized by trophic functional traits that included discrete motility, suspension-feeding, feeding on POM, and sediment resuspension. NMDS ordination agreed well with station clustering, and with the associations between station clusters and trophic functional traits (Fig. 5.6).

Discussion

The trophic functional responses of fish and epifaunal invertebrates to indices of benthic food supply and large-scale oceanography were investigated in two contiguous, but environmentally heterogeneous Arctic shelf ecosystems. Comparisons between traits-based and isotopic functional diversity provided insight regarding spatial variation in potential and realized functional food web structure, but did not reveal the strong differences expected between the Canadian Beaufort Sea and Amundsen Gulf. The distribution of trophic functional traits did not vary significantly with proxies for benthic food supply. Instead, several lines of evidence, including the clustering of stations based on trait compositions, suggested communities near shelf break habitats in both regions were exposed to similar organic matter delivery pathways that made them unique relative to inshore communities. Here, it is argued that trophic functional composition appears to respond to local-scale, dynamic habitat filters that influence benthic food supply, but those habitat filters are not well represented by environmental variables measured at regional scales.

Traits-based and isotopic functional diversity highlighted different regional patterns in functional food web structure, suggesting that each method provided distinct, but complementary information. The most striking observation was the discrepancy between relatively high traits-based functional diversity and low isotopic functional diversity in communities located near the continental shelf break in both the Beaufort Sea and Amundsen Gulf. Frequent but episodic hydrographic events at continental shelf edges are known to affect local production regimes by facilitating exchange of nutrients and biogenic material (e.g., Bering Sea, Springer et al. 1996, Barents Sea, Carroll et al. 2008, Svalbard Bank, Wassmann et al. 2010). Nutrient delivery from shelf break exchange is particularly important for new primary production across the pan-Arctic interior shelves, and upwelling-favourable winds dominate in the Beaufort Sea (Williams & Carmack 2015). Moreover, wind forcing produces a bottom-intensified shelf break jet around 150 m depths characterised by high and temporally variable current velocities, seasonal flow reversals, and eddy formation, all of which enhance the transport and resuspension of particulate matter across the shelf break (Nikolopoulos et al. 2009, O'Brien et al. 2011, Forest et al. 2015, 2016). It is proposed here that high trophic functional trait diversity at shelf edge habitats facilitates the sharing of pulsed food inputs, which may have relatively homogeneous isotopic compositions, by providing a variety of means for sequestering the energy (e.g., capture of different particle sizes, use of fractions that have undergone varying degrees of bacterial processing).

Although polar benthic communities respond quickly and opportunistically to freshly sedimented or advected organic matter, they derive the majority of their nutrition from a sedimentary “food bank” (Mincks et al. 2005, Renaud et al. 2008). Consequently, benthic biomass and consumer stable isotope values in polar seas tend to reflect long-term indicators of benthic food supply rather than seasonal or episodic food inputs (Renaud et al. 2008, Kędra et al. 2012). If benthos rely primarily on sedimentary organic matter, spatial variation in $\delta^{15}N$ and $\delta^{13}C$ would be expected to reflect prominent organic matter sources, regardless of whether communities possess trophic traits to capture episodic food inputs. For example, isotopic functional diversity was especially low near the outflow of the Mackenzie River where terrestrial organic matter is thought to have a strong influence on trophic structure (e.g., Bell et al. 2016, Chapter 3 of this thesis). In contrast, the only “hotspot” in isotopic functional diversity was near Cape Bathurst. Cape Bathurst is known to experience frequent upwelling, regionally high rates of vertical organic matter export, and high benthic remineralisation rates (Williams & Carmack 2008, Sampei et al. 2011, Link et al. 2013) similar to those found in other Arctic hotspots with tight benthic-pelagic coupling (e.g., Chukchi Shelf, Grebmeier et al. 1989, Barents Sea marginal ice zone, Tamelander et al. 2006). Most polar benthic communities, however, likely exhibit limited temporal fluctuation in stable isotope values even if they do consume pulsed food inputs (Kędra et al. 2012).

The clustering of Amundsen Gulf shelf break communities supports the notion that episodic organic matter pathways contribute to structuring benthic functional composition. Station locations in this cluster were coincident with distinct taxonomic composition relative to other areas in the Canadian Arctic Archipelago (Roy et al. 2014), and were defined by traits that suggest suspended particulate organic matter was a dominant basal resource. Three stations in the Amundsen Gulf shelf break cluster, along the northern margins of the gulf, had the highest traits-based functional diversity observed across the entire study region. Similarly, most stations within the deposit-feeding dominated cluster occurred near the upper slopes at Cape Bathurst, Kugmallit Valley, or Mackenzie Trough. Bathymetric features at these locations, as well as at other submarine canyons that intersect Arctic shelves, are known to enhance the upwelling of nutrient-rich waters (Carmack & Kulikov 1998, Williams & Carmack 2008, 2015, Williams et al. 2008). A large proportion of the resultant new primary production sinks ungrazed to the benthos (e.g., Sampei et al. 2011), where it can promote high benthic biomass and a dominance of deposit feeders (Conlan et al. 2013, Link et al. 2013). It remains unclear why other stations near these upwelling hotspots did not have significantly similar trophic functional composition. In addition, the hyperbenthic cluster is less easily explained by known habitat features.

Contrary to study predictions, the distribution of trophic functional traits was not significantly related to sedimentary proxies for organic matter delivery to the benthos. The relationships between trait structure and bottom oceanography was driven by the dominance of hyperbenthic traits on the upper continental slope (200 to 500 m), where oxygen concentrations are lower, temperatures are higher, and where fish reach maximum abundances (Majewski et al. 2017). Recent investigations of Arctic benthos have suggested that some aspects of food web structure and function, such as benthic remineralisation, taxonomic diversity, and benthic-pelagic coupling, are influenced by organic matter input regimes (Tamelander et al. 2006, Link et al. 2013, Roy et al. 2014, Chapter 3 of this thesis). The distribution of trophic functional traits was, therefore, expected to directly respond to indices of benthic food supply (e,g., high abundance of traits promoting the rapid digestion of freshly deposited food where benthic Chl *a* indicated high phytodetrital inputs; Link et al. 2013). However, if episodic processes that influence food availability are indeed linked to regional patterns in trophic trait diversity, then sedimentary proxies for benthic food supply would not be expected to reliably reflect those processes. In the Arctic, sedimentary evidence for pulsed organic matter inputs can be short-lived (e.g., Renaud et al. 2007b). Benthic invertebrates can consume newly sedimented organic matter from phytoplankton blooms within a few weeks, leaving little evidence in the sediment to be measured as part of a regional gradient (e.g., Renaud et al. 2007b, Link et al. 2013).

In large heterogeneous areas, attempts to link specific environmental variables to trait composition may be hampered by local habitat complexity. For example, Moretti et al. (2009) found that functional traits could be used to predict the functional responses of bees to environmental change, but predictions could not be generalized between regions because local habitat configurations altered trait-environment relationships. Similarly, local conditions interrupted any linear associations between the taxonomic composition of benthic invertebrates and benthic habitat variables across the Canadian Arctic Archipelago (Roy et al. 2014). The premise of linking biological traits analysis to environmental gradients assumes a strong role of habitat filtering, wherein a set of abiotic and biotic constraints determine which traits persist in a given location (Keddy 1992). Bremner (2008) advocated the study of trait-environment linkages in benthic marine communities at regional scales, but perhaps the relevant habitat filters acting at local scales on Arctic shelves are not captured by variables measured at regional scales. Because the combined RLQ-fourth corner approach has rarely been used to study benthic marine assemblages, it is difficult to assess how long the gradients in benthic food supply and oceanographic variables must be to detect a strong response in community trait assemblages. The data provided here (Table 5.1) will help future investigations determine the gradient lengths best suited for detecting change.

The absence of significant trait-environment linkages in the current study may demonstrate an underlying advantage of using functional-based indicators to assess food web functioning, even at the regional scale. Stations exposed to similar abiotic forcings had similar trophic functional compositions, even without statistical descriptions of the specific, underlying trait-environmental relationships. Monitoring functional composition may allow detection of environment-driven changes in food web functioning even when trait-environment relationships are not well known, or when they are complicated by interacting local-scale habitat filters (Moretti et al. 2009, van der Linden et al. 2016, Teresa & Casatti 2017). Although emergent patterns in functional composition do not facilitate accurate forecasting of food web structure under future environmental scenarios, they can still be used successfully to inform the designation of marine protected areas (Frid et al. 2008), monitor impacts of stressors such as invasive species and abiotic disturbance (e.g., Mouillot et al. 2013a), and elucidate mechanisms behind climate-driven changes in food web structure (Kortsch et al. 2015). Findings from this study add to growing evidence that indicators based on the composition of functional traits themselves are more powerful tools for detecting community change than those based on functional diversity indices or taxonomy (Mouillot et al. 2013a, van der Linden et al. 2016, Weigel et al. 2016).

Low levels of functional redundancy across the region reinforce the need to monitor trophic functional composition on Arctic shelves, because low functional redundancy can place marine communities at risk of losing entire functional groups from stressors (Micheli & Halpern 2005). Low functional redundancy implies that many species exhibited unique trophic trait compositions. Because biomass-weighted functional and species diversity were not correlated, species with unique trait combinations likely had low relative biomasses. If so, food web function in benthic shelf communities will be especially sensitive to species loss because rare species with unique traits often support unique ecosystem functions (Mouillot et al. 2013b). However, such a conclusion is speculative. More evidence is needed to demonstrate whether the ratio of functional to taxonomic diversity is a reliable indicator of functional redundancy when the traits used in the calculation are qualtitative. Moreover, some of the diversity in the system may have been missed due to the use of a small 3 m benthic beam trawl in the diversity survey. It is not expected that the use of a smaller trawl net would change the conclusions regarding spatial change in relative functional diversity values because any associated biases would be applied across all sampling stations. However, every method of capture has its biases, and a larger trawling net or longer trawling times may have captured greater diversity than that measured in this study.

Indices of food web structure based on $\delta^{15}N$ and $\delta^{13}C$ have been used for over a decade, but they do not provide a framework for considering species' relative biomasses (Bearhop et al. 2004, Layman et al. 2007). Rigolet et al. (2015) argued that omitting biomass distributions from isotopic trophic indices ignored the role of energy flow, and in doing so distorted the relative importance of trophic processes. Complete datasets of both biomass estimates and stable isotope measurements are time consuming and difficult to collect. Where such datasets exist, the results of this study demonstrate that isotopic functional diversity is a useful descriptor of realized food web diversity, especially when used with traits-based metrics that provide important information regarding a community's potential range of trophic functions. The joint use of traits-based and isotopic functional diversity suggested that (1) most communities relied on a similar diversity of sedimentary organic matter sources, but (2) shelf edge communities maintained relatively high trophic trait diversity to exploit pulsed food inputs. More studies are needed to establish whether high trophic functional trait diversity is characteristic of interior Arctic shelf break communities.

Table 5.1. Mean, standard deviation (SD), maximum, and minimum values for oceanographic variables and sedimentary proxies for benthic food supply measured at 39 sites in the Canadian Beaufort Sea and Amundsen Gulf.

Environmental Variable	**Mean**	**SD**	**Max.**	**Min.**
Bottom oxygen (ml L^{-1})	7.18	1.02	10.44	5.90
Bottom salinity (PSU)	33.34	1.40	34.86	29.43
Bottom temperature (°C)	-0.44	0.76	0.75	-1.43
Sediment Chl *a* (m^{-2})	5.00	5.70	27.15	0.31
Sediment Chl *a* : phaeopigments	0.17	0.11	0.53	0.06
% Sediment organic matter	9.63	2.29	14.58	3.67
Mean grain size (μm)	9.81	6.62	32.36	0.20
% Silt	70.37	17.17	90.34	0.20

Table 5.2. Descriptions of functional traits and trait modalities selected for analysis. Codes are used to represent traits in figures.

Trait	Modality	Code	Description
Motility	sessile	M.sess	Generally does not move; may be attached.
	discretely mobile	M.dismob	Capable of free movement, but does not actively move to feed (e.g., sea anemones)
	crawler	M.crawler	Crawls freely on the sediment surface
	swimmer	M.swimmer	Not restricted to movement directly on the seafloor; water-associated.
	burrower	M.burrower	Capable of free movement, but dwells in burrows in the sediment
	tubiculous	M.tubiculous	Tube-dwelling; restricted movement
Feeding type	suspension feeder	FM.susp	Feeds on fresh or resuspended particulate organic matter (no restriction on particle size)
	deposit feeder	FM.dep	Feeds on material deposited on the sediment surface including, but not limited to, large food falls, detritus, carcasses and fecal pellets from the overlying water column, bacteria, and bacterial products
	predator	FM.pred	Feeds by actively capturing live animal prey
	scavenger	FM.scav	Feeds on dead animal material
Body size	20 mm	BS.20	Maximum recorded body size ≤ 200 mm
	100 mm	BS.100	Maximum recorded body size ≤ 100 mm
	250 mm	BS.250	Maximum recorded body size ≤ 250 mm
	500 mm	BS.500	Maximum recorded body size ≤ 500 mm
	750 mm	BS.750	Maximum recorded body size ≤ 750 mm
	1000 mm	BS.1200	Maximum recorded body size ≤ 1200 mm
Particle transport	resuspension	PT.resusp	Actions of the organism resuspend particulate matter
	sediment mixing	PT.mix	Actions of the organism mix the sediment; no restriction on depth of mixing
	advective	PT.adv	Actions of the organism advect particlate matter from relatively long distances, either horizontally or vertically (e.g., fish migrations)
Food source	POM	FS.pom	Feeds on particulate organic matter (POM)
	detritus	FS.det	Feeds on detritus at the sediment surface
	microfauna	FS.mic	Feeds on microfauna (e.g., diatoms, bacteria, and other single-celled organisms)
	macrofauna	FS.mac	Feeds on macrofauna
	phytoplankton	FS.phy	Feeds on phytoplankton that has settled to the seafloor
	zooplankton	FS.zoo	Feeds on zooplankton

Table 5.3. Results of Spearman's rank correlation analyses between pairwise combinations of functional diversity (FDis), isotopic functional diversity (IFDis) and taxonomic diversity (H'). The relationship between FDis and H' appeared quadratic and was tested with polynomial regression instead.

Test	**Method**	r_s	R^2	p
FDis vs. IFDis	Spearman rank correlation	0.16		0.45
FDis vs. H'	Polynomial regression		0.17	0.27
IFDis vs. H'	Spearman rank correlation	0.09		0.66

Table 5.4. Significant indicator traits associated with each station cluster identified by hierarchical cluster analysis of community-weighted mean trait values. An IndVal index of 100% indicates a trait that is observed at all stations of one cluster and not in any other cluster. The functional diversity (FDis), isotopic functional diversity (IFDis), taxonomic diversity (H'), taxonomic distinctness (Δ*), and functional redundancy values are also presented for each cluster as means ± standard deviation. Station depth is presented as a mean and range.

Station cluster	**N sites**	**Significant indicator traits**	**IndVal (%)**	***p***	**Station depth (m)**	**FDis**	**IFDis**	**H'**	**Δ***	**Functional redundancy**
Hyperbenthic communities	4	FS.zoo	43.33	0.001	249 (350, 20)	0.14 ± 0.01	0.26 ± 0.06	1.31 ± 0.22	76.32 ± 18.25	0.11 ± 0.03
		M.swimmer	37.51	0.004						
		PT.adv	37.47	0.008						
		FT.pred	35.76	0.001						
Deposit-feeding dominated	5	FT.dep	34.86	0.026	228 (350, 40)	0.19 ± 0.01	0.27 ± 0.04	1.94 ± 0.39	87.35 ± 2.17	0.10 ± 0.01
		BS.100	32.51	0.045						
		PT.mix	31.43	0.043						
Amundsen Gulf shelf break	7	M.dismob	66.14	0.001	129 (200, 75)	0.20 ± 0.01	0.26 ± 0.04 [a]	1.15 ± 0.39	94.68 ± 3.84	0.19 ± 0.05
		FS.pom	64.71	0.001						
		FT.susp	56.34	0.001						
		PT.resusp	39.70	0.006						

[a] Based on 4 of 7 sites with sufficient stable isotope data to compute IFDis

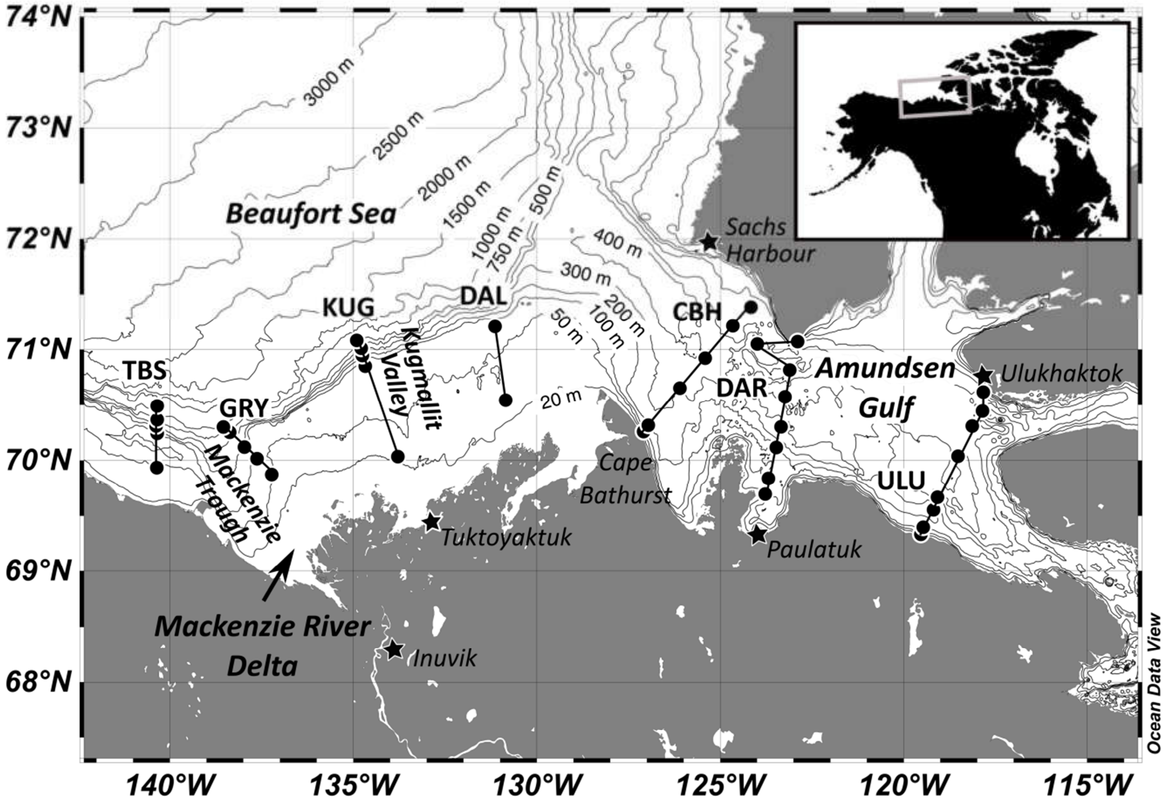


Figure 5.1. Map of the Canadian Beaufort Sea and Amundsen Gulf region, showing the locations of sampling stations. Transects TBS, GRY, KUG, and DAL were sampled in 2012, whereas transects CBH, DAR, and ULU were sampled in 2013.

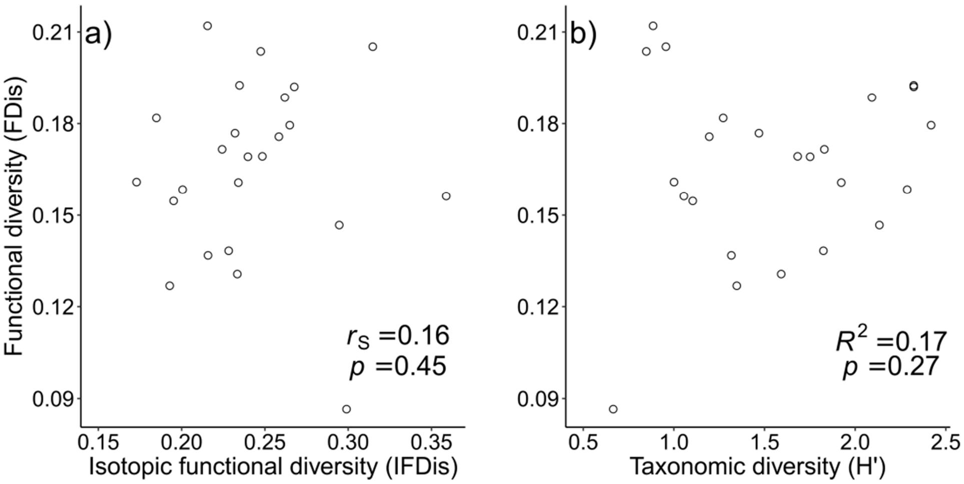


Figure 5.2. Traits-based functional diversity versus a) isotopic functional diversity, with Spearman's rho (r_S) and *p* value from Spearman's rank correlation analyses, and b) taxonomic diversity, with R^2 and *p* value from polynomial regression. There were no significant relationships between any pairwise combinations of diversity indices.

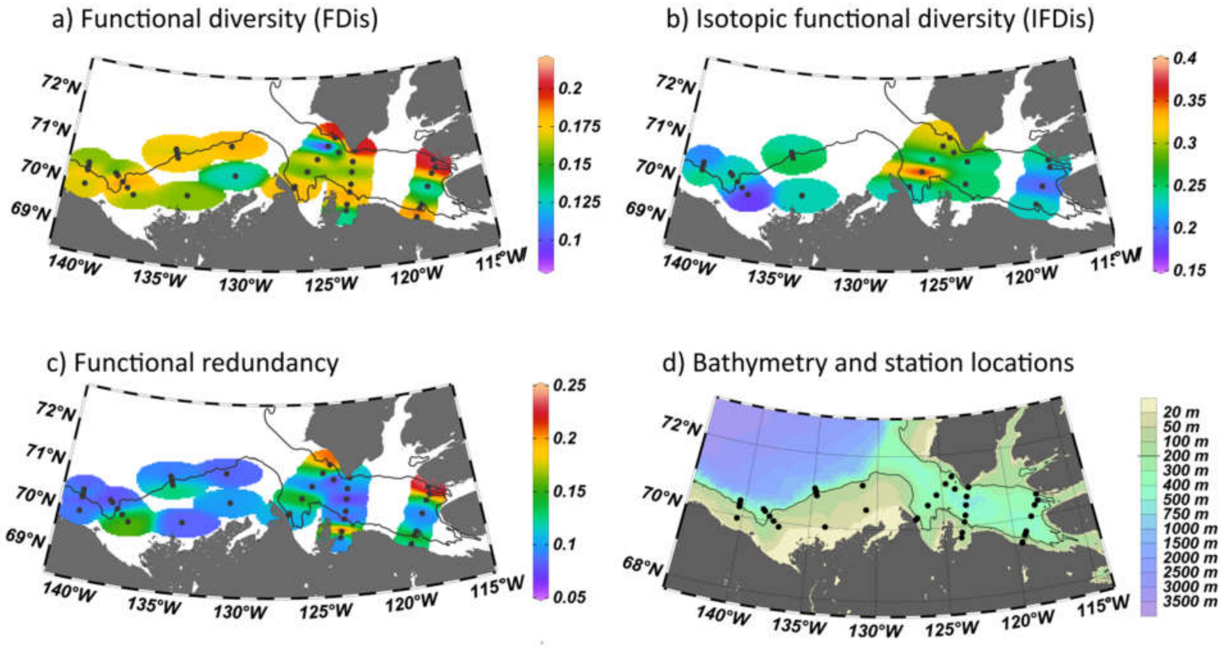


Figure 5.3. Maps showing regional values for a) functional diversity (FDis), b) isotopic functional diversity (IFDis), c) functional redundancy, and d) the locations of sampling stations in relation to bathymetry, with the shelf break at 200 m outlined. Data for IFDis are only displayed for sampling stations where stable isotope data were available for taxa that comprised ≥ 70% of the total biomass of the community. FDis highlights a relatively high diversity of traits within communities located near shelf break, whereas IFDis remains relatively low across both the Beaufort Sea and Amundsen Gulf aside from a community off Cape Bathurst (consult Fig. 5.1 for place names). Functional redundancy is mostly low across the region.

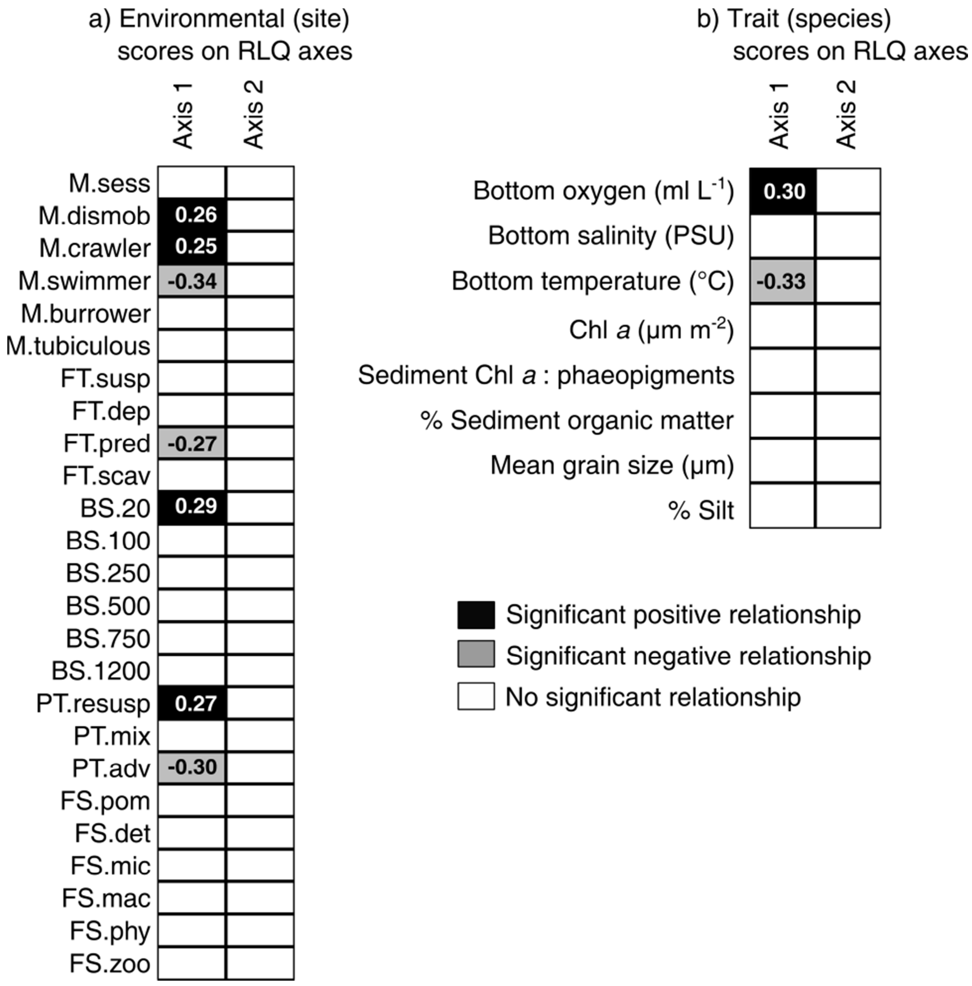


Figure 5.4. Combination of the RLQ and fourth-corner results (Dray et al. 2014), displaying relationships between a) the overall structure of environmental gradients (represented by site scores on RLQ axes) and specific trophic functional traits, and b) between the overall structure of traits (represented by species scores on RLQ axes) and specific environmental variables. Numbers in boxes represent square correlation coefficients measuring linkages between variables in the fourth-corner analysis. Codes for traits are defined in Table 5.1. The overall structure of traits was significantly related to bottom oxygen and temperature, reflecting a separation of traits associated with obligate benthic species in shallower habitats from traits associated with hyperbenthic species in deeper habitats, where there are higher temperatures and lower oxygen concentrations.

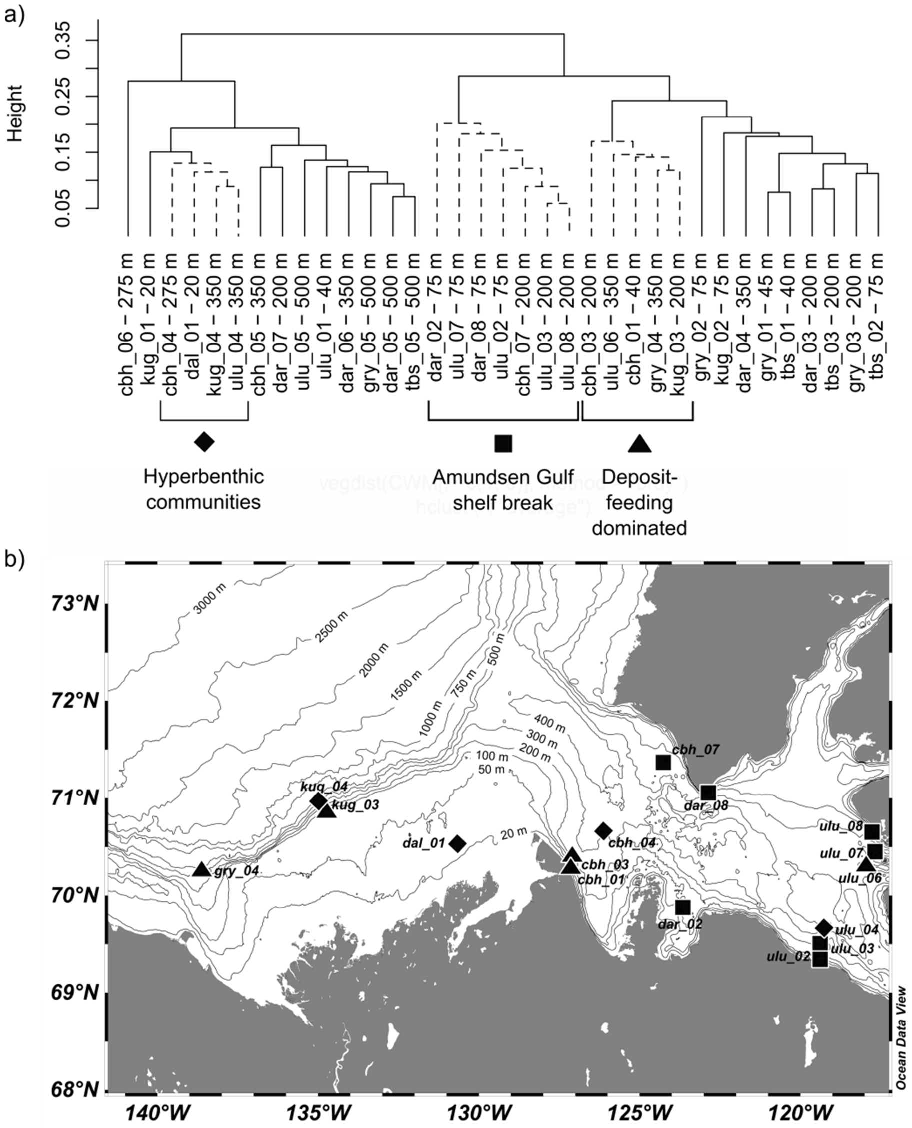


Figure 5.5. a) Dendrogram of station clusters resulting from a hierarchical clustering of community-weighted mean trait values, and b) the locations of clustered stations. Amundsen Gulf shelf break communities were located in a narrow depth range (72 to 200m) on the hydrographically dynamic continental shelf edge surrounding the Amundsen Gulf, and deposit-feeding dominated stations were mostly located near areas with topographically-enhanced upwelling. Habitat features that linked stations in the hyperbenthic communities cluster were less apparent.

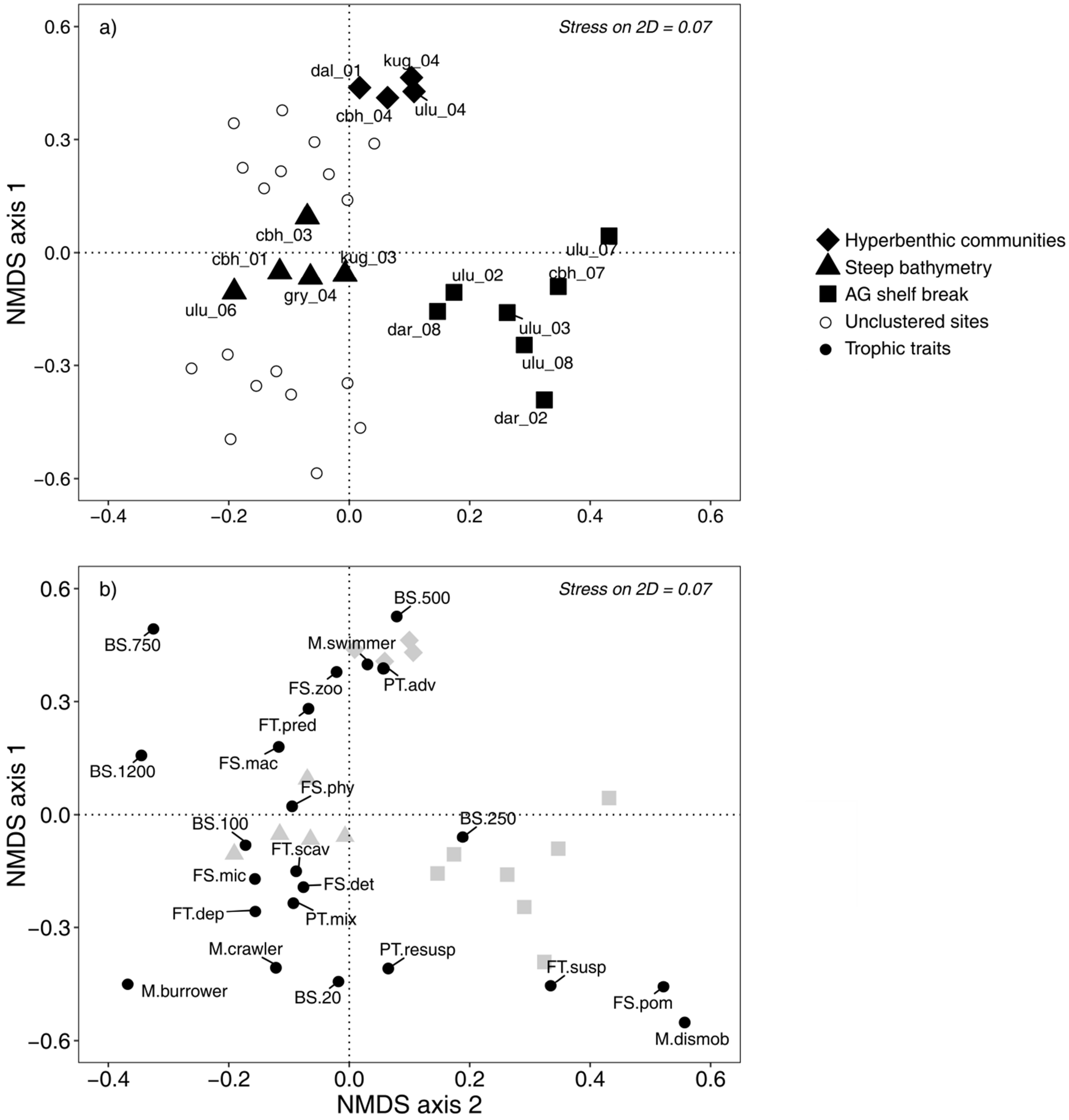


Figure 5.6. Non-metric multidimensional scaling (NMDS) ordination of a) stations and b) traits. Stations belonging to significant clusters identified by hierarchical cluster analysis of community-weighted mean trait values are shown as black symbols in (a), and as grey symbols in (b) to illustrate cluster associations with trait values. Codes for trophic functional traits are defined in Table 5.1. The distribution of stations relative to traits in NMDS ordination aligned closely with the results of hierarchical clustering and IndVal analyses that assigned indicator traits to each cluster.

6 General Conclusion

Synopsis

The research presented in this thesis filled substantial knowledge gaps regarding the overall trophic structure of demersal fish and invertebrates in the Canadian Beaufort Sea and Amundsen Gulf by quantifying isotopic and biomass-weighted trophic structure, and by examining how food web structure responded to gradients of benthic food supply and oceanography (key findings are summarised graphically in Figs. 6.1 and 6.2).

Results of the second thesis chapter demonstrated that fish communities in the Canadian Beaufort Sea were strongly size-structured at all habitat depths down to 1000 m, such that the largest individuals occupied the highest trophic levels. Biomass production for small-bodied fishes declined with depth, resulting in significantly shallower (less negative) relationships between biomass and body size with increasing habitat depth. In the two deeper habitats, $\delta^{13}C$ indicated low dietary differentiation between benthic and benthopelagic fishes. Large size classes in deeper habitats were dominated by Greenland Halibut (*Reinhardtius hippoglossoides* (Walbaum)), known to undertake vertical migrations to obtain pelagic prey (e.g., Jørgensen 1997). Overall, results suggested that decreasing benthic resources with depth limited the production of small size classes of fish in deeper habitats, whereas the biomass of larger size classes was maintained by their ability to obtain pelagic subsidies. Benthic-pelagic coupling via active biological transport was determined to be important for fish production at depth in the Canadian Beaufort Sea.

In Chapter 3, spatial patterns of organic matter input and water mass structure were shown to influence trophic connectivity between benthic and pelagic functional groups down to 1000 m downslope. First, benthic-pelagic trophic coupling weakened alongshore from west to east regardless of primary production at the surface, and coincident with the use of a more diverse range of dietary carbon sources among benthic functional groups. Benthic-pelagic coupling was weakest in the Amundsen Gulf where strong pelagic grazing has been previously observed to limit POM sinking flux, intermediate in the central Canadian Beaufort Sea where benthic communities are thought to be at least partially sustained by terrestrial organic matter, and strongest west of the Mackenzie River where a greater influence of Pacific-origin water likely enhances particulate organic matter (POM) delivery to the benthos. Second, the weakest benthic-pelagic coupling consistently occurred on the upper slope across the entire study region. Here, biological activity at the transition between Pacific and Atlantic water masses may limit POM sinking flux to the benthos. In turn, benthos likely rely to a larger degree on organic matter that is resuspended by dynamic shelf break hydrography. Benthic-pelagic coupling was consistently strongest on the nearshore shelf across all study regions, where POM has a short distance to sink from the chlorophyll maximum depth.

Findings in Chapter 4 revealed that the $\delta^{15}N$ of suspension/filter feeders, infaunal deposit feeders and bulk sediment increased as a function of water depth, which was attributed to preferential uptake of ^{14}N from sinking POM by microbes. Significant $\delta^{15}N$–depth relationships are commonly observed for benthic primary consumers, but not for mobile predators, presumably because they can access pelagic prey that do not rely on ^{15}N-enriched POM at the seafloor (e.g., Mintenbeck et al. 2007, Bergmann et al. 2009, Roy et al. 2015). The work in this chapter demonstrated for the first time that mobile epifaunal predators can exhibit significant δ^{15}N–depth relationships when they are considered independent of their benthopelagic and infaunal counterparts. The slope of δ^{15}N–depth relationships for suspension/filter feeders, infaunal deposit feeders and bulk sediment were steeper in the Amundsen Gulf than in the Beaufort Sea. Sedimentary analyses indicated that regional differences in the relationships could be attributed to differences in the prevalent POM sources available to the benthos. In the Beaufort Sea, the dominance of terrestrial POM discharged from the Mackenzie River was thought to dampen change in δ^{15}N of POM with depth. In contrast, high primary production in the Amundsen Gulf likely promoted intensified biological transformation of autochthonous POM in the pelagic zone, resulting in lower downward POM flux and a faster rate of change in consumer δ^{15}N with depth.

The influence of trophic functional trait composition on regional differences in food web structure between the Canadian Beaufort Sea and Amundsen Gulf was explored in Chapter 5. Biomass-weighted isotopic functional diversity was generally higher in the Amundsen Gulf compared to the Beaufort Sea. However, the differences were more subtle than expected given the differences in benthic food web structure and benthic-pelagic coupling identified in Chapters 3 and 4. Biological communities across both regions appeared to rely on a similar diversity of sedimentary organic matter sources, regardless of the origin of organic matter. Wider community niche breadths along the δ^{13}C axis in the Amundsen Gulf (observed in Chapter 3) may have been driven by species with lower relative biomass having relatively distinct δ^{13}C values, suggesting a unique trophic role for rarer species. High isotopic functional diversity was only observed in biological communities near the Cape Bathurst upwelling hotspot, and those near coastal human settlements. In contrast, analyses of traits-based functional diversity revealed that communities at the shelf edge maintained relatively higher trophic trait diversity than other communities, presumably to allow the exploitation of pulsed food inputs associated with dynamic shelf break hydrography. The influence of shelf break on benthic functional food web structure was not obvious from isotopic functional diversity data in Chapter 5, but was consistent with the unique trophic structure observed for upper slope communities in Chapter 3. Cluster analyses supported the notion that benthic trophic trait composition was influenced by episodic organic matter inputs at the shelf edge. However, there were no significant pairwise relationships between trophic traits and indicators of benthic food supply at the regional scale. The findings of this chapter add to the growing evidence that local habitat complexity can hamper the use of trait-environment relationships to describe and/or predict community functional responses at a regional scale. Finally, functional redundancy was low across most of the region, suggesting benthic food web function will be sensitive to species loss.

What did we learn?

Emergent properties

When the research in this thesis is considered as a whole, several principal properties emerge as characteristic of demersal food webs in the Canadian Beaufort Sea and Amundsen Gulf:

The Canadian Beaufort Sea and Amundsen Gulf should be considered separate but interconnected ecosystems. Despite mounting evidence for physical differences in sediment composition (e.g., Magen et al. 2010), POM sinking flux (Sallon et al. 2011, Sampei et al. 2011), and primary production (Carmack et al. 2004, Morata et al. 2008, Ardyna et al. 2013), few differences in taxonomic benthic community structure have been identified between the two contiguous regions (Conlan et al. 2008, Roy et al. 2014). However, the work in this thesis confirms that habitat differences are linked to differences in benthic-pelagic coupling (Chapter 3), the diversity of dietary carbon sources used by benthic functional groups (Chapter 3), the rate of change in $\delta^{15}N$ with water depth (Chapter 4), and to a lesser degree biomass-weighted isotopic functional diversity (Chapter 5). Food webs in the Canadian Beaufort Sea and Amundsen Gulf are likely to respond differently to environmental changes because they are sustained by significantly different organic matter pathways.

Organic matter pathways are key properties that define and determine trophic structure in the study systems. Trophic structure was found to be influenced by the types of organic matter available to benthos and by their modes of delivery, including: active benthic-pelagic coupling via vertical migrations (Chapter 2, Giraldo et al. 2016 in Appendix A), passive benthic-pelagic coupling controlled by the sinking flux of pelagic POM (Chapters 2, 3 and 4), horizontal flux of terrestrial discharge from the Mackenzie River (Chapter 3 and 4), and resuspension/advection of sedimentary organic matter facilitated by dynamic hydrography near the shelf break (Chapter 5). This emergent property confirms that benthic food web structure will be impacted by predicted shifts in production regimes under future climate scenarios (Wassmann & Reigstad 2011). However, those impacts may not all be negative and will depend on the specific organic matter source or pathway being affected.

Local habitat complexity interrupts linear associations between environmental gradients and trophic structure at the regional scale. Although trophic structure was influenced by organic matter input regimes (Chapters 3, 4, and 5) and hydrography (Chapters 4 and 5), neither of these gradients had linear correlations with specific metrics of isotopic trophic structure (Chapter 3) or with specific trophic traits (Chapter 5). Consequently, trophic structure will not be easily predicted from any single environmental variable, and perhaps not even from a combination of local sedimentary or oceanographic measurements from a single temporal sampling event. Instead, trophic structure may be more associated with rate processes such as annual POM export past the euphotic zone, or the average frequency of upwelling/downwelling events. This may be especially true for shelf break communities (Chapter 5), but the validity of such a hypothesis has yet to be tested.

Considerations for management

Canada has become a global leader in applying an ecosystem-based management approach to fisheries, although there is much room for improvement (Pitcher et al. 2009). Ecosystem-based management begins with conservation of the ecosystem on which species rely, rather than focusing on conservation of a specific target species (e.g., Pikitch et al. 2004). The Beaufort Sea is one of five priority management areas in Canada's Oceans Action Plan, but the lack of knowledge regarding food web structure and function restricts effective ecosystem-based management in the face of climate change and potential industrial development (e.g., hydrocarbon extraction, shipping, fisheries). The research outlined in this thesis has contributed knowledge that is directly applicable to management planning in the

Beaufort Sea and Amundsen Gulf, outlined below. Although knowledge of food web structure and function is still inadequate to precisely predict the impacts of climate change, some conjectures can be provided with respect to the implications of thesis findings for management.

First, Greenland Halibut was identified as an important benthic-pelagic ecosystem integrator (Chapter 2), and should be a candidate species for monitoring. Vertical migrations made by Greenland Halibut and other benthopelagic species likely support total production in benthic communities by transporting pelagic nutrients to benthic habitats through respiration, defecation, and carcasses (e.g., Trueman et al. 2014). The delivery of pelagic subsidies to benthic habitats may mitigate some of the negative effects of decreased POM sinking flux predicted to occur with sea ice loss (Wassmann & Reigstad 2011).

Second, size spectra relationships are a useful tool for detecting shifts in community structure associated with disturbances such as fishing (e.g., Jennings & Blanchard 2004). The Beaufort Sea ecosystem has never been exploited by commercial fisheries, so the size spectra relationships quantified in Chapter 2 could act as a baseline for monitoring future changes in community structure associated with development or climate change.

Third, the discharge of suspended particulate matter from the Mackenzie River has increased by 50% since 2003 (Doxaran et al. 2015). Because terrestrial organic carbon appears to be an important regulator of food web structure on the Mackenzie Shelf (Chapters 3 and 4), benthic food web structure in the Canadian Beaufort Sea may be in a state of change. In contrast, benthic communities in the central Amundsen Gulf may be less sensitive to climate-driven changes in organic matter inputs because they currently receive little autochthonous or terrestrial organic matter. However, care needs to be taken when making inter-regional food web comparisons based on stable isotopes, because depth-related changes in consumer $\delta^{15}N$ occur at different rates in the Amundsen Gulf and Beaufort Sea independent of diet (Chapter 4).

Finally, analyses suggested that functional redundancy was low across most of the Canadian Beaufort Sea and Amundsen Gulf, and that species with unique trait composition had lower biomasses (Chapter 5). Consequently, food web function in benthic shelf communities will be especially sensitive to species loss in the face of decreasing POM sinking flux because rare species with unique traits often support unique ecosystem functions (Mouillot et al. 2013b). Monitoring of functional trait composition, in addition to taxonomic composition, will provide a better indicator of functional food web responses to changing environmental conditions.

Future directions

As this thesis represents some of the first empirical research on offshore food webs in the region, it revealed more questions than answers. However, findings from this research can help steer future investigations toward developing a mechanistic food web model for the Canadian Beaufort Sea and Amundsen Gulf. Some of the most fruitful avenues for future study include the following questions:

What are the direct feeding linkages between species?

Species-specific studies are still needed. This thesis primarily analysed food webs at aggregated structural levels, such as functional groups or communities. Although aggregate-level analyses allowed the identification of important physical-biological forcings acting on food web structure and function, feeding linkages and behaviours among specific species have yet to be elucidated. Building a database of specific trophic linkages between species and/or aggregated food web components will be critical for ecosystem-based management plans. An understanding of energy flow and feeding dynamics will be necessary to conserve species of interest. Because species with the highest biomasses are likely to have the greatest influence on ecosystem function (Grime 1998), dominant species with poorly understood diets, such as eelpouts, brittle stars, and some decapods, may be a good place to start.

How does functional food web structure relate to indicators of ecosystem function?

Functional diversity and composition were determined for benthic communities on the shelf and upper slope (Chapter 5), but they were not linked to actual measurements of ecosystem function. A next important step is to understand how, or if, functional composition is linked to measurements of ecosystem function. Higher diversity does not always lead to higher ecosystem functioning (Mouillot et al. 2013a). For example, trophic functional diversity is especially low near the Mackenzie River outflow (Chapter 4), but other studies have measured regionally high benthic remineralisation rates there (Darnis et al. 2012). In benthic environments, benthic carbon remineralization is often used as an indicator of biological functioning because it measures the rate of detrital recycling and nutrient release into the water column (e.g., Renaud et al. 2007b, Darnis et al. 2012, Link et al. 2013). Such a measurement would improve our understanding of how food web structure influences actual ecosystem function, and would be especially powerful if combined with biomass-weighted isotopic food webs.

Are shelf break food webs unique?

Thesis findings demonstrated that benthic communities near the shelf break are more trophically distinct from the pelagos than communities at other depths (Chapter 3), and that shelf break communities exhibit a relatively more diverse set of trophic traits (Chapter 5). It is plausible that shelf break communities have distinct functional and food web attributes due to the specific water mass structure of the area. For example, biological activity at the transition between Pacific and Atlantic water masses may restrict POM sinking flux, forcing benthic food webs to be more reliant on the frequent resuspension events that occur along the Mackenzie Shelf edge. Continental shelf edges in many regions are typified by dynamic hydrography and unique circulation (e.g., Bering Sea, Springer et al. 1996, Barents Sea, Carroll et al. 2008, Svalbard Bank, Wassmann et al. 2010), which may select for communities that can exploit pulsed resuspension events. It remains uncertain whether distinct trophic functional composition and food web structure are characteristic of shelf break communities at a pan-Arctic scale, or whether these properties are unique to the Beaufort Sea and Amundsen Gulf.

How does benthic trophic ecology differ in winter?

Very little is known about benthic food web structure and function during winter in the Canadian Beaufort Sea and Amundsen Gulf. Winter-time studies in the Bering Sea and in a Norwegian fjord system suggested little seasonal change in benthic food web structure based on low seasonal variation is stable isotope values (Lovvorn et al. 2005, Kędra et al. 2012). However, vertically migrating fish and zooplankton (e.g., Geoffroy et al. 2011, Connelly et al. 2014), as well as intensified winter resuspension events (e.g., Mundy et al. 2009, Forest et al. 2015) may have important and unquantified consequences for winter food web structure in the Beaufort region.

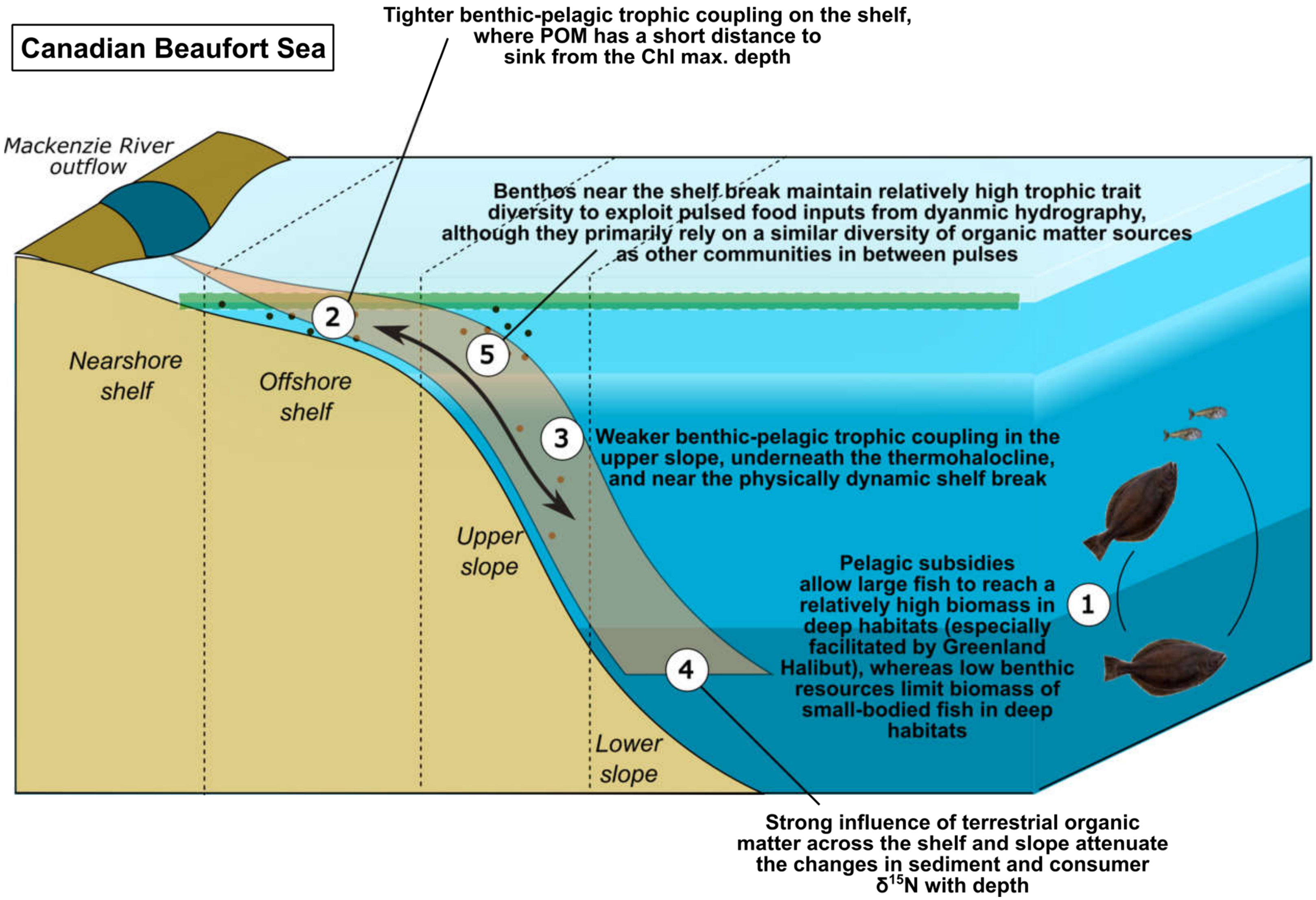
What is the general, over-arching food web model for the Canadian Beaufort Sea and Amundsen Gulf?

Finally, an overall food web model should be a key and over-arching objective for future research in the region. General descriptions of food web structure and/or quantitative mass-balanced models have been published for the Barents Sea (Blanchard et al. 2002, Wassmann et al. 2006), Chukchi Sea (Grebmeier et al. 2006, Whitehouse et al. 2014), the deep Arctic Basin (Iken et al. 2005), Lancaster Sound (Hobson & Welch 1992), and the North Water Polynya of northern Baffin Bay (Hobson et al. 2002). Combining knowledge gained from the work in this thesis, species-specific studies, functional traits databases, relative biomasses of predators and prey, and a description of the major spatial changes in food web structure may help piece together a general food web model structure in the Beaufort Sea and Amundsen Gulf. Food web models can be important for predicting community-level responses to disturbance. For example, simulations from a general metadata model for Arctic ice-associated food webs predicted a total species loss of ~ 50 % as a consequence of cascade effects after removing only 8 % of species (Carscallen & Romanuk 2012). A similar model developed specifically for the Beaufort Sea and Amundsen Gulf ecosystems would be a valuable tool for prioritising species or groups of species for conservation and management planning.

Concluding remarks

The work in this thesis represents a significant contribution to understanding demersal fish and invertebrate food web structure in the Canadian Beaufort Sea and

Amundsen Gulf. Although substantial knowledge gaps remain, the information gained through this research can direct future efforts toward developing a mechanistic food web model for benthic habitats and, ultimately, predicting the consequences of climate-driven change to regional ecosystem function. In the past decade, the formation of a pan-Arctic understanding of ecosystem structure and function has become a leading priority for investigators working in the Arctic, especially in light of fast-paced environmental change and associated implications for international governance (Wassmann et al. 2011). The research here contributes to that broader understanding by providing information on the ecology of two highly understudied interior Arctic shelf ecosystem.



Tighter benthic-pelagic trophic coupling on the shelf, where POM has a short distance to sink from the Chl max. depth

Benthos near the shelf break maintain relatively high trophic trait diversity to exploit pulsed food inputs from dyanmic hydrography, although they primarily rely on a similar diversity of organic matter sources as other communities in between pulses

Weaker benthic-pelagic trophic coupling in the upper slope, underneath the thermohalocline, and near the physically dynamic shelf break

Pelagic subsidies allow large fish to reach a relatively high biomass in deep habitats (especially facilitated by Greenland Halibut), whereas low benthic resources limit biomass of small-bodied fish in deep habitats

Strong influence of terrestrial organic matter across the shelf and slope attenuate the changes in sediment and consumer δ^{15}N with depth

Figure 6.1. Schematic diagram of key thesis findings regarding food web structure in the Canadian Beaufort Sea, numbered in order of their presentation in the thesis. Key findings 2, 3, and 5 are also applicable to food web structure in the Amundsen Gulf (see Fig. 6.2).

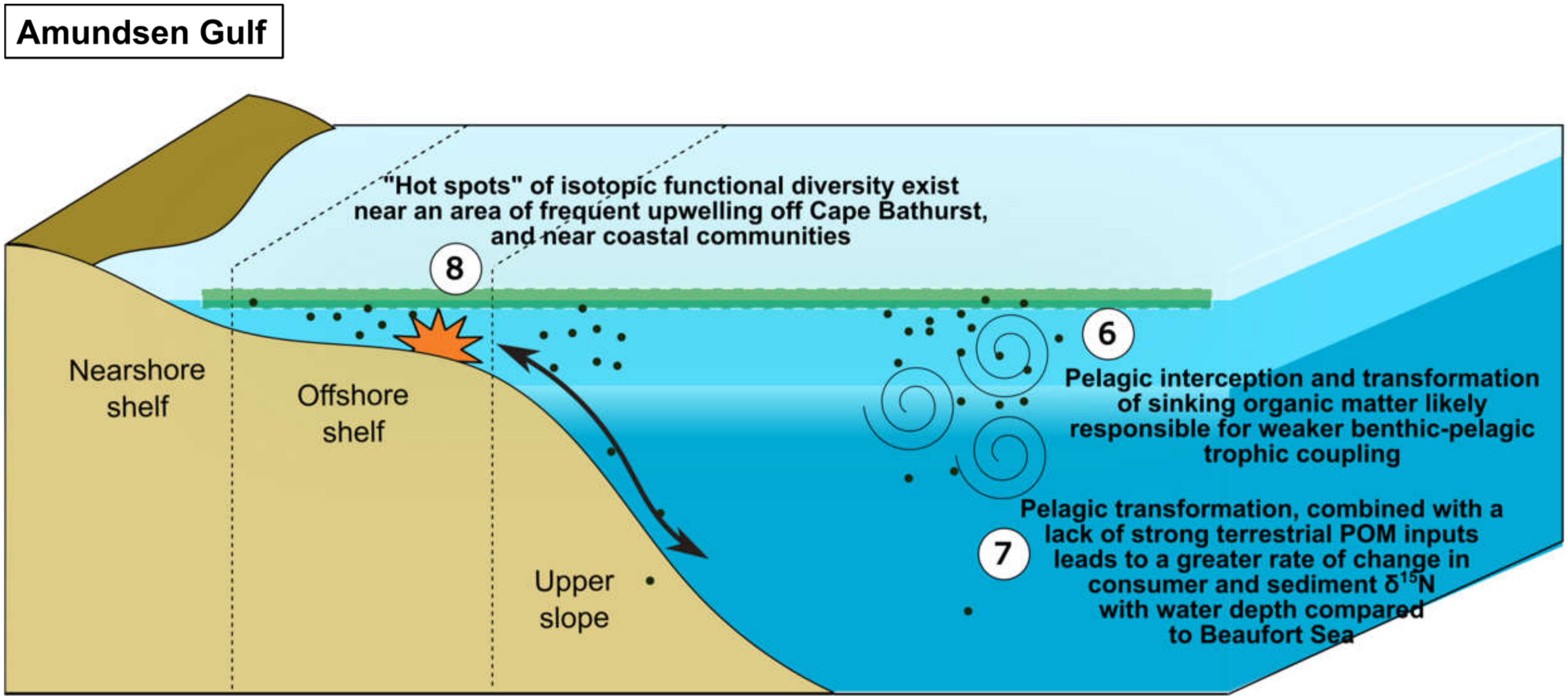


Figure 6.2. Schematic diagram of key thesis findings regarding food web structure in the Amundsen Gulf, numbered in order of their presentation in the thesis. Key findings 2, 3, and 5 from Fig. 6.1 are also applicable to food web structure in the Amundsen Gulf.

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Appendix A: Additional publications

Two publications resulted from data produced for the thesis in addition to the chapters presented: 1) a collaborative paper led by a colleague, and 2) a government data report that synthesised stable isotope methodology and raw data. Their abstracts and a statement of my contributions are presented here.

Girlado C, Stasko A, Choy ES, Rosenburg B, Majewski A, Power M, Swanson H, Loseto L, Reist JD (2016) Trophic variability of Arctic fishes in the Canadian Beaufort Sea: a fatty acids and stable isotope approach. Polar Biol 39:1267-1282

Trophic ecology of most demersal Arctic fishes remains one of the major knowledge gaps for understanding food web dynamics and connectivity among ecosystems. In this study, fatty acids (FA) and stable isotopes (SI) were used to study the feeding ecology of seven species (n = 106) of the most abundant benthic fishes (eelpouts, sculpins and agonids) in the Canadian Beaufort Sea from shallow (20–75 m), slope (200–350 m) and deep (500–1000 m) habitats. Both FA and SI results revealed among- and within-species variability in diet composition. Correspondence analysis of FA signatures identified high within-species variability in diet, resulting in high overlap among species. Calanus-derived FA were present in all species (Calanus markers up to 13 % of total FA) and were particularly important in Ribbed Sculpin, Adolf's and Longear Eelpout collected in deep habitats, suggesting a strong contribution of pelagic-derived FA to benthic fish communities. Incorporation of this signal in the benthos may result from either direct consumption of deep over- wintering copepods (i.e., off-bottom feeding) or through detrital accumulation in benthic invertebrate prey. Mean SI

values differed among species and indicated that a large range of trophic positions (δ^{15}N varied from 14.09 to 17.71 % for Canadian Eelpout and Adolf's Eelpout, respectively) and carbon dietary sources are preyed upon (δ^{13}C range from -21.13 to -23.85 % for Longear Eelpout and Ribbed Sculpin, respectively). SI analyses suggested that most species examined were low- to mid- trophic generalist benthic carnivores, with the exception of Ribbed Sculpin, which was a low-trophic pelagic predator.

Statement of contribution: I provided the data and statistical analyses for the stable isotope portions of the paper. I contributed some writing for methodology and results, and contributed significantly to editing the manuscript.

Stasko A, Swanson H, Atchison S, MacPhee S, Majewski A, de Montety L, Archambault P, Walkusz W, Reist J, Power M (2017) Stable isotope data (δ^{15}N, δ^{13}C) for marine fish and invertebrates from the Beaufort Sea Marine Fishes Project, August-September 2012 and 2013. Can Data Rep Fish Aquat Sci 1270:vi + 63 p

This report presents stable isotope data (δ15N, δ13C and C:N ratios) for marine fishes, benthic invertebrates, zooplankton and sediments collected as part of the Beaufort Regional Environmental Assessment Marine Fishes Project. Sampling was conducted along 12 transects in the Canadian Beaufort Sea and Amundsen Gulf during the open water seasons of 2012 and 2013. A total of 113 taxa were selected for stable isotope analyses. The δ15N, δ13C and C:N values for all taxa are reported as means for the entire study region, as well as means for four water mass assemblages that differ in vertical water mass profile, nested within three large-scale regions that differ in organic matter input regimes. These data provide key information to infer food web structure and feeding linkages among offshore marine fishes and invertebrates, thus may be used as a baseline for future monitoring and regulatory decision-making.

Statement of contribution: I produced the stable isotope data and statistical analyses presented in the report. I wrote the report, but all co-authors authors contributed to editing. Additionally, SA managed metadata, sample processing, inventory and species identifications for fish. SM managed metadata, sample inventory, and some species identifications for epifaunal and infaunal invertebrates. LdM provided certified taxonomy for epifaunal and infaunal invertebrates. PA managed metadata and study design for sample collections of epifaunal and infaunal invertebrates. WW managed sample inventory and species identifications for zooplankton. JR facilitated publication in the DFO data report framework.

Appendix B: Taxonomic classifications

Full taxonomic classifications for all taxa included in thesis research. Taxa with available stable isotope data (SI) and those included in biological traits analyses (BTA) in Chapter 5 are indicated by X. Taxa are listed alphabetically, by Phylum.

Taxon	SI	BTA	Authority	Class	Order	Family	Genus
Annelida							
Abyssoninoe sp.	X		Orensanz, 1990	Polychaeta	Eunicida	Lumbrineridae	Abyssoninoe
Aglaophamus malmgreni	X	X	(Théel, 1879)	Polychaeta	Phyllodocida	Nephtyidae	Aglaophamus
Aglaophamus sp.	X		Kinberg, 1865	Polychaeta	Phyllodocida	Nephtyidae	Aglaophamus
Ampharetidae	X		Malmgren, 1866	Polychaeta	Terebellida	Ampharetidae	
Cistenides hyperborea	X		Malmgren, 1866	Polychaeta	Terebellida	Pectinariidae	Cistenides
Eucranta sp.	X	X	Malmgren, 1866	Polychaeta	Phyllodocida	Polynoidae	Eucranta
Eucranta villosa	X		Malmgren, 1866	Polychaeta	Phyllodocida	Polynoidae	Eucranta
Jasmineira sp.	X	X	Langerhans, 1880	Polychaeta	Sabellida	Sabellidae	Jasmineira
Maldane arctica	X		Detinova, 1985	Polychaeta		Maldanidae	Maldane
Maldane spp.		X	Grube, 1860	Polychaeta		Maldanidae	Maldane
Melinna cristata	X		(M. Sars, 1851)	Polychaeta	Terebellida	Ampharetidae	Melinna
Nephtys ciliata	X		(Müller, 1788)	Polychaeta	Phyllodocida	Nephtyidae	Nephtys
Nephtys sp.	X		Cuvier, 1817	Polychaeta	Phyllodocida	Nephtyidae	Nephtys
Nothria conchylega		X	(Sars, 1835)	Polychaeta	Eunicida	Onuphidae	Nothria
Pista maculata		X	(Dalyell, 1853)	Polychaeta	Terebellida	Terebellidae	Pista
Arthropoda							
Acanthostepheia malmgreni	X	X	(Goës, 1866)	Malacostraca	Amphipoda	Oedicerotidae	Acanthostepheia
Anonyx nugax		X	(Phipps, 1774)	Malacostraca	Amphipoda	Uristidae	Anonyx
Argis dentata	X	X	(Rathbun, 1902)	Malacostraca	Decapoda	Crangonidae	Argis
Boreomysis sp.	X	X	G.O. Sars, 1869	Malacostraca	Mysida	Mysidae	Boreomysis
Bythocaris payeri	X		(Heller, 1875)	Malacostraca	Decapoda	Bythocarididae	Bythocaris
Bythocaris spp.		X	G.O. Sars, 1870	Malacostraca	Decapoda	Bythocarididae	Bythocaris

Taxon	SI	BTA	Authority	Class	Order	Family	Genus
Calanus glacialis	X		Jaschnov, 1955	Hexanauplia	Calanoida	Calanidae	Calanus
Calanus hyperboreus	X		Krøyer, 1838	Hexanauplia	Calanoida	Calanidae	Calanus
Colossendeis proboscidea		X	(Sabine, 1824)	Pycnogonida	Pantopoda	Colossendeidae	Colossendeis
Decapoda (Hippolytidae?)	X		Latreille, 1802	Malacostraca	Decapoda		
Epimeria loricata		X	G. O. Sars, 1879	Malacostraca	Amphipoda	Epimeriidae	Epimeria
Eualus gaimardii gaimardii	X	X	(H. Milne Edwards, 1837 [in Milne Edwards, 1834-1840])	Malacostraca	Decapoda	Thoridae	Eualus
Halirages qvadridentatus		X	G.O. Sars, 1877	Malacostraca	Amphipoda	Calliopiidae	Halirages
Haploops laevis	X		Hoek, 1882	Malacostraca	Amphipoda	Ampeliscidae	Haploops
Hyas coarctatus	X		Leach, 1816	Malacostraca	Decapoda	Oregoniidae	Hyas
Hymenodora glacialis	X		(Buchholz, 1874)	Malacostraca	Decapoda	Acanthephyridae	Hymenodora
Hymenodora sp.	X		G.O. Sars, 1877	Malacostraca	Decapoda	Acanthephyridae	Hymenodora
Hyperia galba	X		(Montagu, 1815)	Malacostraca	Amphipoda	Hyperiidae	Hyperia
Lebbeus groenlandicus		X	(Fabricius, 1775)	Malacostraca	Decapoda	Thoridae	Lebbeus
Lebbeus polaris	X	X	(Sabine, 1824)	Malacostraca	Decapoda	Thoridae	Lebbeus
Michthyops theeli		X	(Ohlin, 1901)	Malacostraca	Mysida	Mysidae	Michthyops
Mysida	X	X	Boas, 1883	Malacostraca	Mysida		
Mysis oculata	X		(Fabricius, 1780)	Malacostraca	Mysida	Mysidae	Mysis
Mysis polaris	X		Holmquist, 1959	Malacostraca	Mysida	Mysidae	Mysis
Mysis spp.		X	Latreille, 1802	Malacostraca	Mysida	Mysidae	Mysis
Nymphon hirtipes		X	Bell, 1855	Pycnogonida	Pantopoda	Nymphonidae	Nymphon
Onisimus plautus		X	(Krøyer, 1845)	Malacostraca	Amphipoda	Uristidae	Onisimus
Paraeuchaeta sp.	X		Scott A., 1909	Hexanauplia	Calanoida	Euchaetidae	Paraeuchaeta
Rhachotropis aculeata		X	(Lepechin, 1780)	Malacostraca	Amphipoda	Eusiridae	Rhachotropis
Rhachotropis sp.		X	S.I. Smith, 1883	Malacostraca	Amphipoda	Eusiridae	Rhachotropis
Sabinea septemcarinata	X	X	(Sabine, 1824)	Malacostraca	Decapoda	Crangonidae	Sabinea
Saduria sabini	X	X	(Krøyer, 1849)	Malacostraca	Isopoda	Chaetiliidae	Saduria
Saduria sibirica	X	X	(Birula, 1896)	Malacostraca	Isopoda	Chaetiliidae	Saduria
Sclerocrangon boreas		X	(Phipps, 1774)	Malacostraca	Decapoda	Crangonidae	Sclerocrangon

Taxon	SI	BTA	Authority	Class	Order	Family	Genus
Sclerocrangon ferox	X	X	(Sars G.O., 1877)	Malacostraca	Decapoda	Crangonidae	Sclerocrangon
Synidotea bicuspida	X	X	(Owen, 1839)	Malacostraca	Isopoda	Idoteidae	Synidotea
Synidotea sp.	X		Harger, 1878	Malacostraca	Isopoda	Idoteidae	Synidotea
Themisto abyssorum	X		(Boeck, 1871)	Malacostraca	Amphipoda	Hyperiidae	Themisto
Themisto libellula	X		(Lichtenstein in Mandt, 1822)	Malacostraca	Amphipoda	Hyperiidae	Themisto
Thysanoessa inermis	X		(Krøyer, 1846)	Malacostraca	Euphausiacea	Euphausiidae	Thysanoessa
Thysanoessa raschii	X		(M. Sars, 1864)	Malacostraca	Euphausiacea	Euphausiidae	Thysanoessa
Tmetonyx sp.		X	Stebbing, 1906	Malacostraca	Amphipoda	Uristidae	Tmetonyx
Brachiopoda							
Brachiopoda		X	Duméril, 1805				
Bryozoa							
Alcyonidium spp.		X	J.V.F.Lamouroux, 1813	Gymnolaemata	Ctenostomatida	Alcyonidiidae	Alcyonidium
Cephalorhyncha							
Priapulopsis bicaudatus		X	(Koren & Danielssen, 1868)	Priapulida		Priapulidae	Priapulopsis
Chaetognatha							
Chaetognatha	X						
Eukrohnia hamata	X		(Möbius, 1875)	Sagittoidea	Phragmophora	Eukrohniidae	Eukrohnia
Parasagitta elegans	X		(Verrill, 1873)	Sagittoidea	Aphragmophora	Sagittidae	Parasagitta
Chordata							
Amblyraja hyperborea	X	X	(Collett, 1879)	Elasmobranchii	Rajiformes	Rajidae	Amblyraja
Anisarchus medius	X	X	(Reinhardt, 1837)	Actinopterygii	Perciformes	Stichaeidae	Anisarchus
Artediellus uncinatus	X		(Reinhardt, 1834)	Actinopterygii	Scorpaeniformes	Cottidae	Artediellus
Ascidia obliqua		X	Alder, 1863	Ascidiacea	Phlebobranchia	Ascidiidae	Ascidia
Aspidophoroides olrikii	X		Lütken, 1877	Actinopterygii	Scorpaeniformes	Agonidae	Aspidophoroides
Benthosema glaciale	X		(Reinhardt, 1837)	Actinopterygii	Myctophiformes	Myctophidae	Benthosema
Boreogadus saida	X	X	(Lepechin, 1774)	Actinopterygii	Gadiformes	Gadidae	Boreogadus
Careproctus mollis		X	Gilbert & Burke, 1912	Actinopterygii	Scorpaeniformes	Liparidae	Careproctus
Careproctus rastrinus		X	Gilbert & Burke, 1912	Actinopterygii	Scorpaeniformes	Liparidae	Careproctus
Careproctus sp.		X	Krøyer, 1862	Actinopterygii	Scorpaeniformes	Liparidae	Careproctus

Taxon	SI	BTA	Authority	Class	Order	Family	Genus
Cottunculus microps		X	Collett, 1875	Actinopterygii	Scorpaeniformes	Psychrolutidae	Cottunculus
Cyclopteridae		X	Bonaparte, 1831	Actinopterygii	Scorpaeniformes	Cyclopteridae	
Eumicrotremus derjugini	X		Popov, 1926	Actinopterygii	Scorpaeniformes	Cyclopteridae	Eumicrotremus
Eumicrotremus spinosus	X		(Fabricius, 1776)	Actinopterygii	Scorpaeniformes	Cyclopteridae	Eumicrotremus
Gymnelus hemifasciatus	X		Andriashev, 1937	Actinopterygii	Perciformes	Zoarcidae	Gymnelus
Gymnocanthus tricuspis	X		(Reinhardt, 1830)	Actinopterygii	Scorpaeniformes	Cottidae	Gymnocanthus
Icelus bicornis	X		(Reinhardt, 1840)	Actinopterygii	Scorpaeniformes	Cottidae	Icelus
Icelus sp.		X	Krøyer, 1845	Actinopterygii	Scorpaeniformes	Cottidae	Icelus
Icelus spatula	X		Gilbert & Burke, 1912	Actinopterygii	Scorpaeniformes	Cottidae	Icelus
Leptagonus decagonus	X		(Bloch & Schneider, 1801)	Actinopterygii	Scorpaeniformes	Agonidae	Leptagonus
Liparidae		X	Gill, 1861	Actinopterygii	Scorpaeniformes	Liparidae	
Liparis fabricii	X		Krøyer, 1847	Actinopterygii	Scorpaeniformes	Liparidae	Liparis
Liparis sp.	X		Scopoli, 1777	Actinopterygii	Scorpaeniformes	Liparidae	Liparis
Liparis tunicatus	X	X	Reinhardt, 1836	Actinopterygii	Scorpaeniformes	Liparidae	Liparis
Lumpenus fabricii	X	X	Reinhardt, 1836	Actinopterygii	Perciformes	Stichaeidae	Lumpenus
Lycodes adolfi	X		Nielsen & Fosså, 1993	Actinopterygii	Perciformes	Zoarcidae	Lycodes
Lycodes eudipleurostictus		X	Jensen, 1902	Actinopterygii	Perciformes	Zoarcidae	Lycodes
Lycodes pallidus	X	X	Collett, 1879	Actinopterygii	Perciformes	Zoarcidae	Lycodes
Lycodes polaris	X		(Sabine, 1824)	Actinopterygii	Perciformes	Zoarcidae	Lycodes
Lycodes rossi	X	X	Malmgren, 1865	Actinopterygii	Perciformes	Zoarcidae	Lycodes
Lycodes sagittarius	X	X	McAllister, 1976	Actinopterygii	Perciformes	Zoarcidae	Lycodes
Lycodes seminudus	X	X	Reinhardt, 1837	Actinopterygii	Perciformes	Zoarcidae	Lycodes
Lycodes sp.		X	Reinhardt, 1831	Actinopterygii	Perciformes	Zoarcidae	Lycodes
Lycodes squamiventer	X		Jensen, 1904	Actinopterygii	Perciformes	Zoarcidae	Lycodes
Reinhardtius hippoglossoides	X	X	(Walbaum, 1792)	Actinopterygii	Pleuronectiformes	Pleuronectidae	Reinhardtius
Stichaeidae		X	Gill, 1864	Actinopterygii	Perciformes	Stichaeidae	
Triglops nybelini	X	X	Jensen, 1944	Actinopterygii	Scorpaeniformes	Cottidae	Triglops
Triglops pingelii	X	X	Reinhardt, 1837	Actinopterygii	Scorpaeniformes	Cottidae	Triglops
Cnidaria							

Taxon	SI	BTA	Authority	Class	Order	Family	Genus
Actiniaria	X	X		Anthozoa	Actiniaria		
Aglantha digitale	X		(O. F. Müller, 1776)	Hydrozoa	Trachymedusae	Rhopalonematidae	Aglantha
Catablema vesicarium	X		(A. Agassiz, 1862)	Hydrozoa	Anthoathecata	Pandeidae	Catablema
Lafoeidae		X	Hincks, 1868	Hydrozoa	Leptothecata	Lafoeidae	
Nephtheidae		X	Gray, 1862	Anthozoa	Alcyonacea	Nephtheidae	
Zoanthidae		X	Rafinesque, 1815	Anthozoa	Zoantharia	Zoanthidae	
Ctenophora							
Beroe cucumis	X		Fabricius, 1780	Nuda	Beroida	Beroidae	Beroe
Mertensia ovum	X		(Fabricius, 1780)	Tentaculata	Cydippida	Mertensiidae	Mertensia
Echinodermata							
Asteriidae		X	Gray, 1840	Asteroidea	Forcipulatida	Asteriidae	
Crossaster papposus		X	(Linnaeus, 1767)	Asteroidea	Valvatida	Solasteridae	Crossaster
Ctenodiscus crispatus	X	X	(Retzius, 1805)	Asteroidea	Paxillosida	Ctenodiscidae	Ctenodiscus
Cucumaria sp.		X	de Blainville, 1830	Holothuroidea	Dendrochirotida	Cucumariidae	Cucumaria
Eupyrgus scaber	X	X	Lütken, 1857	Holothuroidea	Molpadida	Eupyrgidae	Eupyrgus
Gorgonocephalus arcticus	X	X	Leach, 1819	Ophiuroidea	Euryalida	Gorgonocephalidae	Gorgonocephalus
Gorgonocephalus sp.	X	X	Leach, 1815	Ophiuroidea	Euryalida	Gorgonocephalidae	Gorgonocephalus
Heliometra glacialis	X	X	(Owen, 1833 ex Leach MS)	Crinoidea	Comatulida	Antedonidae	Heliometra
Holothuroidea	X			Holothuroidea			
Hymenaster pellucidus		X	Thomson, 1873	Asteroidea	Velatida	Pterasteridae	Hymenaster
Leptasterias sp.	X	X	Verrill, 1866	Asteroidea	Forcipulatida	Asteriidae	Leptasterias
Molpadia spp.	X	X	Cuvier, 1817	Holothuroidea	Molpadida	Molpadiidae	Molpadia
Myriotrochus sp.	X	X	Steenstrup, 1851	Holothuroidea	Apodida	Myriotrochidae	Myriotrochus
Ophiacantha bidentata	X	X	(Bruzelius, 1805)	Ophiuroidea	Ophiurida	Ophiacanthidae	Ophiacantha
Ophiocten sericeum	X	X	(Forbes, 1852)	Ophiuroidea	Ophiurida	Ophiuridae	Ophiocten
Ophiocten sp.		X	Lütken, 1855	Ophiuroidea	Ophiurida	Ophiuridae	Ophiocten
Ophiopleura borealis	X	X	Danielssen & Koren, 1877	Ophiuroidea	Ophiurida	Ophiuridae	Ophiopleura
Ophioscolex glacialis		X	Müller & Troschel, 1842	Ophiuroidea	Ophiurida	Ophiomyxidae	Ophioscolex
Ophiura robusta		X	(Ayres, 1852)	Ophiuroidea	Ophiurida	Ophiuridae	Ophiura

Taxon	SI	BTA	Authority	Class	Order	Family	Genus
Poliometra prolixa		X	(Sladen, 1881)	Crinoidea	Comatulida	Antedonidae	Poliometra
Pontaster tenuispinus	X	X	(Düben & Koren, 1846)	Asteroidea	Notomyotida	Benthopectinidae	Pontaster
Psilaster andromeda	X	X	(Müller & Troschel, 1842)	Asteroidea	Paxillosida	Astropectinidae	Psilaster
Psolus sp.	X	X	Oken, 1815	Holothuroidea	Dendrochirotida	Psolidae	Psolus
Pteraster obscurus		X	(Perrier, 1891)	Asteroidea	Velatida	Pterasteridae	Pteraster
Solaster endeca		X	(Linnaeus, 1771)	Asteroidea	Valvatida	Solasteridae	Solaster
Strongylocentrotus sp.		X	Brandt, 1835	Echinoidea	Camarodonta	Strongylocentrotidae	Strongylocentrotus
Urasterias lincki	X	X	(Müller & Troschel, 1842)	Asteroidea	Forcipulatida	Asteriidae	Urasterias
Mollusca							
Astarte borealis	X	X	(Schumacher, 1817)	Bivalvia	Carditida	Astartidae	Astarte
Astarte montagui/crenata	X	X	(Dillwyn, 1817) / Gray, 1824	Bivalvia	Carditida	Astartidae	Astarte
Astarte sp.	X		Sowerby 1816	Bivalvia	Carditida	Astartidae	Astarte
Bathyarca glacialis	X	X	(Gray, 1824)	Bivalvia	Arcida	Arcidae	Bathyarca
Bathyarca sp.	X		Kobelt, 1891	Bivalvia	Arcida	Arcidae	Bathyarca
Bathypolypus arcticus	X	X	(Prosch, 1849)	Cephalopoda	Octopoda	Bathypolypodidae	Bathypolypus
Buccinidae		X	Rafinesque, 1815	Gastropoda	Neogastropoda	Buccinidae	
Buccinum hydrophanum		X	Hancock, 1846	Gastropoda	Neogastropoda	Buccinidae	Buccinum
Buccinum scalariforme		X	Møller, 1842	Gastropoda	Neogastropoda	Buccinidae	Buccinum
Buccinum sp.		X	Linnaeus, 1758	Gastropoda	Neogastropoda	Buccinidae	Buccinum
Buccinum undatum		X	Linnaeus, 1758	Gastropoda	Neogastropoda	Buccinidae	Buccinum
Clione limacina	X		(Phipps, 1774)	Gastropoda	Gymnosomata	Clionidae	Clione
Colus sabini		X	(Gray, 1824)	Gastropoda	Neogastropoda	Buccinidae	Colus
Cylichna alba	X		(Brown, 1827)	Gastropoda	Cephalaspidea	Cylichnidae	Cylichna
Dendronotus sp.		X	Alder & Hancock, 1845	Gastropoda	Nudibranchia	Dendronotidae	Dendronotus
Ennucula tenuis	X		(Montagu, 1808)	Bivalvia	Nuculida	Nuculidae	Ennucula
Limacina helicina	X		(Phipps, 1774)	Gastropoda	Thecosomata	Limacinidae	Limacina
Macoma calcarea	X		(Gmelin, 1791)	Bivalvia	Cardiida	Tellinidae	Macoma
Macoma moesta	X		(Deshayes, 1855)	Bivalvia	Cardiida	Tellinidae	Macoma
Macoma spp.		X	Leach, 1819	Bivalvia	Cardiida	Tellinidae	Macoma

Taxon	SI	BTA	Authority	Class	Order	Family	Genus
Neptunea heros		X	(Gray, 1850)	Gastropoda	Neogastropoda	Buccinidae	Neptunea
Nuculana minuta	X		(O. F. Müller, 1776)	Bivalvia	Nuculanida	Nuculanidae	Nuculana
Nuculana pernula	X	X	(O. F. Müller, 1779)	Bivalvia	Nuculanida	Nuculanidae	Nuculana
Similipecten greenlandicus	X	X	(G. B. Sowerby II, 1842)	Bivalvia	Pectinida	Propeamussiidae	Similipecten
Thyasira sp.	X		Lamarck, 1818	Bivalvia	Lucinida	Thyasiridae	Thyasira
Thyasiridae	X		Dall, 1900 (1895)	Bivalvia	Lucinida	Thyasiridae	
Yoldiella sp.		X	A. E. Verrill & Bush, 1897	Bivalvia	Nuculanida	Yoldiidae	Yoldiella
Nemertea							
Nemertea	X	X					
Porifera							
Radiella hemisphaerica		X	(Sars, 1872)	Demospongiae	Polymastiida	Polymastiidae	Radiella
Sipuncula							
Phascolionidae		X	Cutler & Gibbs, 1985	Sipunculidea	Golfingiida	Phascolionidae	
Sipunculidae	X		Rafinesque, 1814	Sipunculidea	Golfingiida	Sipunculidae	

Appendix C: Information on trophic attributes

Notes on feeding and functional attributes for all taxa included in thesis research, based extensive literature review. References are included. Information collected was used to estimate trophic functional guilds (Chapters 2, 3 and 4) and to assign trophic functional trait affinities for biological traits analyses (Chapter 5).

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Annelida				
Abyssoninoe sp.	Benthic SS Carnivore	Most Lumbrineridae are burrowers. Somewhat motile. Most Lumbrineridae are carnivores on sessile and motile prey but some are herbivorous or sub-surface deposit feeders. Macdonald et al. (2010) classified Lumbrinidae generally as mobile predatory carnivores that feed sub-subsurface on meiofauna and macrofauna (>500 µm).	(Macdonald et al. 2010, Jumars et al. 2015)	
Aglaophamus malmgreni	Benthic SS Carnivore	Nephtyidae are burrowers in soft sediments at any water depth; very active. Macdonald et al. (2010) classified this species as a free-living, mobile, carnivorous predator that feeds below the sediment surface on macrofauna (>500 µm).Kędra et al. (2010) reported this species as a mobile carnivore with Boreal distribution. Maximum size found in literature was 120 mm, taken from the Marine Species Identification Portal.	(Kędra et al. 2010, Macdonald et al. 2010, Jumars et al. 2015)	Marine Species Identification Portal
Aglaophamus sp.	Benthic SS Carnivore	Nephtyidae are burrowers in soft sediments at any water depth; very active. Macdonald et al. (2010) classified *Aglaophamus* spp. generally as free-living, motile, carnivorous predators that feed sub-surface on macrofauna (>500 µm).	(Macdonald et al. 2010, Jumars et al. 2015)	
Ampharetidae	Benthic SDF	Tube-building and infaunal at all depths. Macdonald et al. (2010) classified Ampharetidae generally as discretely motile (can move but don't need to for feeding), omnivorous detrivores that feed at the sediment surface on sediment, POM, microfauna (<500 µm) and diatoms.	(Macdonald et al. 2010, Jumars et al. 2015)	
Cistenides hyperborea	Benthic SSDF	Head-down sub-surface deposit feeders, possibly feeding on fresh detritus in Kongsfjorden.	(Jumars et al. 2015)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Eucranta sp.	Benthic Carnivore	No genus-specific information found for *Eucranta*. Fauchald & Jumars (1979) report that Polynoidea are generally considered carnivores that feed on small crustaceans, echinoderms, polychaetes, gastropods, sponges, and hydroids, but *Eucranta* spp. were not among those reviewed. Size of 53 mm based on cogener *E. villosa*, which was also fund in beam trawls for this study.	(Fauchald & Jumars 1979)	
Eucranta villosa	Benthic Carnivore	No specific information on this species. Functional group and trophic traits classifications are based on cogeners. See also *Eucranta* sp.	(Fauchald & Jumars 1979)	
Jasmineira sp.	Benthic SDF/SF	No species-specific information found. Macdonald et al. (2010) classified species within this genus as epibenthic, tubiculous suspension-feeding omnivores that feed at the surface on POM and phytoplankton. Size of 20 mm based on sizes reported for cogeners in the Marine Species Identification Portal.	(Macdonald et al. 2010)	Marine Species Identification Portal
Maldane arctica	Benthic SSDF	No species-specific diet information found. Functional group and trophic trait classifications are based on feeding information for cogeners. See also *Maldane* sp.		
Maldane spp.		Maldanids are generally considered subsurface deposit feeder by Jumars et al. (2015), with more evidence for deposit feeding based on fatty acid biomarkers reported by Søreide et al. (2013). Macdonald et al. (2010) classified *Maldane* spp. generally as discretely motile, omnivorous detrivores that feed sub-surface on sediment, particulate organic matter, and microfauna. Holte & Gulliksen (1998) report that the cogener *M. sarsi* is a head-down deposit feeder. Size of 32 mm reported for cogener *M. arctica* on the Marine Species Identification Portal, although other northern *Maldane* spp. can reportedly get up to 110 mm. *M. arctica* was also caught in this study.	(Holte & Gulliksen 1998, Macdonald et al. 2010, Søreide et al. 2013, Jumars et al. 2015)	Marine Species Identification Portal
Melinna cristata	Benthic SDF	Tube-building and infaunal at all depths according to Jumars et al. (2015). Macdonald et al. (2010) classified this species as a discretely motile (can move but doesn't need to for feeding), omnivorous detrivore that feeds at the sediment surface on sediment, POM, microfauna (<500 μm) and diatoms.	(Macdonald et al. 2010, Jumars et al. 2015)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Nephtys ciliata	Benthic SS Carnivore	Burrowers in soft sediment according to Jumars et al. (2015). Søreide et al. (2013) found high levels of *Calanus* and bacterial fatty acid markers in this genus. Macdonald et al. (2010) classified it as a free-living, motile, carnivorous predator that feeds on sub-surface macrofauna (>500 μm).	(Macdonald et al. 2010, Søreide et al. 2013, Jumars et al. 2015)	
Nephtys sp.	Benthic SS Carnivore	Burrowers in soft sediment according to Jumars et al. (2015). Søreide et al. (2013) found high levels of *Calanus* and bacterial fatty acid markers in this genus. Macdonald et al. (2010) classified this genus as a free-living, motile, carnivorous predator that feeds on macrofauna (>500 μm) below the sediment surface. Kędra et al. (2010) also classified this species as a motile carnivore.	(Kędra et al. 2010, Macdonald et al. 2010, Søreide et al. 2013, Jumars et al. 2015)	
Nothria conchylega		According to Jumars et al. (2015), there is strong evidence for omnivory in Onuphidae, including macrophagous and microphagous feeding. Their jaws can handle food items larger than their mouths. They review that stable isotopic evidence supports broad omnivory. Gaston et al. (1987) examined stomach contents and literature information for many polychaetes in the Middle Atlantic Bight, and found this species to be a motile, jawed, surface-deposit feeder that had detritus and forams in its stomach. Size of 150 mm reported on the Marine Species Identification Portal, which agrees with size reported by Pollock (1998).	(Gaston 1987, Pollock 1998, Jumars et al. 2015)	Marine Species Identification Portal
Pista maculata		Macdonald et al. (2010) classify *Pista* spp. generally as discretely motile, tube-dwelling, omnivorous detrivores that feed at the sediment surface on sediment, particulate organic matter, microfauna, and diatoms. According to Pollock (1998), *P. maculata* prefers sand and mud. Jumars et al. (2015) report that Terebellidae are generally surface deposit feeders. Maximum size of 153 mm reported by Pollock (1998).	(Pollock 1998, Macdonald et al. 2010, Jumars et al. 2015)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Arthropoda				
Acanthostepheia malmgreni	Benthopelagic Carnivore	Inhabits soft bottoms. Highly motile. Adults are mainly carnivorous, feeding on small zooplankton such as harpacticoid and calanoid copepods. Juveniles feed on phytoplankton and/or detritus. No known diel vertical migration, but individuals are commonly found as high as 100 m off bottom in the Gulf of the St. Lawrence (reviewed in Richoux et al. 2004). Węsławski et al. (2010) and Kędra et al. (2010) report this species as a motile carnivore with Arctic distribution. Maximum body size found reported in literature was 36 mm by Węsławski et al. (2010).	(Richoux et al. 2004, Kędra et al. 2010, Węsławski et al. 2010)	
Anonyx nugax		Macdonald et al. (2010) describe *Anonyx* spp. generally as free living, motile carnivores that feed at the surface by scavenging macrofauna (> 500 μm).Sainte-Marie et al. (1989) suggested *Anonyx nugax* may be an obligate carnivore, and found the species to be a very efficient feeder. Starvation for up to 30 days did not impact their feeding ability or survivorship. Legeżyńska (2008) observed that only mature adult *A. nugax* are true scavengers, and that younger individuals feed on both animal and non-animal (detritus) food. Fatty acid analyses by Graeve et al. (1997) indicated that they may feed to some extent on copepods. Legeżyńska (2008) reviewed a lab study that documented *A. nugax* showing mild interest in zooplankton prey when offered. Nygård et al. (2012) observed *Anonyx* spp. preying extensively on *Calanus* copepods in two Arctic fjords. Fatty acid and stable isotope analyses in Legeżyńska et al. (2012) suggested carrion comprised 90 % of diet in both summer and winter. Kędra et al. (2010) reported this species as a motile carnivore with Arctic distribution. Węsławski et al. (2010) reported this species as a nectobenthic, motile carnivore with Arctic distribution. Maximum size taken from Węsławski et al. (2010) and Steele & Brunel (1968) was 44 mm.	(Steele & Brunel 1968, Sainte-Marie et al. 1989, Graeve et al. 1997, Legezyńska 2008, Macdonald et al. 2010, Węsławski et al. 2010, Kędra et al. 2012, Legeżyńska et al. 2012, Nygård et al. 2012)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Argis dentata	Benthopelagic Carnivore	Stable isotope values in Sherwood & Rose (2005) places this species near the top of the food chain. Carnivore? Reportedly circumpolar Arctic distribution from Sokolov (2001). Difficult to find general data on size, but Sherwood & Rose (2005) reported a length of 100 mm for a specimen they captured. Based on other Crangonid shrimps, there is probably some degree of deposit feeding or scavenging. See also *Sclerocrangon* spp.	(Sokolov 2001, Sherwood & Rose 2005)	
Astarte montagui/crenata	Benthic SF	Macdonald et al. (2010) classified *Astarte* spp. generally, and *A. montagui* specifically, as discretely motile, epibenthic omnivores that live in burrows and feed on particulate organic matter and phytoplankton via suspension feeding. Søreide et al. (2013) classified *A. crenata* as a benthic suspension feeder that feeds between trophic levels 2.0 and 2.6. Gallagher et al. (1998) studied the biochemical composition of *A. crenata* and described it as a facultative deposit-feeding bivalve. Kędra et al. (2010) reported *A. montagui* as a discretely motile filter feeder with Arctic-boreal distribution. Size from the Encyclopedia of Life for *A. crenata* was 18.4 mm. Size for *A. montagui* on the Marine Species Identification Portal was 13 mm, but Kędra et al. (2010) observed a length of 21.7 mm.	(Gallagher et al. 1998, Kędra et al. 2010, Macdonald et al. 2010, Søreide et al. 2013)	Enclyclopedia of Life, Marine Species Identification Poral
Boreomysis sp.	Benthopelagic Carnivore	Specific Boreomysids (*B. arctica*) in the Mediterrannean Sea fed on crustacean remains, including those of pelagic origin. Pytodetritus became more important with depth (Cartes & Sorbe 1998). Fatty acid markers in Cartes (2011) suggested a wide range of diet items including carnivory, likely on Calanoid copepods, and a link to surface production. Fatty acid and stable isotope markers in Connelly et al. (2014) also suggested a link to Calanoid copepods in *B. arctica* from the Beaufort Sea and Amundsen Gulf. Size of 27 mm based on specimens reported in Connelly et al. (2014) from the Canadian Beaufort Sea, and on Marine Species Identification Portal records for *B. arcticus.*	(Cartes & Sorbe 1998, Cartes 2011, Connelly et al. 2014)	Marine Species Identification Portal

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Bythocaris payeri	Benthic Carnivore	No species-specific diet information found. Functional group and trophic trait classifications are based on cofamilials. Macdonald et al. (2010) classified Hippolytidae generally as free-living, motile, carnivorous predators that feed on macrofauna (>500 μm).	(Macdonald et al. 2010)	
Bythocaris spp.		Difficult to find genus-specific information on *Bythocaris* in the literature. Based on cofamilials, Macdonald et al. (2010) classified Hippolytidae generally as free-living, motile, carnivorous predators that feed on macrofauna. Bergmann et al. (2009) classified *Bythocaris* spp. as predator/scavengers. Nitrogen stable isotope data from Bergmann et al. (2009) indicated a mid-trophic level, and carbon stable isotope data indicated a fairly benthic diet. Connelly et al. (2014) reported stable isotope data that indicated a high trophic level of 4.0 for *Bythocaris* spp., and fatty acid data indicated come consumption of copepods. Maximum size of 47 mm taken from sizes reported for *Bythocaris* spp. in the Canadian Beaufort Sea by Connelly et al. (2014).	(Bergmann et al. 2009, Macdonald et al. 2010, Connelly et al. 2014)	
Calanus glacialis	Pelagic Herbivore	Pelagic filter feeder. According to Mauchline (1998), most *Calanus* spp are predominantly herbivorous. However, they review research that indicates *Calanus* spp. also eat pelagic detritus and heterotrophs. Observational, fatty acid, and stable isotope biomarker data reported by Søreide et al. (2008) indicated that *C. hyperboreus* and *C. glacialis* were essentially herbivores in the spring when algal biomass is highest, and generally occur at the same depths as maximum algal biomass. *C. glacialis* preferred diatom species. Outside of the bloom, *Calanus* spp. become more omnivorous and have increased trophic levels, likely from consuming higher proportions heterotrophs and detritus (Basedow et al. 2010). The literature on *Calanus* feeding and lifecycles is extensive.	(Mauchline 1998, Søreide et al. 2008, Basedow et al. 2010)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Calanus hyperboreus	Pelagic Herbivore	Pelagic filter feeder. According to Mauchline (1998), most *Calanus* spp are predominantly herbivorous. However, they review research that indicates *Calanus* spp. also eat pelagic detritus and heterotrophs. Conover et al. (1960) report that *C. hyperboreus* ate all types of phytoplankton and diatoms offered, and would consume their own eggs when starved. Observational, fatty acid, and stable isotope biomarker data reported by Søreide et al. (2008) indicated that *C. hyperboreus* and *C. glacialis* were essentially herbivores in the spring when algal biomass is highest, and generally occur at the same depths as maximum algal biomass. *C. hyperboreus* preferred Phaecystis. Outside of the bloom, *Calanus* spp. become more omnivorous and have increased trophic levels, likely from consuming higher proportions heterotrophs and detritus (Basedow et al. 2010). The literature on *Calanus* feeding and lifecycles is extensive.	(Conover 1960, Mauchline 1998, Søreide et al. 2008, Basedow et al. 2010)	
Colossendeis proboscidea		According to fact page on the Institute of Marine Research website, pycnogonids are benthic predators that are genereally slow moving on the surface. They eat stationary or slow-moving prey such as sea nettles, sponges, gastropods, bristle worms, and algae. Braby et al. (2009) observed other *Colossendeis* spp. preying on sponges. In their introduction, Braby et al. (2009) review the evidence in the literature for large pycnogonids as suctorial predators on slow-moving benthos (sponges, cnidarians, molluscs, broyozoans, and small polychaetes). They report that feeding information for *Colossendeis* spp. is particularly scarce, although they have been observed feeding on limpets, sea anemones, and polychaates during Antarctic sampling programs.	(Braby et al. 2009)	Institute of Marine Research website (http://www.imr.no/temasider/havedderkopp/en),
Decapoda (Hippolytidae?)	Benthopelagic Carnivore	Macdonald et al. (2010) classified Hippolytidae generally as free-living, motile, carnivorous predators that feed on macrofauna (>500 μm).	(Macdonald et al. 2010)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Epimeria loricata		No species-specific information found on feeding. Functional group and trophic trait classifications are based on cogeners. *Epimeria robusta* collected in the Antarctic accepted all kinds of foods offered in a laboratory experiment, including pieces of fish, krill, and living zooplankton (Klages and Gutt 1990). Cannibalism and feeding on other amphipods was also observed. Individuals were up to 50 mm. Similarly, de Broyer & Klages (1991) observed *E. rubrieques* grasped and fed on fish and krill tissue offered in the lab, as well as live Artemia and chironomid larvae. They suggested *E. rubrieques* was an ambush predator. Both studies observed limited movement, unless food was nearby. Specimens mostly stayed on the bottom, often walking rather than swimming.	(Klages & Gutt 1990, de Broyer & Klages 1991)	
Eualus gaimardii gaimardii	Benthopelagic Carnivore	Graeve et al. (1997) reported that fatty acid biomarkers measured in this species aligned with carnivory. Macdonald et al. (2010) classified *Eulaus* spp. generally as free-living, motile, carnivorous predators. Birkely & Gulliksen (2003) observed pelagic feeding on copepods and amphipods, but sediment present in the stomach indicated feeding near the seafloor as well. Zimina et al. (2015) classified *E. gaimadrii gaimadrii* as a high boreal-Arctic species, but distribution extends into the northern Atlantic. Węsławski et al. (2010) classified this species as a motile carnivore with Arctic-boreal distribution. Size on the Marine Species Identification Portal is 70 mm, but Pollock (1998) reported 101 mm.	(Graeve et al. 1997, Pollock 1998, Birkely & Gulliksen 2003, Macdonald et al. 2010, Węsławski et al. 2010, Zimina et al. 2015)	Marine Species Identification Portal
Halirages qvadridentatus		No species-specific feeding information found. Stable isotope data in Connelly et al. (2014) indicated a trophic level of 3.1. Isotopic and fatty acid markers indicate that biomarker values measured in this species generally fall within the middle range of other species. Kędra et al. (2012) classified another Arctic *Halirages* sp. as a deposit-feeder. Węsławski et al. classified the same *Halirages* sp. (*fulvocinctus*) as a deposit feeder in their 2006 paper, and as a suspension-feeder in their 2010 paper. Stable isotope data in Legezyńska et al. (2012) suggested the genus occupies a low trophic level, but has a more "pelagic" carbon stable isotope value than other amphipods (still not truly pelagic). Possibly feeding on phytodetritus to some extent? Size of 31 mm based on individuals caught by Connelly et al. (2014).	(Węsławski et al. 2006, Węsławski et al. 2010, Kędra et al. 2012, Legeżyńska et al. 2012, Connelly et al. 2014)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Haploops laevis	Benthic SF	*Haploops* spp. generally live in mud and stone. Use a mix of benthic and pelagic feeding strategies including feeding on sinking POM. Rich in phytoplankton fatty acid markers but low in $\delta^{15}N$ and $\delta^{13}C$, indicating direct POM consumption. Stomach contents show diatoms, protist cysts, and formaniferans. Ampelescid amphipods are generally considered benthic suspension feeders that collect particles with their antennae.	(Rigolet et al. 2011, Legeżyńska et al. 2012)	
Hyas coarctatus	Benthic Carnivore	Difficult to find specific diet information in the literature. Stable isotope analysis by Gorbatenko et al. (2008) indicated benthic $\delta^{13}C$ values and high trophic level, suggesting benthic carnivory.	(Gorbatenko et al. 2008)	
Hymenodora glacialis	Pelagic Carnivore	*Hymenodora glacialis* are found in the water column (most abundant between 350-1000 m), but have also been caught near the seafloor. Stomach contents revealed a diverse diet, with copepods as the most important prey followed by chaetognaths and radiolarians (Havens & Rork 1969). Vertical migration and use of hyperbenthic habitat confirmed by Domanaski (1986).	(Havens & Rork 1969, Domanski 1986)	
Hymenodora sp.	Pelagic Carnivore	No genus-specific information found for this species. Functional group and trophic trait classifications are based on feeding information for cogeners (see also *Heliometra glacialis*).	(Havens & Rork 1969, Domanski 1986)	
Hyperia galba	Pelagic Carnivore	Conover et al. (1960) found this species readily took all animal prey offered in laboratory experiments, including bits of mussel, smashed snails, and living/dead copepods. In general, Hyperiid amphipods may also be parasitic/symbiotic on gelatinous zooplankton (Dittrich 1987). Węsławski et al. (2010) classified this species as a pelagic carnivore with Boreal distribution.	(Conover 1960, Dittrich 1987, Węsławski et al. 2010)	
Lebbeus groenlandicus		Birkely & Gulliksen (2003) observed epibenthic feeding mostly on hydrozoans and amphipods in *Lebbeus* spp. Macdonald et al. (2010) classified *Lebbeus* spp. generally as free-living, motile, carnivorous predators that feed on macrofauna. Squires (1968) observed detritus (including phytodetritus), crustaceans, ostracods, euphasids, faraminifera, gastropods, kelp, and pelecypods in the stomachs of 25 specimens collected in the Canadian Arctic Archipelago. According to a literature review by	(Squires 1968, Pollock 1998, Sokolov 2001, Birkely & Gulliksen 2003, Macdonald et al. 2010)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
		Sokolov (2001), *L. groenlandicus* has an Arctic-Pacific distribution. Size of 107 mm reported by the Census of Marine Life's Arctic Ocean Biodiversity database, and a size of 101 mm reported by Pollock (1998).		
Lebbeus polaris	Benthopelagic Carnivore	Squires (1968) observed mostly phytobenthos and detritus in stomachs, but occassionally found foraminiferans, ostracods, euphasiids, and copepods as well. Fatty acid and stable isotope analyses performed by Søreide et al. (2013) and by Graeve et al. (1997) suggested carniviory and a link to pelagic production. Birkely & Gulliksen (2003) observed epibenthic feeding mostly on hydrozoans and amphipods in *Lebbeus* spp. Macdonald et al. (2010) classified *Lebbeus* spp. generally as free-living, motile, carnivorous predators that feed on macrofauna. Zimina et al. (2015) reported that this is a circumpolar Arctic, high-boreal species. Węsławski et al. (2010) classified this species as a mobile carnivore with Arctic-boreal distribution. Søreide et al. (2013) classified this species as a benthic suspension feeder. Size of 90 mm reported on the Marine Species Identification Portal, and a size of 89 mm reported by Pollock (1998).	(Squires 1968, Graeve et al. 1997, Pollock 1998, Birkely & Gulliksen 2003, Macdonald et al. 2010, Węsławski et al. 2010, Søreide et al. 2013, Zimina et al. 2015)	
Michthyops theeli		Stable isotope data in Connelly et al. (2014) suggested a trophic level of 3. Fatty acid analyses from Connelly et al. (2014) suggested an omnivorous diet with higher *Calanus* markers and lower diatom markers than other mysids. The authors review that diet data are scarce for the mysid species considered in their study. Size of 22 mm based on individuals caught by Connelly et al. (2014).	(Connelly et al. 2014)	
Mysida	Pelagic Herbivore	In a review of Mysid taxonomy, Meland et al. (2015) describe Mysida as generally epi- to hyperbenthic, omnivorous filter-feeders ranging in size from 5 to 25 mm. Connelly et al. (2014) measured stable isotopes and fatty acids in a variety of benthic Mysida collected in the Beaufort Sea and Amundsen Gulf (under the older name Mysidacea) and found they generally fell within trophic levels 2 and 3. Connelly et al. (2014) review that Mysids are generally omnivorous, feeding on a wide variety of food sources dependent on life history and food availability, although some may be opportunistic predators.	(Connelly et al. 2014, Meland et al. 2015)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Mysis oculata	Pelagic Herbivore	Difficult to find species-specific feeding information. Individuals collected from the Yenisei estuary fed on phytoplankton in one experiment (Drits et al. 2015). Węsławski et al. (2010) classified this species as a pelagic suspension feeder.	Węsławski et al. 2010; Drits et al. 2015	
Mysis polaris	Pelagic Herbivore	Ice-associated (Gulliksen & Lønne 1989), but no species-specific feeding information available. Functional group and trophic trait classifications are based on feeding information for cogeners. See also *Mysidae* sp. and *Mysis oculata.*	(Gulliksen & Lønne 1989)	
Mysis spp.		No genus-specific feeding information available. Functional group and trophic trait classifications are based on information from other Arctic cogeners. There is evidence for vertical migration in the genus, with juveniles migrating higher than adults in *Mysis mixta* (Rudstam et al. 1989, Richoux 2004). *M. mixta* fed on phytoplankton, detritus, copepods, cladocerans, rotifers, and tintinnids. Mysids lower in the water column had higher ingestion of zooplankton and detritus (Rudstam et al. 1989, Richoux 2004). *M. oculata* collected from the Yenisei estuary were successfully fed phytoplankton in one experiment (Drits et al. 2015). Węsławski et al. (2010) classified *M. oculata* as a pelagic suspension feeder with Arctic distribution. Maximum size found for any cogener was 30 mm (Keast & Lawrence 1990).	(Rudstam et al. 1989, Keast & Lawrence 1990, Richoux et al. 2004, Węsławski et al. 2010, Drits et al. 2015)	
Nymphon hirtipes		Suctorial predators that feed by puncturing a hole in prey and sucking out fluid through a probiscus. Feed on sessile, small-sized prey such as hydrozoans, alyconarians, and bryozoans (Arnaud & Bamber 1987). Macdonald et al. (2010) classified *Nymphon* spp. generally as freely motile, carnivorous predators that feed on macrofauna at the sediment surface. Adult size reported by Mercier et al. (2015) was 55 mm. Mercier et al. (2015) observed adults feeding on sea anemones, nudibranchs, and possibly coral polyps in the laboratory. Large sponges did not die after feeding. Juveniles ate colonial hydroid polyps. Richards & Fry (1978) reported observing polar *Nymphon* spp. consume detritus and dead amphipods.	(Richards & Fry 1978, Arnaud & Bamber 1988, Macdonald et al. 2010, Mercier et al. 2015)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Onisimus plautus		Very little species-specific information found. Functional group and trophic trait classifications are based mostly on cogeners. Fatty acid and stable isotope data reported by Nygård et al. (2012) suggested some *Onisimus* spp. are somewhat herbivorous (*O. Caricus* and *O. nanseni*), and *O. litoralis* was primarily herbivorous. Legezyńska et al. (2012) reported that some *Onisimus* spp. are sympagic. Boudrias and Carey (1988) found that *Onisimus plautus* occurred only in the sediment as opposed to some other *Onisimus* spp. that were also found near the ice. In a study of symapgic fauna in the Beaufort Sea, Carey (1992) found that the sympagic amphipod community was primarily comprised of benthic species, including *O. littorialis*, but did not mention *O. plautus*. Size of 25 mm based on sizes for cogeners reported in Węsławski et al. (2010).	(Boudrias & Carey 1988, Carey 1992, Węsławski et al. 2010, Legeżyńska et al. 2012, Nygård et al. 2012)	
Paraeuchaeta sp.	Pelagic Carnivore	Predatory pelagic copepod genus. Adult *Paraeuchaeta* spp. occupy bathypelagic zones of the water column, but in polar regions have also colonised shallower epipelagic depths (Fleddum 2001, Auel & Hagen 2005). For example, adult *P. norvegica* in the Norwegian Sea were most abudant between 400 and 500 m, whereas younger life stages were most abundant between 100 and 300 m (Fleddum et al. 2001). *Paraeuchaeta* spp. are tactile predators that prey on moving animals such as other mesozooplankton, especially copepods, and fish larvae (Fleddum et al. 2001, reviewed in Auel & Hagen 2005). Vertical migration does occur, but in the summer they do not occupy the upper 100 m of the water column such that they do not coincide with copepod prey (Fleddum 2001). Iken et al. (2005) reported stable isotope values that indicated this genus is predatory.	(Fleddum et al. 2001, Auel & Hagen 2005, Iken et al. 2005)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Rhachotropis aculeata		Węsławski et al. (2010) classified this species as a motile carnivore with Arctic distribution. Stable isotope values and fatty acid profiles reported by Legeżyńska et al. (2012) suggest carnivory with a mix of benthic and pelagic diets items. The authors review the literature on feeding for *R. aculeata* and describe the species as far-ranging and a strong swimmer (based on Sainte-Marie & Brunel 1985). Legeżyńska et al. (2012) suggest pelagic crustaceans may be an important part of the diet. High levels of phytoplankton-derived fatty acid markers suggest strong links to pelagic production. Size of 28 mm was maximum found in literature, from Węsławski et al. (2010).	(Sainte-Marie & Brunel 1985 referenced in Legeżyńska et al. 2012, Węsławski et al. 2010, Legeżyńska et al. 2012)	
Rhachotropis sp.		Functional group and trophic trait classifications are based on cogeners. See also *R. aculeata*. Size of 17 mm reported in Connelly et al. (2014).	(Connelly et al. 2014)	
Sabinea septemcarinata	Benthic Carnivore	Most stomachs observed by Squires (1968) contained phytobenthos and detritus. However, some specimens had foramineriferans, small gastropods, and polychaetes in their stomachs. Graeve et al. (1997) also observed fatty acid biomarkers indicative of diatoms in a number of decapods including this species, but based on previous knowledge of predatory behaviour and high proportions of carnivory biomarkers, the authors suggested the diatom markers may have been transferred through prey. Fatty acid markers in McGovern (2016) suggested that this species is probably reliant much on bacteria, phytodetrutis, or small benthic organisms that eat those food sources. Zimina et al. (2015) classified this species as a circumpolar Arctic and high-boreal species. Węsławski et al. (2010) classified this species as a motile carnivore with Arctic distribution. Size of 91 mm reported by Pollock (1998).	(Squires 1968, Graeve et al. 1997, Pollock 1998, Birkely & Gulliksen 2003, Węsławski et al. 2010, Zimina et al. 2015, McGovern 2016)	
Saduria sabini	Benthic Carnivore	Euryhaline species. *Saduria* spp. generally act as omnivores and predators according to review by Percy (1983). Premke et al. (2003) observed this species scavenging on bait in deep-sea experiment, indicating chemoreceptivity. Size of 102 mm reported in Bray (1962).	(Bray 1962, Percy 1983, Premke et al. 2003)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Saduria sibirica	Benthic Carnivore	Euryhaline species. *Saduria* spp. act as both omnivores and predators according to short review by Percy (1983). See also cogener *S. sabini*. Size of 102 mm reported in Bray (1962).	(Bray 1962, Percy 1983)	
Sclerocrangon boreas		Birkely & Gulliksen (2003) observed a high diversity of foods in the stomachs of *S. boreas*, making it the most opportunistic of the shrimp they observed. Diet included polychaetes (highest proportion), amphipods (second highest proportion), molluscs, and hydrozoa. Males had more epibenthic diets while females had more infaunal diets. Zimina et al. (2015) reported *S.boreas* as a circumpolar Arctic, high-boreal species. Węsławski et al. (2010) classified this species as a motile carnivore with Arctic distribution. Squires (1968) observed mostly phytobenthos and detritus but also found some ostracads, euphasiids, copepods, small gastropods, and polychaetes in stomachs. Graeve et al. (1997) observed fatty acid markers indicative of diatoms in a number of decapods including this species, but based on previous knowledge of predatory behaviour and high proportions of carnivory biomarkers, the authors suggested the diatom markers may have been transferred through prey. Largest size found was 129 mm.	(Squires 1968, Graeve et al. 1997, Birkely & Gulliksen 2003, Węsławski et al. 2010, Zimina et al. 2015)	
Sclerocrangon ferox	Benthic Carnivore	No species-specific information found for this species, but high proportions of carnivory biomarkers were observed by Graeve et al. (1997). Birkley & Gulliksen (2003) observed high diet variability in another *Sclerocrangon* sp. Squires (1968) observed mostly phytobenthos and detritus in stomachs but also found some ostracads, euphasiids, copepods, small gastropods, and polychaetes in the stomach of cogener *Sclerocrangon boreus*. Zimina et al. (2015) reported *S. ferox* as a circumpolar Arctic, high-boreal species. No size information found, but images on WoRMS and the Arctic Megabenthos Database suggest they can get at least 70 mm. See also size from cogener *S. boreas*.	(Squires 1968, Graeve et al. 1997, Birkely & Gulliksen 2003, Zimina et al. 2015)	Arctic Megabenthos Database ; WoRMS

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Synidotea bicuspida	Benthic SDF	Macdonald et al. (2010) classified *Synidotea* spp. generally as herbivorous browsers that feed by tearing or gathering particular items at the surface, and that consume macrofaunal algae. Image with size guide on the Barcode of Life database suggests a size of at least about 25 mm. Morris et al. (1980) claimed this species only reached size of 12 mm in its southern range near California.	(Morris et al. 1980, Macdonald et al. 2010)	Barcode of Life
Synidotea sp.	Benthic SDF	Macdonald et al. (2010) classified *Synidotea* spp. generally as herbivorous browsers that feed by tearing or gathering particular items, and that feed at the sediment surface on macrofaunal algae.	(Macdonald et al. 2010)	
Themisto abyssorum	Pelagic Carnivore	Carnivorous predator of zooplankton. Fatty acid biomarkers observed by Auel et al. (2002) suggested this species had a higher trophic level than *T. libellula* and occurred deeper in the water column where it may feed on some omnivorous or carnivorous prey. Biomarker data in Søreide et al. 2013 support pelagic carnivory. Węsławski et al. (2010) classified this species as a pelagic carnivore.	(Auel et al. 2002, Węsławski et al. 2010, Søreide et al. 2013)	
Themisto libellula	Pelagic Carnivore	Carnivorous predator of zooplankton. Fatty acid biomarkers observed by Auel et al. (2002) suggest predation mainly on herbivorous *Calanus* spp., and a close association with sympagic production. Lower trophic level than *T. abyssorum* is also in agreement with the notion that this species relies on herbivorous prey while *T. abyssorum* probably relies to some degree on omnivorous/carnivorous prey. Węsławski et al. (2010) classified this species as a pelagic carnivore.	(Auel et al. 2002, Węsławski et al. 2010, Søreide et al. 2013)	
Thysanoessa inermis	Pelagic Herbivore	Generally herbivorous, and likely a more truly polar life cycle than *Thysanoessa rashii* because it relies solely on lipid reserves during the winter (reviewed in Smith 1991). Sameoto (1980) observed a small percentage of stomachs contained copepod remains, but mostly algae. Węsławski et al. (2010) classified this species as a pelagic herbivore.	(Sameoto 1980, Smith 1991, Węsławski et al. 2010)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Thysanoessa raschii	Pelagic Herbivore	Composition of lipids suggests that it relies to some degree on omnivory (animal prey and detritus) during the winter, but during the productive season mostly relies on herbivory. Sameoto (1980) observed a small percentage of stomachs contained copepod remains, but mostly algae. Węsławski et al. (2010) classified this species as a pelagic herbivore.	(Sameoto 1980, Falk-Petersen et al. 1982, Smith 1991, Węsławski et al. 2010)	
Tmetonyx sp.		*Tmetonyx* spp.are scavenging amphipods. Premke et al. (2006) observed them as one of the abundant scavengers feeding at large food falls, and they were attracted to baited traps near Svalbard (see references in Connelly et al. 2014). These observations suggest they can swim far distances in search of food. Marine Species Identification Portal has sizes for two *Tmetonyx* spp. (*cicada* = 25 mm, *similis* = 15 mm), both of which have circumpolar distributions. Fatty acid biomarkers in Connelly et al. (2014) and Graeve et al. (1997) suggest a scavenging lifestyle, which is a general characteristic of Lysianassid amphipods (see short review and references in Discussion of Connelly et al. 2014).	(Graeve et al. 1997, Premke et al. 2006, Connelly et al. 2014)	Marine Species Identification Portal
Brachiopoda				
Brachiopoda		Macdonald et al. (2010) classified Brachiopoda generally as sessile, epibenthic omnivores that use suspension-feeding to feed on phytoplankton. Live attached to hard substrate. Taxonomic classification too broad to assign a size.	(Macdonald et al. 2010)	
Bryozoa				
Alcyonidium spp.		According to the Smithsonian Institute website, *Alcyonidium* sp. is an encrusting bryozoan, having gelatinous colonies. Suspension feeder that filters phytoplankton from the water column. Kukliński & Porter (2004) describe *A. disciformes* as the only free-living species of Arctic bryozoan. Since our specimens were not identified as this unique species, our specimens are likely one of the encrusting species. Taxonomic classification was too broad to estimate maximum body size.	(Kukliński & Porter 2004)	Smithsonian Institute (http://www.sms.si.edu/irlspec/alcyon_sp.htm), Marine Species Identification Portal

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Cephalorhyncha				
Priapulopsis bicaudatus		Schmidt-Rhaesa (2013) discussed that Priapulida in general are burrowers, and reported longest trunk size for *P. bicaudatus* as 100 mm. Also suggested that Priapulida are predators that "plough through muddy sediments in search of food", but no specific prey items given. Macdonald et al. (2010) describe Priapulids generally as mobile, burrowing predatory carnivores that feed subsurface on meiofauna.	(Macdonald et al. 2010, Schmidt-Rhaesa 2013)	
Chaetognatha				
Chaetognatha	Pelagic Carnivore	Chateognaths are important pelagic predators that prey mostly on copepods, and Generally, prey size increases with chaetognath body size (Pearre 1980).	(Pearre 1980)	
Eukrohnia hamata	Pelagic Carnivore	This species occurs mostly below the upper mixed layer in the water column (Sullivan 1980). Preys mostly on copepods. Stable isotope data reported in Iken et al. (2005) suggest carnivory. Generally, prey size increases with chaetognath body size (Pearre 1980).	(Pearre 1980, Sullivan 1980, Iken et al. 2005)	
Parasagitta elegans	Pelagic Carnivore	Pelagic carnivore that lives and feeds mostly in the upper 25 m of the water column where prey densities are high (Sullivan 1980). Preys mostly on copepods (Sullivan et al. 1980). Generally, prey size increases with chaetognath body size (Pearre 1980). Biomarkers reported in Søreide et al. (2013) agree with carnivory.	(Pearre 1980, Sullivan 1980, Søreide et al. 2013)	
Chordata				
Amblyraja hyperborea	Benthic Carnivore	Feeds on some benthic crustaceans (krill, decapods, amphipods) but mostly on fish. Pelagic fish have been found in stomachs in Norwegian/Barents Seas, but may be the result of scavenging waste from the fish industry. Some evidence for water column feeding. Discussion with S. Atchison (DFO, Canada) indicated the Beaufort Sea population fed heavily on mysids and may switch to larger prey including fish as they grow, but current evidence points to very slow maturation rates and mostly benthic feeding. Peklova (2012) suggested that Arctic skates may switch between benthic and pelagic feeding modes. Coad and Reist (2004) report a distribution throughout Arctic Canada, as well as in the northern Atlantic and Eurasia. Coad and Reist (2004) report 870 mm as the maximum recorded body size, but Byrkjedal et al. (2015) report a female with 903 mm total length.	(Bjelland et al. 2000, Coad & Reist 2004, Peklova 2012, Byrkjedal et al. 2015, S. Atchison, DFO Canada, pers.comm.)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Anisarchus medius	Benthic Carnivore	Feeds on amphipods, copepods, and polychaetes. Norcross et al. (2009) found prey were primarily benthic. Nematodes were eaten by fish > 50 mm. Mainly harpactacoid copepods for all size classes. Increasing consumption of gamarid amphipods with size. Maximum known length reported by Mecklenburg et al. (2007) is 180 mm.	(Mecklenburg et al. 2007, Norcross et al. 2011)	
Artediellus uncinatus	Benthic Carnivore	Feed on invertebrates. Whitehouse et al. (2017) classified another *Artedellius* sp. (*scaber*) as a Gammerid consumer.	(Coad & Reist 2004, Whitehouse et al. 2017)	
Ascidia obliqua		Jorgensen et al. (1984) describe the mucous-net filter feeding of this species as highly efficient at capturing small particles. Macdonald et al. (2010) describe Ascidiacea generally as epibenthic , sessile attached omnivores that use suspension feeding to feed on POM and phytoplankton. According to the Marine Species Identification Portal, this species can be up to 80 mm long. Lives attached to a hard substrate by the base and left side. Nearly circumpolar distribution.	(Jørgensen et al. 1984, Macdonald et al. 2010)	Marine Species Identification Portal
Aspidophoroides olrikii	Benthic Carnivore	Feeds on benthic amphipods, polychaetes, bivalves, gastropods. Note: formerly known as *Ulcina olrikii.* Under this older name, Whitehouse et al. (2017) classified this species as a Gammarid consumer. Cui et al. (2012) found mostly benthic amphipods in stomachs, and large numbers of bivalve siphons and crabs. Fatty acid and stable isotope data in Giraldo et al. (2015), along with dietary literature reviews, suggested this species is a low-trophic benthic feeder with a preference for bivalves and molluscs.	(Atkinson & Percy 1992, Cui et al. 2012, Giraldo et al. 2016, Whitehouse et al. 2017)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Benthosema glaciale	Benthopelagic Carnivore	Feeds on copepods, amphipods, chaetognaths, gastropods, polychaetes. Vertical migrator. Increasing prey size and diversity with fish size. Dypvik et al. (2012) reported that most individuals occupied waters deeper than 200 m, but displayed vertical migrations. Individuals 2+ years migrated up to depths between 270-200 m in daytime and descended below 270 m at night. Stomach contents revealed increased daytime feeding on overwintering *Calanus* spp. Review in Dypvik et al. (2012) indicates that this species feeds mainly on *Calanus* spp. and other plankton. García-Seone et al. (2013) point out that although this species feeds mainly on pelagic planktonic crustaceans, benthic prey such as gastropods and polychaetes are also found in stomachs. Although there was increased use of amphipods with increasing size, the smallest size classes (31-40 mm) still mostly fed on pelagic prey	(Sameoto 1988, Dypvik et al. 2012, García-Seoane et al. 2013)	
Boreogadus saida	Pelagic Carnivore (< 80 mm) / Benthopelagic Carnivore (> 80 mm)	According to Cui et al. (2012), small cod (total length 70-110 mm) mainly consumed calanoid copepods followed by euphasids and oedicerotid amphipods. Large cod (total length 140-220 mm) consumed mainly amphipods including both benthic (Ampeliscidae and Lysianassidae) and pelagic (Hyperidae) taxa. They also consumed fish, and euphausids were secondarily important behind fish and amphipods. Differences between size groups were significant. Matley et al. (2013) found no overlap between fish with fork length > 185 mm and those with smaller fork length based on Schoener's index (percent compositon of prey sizes). There was no overlap between 4 size classes (fork length of 56-93, 123-159, 160-183, 185-256 mm) when prey items rather than prey size were the variable used in Schoener's Index. Stable isotopic niche analysis, however, showed that only the smallest size class appeared significantly separated from the other size classes. Norcross et al. (2009) found evidence for mostly pelagic diets, with some benthic amphipods. All cod < 75 mm ate mostly calanoid copepods. Cod > 75 mm also consumed gammarid and hyperiid amphipods, euphasiids, and fish. Walkusz et al. (2013) observed that demersal Arctic Cod with standard length < 80 mm generally consumed strictly pelagic zooplankton, while adults occupied deeper waters and consumed more mysids and amphipods. Geoffroy et al. (2011) used	(Geoffroy et al. 2011, Norcross et al. 2011, Cui et al. 2012, Matley et al. 2013, Walkusz et al. 2013, Majewski et al. 2016)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
		hydroacoustics to show that age 0 cod occupied surface waters and eventually descended to deeper demersal habitats as they grew.		
Careproctus mollis		No species-specific dietary information found. Functional group and trophic trait classifications are based on cogeners. See also *C. rastrinus*, *C. reinhardti*, and *Careproctus* sp. Size reported on FishBase is 74 mm, but BREA MFP caught an individual with standard length of 82 mm.		FishBase
Careproctus rastrinus		Laboratory observations of feeding behaviour revealed this species uses rays on its pectoral fins to search for food in the sediment surface (Sakurai and Kido 1992). Glubokov (2010) reported observations within the northern Pacific and Pacific-Arctic areas. Individuals observed off the coast of Japan fed mostly on gammarid amphipods, with smaller contributions from hermit crab, polycheates, euphasiids, copepods, large decapods (Pandalidae), and fish (Glubokov 2010). Napazakov & Chuchukalo (2005) report a dietary dominance of amphipods and *Pandalus borealis* in waters off Kamchatka, with smaller contributions from other decapods, *Actiniaria* spp, cheatognaths, bivalves, octopus, fish, and fish eggs. The importance of decapods increased with size. Size of 510 mm reported on FishBase.	(Sakurai & Kido 1992, Napazakov & Chuchukalo 2005, Glubokov 2010)	FishBase
Careproctus sp.		Functional group and trophic trait classifications are based on feeding information for cogeners. See also *C. rastrinus* and *C. mollis*. Size taken as maximum potential body size reported for other *Careproctus* spp. caught in the beam trawl nets of the BREA program (*C. rastrinus*).		
Cottunculus microps		Coad & Reist (2004) reported benthic feeding on polychaetes, crustaceans, and sea spiders. Houston & Haedrich (1986) reported finding euphasiids, amphipods (most common), cumaceans, polychaetes, and molluscs in stomachs of individuals from the Grand Banks. The authors concluded diet primarily consisted of benthic organisms. Bjelland et al. (2000) reported diets dominated by benthic prey, mostly pycnogonids and polychaetes, but also hyperbenthic amphipods. Both Mecklenburg et al. (2013) and Coad & Reist (2004) reported Arctic-Atlantic distributions. Size of 300 mm reported by Coad & Reist (2004)	(Houston & Haedrich 1986, Bjelland et al. 2000, Coad & Reist 2004, Mecklenburg et al. 2013)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Cyclopteridae		Functional group and trophic trait classifications are based on information for cogeners. See also *Eumicrotremus derjugini* and *E. spinosus*. Size of 132 mm taken as maximum size observed for other Cyclopteridae caught in beam trawl nets (*E. spinosus*).		
Eumicrotremus derjugini	Benthic Carnivore	Feeds on benthic crustaceans and oikopleura. See also cogener *Eumicrotremus spinosus*.	(Coad & Reist 2004)	
Eumicrotremus spinosus	Benthopelagic Carnivore	Feeds on benthic crustaceans, oikopleura, and fishes. Berge et al. (2013) found almost exclusively *Themisto libella* in stomachs near Svalbard, regardless of size class. Other lumpsuckers also make vertical migrations.	(Coad & Reist 2004, Berge & Nahrgang 2013)	
Gymnelus hemifasciatus	Benthic Carnivore	No species-specific information found. Functional group and trophic trait classifications are based on feeding information for cogeners listed in Coad & Reist (2004), which are benthic and eat clams, crustaceans, and worms.	(Coad & Reist 2004)	
Gymnocanthus tricuspis	Benthic Carnivore	Atkinson & Percy (1992) identified 86 invertebrate species in stomachs. Mostly benthic amphipods, some polychaetes, cumaceans, and cropped siphons from bivalves. Fish have been observed. Generalist benthic feeder according to fatty acid and stable isotope analyses in Giraldo et al. (2016). Whitehouse et al. (2017) classified this species as a Gammarid consumer. Norcross et al. (2009) found prey in stomachs were primarily benthic. Fish of all length classes ate gammarid amphipods. Fish > 51 mm mainly ate gammarid amphipods and demersal polychaete worms, and some pelagic euphasiids. Cui et al. (2012) found benthic amphipods were the most important prey item with Ampeliscidae being the most common. Polychaetes were secondarily important, followed by significant numbers of cropped bivalve siphons.	(Atkinson & Percy 1992, Coad & Reist 2004, Norcross et al. 2011, Cui et al. 2012, Giraldo et al. 2016, Whitehouse et al. 2017)	
Icelus bicornis	Benthic Carnivore	Atkinson & Percy (1992) observed over 91 prey species in stomachs. Amphipods were most abundant in stomachs, but stomachs also contained isopods and some copepods (*Calanus* spp.)	(Atkinson & Percy 1992)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Icelus sp.		No genus-specific information found. Functional group and trophic trait classifications are based on feeding information for cogeners (see also *Icelus spatula* and *I. bicornis*).		
Icelus spatula	Benthopelagic Carnivore	Most prevalent prey items in stomachs were mysids (*Erythrops* sp.), cumaceans, and amphipods (Atkinson & Percy 1992) Reportedly seen feeding on plankton 1 m below surface. Worms and molluscs also reported as prey by Coad & Reist (2004). Whitehouse et al. (2017) classified this species as a Gammarid consumer.	(Atkinson & Percy 1992, Coad & Reist 2004, Whitehouse et al. 2017)	
Leptagonus decagonus	Benthopelagic Carnivore (< 85 mm) / Benthic Carnivore (> 85 mm)	This species fed mainly on copepods in a Norwegian fjord (Källgren et al. 2015), but stable isotopes and fatty acid profiles measured by Giraldo et al. (2015) in the Beaufort Sea indicated a mid-trophic benthic carnivore. Tamelander et al. (2006) classified this species as benthopelagic based on Pethon (1998). Källgren et al. (2015) found that the smallest individuals (50-85 mm) fed mainly on copepods and amphipods. Larger individuals (140-180 mm) included similar proportions of calanoid copepods, amphipods, and other large crustaceans such as the decapod *P. borealis* and krill. The two size classes had significantly different diets according to Schoener's index.	(Tamelander et al. 2006, Källgren et al. 2015, Giraldo et al. 2016)	
Liparidae		No feeding information found for the general family level. Functional group and trophic trait classifications are based on cofamilials, the majority of which prey on a mixture of benthic and pelagic species. See also *Careproctus rastrinus*, *C. reinhardtii*, and *L. tunicatus*. Size of 524 mm taken as the maximum size for other Liparidae spp. caught in the beam trawl (*Liparis gibbus*).		
Liparis fabricii	Benthic Carnivore	Benthic. Feeds mostly on crustaceans and worms.	(Coad & Reist 2004)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Liparis sp.	Benthopelagic Carnivore	Not much genus-specific information found. Functional group and trophic trait classifications are largely based on feeding information for cogeners. See also *Liparis fabricii* and *Liparis tunicatus*. Cui et al. (2012) found that benthic amphipods were the most important prey for general Liparidae spp. Most common amphipod prey in stomachs were Ampeliscidae followed by Lysianassidae and Melitidae.	(Cui et al. 2012)	
Liparis tunicatus	Benthopelagic Carnivore	Feeds on crustaceans (Coad & Reist 2004), but stable isotope values from the thesis show it clearly falls within the benthopelagic guild of fishes. Whitehouse et al. (2017) classified this species as a Gammarid consumer. Size of 200 mm reported by Coad & Reist (2004).	(Coad & Reist 2004, Whitehouse et al. 2017, data from this thesis)	
Lumpenus fabricii	Benthic Carnivore	Atkinson & Percy (1992) observed 86 prey species in stomachs, dominated by polychaetes. Amphipods were of secondary importance, as well as cropped siphons from *Macoma* spp. and small crustaceans. Whitehouse et al. (2017) classified this species as a Gammarid consumer in the Chukchi Sea. Size of 365 mm reported by Coad & Reist (2004).	(Atkinson & Percy 1992, Coad & Reist 2004, Whitehouse et al. 2017)	
Lycodes adolfi	Benthic Carnivore	Feeds on polychaetes, some fish, and crustaceans (Coad & Reist 2004). High number of diet items, highly variable diets, and heavy reliance on demersal prey suggests generalist benthic diet. Fatty acid and stable isotope analyses in Giraldo et al. (2016) indicated it was a benthic consumer.	(Coad & Reist 2004, Giraldo et al. 2016)	
Lycodes eudipleurostictus		Bjelland et al. (2000) review feeding literature for this species, and found stomachs contained polychaete fragments, *Themisto libellula*, and a mixture of other benthic prey (brittle stars, isopods, polychaetes, priapulids) and pelagic prey (other *Themisto* spp., carideans). Coad & Reist (2004) classified this species as benthic, and reported feeding on crustaceans. Circumpolar distribution reported by both Coad & Reist (2004) and Mecklenburg et al. (2013). Size of 450 mm reported by from Coad and Reist (2004).	(Bjelland et al. 2000, Coad & Reist 2004, Mecklenburg et al. 2013)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Lycodes pallidus	Benthic Carnivore	Feeds on polychaetes, crustacean fragments, amphipods, and molluscs (Bjellend et al. 2000). Size of 287 mm reported by Coad & Reist (2004).	(Bjelland et al. 2000, Coad & Reist 2004)	
Lycodes polaris	Benthic Carnivore	Feeds on isopods and some copepods (Coad & Reist 2004). Previously reported to eat bivalves and cropped siphons from *Macoma* spp., but no evidence for it in the Beaufort Sea from fatty acid and stable isotope data reported by Giraldo et al. (2016), and little evidence for *Macoma* in the diet reported by Dissen (2015). Whitehouse et al. (2017) classified this species as a Gammarid consumer in the Chukchi Sea. Norcross et al. (2009) found that fish of all length classes ate gammarid amphipods, and fish > 51 mm also ate fish.	(Coad & Reist 2004, Norcros et al. 2009, Dissen 2015, Giraldo et al. 2016, Whitehouse et al. 2017)	
Lycodes rossi	Benthic Carnivore	Feeds on decapods, benthic amphipods, polychaetes, and clams. Size of 380 mm reported by Coad & Reist (2004).	(Dolgov 1994, Coad & Reist 2004)	
Lycodes sagittarius	Benthic Carnivore	High number of diet items, highly variable diets, and heavy reliance on demersal prey suggests generalist benthic diet. Poster presented by S. Aspens (MSc., University of Alaska Fairbanks) reported that polychaetes, benthic amphipods, brittle stars, and harpacticoid copepods composed a large part of the diet in the Alaskan Beaufort Sea (abstract available from ASLO Ocean Sciences Meeting, but thesis not available at the time this database was compiled). Diet for *L. Sagittarius* was correlated with longitude and depth (S. Aspens). Size of 273 mm reported on FishBase.	(Coad & Reist 2004)	FishBase, S. Aspens abstract from ASLO Ocean Sciences Meeting 21-26 Feb 2016 available at: https://agu.confex.com/agu/os16/preliminaryview.cgi/Paper92722.html)
Lycodes seminudus	Benthic Carnivore	Feeds on bivalves, molluscs, brittle stars, polychaetes, and fish. Mid- to high-trophic benthic generalist according to stable isotope and fatty acid analyses reported by Giraldo et al. (2016). High number of diet items, highly variable diets, and heavy reliance on demersal prey suggests generalist benthic diet. Size of 560 mm reported by Coad & Reist (2004).	(Coad & Reist 2004, Giraldo et al. 2016)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Lycodes sp.		Functional group and trophic trait classifications are based on cogeners. Hildebrandt et al. (2011) briefly review the ecology of Zoarcidae (eelpouts), including their preference for deep soft bottom habitats at the outer shelves and slopes and cold temperatures. Hildebrandt et al. (2011) also review the feeding habits of cogeners *L. squamiventer* and *L. frigidus*, indicating that both are benthic carnivores that eat benthic fauna including polychaetes, crustaceans, ophiuroids, molluscs, sipunculids, gastropods, amphipods, copepods, and sometimes fish. See also *L. eudipleurostictus*, *L. pallidus*, *L. rossi*, *L. sagittarius*, and *L. seminudus*. Size of 560 mm taken as maximum size observed for other *Lycodes* spp. caught in beam trawls (see *L. seminudus*).	(Hildebrandt et al. 2011)	
Lycodes squamiventer	Benthic Carnivore	Growth rates increase with increasing temperature, but maximum age declines with temperature (Hildebrandt et al. 2011). Prefers soft-bottom habitats and is mostly recorded between 700 and 1800 m depths at subzero temperatures (Andriyashev 1986, Møller 2001; referenced in Hildebrandt et al. 2011). Stable isotope data and stomach contents observed by Gebruk et al. (2003) supported benthic carnivory on benthic fauna including pogonophores, gastropods, amphipods, polychaetes, and copepods. Maximum size reported was 260 mm.	(Gebruk et al. 2003, Hildebrandt et al. 2011 & references therein)	
Reinhardtius hippoglossoides	Benthopelagic Carnivore	Euphasids were important for young (< 200 mm) Halibut, otherwise squid and fish, including Zoarcidae, Capelin, and Arctic Cod were important prey. Some cannibalism reported. Hovde et al. (2002) found that spatial and temporal factors were more important in determining diet than biotic variables such as predator size, maturity, and sex. Hovde et al. (2002) found some clear ontogenetic shifts on the slope where smaller Greenland Halibut (< 500 mm) preyed mostly on cephalopods and crustaceans while larger specimens fed more on fish. Smaller fish appeared to be foraging at greater depths than larger fish (< 700 m). Much literature confirms carnivorous diet on benthic invertebrates and fish, as well as foraging migrations to the upper water column for benthopelagic prey. Maximum size of 1190 mm reported by Coad & Reist (2004).	(Rodríguez-Marín et al. 1995, Jørgensen 1997, Michalsen & Nedreaas 1998, Bjelland et al. 2000, Hovde et al. 2002, Coad & Reist 2004)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Stichaeidae		No general diet information found for family level. Diet and size inferred from cofamilials (see also *Lumpenus fabricii*). Size taken as 365 mm.		
Triglops nybelini	Benthopelagic Carnivore	Ottesen (2004) found crustaceans and some fish in stomachs, with evidence for possible cannibalism in Norwegian waters. Otherwise, see cogener *Triglops pingelii*. Stable isotope values from this thesis indicate *T. nybelini* clearly falls within the benthopelagic fishes guild. Size of 200 mm reported on FishBase, which was larger than that reported by Coad & Reist (2004).	(Coad & Reist 2004, Ottesen 2004)	FishBase
Triglops pingelii	Benthopelagic Carnivore	Feeds on zooplankton, *Mysis relicta*, amphipods, *Themisto libellula*, *Calanus glacialis*, *Thysanoessa inermis*, and *Sagitta elegans* according to Atkinson & Percy (1992). Some fish in diet also reported by Coad & Reist (2004). Whitehouse et al. (2017) classified this species as a benthic invertebrate consumer. Size of 202 mm reported by Coad & Reist (2004).	(Atkinson & Percy 1992, Coad & Reist 2004, Whitehouse et al. 2017)	
Cnidaria				
Actiniaria	Benthic Carnivore	Sea anemone. Generalist, carnivorous predator that consumes a wide variety of animals from algae to invertebrates (Acuna & Zamponi 1995). Macdonald et al. (2010) classified Actiniaria generally as motile, free-living, animals that feed at the sediment surface on macrofaunal prey (>500 μm). Stable isotope values for Actinaridae reported by Søreide et al. (2013) suggest a mid-trophic carnivore, but a potential reliance on phytoplankton-derived carbon sources. Taxonomic classification is too broadly defined to pinpoint a body size.	(Acuña & Zamponi 1995, Macdonald et al. 2010, Søreide et al. 2013)	
Aglantha digitale	Pelagic Carnivore	Ambush predator that feeds while drifting. Consumes copoepods and eggs of other pelagic predators.	(Matsakis & Conover 1991, Colin et al. 2003)	
Catablema vesicarium	Pelagic Carnivore	Preys on fish larvae, with some evidence for feeding on plankton.	(de Lafontaine & Leggett 1988)	
Lafoeidae		Macdonald et al. (2010) classified Lafoeidae as sessile, epibenthic carnivores that feed on zooplankton using suspension feeding. They live attached. Size of 100 mm reported on the Encyclopedia of Marine Life of Britain and Ireland database.	(Macdonald et al. 2010)	Encyclopedia of Marine Life of Britain and Ireland

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Nephtheidae		Imbs et al. (2016) studied the fatty acid profiles of cold water corals for the first time and found that species in the Nephtheidae family likely fed opportunistically from a variety of food sources, including particulate organic matter and phytoplankton/phytodetritus that is likely advected from shallower habitats or the upper water column. The authors explain that in the absence of zooxanthellae, some species of soft corals rely entirely on heterotrophy.	(Imbs et al. 2016)	
Zoanthidae		Review by Kenchington et al. (2012) describes Arctic corals as sessile, benthic suspension feeders.	(Kenchington et al. 2012)	
Ctenophora				
Beroe cucumis	Pelagic Carnivore	Prefers *Mertensia ovum*. Probably cannot digest crustaceans, so relies on other gelatinous prey.	(reviewed in Falk-Petersen et al. 2002)	
Mertensia ovum	Pelagic Carnivore	Opportunistic plankton feeder, but prefers calanoid copepods (*Calanus* spp. in Svalbard waters).	(reviewed in Falk-Petersen et al. 2002)	
Echinodermata				
Asteriidae		Jangoux (1982) describes Asteroidea as mostly benthic predators that will occasionally eat carrion. Size and trophic traits estimated from cofamilials (see also *Lepasterias* sp. and *Urasterias linckii*).	(Jangoux 1982)	
Crossaster papposus		A study of echinoderm predators in commercial sea scallop beds in Iceland identified that *C. papposus* fed mostly on other echinoderms such as sea urchins and sea cucumbers (Zolotarev 2002). Gale et al. (2015) found that *C. papposus* and *Lepasterias* spp. were commonly associated with invertebrates known to be asteroid prey, such as *Strongylocentrotus* spp., ophiuroids, holothuroideans, and bivalves. Other observations of preatory behaviour on various benthic invertebrate prey are found in Himmelman and Dutil (1991), Mauzey et al. (1968) and Mortensen (1927). Deja et al. (2016) classified this species as a boreal-Arctic carnivore, omnivore, and scavenger that prefers rocky bottom. Size reported on the Marine Species Identification Portal was 340 mm, but the 178 mm reported by Pollock (1998) was more typical of the specimens observed in this thesis.	(Mortensen 1927, Mauzey et al. 1968, Himmelman & Dutil 1991, Pollock 1998, Zolotarev 2002, Gale et al. 2015, Deja et al. 2016)	Marine Species Identification Portal

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Ctenodiscus crispatus	Benthic SDF	Combined use of stable isotopes and stomach contents by Gale et al. (2013) suggested this species is a mud ingester and infaunal predator. Macdonald et al. (2010) classified *C. crispatus* as an omnivorous, motile detrivore that feeds on sediment, microfauna and diatoms. Søreide et al. (2013) classified it as a carnivore, and stable isotope values indicated a high trophic level of 3.3. Gale et al. (2015) observed its infaunal burrowing behaviour directly using ROV surveys. Shick et al. (1981) conducted a thorough study of deposit feeding in this species and concluded that it subsides off POM in detritus, and likely much nutrition comes from bacteria in the sediment. Deja et al. (2016) classified this species as a boreal-Arctic deposit feeder that prefers mixed sediment and mud. Size of 50 mm reported on Arctic Megabenthos database.	(Shick et al. 1981, Jangoux 1982, Gale et al. 2013, 2015, Søreide et al. 2013, Deja et al. 2016)	Arctic Magebanthos database
Cucumaria sp.		No genus-specific feedinf information found. Functional group and trophic traits are inferred from cogeners. In the St. Lawrence estuary, Hamel and Mercier (1998) observed distinct seasonal feeding cycles in *Cucumaria frondosa* with most feeding occurring in spring and summer. They found *C. frondosa* ate mostly phtoplankton cells, and occasionally ate small crustaceans, eggs, and larvae. Fish (1967) reported that *C. elongata* was a suspension feeder, using its tentacles to gather suspended particulate matter. Many other studies available on the suspension-feeding behaviour of *C. elongata* and *C. frondosa*. Fankboner (1978) provides a good review of how various *Cucumaria* spp. use suspension feeding to feed on small planktonic crustaceans and diatoms. Size of 152 mm based on that reported for *C. frondosa* by Pollock (1998).	(Fish 1967, Fankboner 1978, Hamel & Mercier 1998, Pollock 1998)	
Eupyrgus scaber	Benthic SSDF	No species-specific diet information found. Diet and trophic trait classifications are inferred from coarser taxonomic levels. Massin et al. (1982) state that Molpadida are generally conveyor-belt feeders that ingest sediment to extract nutrition. Macdonald et al. (2010) classified Dendrochirotidae spp. generally as disceretly motile omnivores that feed via detrivory on sediment, POM, microfauna, and diatoms. Deja et al. (2016) classified this species uncertainly as a deposit feeder with boreal-Arctic distribution.	(Massin 1982, Macdonald et al. 2010, Deja et al. 2016)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Gorgonocephalus arcticus	Benthic Carnivore	Predatory suspension feeder on macroscopic prey. Uses specialised hooks and spines on its arms to capture live prey such as krill and zooplankton. *Meganyctiphanes norvegica* was the principal prey in the Bay of Fundy. This species is euryhaline and adapted for strong currents (Emson et al. 1991). Review of Arctic brittle star zoogeography by Piepenburg (2000) reported *Gorgoncephalus* spp. as Atlantic boreal-Arctic, nearly cicrumpolar. Size of 38 mm for the lantern reported by Pollock (1998).	(Emson et al. 1991, Pollock 1998, Piepenburg 2000)	
Gorgonocephalus sp.	Benthic Carnivore	No genus-specific diet information found. Functional group and trophic traits inferred from cogener *G. arcticus.*		
Heliometra glacialis	Benthic SF	Not much species-specific diet information available from the literature for this species, but suspension-feeding diet confirmed in a review by Baumiller (2008). Deja et al. (2016) classified this species as a boreal-Arctic suspension-feeder that prefers silt and sandy silt bottoms. Some trophic traits inferred from general Crinoida. Maximum size of 200 mm reported on the Marine Species Identification Portal.	(Baumiller 2008, Deja et al. 2016)	Marine Species Identification Portal
Holothuroidea	Benthic SDF	Can be deposit feeders or suspension feeders. See also *Cucumaria* sp.	(Massin 1982)	
Hymenaster pellucidus		No species-specific diet information found. Functional group and trophic traits inferred from cogeners. Wagstaff et al. (2014) classified this species as a carnivore based on Howell et al. (2003), who studied the stomach contents and fatty acid profiles of *Hymenaster membranaceus* and found them to feed on small benthic invertebrates (small crustaceans and foraminifera) and planktonic fall-out (pteropod moults, planktonic faraminifera). These food items agree with those reported by Mortensen (1927). Fatty acid profiles suggest that *H. membranacues* was a predator/scavengers, but with some reliance on benthic bacterial and pelagic-detrital food sources (Howell et al. 2003). Deja et al. (2016) classified this species uncertainly as an Arctic deposit feeder that prefers muddy bottom. No actual references for size found. A size of 30 mm was estimated from pictures on the WoRMS database that included a size reference.	(Mortensen 1927, Howell et al. 2003, Wagstaff et al. 2014, Deja et al. 2016)	WoRMS

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Leptasterias sp.	Benthopelagic Carnivore	Zolotarev (2002) studied echinoderms in commercial scallop beds in Iceland and found one *Lepasterias* spp. (*muelleri hyperborea*) was carnivorous and preyed on scallops. Gale et al. (2015) observed that the distributions of *Lepasterias* spp. and *Crossaster papposus* on the Grand Banks were associated with several common macroinvertebrate species considered to be their prey. Direct observations of predatory feeding are also available in Himmelman and Dutil (1991). Maximum size of 100 mm was estimated from the cogener *L. muelleri* from the Marine Species Identification Portal.	(Himmelman & Dutil 1991, Zolotarev 2002, Gale et al. 2015)	Marine Species Identification Portal
Molpadia spp.	Benthic SSDF	Macdonald et al. (2010) classified *Molpadia* spp. generally as subsurface, discretely motile, omnivores that feed on sediment, detritus, particulate organic matter, microfauna, and meiofauna. Massin et al. (1982) state that Molpadida are generally conveyor-belt feeders that bury themselves and ingest sediment to extract nutrition. Size of 200 mm based on cogener *M. borealis*, decsribed as a "20-cm long holothurian" by Drozdov et al. (2012), and *M. oolitic,a* for which Pollock (1998) reported a size of 254 mm. No other size information found.	(Massin 1982, Pollock 1998, Macdonald et al. 2010, Drozdov et al. 2012)	
Myriotrochus sp.	Benthic SDF	No genus-specific information found. Functional group and trophic trait classifications inferred from cogeners and coarser taxonomic levels. Deep-sea holothurians are typically deposit-feeders (Billett 1991, in Wagstaff et al. 2014). According to Massin (1982), Apopids are either surface, rake, or funnel feeders, all consuming detritus along with algae, small crustaceans, worms, and diatoms. Deja et al. (2016) classified *Myriotrochus rinckii* as a boreal-Arctic deposit-feeder that prefers muddy gravel and mixed sediments. No size information found.	(Massin 1982, Wagstaff et al. 2014, Deja et al. 2016)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Ophiacantha bidentata	Benthic SDF/SF	Brittle stars are generally known to be very opportunistic (Warner 1982, in Jangoux 1982). This species can act at least temporarily as suspension feeders. Graeve et al. (1997) observed diatom markers in specimens collected near Greenland. Gallagher et al. (1998) studied the biochemical composition of this species and described it as a deposit-feeding ophiurid that can modify its feeding strategies to deposit feeding, scavenging, or suspension-feeding. A review of Arctic brittle star zoogeography by Piepenburg (2000) reported that this species occurs nearly circumpolar, but is also found in temperate regions of the Atlantic and Pacific. Deja et al. (2016) classified this species as a boreal-Arctic suspension feeder that prefers mixed sediments. Disk diameter of 11 mm reported by Pollock (1998). Largest individuals observed by Brooks et al. (2007) were 11.1 mm in diameter.	(Jangoux 1982, Graeve et al. 1997, Gallagher et al. 1998, Pollock 1998, Piepenburh 2000, Brooks et al. 2007, Deja et al. 2016)	
Ophiocten sericeum	Benthic SDF/SF	Ophiurids are generally known to be opportunistic facultative deposit or suspension feeders (Warner 1982, in Jangoux 1982). Kędra et al. (2010) classified this species as a discretely motile surface deposit feeder with Arctic-boreal distribution. Deja et al. (2016) classified this species as a boreal-Arctic deposit feeder that prefers soft bottom. A review of Arctic brittle star zoogeography by Piepenburg (2000) reported that this is chiefly a cold-water species with circumpolar distribution, and while it is found in some deeper waters of the north Atlantic it is absent from the Pacific. Maximum observed disk diameter by in the Chukchi and Alaskan Beaufort Sea was 18 mm (Ravelo 2015).	(Jangoux 1982, Pollock 1998, Piepenburg 2000, Kędra et al. 2010, Ravelo et al. 2015, Deja et al. 2016)	
Ophiocten sp.		Functional group and trophic traits inferred from cogeners. Ophiuroids are generally known to be opportunistic facultative deposit or suspension feeders (Warner 1982, in Jangoux 1982). According to Jangoux (1982) and Piepenburg (2000), Ophiurids can have a very broad range of benthic food items including predation, scavenging, and surface deposit feeding. See also *Opiocten sericeum*. Maximum size of 18 mm reported for cogener *O. sericeum*.	(Jangoux 1982, Piepenburg 2000)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Ophiopleura borealis	Benthic SDF/SF	Brittle stars generally known to be very opportunistic (Warner 1982, in Jangoux 1982). Graeve et al. (1997) reported relatively high carnivory markers for *O. borealis* based on fatty acid analyses. According to Jangoux (1982) and Pipenburg (2000), Ophiuroids can have a very broad range of benthic food items and use a number of strategies including predation, scavenging, and surface deposit feeding. Mortensen (1933) suggested that larger ophiurids like *O. borealis* and *O. glacialis* prefered to forage as macrophagous predators/scavengers. Gallagher et al. (1998) studied the biochemical composition of this species and described it as a deposit-feeding ophiuroid that can modify its feeding strategies to deposit feeding, scavenging, or suspension-feeding. A review of Arctic brittle star zoogeography by Piepenburg (2000) reported that this is an endemic Arctic species. Deja et al. (2016) classified this species as an Arctic carnivore/omnivore that prefers soft bottom and mud. Blicher and Sejr (2011) observed *O. borealis* with disk diameter up to 35 mm.	(Mortensen 1933, Jangoux 1982, Graeve et al. 1997, Gallagher et al. 1998, Piepenburg 2000, Blicher & Sejr 2011, Deja et al. 2016)	
Ophioscolex glacialis		According to Jangoux (1982) and Pipenburg (2000), Ophiuroids can have a very broad range of benthic food items and use a number of strategies including predation, scavenging, and surface deposit feeding. Mortensen (1933) suggested that larger ophiuroids like *Ophiopleura borealis* and *O. phioscolex glacialis* prefer to forage as macrophagous predators/scavengers. A review of Arctic brittle star zoogeography by Piepenburg (2000) reported that this species has a west Atlantic boreal-Arctic distribution, ranging from the continental slope of the Siberian Chukchi Sea to the northwestern Atlantic. Apparently prefers soft sediments. Deja et al. (2016) classified this species as a boreal-Arctic carnivore that prefers soft bottom and mud. Piepenburg and Schmid (1996) reported observing *O. glacialis* > 30 mm in the Barents Sea.	(Mortensen 1933, Jangoux 1982, Piepenburg & Schmid 1996, Piepenburg 2000, Deja et al. 2016)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Ophiura robusta		Brittle stars generally known to be very opportunistic (Warner 1982, in Jangoux 1982). According to Jangoux (1982) and Pipenburg (2000), Ophiurids can have a very broad range of benthic food items and use a number of strategies including predation, scavenging, and surface deposit feeding. Pollock (1998) reports this species as a deposit feeder and predator that prefers sand and mud. Size of 10 mm reported in Pollock (1998)	(Jangoux 1982, Pollock 1998, Piepenburg 2000)	
Poliometra prolixa		Taylor et al. (2016) classified this species as a suspension feeder, and crinoids are generally mobile species. Functional group and trophic traits are mostly inferred from general Crinoida. Not much species-specific diet information found, but suspension-feeding diet confirmed in review by Baumiller (2008) and by Encyclopedia of Life. Anisimova and Cochrane (2003) reported an Arctic distribution for this species. Deja et al. (2016) classified this species as an Arctic suspension feeder that prefers silt and sandy silt bottoms. Size of 200 mm (Dyer et al. 1984, references in Jorgensen 2016).	(Anisimova & Cochrane 2003, Baumiller 2008, Deja et al. 2016, Jørgensen et al. 2016, Taylor et al. 2016)	Encyclopedia of Life
Pontaster tenuispinus	Benthic SDF	Carnivore according to Wagstaff et al. (2014), but this seems to be a mistake as the reference used to establish this claim is Mortensen (1927). Mortensen (1927) reports that ciliary currents appear to play a role in feeding for *P. tenuispinus*, and that its food consists of minute organisms and detritus. Summary of feeding observations in Jangoux (1982) agrees with Mortensen (1927). High $\delta^{13}C$ values reported in Søreide et al. (2013) indicate a closer link to pelagic production, although the species exhibits relatively high $\delta^{15}N$ values and is classified as a carnivore. Stable isotope values reported in Tamelander et al. (2006) are closer to those of other deposit feeders, and $\delta^{15}N$ indicates a mid-trophic level. Feeding strategy unclear but may be a mix? Deja et al. (2016) classified this species as a boreal-Arctic deposit feeder that prefers soft bottom and mixed sediment. Size of 200 mm reported by the Arctic Megabenthose Database.	(Mortensen 1927, Jangoux 1982, Tamelander et al. 2006, Søreide et al. 2013, Wagstaff et al. 2014, Deja et al. 2016)	Arctic Megabenthos Database

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Psilaster andromeda	Benthic Carnivore	Carnivore according to Wagstaff et al. (2014), who reference Mortensen (1927). Jangoux (1982) summarizes earlier observations of this species preying mostly on molluscs, some echinoderms, small bivalves, and foraminifera. These prey items are also listed in Mortensen (1927). Maximum size found for this species was 100 mm.	(Mortensen 1927, Jangoux 1982, Wagstaff et al. 2014)	
Psolus sp.	Benthic SDF/SF	Macdonald et al. (2010) classified Psolidae generally as epibenthic, discretely motile omnivores that use suspension feeding to feed on POM, phytoplankton, and zooplankton. Deja et al. (2016) classified another Arctic Psolus sp. (*P. squamatus*) as a deposit feeder. Size of 200 mm based on size reported for cogener *P. phantapus*, which also has an Arctic distribution, on Marine Species Identification Portal. This size agrees with those reported for two other *Psolus* spp. by Pollock (1998). Fankboner (1978) gives a good review of suspension-feeding sea cucumbers and studies the suspension-feeding mechanisms of *P. chitinoides*. Fankboner et al. (1978) observed fragments and whole crustacean larvae and copepods, diatoms, and algal debris in stomachs.	(Fankboner 1978, Pollock 1998, Macdonald et al. 2010, Deja et al. 2016)	Marine Species Identification Portal
Pteraster obscurus		Difficult to find species-specific feeding information. Functional group and trophic traits inferred from cogeners and coarser taxonomic levels. Jangoux (1982) described Asteroidea in general as mostly benthic predators that will occasionally eat carrion. Review in the introduction of Gale et al. (2013) states that Asteroidea are often important benthic predators, but say that explicit studies of feeding in deep-water Asteroids are rare, and deposit-feeding, mud ingestion, and suspension feeding have been observed. Wagstaff et al. (2014) classified *Pteraster* spp. generally as carnivores, inferred from cogeners in Mauzey et al. (1968) who observed predatory feeding habits of various Asteroids in Puget Sound, inlcuding one *Pteraster* spp. Macdonald et al. (2010) classified *Pteraster* spp generally as mobile, free-living carnivorous predators that feed at the sediment surface on macrofauna. Deja et al. (2016) classified this species as boreal-Arctic, potentially a deposit-feeder, with a preference for mixed sediments and muddy gravel. Size of 35 mm reported on the Russin Arctic Megabenthos Database.	(Jangoux 1982, Mauzey et al. 1968, Macdonald et al. 2010, Gale et al. 2013, Wagstaff et al. 2014, Deja et al. 2016)	Russin Arctic Megabenthos Database.

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Solaster endeca		Jangoux (1982) described Asteroidea in general as mostly benthic predators that will occasionally eat carrion. Review in the introduction of Gale et al. (2013) states that Asteroidea are often important benthic predators, but say that explicit studies of feeding in deep-water Asteroids are rare, and deposit-feeding, mud ingestion, and suspension feeding have been observed. Direct observations of predatory behaviour for this species, in the context of a predator-avoidance study, can be found in Legault & Himmelman (1993). Direct observations of predatory behaviour are found in Himmelman & Dutil (1991). Size of 203 mm reported by Pollock (1998). The Marine Species Identification reported this species can reach 400mm, which seems less likely for the specimens collected for this project.	(Jangoux 1982, Himmelman & Dutil 1991, Legault & Himmelman 1993, Pollock 1998, Gale et al. 2013)	Marine Species Identification Portal
Strongylocentrotus sp.		*Strongylocentrotus* spp. fatty acid biomarkers implied ice algae was a dietary component for this species (Brown & Belt 2012; Brown et al. 2012). Macdonald et al. (2010) classified *Strongylocentrotus* spp. generally as free-living, mobile herbivores that graze algae on the sediment surface. Stable isotope evidence in Renaud et al. (2015) suggested this genus acted as a herbivorous grazer, and the authors classified it as a benthic, omnivorous grazer. Direct observations of macroalgal diets were recorded in Kongsfjord (Wessels et al. 2006). Deja et al. (2016) classified *Strongylocentrotus droebachiensis,* which is an Arctic species, as a boreal-Arctic herbivore that prefers rocky bottom. Anisimova and Cochrane (2003) reported a boreal-Arctic distribution for two Arctic *Strongylocentrotus* species. Size of 80 mm based on size reported for northern cogener *S. droebachiensis* on Marine Species Identification Portal.	(Anisimova & Cochrane 2003, Wessels et al. 2006, Macdonald et al. 2010, Brown & Belt 2012, Brown et al. 2012, Renaud et al. 2015, Deja et al. 2016)	Marine Species Identification Portal

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Urasterias lincki	Benthic Carnivore	Jangoux (1982) described Asteroidea as mostly benthic predators that will occasionally eat carrion. A study of commercial scallop beds in Iceland reported that *U. linckii* was carnivorous and preyed upon scallops (Zolotarev 2002). Atlantic in origin according to ITIS report, but distribution map shows it has been sampled throughout the Arctic and does appear to be more common in the north Atlantic than in other places. Deja et al. (2016) reported *U. linckii* as a boreal-Arctic opportunistic species that prefers mixed sediment, and classified them as facultative carnivores, omnivores, and scavengers. Maxmimum size of 220 mm was reported on the Russian Arctic Megabenthos Database.	(Jangoux 1982, Himmelman & Hamel 1993, Zolotarev 2002, Deja et al. 2016)	IT IS; Russian Arctic Megabenthos Database
Mollusca				
Astarte borealis	Benthic SF	Fatty acid and stable isotope analyses performed by Søreide et al. (2013) suggest low trophic level. Macdonald et al. (2010) classified *Astarte borealis* as an epibenthic, discretely motile, suspenion-feeding omnivore that feeds on particulate organic matter and phytoplankton. Live in burrows. Aitken & Gilbert (1996) referred to *Astarte* spp. as suspension-feeding bivalves and noted the distribution of *A. borealis* in the eastern Canadian Archipelago was associated with greater availability of phytoplankton and benthic macroalgae. Absence was associated with high sediment loads that presumably hampered feeding. Kędra et al. (2010) reported this species as a discretely motile filter feeder with Arctic-boreal distribution. Size from Marine Species Identification Portal was 45 mm, and 51 mm was reported by Pollock (1998).	(Aitken & Gilbert 1996, Pollock 1998, Kędra et al. 2010, Macdonald et al. 2010, Søreide et al. 2013)	Marine Species Identification Portal
Astarte sp.	Benthic SF	Fatty acid and stable isotope analyses performed by Søreide et al. (2013) suggest low trophic level. Macdonald et al. (2010) classified *Astarte* spp. generally as epibenthic, discretely mobile (can move but don't need to for feeding), suspenion-feeding omnivores that feed on POM and phytoplankton. Aitken & Gilbert (1996) referred to *Astrate* spp. as suspension-feeding bivalves. See also *Astarte borealis.*	(Aitken & Gilbert 1996, Macdonald et al. 2010, Søreide et al. 2013)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Bathyarca glacialis	Benthic SDF/SF	Fatty acid biomarkers analysed by Gaillard et al. (2015) indicated this species was a non-selective filter feeder that ate microalgae, zooplankton, and bacteria. Coastal populations in the Beaufort Sea depended mostly on microalgae. Zooplankton and bacteria were more important to diet in bathyal populations. Stable isotope analyses in Renaud et al. (2011) suggested this species fed to some extent on detritus or resuspended material rather than just on fresh phytodetritus. Søreide et al. (2013) classified this species as a benthic suspension feeder, and reported stable isotope values that indicated feeding at trophic levels between 2.0 and 2.6. Stable isotope analyses for a *Bathyarca* sp. reported in Iken et al. (2005) agree with suspension feeding, and the authors classified *Bathyarca* sp. as an unselective surface deposit feeder. Size of 19 mm taken from Sea Life Base.	(Iken et al. 2005, Renaud et al. 2011, Søreide et al. 2013, Gaillard et al. 2015)	Sea Life Base
Bathyarca sp.	Benthic SF	Iken et al. (2005) classified *Bathyarca* spp. as an 'unselective' surface deposit feeder. See also *B. glacialis*.	(Iken et al. 2005)	
Bathypolypus arcticus	Benthopelagic Carnivore	O'Dor and Macalaster (1983) described this species as an opportunistic feeder that would "eat almost anything" according to laboratory experiments and stomach contents analyses. Sit-and-wait predators. Food items found in stomachs from wild-caught specimens included cumaceans, sipunculids, Foraminifera, gastropods, bivalves, polychaetes, crustaceans, and ophiuroids. Does not appear to require vision for hunting, and may feed by probing bottom sediments or taking any mobile prey that brush against it. Size of 100 mm taken from Sea Life Base. Pollock (1998) reported a maximum length of 610 mm for this species, but that is much larger than any of the specimens observed in the thesis.	(O'Dor and Macalaster 1983, Pollock 1998)	Sea Life Base
Buccinidae		Functional group and trophic traits inferred from co-familials. Macdonald et al. (2010) classified Buccinidae generally as freely motile predatory carnivores that feed on macrofauna at the sediment surface. Information for *Buccinum* spp. (Family: Buccinidae) agree with these classifications. See also *Buccinum* sp., *Buccinum undatum*, *B. hydrophanum*, and *B. scaliarforme*. Maximum size of 110 mm based on cofamilials.	(Macdonald et al. 2010)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Buccinum hydrophanum		No species-specific information found. Functional group and trophic trait classifications inferred from cogeners. Macdonald et al. (2010) described *Buccinum* spp. generally as motile, free-living, predatory carnivores that feed at the surface on macrofauna. See also *B. undatum*. Maximum size of 70 mm taken from Marine Species Identification Portal	(Macdonald et al. 2010)	Marine Species Identification Portal
Buccinum scalariforme		Not much species-specific information found. Functional group and trophic trait classifications inferred from cogeners. Macdonald et al. (2010) described *Buccinum* spp. generally as motile, free-living, predatory carnivores that feed at the sediment surface on macrofauna. See also *B. undatum*. Maximum size of 51 mm taken from Pollock (1998), who classified the species uncertainly as a predator.	(Pollock 1998, Macdonald et al. 2010)	
Buccinum sp.		Functional group and trophic trait classifications inferred from. Macdonald et al. (2010) described *Buccinum* spp. generally as motile, free-living, predatory carnivores that feed at the sediment surface on macrofauna. Information for other *Buccinum* spp. agree with these classifications See also *B. undatum*. Maximum size of 110 mm based on cogener *B. undatum*.	(Macdonald et al. 2010)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Buccinum undatum		Nielson (1974) reports that *B. undatum* hunts bivalve prey by waiting for them to open, then inserting its lip in between the valves so they cannot close. He observed that *Cardium* spp. were especially vulnerable to this type of predation, but some others were not (e.g., *Nuculana pernula* swam away quickly and *Astarte montagui* remained closed until the predator left). Nielson (1974) concluded generally that *B. undatum* mainly takes weak or dead bivalves. Martel et al. (1986) observed that food consumption declines from June to October coincident with breeding. Martel et al. (1986) found stomachs full of tissue (which the authors thought was likely bivalve tissue) and dark silt-like sediment. They directly observed feeding on bivalves. Himmelman & Hamel (1993) also found low feeding rates during breeding throughout summer, and found fragments of organisms such as polychaetes, bivalves, and urchins in *B. undatum* stomachs, suggesting they are active predators. The species also feeds on carrion. They are frequently observed near seastars that are feeding on bivalves pulled from the sediment, so may benefit from scavenging on prey remains or foraging in disturbed sediments. Size of 110 mm reported on Marine Species Identification Portal. Pollock (1998) classified this species as a predator-scavenger that prefers hard substrate or sand, and reported a maximum size of 140 mm.	(Nielsen 1974, Martel et al. 1986, Himmelman & Hamel 1993, Pollock 1998)	Marine Species Identification Portal
Clione limacina	Pelagic Carnivore	Pelagic shell-less gastropod. Specializes on two related species of pteropods. Appears to elicit a predatory response only after it has come into direct contact with prey, after which it very quickly grasps the pteropod. Slowly pulls the animal out of its shell to swallow it whole.	(Lalli 1970)	
Colus sabini		Most Buccinidae are predatory (see also Buccinidae spp, and co-familial *Buccinum undatum*). Macdonald et al. (2010) classified *Colus* sp. generally as free-living, motile, predatory carnivores that feed at the sediment surface on macrofauna. Jones et al. (1998) directly observed *Colus sabini* attracted to and feeding on a whale carcass approximately 12 hours after baiting. Sea Life Base indicates the distribution is north Atlantic and Arctic. Size of 60 mm reported on Arctic Register of Marine Species.	(Jones et al. 1998, Macdonald et al. 2010)	Arctic Register of Marine Species; Sea Life Base

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Cylichna alba	Benthic Carnivore	Macdonald et al. (2010) classified this species as a motile, predatory carnivore that feeds on subsurface meiofauna.	(Macdonald et al. 2010)	
Dendronotus sp.		Swennen (1961) reviews the feeding of nudibrachs in the Netherlands and concludes that many are specialists, but mostly the specialisation is on slow moving species like sponges, hydroids, and sea anemones. A few are Bryozoan or Ascidian specialists. There is much literature on the predatory behaviours of specific nudibranch species. Macdonald et al. (2010) classify *Dendronotus* spp. as freely motile, predatory carnivores that feed at the sediment surface on macrofauna. Pollock (1998) reports two *Dendrontus* spp. as predators, with maximum size 11.4 mm.	(Swennen 1961, Pollock 1998, Macdonald et al. 2010)	
Ennucula tenuis	Benthic SDF	Sessile surface deposit feeder according to Kędra et al. (2010), but Divine et al. (2015) classified this species as subsurface. North et al. (2014) used stable isotope, fatty acid, and stomach contents analyses to confirm it was a deposit feeder. The algae consumed followed seasonal patterns in phytoplankton in the upper water column, being dominated by ice-associated diatoms at the beginning of the spring phytoplankton bloom, and open-water diatoms after the spring bloom was well underway (North et al. 2014). The specimens observed by North et al. (2014) from the Bering Sea had shell lengths of 9.8 to 16.3 mm.	(Kędra et al. 2010, North et al. 2014, Divine et al. 2015)	
Limacina helicina	Pelagic Herbivore	Mostly herbivorous based on stable isotope and fatty acid analyses from Søreide et al. (2013). Fatty acid analyses by Gannefors et al. (2005) found a switch from diatoms to dinoflaggellates in late summer/fall. Some evidence for copepod ingestion.	(Gannefors et al. 2005 and references therein, Søreide et al. 2013)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Macoma calcarea	Benthic SDF/SF	Søreide et al. (2013) classified this genus as a benthic deposit feeder, with intermediate levels of bacterial fatty acid markers. Divine et al. (2015) classified it as a suspension feeder. Macdonald et al. (2010) classified it as a free-living, discretely motile (can move but doesn't need to for feeding) omnivore that lives at the sediment surface and uses a combination of detrivory and suspension feeding to feed on sediment, POM, and microfauna (<500 μm). Kędra et al. (2010) classified *M. calcarea* as a sessile filter feeder with Arctic-boreal distribution. North et al. (2014) observed fatty acid signatures in *M. calcarea* indicated a quick response to freshly deposited algae, but longer-term stable isotope markers suggested algae likely did not contribute significantly to overall carbon assimilation. Instead, *M. calcarea* likely consumed a fairly consistent fraction of heterotrophic organisms/bacteria and reworked phytodetritus from the sediment. Gut contents examined by North et al. (2014) were dominated by centric diatoms, followed by pennate diatoms and amorphous detritus. The specimens observed by North et al. (2014) had shell lengths from 23.4 to38.7 mm. Maximum sizes of 51 and 44 mm reported on the Marine Species Identification Portal and by Pollock (1998), respectively.	(Pollock 1998, Kędra et al. 2010, Macdonald et al. 2010, Søreide et al. 2013, North et al. 2014)	Marine Species Identification Portal
Macoma moesta	Benthic SDF/SF	Søreide et al. (2013) classified this genus as benthic, with intermediate levels of bacterial fatty acid markers. Macdonald et al. (2010) classified the species as a free-living, discretely motile (can move but doesn't need to for feeding) omnivore that lives at the sediment surface and uses a combination of detrivory and suspension feeding to feed on sediment, POM, and microfauna (<500 μm). Kędra et al. (2010) classified *M. moesta* as a sessile filter feeder with Arctic-boreal distribution. Size of 30 mm reported on Sea Life Base.	(Kędra et al. 2010, Macdonald et al. 2010, Søreide et al. 2013)	Sea Life Base

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Macoma spp.		Functional group and trophic trait classifications inferred from cogeners *M. calcarea* and *M. moesta*, which were pooled with unidentified *Macoma* spp. species for the purposes of Chapter 5. Macdonald et al. (2010) classified *Macoma* spp. generally as free-living, discretely motile omnivores that live at the sediment surface and use a combination of detrivory and suspension feeding to feed on sediment, particulate organic matter, and microfauna. Size of 40 mm based on median value between *M. calcarea* and *M. moesta*.	(Macdonald et al. 2010)	Marine Species Identification Portal; Sea Life Base
Neptunea heros		Most Buccinidae are predatory (see also Buccinidae spp. and cofamilial *Buccinum undatum*). A review by Smith et al. (2011) summarized their main diet and feeding habits. *Neptunea* spp. are mostly predatory, and likely scavenge only opportunistically. Feed mostly on polychaetes, but also on bivalves, barnacles, and trace occurrences of gastropods, decapods, ophiuroids, and fish (probably as carrion). Macdonald et al. (2010) described Buccinidae generally as motile, free-living, predatory carnivores that feed at the sediment surface on macrofauna. Maximum size of 170 mm reported by Smith et al. (2011).	(Macdonald et al. 2010, Smith et al. 2011)	
Nuculana minuta	Benthic SDF	Macdonald et al. (2010) classified this species as a free-living, discretely motile (can move but doesn't need to for feeding) omnivorous detrivore that lives at the sediment surface and feeds on sediment, POM, and microfauna (<500 μm). No other species-specific feeding information found.	(Macdonald et al. 2010)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Nuculana pernula	Benthic SDF	Fatty acid and stable isotope analyses performed by Søreide et al (2013) suggested a low trophic level and deposit feeding, with a potential connection to ice algal production. Macdonald et al. (2010) classified this species as a free-living, discretely motile omnivorous detrivore that lives at the surface and feeds on sediment, particulate organic matter, and microfauna. Size from Marine Species Identification portal. North et al. (2014) observed fatty acid, stable isotope, and stomach contents for the polar cogener *N. radiata* and found that stomach contents and fatty acid profiles from May-June indicated a quick response to freshly deposited algae, but longer-term stable isotope markers suggested algae likely did not contribute significantly to overall carbon assimilation. Instead, polar deposit feeders were thought to consume a fairly consistent fraction of heterotrophic organisms/bacteria and reworked phytodetritus from the sediment.	(Macdonald et al. 2010, Soreide et al. 2013, North et al 2014)	
Similipecten greenlandicus	Benthic SF	No species-specific feeding information found, but Pieńkowski et al. (2014) and Renaud et al. (2015) classified this species as a filter feeder. It has an Arctic distribution according to the Natural History Museum of Wales and to the distribution map on the Encyclopedia of Life. Size of 30 mm reported on the Arctic Megabenthos Database.	(Pieńkowski et al. 2014, Renaud et al. 2015)	Arctic Megabenthos Database; Encyclopedia of Life; Natural history Museum of Wales
Thyasira sp.	Benthic SF	No genus-specific feeding information found. Functional group and trophic traits classification were mostly inferred from cofamilials. See also Thyasiridae. Kędra et al. (2010) classified three polar *Thyasira* spp. as discretely motile filter feeders.	(Kędra et al. 2010)	
Thyasiridae	Benthic SF	Macdonald et al. (2010) classified Thyasiridae generally as free-living, discretely motile (can move but don't need to for feeding) omnivores that live at the sediment surface and use a combination of suspension feeding on POM and phytoplankton, and chemosynthetic nutrition from symbiotic autotrophic bacteria.	(Kędra et al. 2010, Macdonald et al. 2010)	

Taxon	Functional groups for Chapters 3 & 4	Notes on diet, feeding behaviour, and inferences from biomarkers	References	Online Resources
Yoldiella sp.		Søreide et al. (2013) classified this species as a benthic deposit feeder. Macdonald et al. (2010) classified *Yoldiella* spp. generally as discretely motile, burrow-dwelling, omnivorous detrivores that feed subsurface on sediment, POM, and microfauna. Holte & Gulliksen (1998) described several Arctic *Yoldiella* spp. from Norwegian and Svalbard fjords as subsurface detrivores. Size of 13 mm was reported for Arctic cogeners *Y. frigida* on Marine Species Identification Portal and *Y. intermedia* on the Arctic Megabenthos Database.	(Holte & Gulliksen 1998, Macdonald et al. 2010, Søreide et al. 2013)	Arctic Megabenthos Database; Marine Species Identification Portal
Nemertea				
Nemertea	Benthic SS Carnivore	Macdonald et al. (2010) classified Nemertea generally as free-living, motile, predatory carnivores that feed sub-surface on macrofauna. Taxonomic classification is too broad to estimate size.	(Macdonald et al. 2010)	
Porifera				
Radiella hemisphaerica		No species-specific information on feeding found. Macdonald et al. (2010) classified Porifera generally as sessile, encrusting, epibenthic omnivores that use suspension feeding to consume POM. Size of 50 mm reported on Marine Species Identification Portal.	(Macdonald et al. 2010)	Marine Species Identification Portal
Sipuncula				
Phascolionidae		Macdonald et al. (2010) classified Golfingiidae generally as discretely motile, free-living omnivorous detritivores that feed at the sediment surface on POM, microfauna, and macrofauna. Most sipunculids are deposit feeders, consuming detritus, fecal matter, bacteria, algae, protozoans, and small invertebrates (reviewed by Maiorova & Adrianov 2013). Edmonds (2001) reports that members of this family can have trunks from 5 to 100 mm long.	(Edmonds 2001, Macdonald et al. 2010, Maiorova & Adrianov 2013)	
Sipunculidae	Benthic SDF	Macdonald et al. (2010) classified Sipuncula generally as discretely mobile (can move but don't need to for feeding) herbivorous detrivores and browsers that feed at the sediment surface on POM and algae by tearing or gathering specific particles. Sipuncula are mostly deposit feeders, and may be burrowers that indiscriminately ingest sediment, may occupy vacant shelters and collect detritus, may wait for seston to arrive near them, or may scrape detritus and food from the surface (Murina 1984).	(Murina 1884, Macdonald et al. 2010)	