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A deep life: The application of stable isotopes to understand deep-sea environments with a focus on latitudinal gradients

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A deep life: The application of stable isotopes to understand deep-sea environments with a focus on latitudinal gradients.

By

Laurissa Christie

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A deep life: The application of stable isotopes to understand deep-sea food webs with a focus on latitudinal gradients.

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Declaration of Previous Publication

I. Previous Publication

This thesis includes 2 original papers that have been previously published/submitted for publication in peer reviewed journals in the non-peer reviewed section, as follows:

Thesis Chapter	Publication title/full citation	Publication status
Chapter 3	Christie, L. (2019). A Deep Life: Using Stable Isotopes to Understand Deep-Sea Food Web Metrics from the Poles to the Tropics. *Arctic*, *72*(4), 472-477.	*Published*
Chapter 3	Christie, L. (2018). Understanding How Sea Ice Influences Arctic Deep-Water Food Webs Across a Latitudinal Gradient. *Arctic*, *71*(4), 467-472.	*Published*

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Abstract:

The deep-sea, defined as the area 200 m below the surface, is facing emerging chemical, physical and biological stressors. Currently, very little is known regarding deep-sea ecosystems both globally and in the Arctic. In this thesis I undertook a literature review on the current understanding of global deep-sea ecosystems through the use of stable isotopes. Specifically, I synthesized the available literature on spatial variation, energy pathways, depth, temporal variation, feeding behaviour, niche, trophic position and body size isotopic trends. This thesis then presents a case study examining the isotopic niche of five teleost and two decapod species within Arctic deep-sea food webs across the localized latitudinal gradient of Baffin Island. Spatial variation in isotopic niche was quantified using $\delta^{13}C$ and $\delta^{15}N$ for seven deep-sea species at three locations on Baffin Island, Nunavut to determine whether the "Latitudinal Niche Breadth Hypothesis" which states that niche breadth should increase with latitude holds true in the Arctic. Overall, isotopic patterns in global deep-sea ecosystem are variable; consistent trends are not observed across all taxa and habitats. It was concluded that niche breadth did not consistently increase with latitude in the eastern Canadian Arctic; localized conditions (e.g. sea ice, temperature) and individual condition (e.g. hepatosomatic index) may contribute more to a species' niche than latitude. Overall, this thesis improves our understanding of deep-sea ecosystems globally, contributes baseline data for future monitoring, and by investigating multiple species and locations it will provide input on how climate change may impact Arctic food web diversity, energy dynamics and ecosystem structure to aid in sustainable fishery development.

Dedication:

I would like to dedicate this thesis to my parents, Heather and Larry Christie who have provided unconditional love and support to me. My parents have fostered my passion for science, the Arctic, and community involvement through their endless help with my science fair projects, supporting my figure skating, and raising me on a family farm in rural Midwestern Ontario.

I would also like to dedicate this thesis to my Grandma and Grandpa Stanley. Losing both of them during graduate school was extremely difficult. I am grateful for all of the love, encouragement, meals, and family lessons they provided me. My Grandma encouraged me to take advantage of opportunities that came my way. I know that they are proud.

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Table of Contents:

Declaration of Previous Publication iii

Abstract: v

Dedication: vi

Acknowledgements: vii

List of Tables: xiii

List of Figures: xiv

Chapter 1: General Introduction 1

2.0 References: 8

Chapter 2: A glimpse into the deep: State of knowledge on global deep-sea ecosystems through the application of stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) 20

1.0 Introduction: 20

2.0 Methods: 23

3.0 Results and Discussion: 23

3.1 Spatial variation: 32
3.2 Energy pathways within the deep-sea: Consideration of habitat types 33
3.3 Stable isotopes and depth: 38
3.4 Temporal variation in isotopic profiles in the deep-sea: 43
3.5 Feeding behaviour: 47
3.6 Estimating trophic position in the deep-sea: 51
3.7 Niche and community metrics in the deep-sea: 54
3.8 Body size in the deep-sea: 58

4.0 Future directions: 63

5.0 Summary of findings: 67

6.0 References: 70

Chapter 3: Trophic ecology of five deep-sea teleosts and two decapod species with different functional roles across an Arctic latitudinal gradient. 93

1.0 Introduction: 93

2.0 Materials and Methods: 98

2.1 Study Sites and Environmental Conditions 98
2.2 Sample collection and morphometric characteristics 99
2.2 Sample preparation for stable isotope analysis 103
2.3 Data Analysis 104

3.0 Results: 106

3.1 Environmental characteristics of the three study sites 106
3.2 Morphometric Data 111
3.3 Stable Isotope Data: 114

4.0 Discussion: 128

5.0 Conclusion: 143

6.0 References: 144

Chapter 4: General Conclusions and Future Directions ***169***

2.0 References: 177

Supplemental: ***185***

Vita Auctoris ***186***

List of Tables:

Table 1: All studies examining bulk stable isotope ($\delta^{15}N$ and $\delta^{13}C$) in deep-sea food webs from 1992 – 2017 identified from 'Web of Science' standard literature searches. 27
Table 2: Relationship between $\delta^{15}N$ and $\delta^{13}C$ values of distinct trophic levels or functional groups with depth. 39
Table 3: Relationship between body size and isotopic composition in the deep-sea. 58
Table 4: Studies that specifically used the term ontogenetic variation. 61
Table 5: Ecological characteristics of deep-sea Arctic species collected in Scott Inlet (2013), Qikiqtarjuaq (2018) and Pond Inlet (2017, 2018) (Christie, 2019). 101
Table 6: Stable isotope (white muscle $\delta^{13}C$ and $\delta^{15}N$; ‰) and body size data (all mean ± SD) for five deep-sea fish and two shrimp species across three sites on Baffin Island, Nunavut collected in 2013 (Scott Inlet) and 2018 (Pond Inlet, Qikiqtarjuaq). 113
Table 7: MANOVA and ANOVA results testing whether significant differences were present in $\delta^{15}N$ and $\delta^{13}C$ between species at each location. *** Indicates that there was a significant effect ($p < 0.05$). 118
Table 8: Tukey post hoc test results for $\delta^{13}C$ species comparisons within each location; Pond Inlet (PI), Scott Inlet (SI) and Qikiqtarjuaq (Qik). Species Codes are as follows: Atlantic Poacher (AP), Greenland Halibut (GH), Gelatinous Snailfish (GSF), Northern Shrimp (NS), Bigeye Sculpin (SC), and Sclerocrangon ferox (SFS). *** $p < 0.0001$, ** $p = 0.0001 - 0.009$, * $p = 0.01 – 0.049$. Dark grey area is for Bigeye Sculpin in Pond Inlet which had low sample size ($n < 5$) and therefore was not included in the comparisons. 119
Table 9: Tukey post hoc test results for $\delta^{15}N$ species comparisons within each location; Pond Inlet (PI), Scott Inlet (SI) and Qikiqtarjuaq (Qik). Species Codes are as follows: Atlantic Poacher (AP), Greenland Halibut (GH), Gelatinous Snailfish (GSF), Northern Shrimp (NS), Bigeye Sculpin (SC), and Sclerocrangon ferox shrimp (SFS). *** $p < 0.0001$, ** $p = 0.0001 - 0.009$, * $p = 0.01 – 0.049$. Dark grey area is for Bigeye Sculpin in Pond Inlet which had low sample size ($n < 5$) and was not included. 119
Table 10: Bayesian standard ellipse areas (SEA_B mode, ‰^{2}) for five fish and two shrimp species in Pond Inlet, Scott Inlet and Qikiqtarjuaq, Nunavut. The sample size was not sufficient for Bigeye Sculpin in Pond Inlet to perform the analysis. 124
Table 11: Bayesian estimated isotopic niche overlap probability (%) determined from 40% Bayesian ellipses, separated by location (high to low Arctic: Pond Inlet, Scott Inlet, Qikiqtarjuaq). Overlap estimates are directional and presented based on the amount of species A's niche that overlaps with species B's niche. For example, in Scott Inlet 23.6% of Bigeye Sculpin niche overlaps with Gelatinous Snailfish niche, but only 9.3% of Gelatinous Snailfish niche overlaps with Bigeye Sculpin niche. Bigeye Sculpin is not available in Pond Inlet. * represents significant overlap which is defined as >60%. Species Codes are as follows: Arctic Cod (AC), Atlantic Poacher (AP), Gelatinous Snailfish (GSF), Bigeye Sculpin (BSC), Greenland Halibut (GH), Northern Shrimp (NS), Sclerocrangon ferox (SFS). 125
Table 12: Community-wide metrics (Layman et al., 2007) for 5 deep-sea fishes used to estimate variability in trophic structure for Pond Inlet, Scott Inlet, and Qikiqtarjuaq, Nunavut for white muscle tissue. Note: due to sample size (n=4), Bigeye Sculpin in Pond Inlet were not included 127

Table 13: Mean hepatosomatic index (HSI) in % for deep-sea fishes at three locations in the Eastern Arctic ± standard deviation, values in parentheses indicate the maximum and minimum HSI. 185

List of Figures:

Figure 1: Count of deep-sea ecosystem studies by publication year (1992 - 2017). Bar length reflects publications in orange for the current year and cumulative publications to date from previous years are in blue. 25

Figure 2: Locations of studies using stable isotopes to examine deep-sea ecosystems globally. Each dot represents a relevant identified study. For studies undertaken in two or more distinct locations, one dot was added for each relevant location. 25

Figure 3: Count of studies published by biome and ecoregion. The count is a reflection of ecoregions which are studied but some studies occurred in more than one ecoregion which was therefore counted in each relevant region. Blue represents the distant neritic biome (n=8), purple is the polar biome (n=14), orange is the trade wind biome (n=7), and green is the westerly winds biome (n=26). 26

Figure 4: Count of published studies from 1992-2017 examining deep-sea ecosystems by environment type. 34

Figure 5: Locations of scientific bottom trawl surveys and longline surveys conducted along the Eastern Coast of Baffin Island in 2013 (Scott Inlet) and 2018 (Pond Inlet, Qikiqtarjuaq). The distance between Pond Inlet and Scott Inlet is ~300km; the distance between Scott Inlet and Qikiqtarjuaq is 500km; the full geographic range was ~800km. 99

Figure 6: Average air temperature (°C) for the three locations**:** Pond Inlet (green), Clyde River near Scott Inlet (red), and Qikiqtarjuaq (blue), Nunavut. Points represent daily mean air temperature data which was obtained from Environment Canada. Data was smoothed using a smoothed conditional means and the grey represents standard error bounds. 108

Figure 7: Mean spatially weighted sea ice concentration for Pond Inlet (2018), Scott Inlet (2013), and Qikiqtarjuaq (2018). Sea ice data obtained from the Canadian Ice Survey weekly ice charts. Sea ice concentration >50% is considered formation when the ice concentration is increasing (i.e. fall), <50% is considered sea ice break up when the sea ice concentration is decreasing (i.e. spring) and <10% is considered ice free / open water (i.e. summer period) (Canadian Ice Service, 2019). Pond Inlet (green), Clyde River near Scott Inlet (red), and Qikiqtarjuaq (blue), Nunavut. 109

Figure 8: Hours of daylight illumination (solid) and sky hours of illumination (dashed) at three locations: Pond Inlet (green), Clyde River near Scott Inlet (red) Qikiqtarjuaq (blue). Data obtained from sunrise and sunset calendar from the National Research Council of Canada (https://app.hia-iha.nrc-cnrc.gc.ca/cgi-bin/sun-soleil.pl, September 2019). 110

Figure 9: (A) Boxplot representing the distribution of fork length in cm (Arctic Cod), total length (Gelatinous Snailfish, Atlantic Poacher, Bigeye Sculpin) and (B) Carapace length in (Northern Shrimp, Sclerocrangon ferox) for each species at the three locations. Boxes represent the interquartile range (first quartile, median and third quartile), whiskers representing approximately the 95% confidence interval and outliers. 112

Figure 10: Frequency distribution of Hepatosomatic Index (HSI) (%) for Arctic Cod, Atlantic Poacher, Bigeye Sculpin, Gelatinous Snailfish, and Greenland Halibut at three sites: Pond Inlet, Scott Inlet and Qikiqtarjuaq. Greenland Halibut HSI is unavailable for Pond Inlet and Scott Inlet. The maximum, minimum, mean and standard deviation are in the supplemental material (Table 13). 114

Figure 11: Isotopic biplot ($\delta^{13}C$ versus $\delta^{15}N$) of Arctic Cod, Atlantic Poacher, Bigeye Sculpin, Gelatinous Snailfish, Greenland Halibut, Northern Shrimp and Sclerocrangon ferox collected from three locations in the Canadian Arctic: Pond Inlet, Scott Inlet, and Qikiqtarjuaq. 116

Figure 12: Linear regressions of length and $\delta^{15}N$ (‰) separated by site for (A) four deep-sea fish species separated and (B) two deep-sea shrimp species. Note the different scales on the x-axis between panels. 120

Figure 13: Linear regressions of hepatosomatic index (HSI) and $\delta^{15}N$ for five deep sea Arctic fish species separated by site. 121

Figure 14: Isotopic composition and depth (m) for shrimp and fish in Pond Inlet and Qikiqtarjuaq (A) $\delta^{15}N$ (‰) and (B) $\delta^{13}C$ (‰). Not enough data were available to examine Scott Inlet. 122

Figure 15: Isotopic niches of five deep-sea fishes and two shrimp in Pond Inlet (A), Scott Inlet (B) and Qikiqtarjuaq (C), Nunavut generated from muscle tissue. Ellipses contain 40% of the data. Colours represent each species with codes: Arctic Cod (AC), Atlantic Poacher (AP), Greenland Halibut (GH), Gelatinous Snailfish (GSF), Bigeye Sculpin (SC) Northern Shrimp (NS), and Sclerocrangon ferox (SCF). Estimates were not available for Bigeye Sculpin in Pond Inlet because the sample size was small (n < 5). 124

Figure 16: Linear regressions of length and $\delta^{13}C$ (‰) separated by site for (A) four deep-sea fish species separated and (B) two deep-sea shrimp species. Note the different scales on the y-axis between panels. 185

Chapter 1: General Introduction

Around the world, marine ecosystems are threatened by a variety of stressors (Ashford et al., 2018) including: climate change (Bruno et al., 2018; Levin & Le Bris, 2015), hydrocarbon-related activities (Venegas-Li et al., 2019), invasive species (Seebens et al., 2013), shipping (Melia et al., 2016), fishing (Coll et al., 2008), ghost fishing gear (Bo et al., 2014), tourism (Hardiman & Burgin, 2010), mining (Jones et al., 2018; Sharma, 2015), and plastic pollution (Cózar et al., 2014; Taylor et al., 2016). These stressors impact native diversity and habitat quality and there are increasing concerns about their effects on marine food webs and ecosystem services (Sandifer & Sutton-Grier, 2014).

Two-hundred meters under the ocean surface lies the deep-sea; one of earth's largest (Webb et al., 2010) and least understood habitats (Danovaro et al., 2017). Many species within the deep-sea have highly k-selected traits (i.e. slow maturation, long life, few offspring; Victorero et al., 2018) and have adapted to the low light (Danovaro et al., 2014), limited food availability (Clark, 2001), and the high pressure (Rogers, 2015) environment they inhabit. The deep-sea provides ecosystem functions and services to both humans and oceanic processes through water circulation ("global conveyor belt"), carbon dioxide exchange, nutrient cycling, biological pump for nutrients, in-situ primary and secondary production, waste disposal, and fisheries (Thurber et al., 2014).

Globally, deep-sea ecosystems have diverse biological, physical and chemical characteristics depending on their location and biogeography. Broad-scale patterns in deep-sea temperature variability is largely due to the great ocean conveyor belt transporting water to the deep-sea through global thermohaline circulation (Priede, 2017).

The deep-sea is generally colder in polar regions (typically < 0°C; Priede, 2017) than in temperate and tropical regions (Mediterranean: 12.8 – 15.5°C at 3000 m; Danovaro et al., 2010; Emig & Geistdoerfer, 2005 and Red Sea: 21.7°C at 3000 m; Klausewitz, 1989) because of evaporation, cooling and sinking of warm saline water that occurs in the tropics and temperate regions (Priede, 2017). Deep-sea temperatures are rising due to climate change and it is predicted that by 2100 deep-sea temperatures will increase by up to 4.41°C in some areas, specifically the Atlantic (Sweetman et al., 2017). In Antarctica, impacts of warming in the deep-sea extend beyond the deep-sea into shallow environments because warmer sub-surface waters (depth: 50 – 400 m) have led to ice shelf collapse and recession (Etourneau et al., 2019).

Global species richness dips at the equator, increases in low-mid latitudes (e.g. 5-10°N, the Philippines), dipping and then peaking again in higher latitude locations (e.g. 75-90°N; Saeedi et al., 2019). Deep-sea polar regions have lower species richness compared to tropical and temperate deep-sea regions (Costello & Chaudhary, 2017). Species richness is strongly linked to higher temperatures (Righetti et al., 2019), which increases competition due to higher metabolic rates and thus higher food demands (Costello & Chaudhary, 2017), which drives speciation (Wright & Rohde, 2013). Species richness also declines with increasing depth (Costello & Chaudhary, 2017; Saeedi et al., 2019) as species must be able to withstand the harsh deep-sea conditions. It is difficult to obtain accurate species richness estimates for the deep-sea because there are many undiscovered species (Danovaro et al., 2017).

Stable isotopes (Inger & Bearhop, 2008) have gained popularity in ecology in the past two decades (Carter et al., 2019) as a means to provide inference into a species' niche (Newsome et al., 2007; Bearhop et al., 2004), trophic position (Post, 2002; Turner et al., 2010; Zimmo et al., 2012), habitat utilisation (Inger & Bearhop, 2008), diet (DeNiro & Epstein, 1976; Post, 2002), energy pathways (Gladyshev, 2009) and movements (Shaw & Ryan, 2014; Rubenstein & Hobson, 2004; Carlisle et al., 2012). DeNiro and Epstein (1976) described stable isotopes as "*you are what you eat*" because ratios between stable isotopes in consumer protein tissues reflect the ratios in their consumed prey (Bergmann et al., 2009). Analyzing species' tissues for stable isotopes is inexpensive (Newton, 2010), non-lethal (Shipley et al., 2017) and minimally invasive (Newton, 2010). The approach provides temporally integrated ecological information on a species by analyzing tissues with different isotope turnover rates (Peterson & Fry, 1987). The nitrogen stable isotope ratio (^{15}N:^{14}N) infers trophic position (Fry, 1988; Post, 2002) and food web length whereas the carbon stable isotope ratio (^{13}C:^{12}C) is used to make inferences about habitat usage (Inger & Bearhop, 2008) and primary carbon sources (Bergmann et al., 2009).

Niche was first used to describe an environmental realm in 1917 (Grinnell, 1917). Ten years later, Elton (1927) described niche as the role that species play in an ecosystem under different environmental scenarios. Over the years, niche has evolved and divided into several categories: trophic (Bearhop et al., 2004), climatic (Moen & Wiens, 2017), environmental (Pearman et al., 2007), dietary (Sato et al., 2018) and isotopic (Newsome et al., 2007). Isotopic niche uses stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) to determine the n-dimensional δ-space to understand connections between resource consumption ($\delta^{15}N$) and habitat ($\delta^{13}C$) (Newsome et al., 2007). The isotopic niche consequently provides a tool to understand prey dynamics (Bearhop et al., 2004), inter- and intra- specific variability in resource-habitat use (Yeakel et al., 2016), and competition and response to emerging stressors (Shipley et al., 2019). But few studies have investigated the isotopic niche of species in the deep sea (e.g. Kopp et al., 2017; Demopoulos et al., 2017; Valls et al., 2017).

The "Latitude Niche Breadth Hypothesis" states that niche breadth increases with latitude towards the poles (MacArthur, 1972; Vázquez & Stevens, 2004). Under this scenario, species are deemed more specialized at the tropics (Saupe et al., 2018) because of higher resource diversity (Araújo & Costa-Pereira, 2013) and less seasonality compared to the poles (Vázquez & Stevens, 2004). Moreover, inter-specific competition is higher in tropical species whereas intra-specific competition is higher at the poles (Barnes & Neutel, 2016) because of higher resource diversity in the tropics (Araújo & Costa-Pereira, 2013). The "Latitudinal Niche Breadth Hypothesis" has been observed around the globe in crabs (Papacostas & Freestone, 2016), plants (Saupe et al., 2018), and in lake and stream food webs (Cirtwill et al., 2015). However, it is also suggested that the type of environment can have a greater effect on niche breadth than latitude for species in estuarine, marine and terrestrial ecosystems (Cirtwill et al., 2015). No relationships between latitude, air temperature or ecosystem size and food chain length using stable isotopes have been suggested for marine and aquatic ecosystems (Vander Zanden & Fetzer, 2007). Gilbert (2019) also indicated that temperature predicts food web structure more than latitude, indicating that there is a negative relationship between temperature and the number species. Predators in warmer ecosystems will therefore have more species interactions compared to species in colder ecosystems (Cirtwill et al., 2015). These contrasting trends and hypotheses identify the need to further investigate latitudinal trends in species ecological characteristics at small scales, particularly at the poles.

Limited research has been undertaken to understand how sea ice influences the Arctic deep-sea. The Arctic is a highly seasonal ecosystem and experiences a period of ice formation, ice coverage, ice melt and the open water season which relies on seasonal ice for primary productivity (Ramirez et al., 2017). Summer sea ice in the Arctic is predicted to be diminished by mid-century (Notz et al., 2018) and sea surface temperatures are predicted to increase to 10°C by 2300 (Carton et al., 2015). Regional concerns over declining sea ice include: more stratification (Carton et al., 2015), changes in productivity (Harada, 2016; Coad & Reist, 2017), reduced protection from predators for marine species (Hussey et al., 2017b; Coad & Reist, 2017), and increased sea water temperature (Lind et al., 2018) which will have consequences for food web structure, species diversity and energy dynamics (Kortsch et al., 2015; Murphy et al. 2016). Globally, sea ice plays an important role in regulating climate due to the Albedo effect (NSIDC, 2019) and water freshening (reduced salinity; Bethke, Furevik, & Drange, 2006; Ohshima et al., 2014). In the Okhotsk Sea, water freshening caused by sea ice declines has been observed from the surface to 500 m and is linked to reductions in dense shelf water (Ohshima et al., 2014).

Sea ice connects to the surface to the deep-sea as one of several energy pathways providing nutrition to deep-sea food webs (Bergmann et al., 2009; Iken et al., 2004). Research using highly branched isoprenoid lipid biomarkers determined that Alligator fish (*Asphidophoroides olrikii*), a species known to forage in the Arctic deep-sea, utilized sea ice derived carbon (Brown & Belt, 2011) indicating surface to deep-sea connectivity.

Variation in stable isotopes (specifically, $\delta^{13}C$) can also provide an indication of whether species are utilizing sea ice derived resources (Hobson et al., 1995). Previous Arctic research has focused heavily on understanding shallower water food webs (e.g. Linnebjerg et al., 2016; Hobson & Welch, 1992) with little research on deep-sea food webs. Understanding the link between sea ice and food web dynamics will be key to understanding how Arctic deep-sea food webs may respond to sea ice declines.

Arctic food webs experience greater seasonality than tropical food webs (Vázquez & Stevens, 2004). Seasonal variation in the tropical deep-sea is also present due to hydrological seasons and the resulting temperature variations (Morales-Nin & Panfili, 2005) with diversity found to be highly influenced by climate (Yasuhara et al., 2009). Severe coastal storms transport and sequester large quantities of organic carbon from shallow regions to the deep-sea (Sanchez-Vidal et al., 2012). More frequent tropical storms, therefore, have the potential to alter the deep-sea carbon sequestration potential (Sanchez-Vidal et al., 2012). Whereas in the Arctic, seasonality is largely driven by sea ice formation, and break up followed by phytoplankton blooms in the spring (Hoegh-Guldberg & Bruno, 2010).

This thesis examines global deep-sea food webs through the application of stable isotopes and presents a case study within the Canadian Arctic examining three food webs across a relatively localized latitudinal gradient. It is anticipated that this thesis will provide insight into deep-sea environments both in the Arctic and globally. Specifically, the chapters in this thesis address the following topics:

Chapter 2 is a literature review that examines how stable isotopes have been used to understand deep-sea environments around the world. This chapter focuses on summarizing isotopic trends under the umbrella of nine core ecological topics: niche, feeding behaviour, trophic position, energy pathways, depth, body size, spatial variation and temporal variation. Insight into deep-sea environments will provide an opportunity to make more informed conservation and management decisions in an environment, that until recently, has remained relatively untouched compared to shallower counterparts.

Chapter 3 provides a novel approach using stable isotopes to understand the isotopic niches of Arctic deep-sea species and food web structure across a localized latitudinal gradient. Economically significant species were studied including: Greenland Halibut (*Reinhardtius hippoglossoides*), Northern shrimp (*Pandalus borealis*), and Arctic Cod (*Boreogadus saida*). Non-commercial species that are also part of the deep-sea food web and support economic species include: Bigeye Sculpin (*Triglops nybelini*), Gelatinous Snailfish (*Liparis fabricii*), Atlantic Poacher (*Leptagonus decagonus*), and *Sclerocrangon ferox* (a shrimp). To date, minimal research has been undertaken to fully understand the role that Arctic fauna play in deep-sea food webs, particularly for species with little cultural or economic significance. Greenland halibut, Arctic char and Northern shrimp combined contributed 86.3 million dollars to Nunavut's economy in 2015 (Government of Nunavut, 2016). There is currently one community-based commercial Greenland halibut fishery in Cumberland Sound, Nunavut which in winter 2014 involved over 70 licensed participants (Government of Nunavut, 2016). Due to its positive socioeconomic impact, this has now led other communities to investigate the development of fisheries (Barkley et al., 2018). Findings from Chapter 3 provide necessary baseline data on the trophic roles of different deep-sea species. These baseline data can be used to aid in the monitoring of test fisheries in other communities which would contribute to socio-economic growth, employment and food security in the North (Christie, 2018).

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Chapter 2: A glimpse into the deep: State of knowledge on global deep-sea ecosystems through the application of stable isotopes ($\delta^{15}N$ and $\delta^{13}C$)

1.0 Introduction:

Defined as the area >200 m below the sea surface, the deep-sea represents the largest volumetric space on the planet (99% by volume; Norse et al., 2012), accounting for the majority of earth's surface (65%; Priede, 2017). Deep-sea species grow slowly, mature late and have low metabolic rates compared to shallower-water counterparts (Victorero et al., 2018). These k-selected ecological traits are considered to be a result of light limitation, which prohibits photosynthesis (Danovaro et al., 2014; Drazen & Sutton, 2017; Priede, 2017), limited food availability, low energy (Clark, 2001; Woolley et al., 2016), variable temperatures (Yasuhara & Danovaro, 2016; Klausewitz, 1989; Priede, 2017), and the extreme pressure (Rogers, 2015) of these environments. Within the deep-sea, species span all trophic levels from primary consumers to apex predators and, similar to terrestrial systems, environments are spatially diverse from volcanoes and vents to canyons, trenches and slopes (Priede, 2017).

Advances in technology and the recognized significance of the deep-sea, both economically and ecologically, have driven increased interest in this previously little explored environment in recent decades. As deep-sea habitats face increased exploitation pressures from mining (Glover et al., 2018) and fishing (Morato et al., 2006), it is important that exploration is conducted in a sustainable manner to avoid disrupting ecosystem stability and resilience. The orange roughy, *Hoplostethus atlanticus*, a k-selected species, distributed throughout New Zealand (depths 700-1500 m), for example, was heavily overexploited during the 1980's driving stocks to rapidly decline within a decade (Clark, 2001). At present, there are more than 300 exploited deep-sea species around the world (Priede, 2017) and lack of basic biological-ecological knowledge raises concern over their long-term sustainability. Non-commercial species can also play important roles in food webs that support fisheries (Christie, 2019) and it has been shown that with fishing pressure there are indirect effects on non-commercial species including the decline of mean body mass over time (Jørgensen et al., 2014). Deep-sea environments should not be considered replacements for degrading shallow water environments (Morato et al., 2006), but rather opportunities to develop fisheries in a sustainable manner that are built upon the successes and lessons learned from other fisheries (Hidalgo & Browman, 2019). Protected areas in the deep-sea will help provide refuge for fauna and help reduce stress from fishing and other stressors (e.g. climate change; Levin & Le Bris, 2015).

Stable isotopes have gained popularity over the past twenty years (Carter et al., 2019) as a tool to understand species movements (Rubenstein & Hobson, 2004; Carlisle et al., 2012), dietary history (Post, 2002; DeNiro & Epstein, 1976), trophic level (Turner et al., 2010; Zimmo et al., 2012), habitat utilization (Peterson & Fry, 1987; Inger & Bearhop, 2008; Layman et al., 2011), energy pathways (Gladyshev, 2009) and niche (Newsome et al., 2007; see review by Layman et al 2007). Temporally integrated ecological information derived from stable isotopes can be inferred from multiple tissues that have different turnover rates increasing the power of inference (Peterson & Fry, 1987). The isotopic approach is typically inexpensive when compared to other techniques, such as telemetry, minimally invasive via tissue sampling and release of individuals (Newton, 2001; Shipley et al., 2017), yet can answer questions from the individual to ecosystem level. Furthermore, stable isotope analysis (SIA) can complement traditional methods (e.g. stomach content analysis, telemetry, respirometry, fecal analysis, and fatty acid analysis) to provide insight on both recent and longer-term ecological characteristics of species.

Observed trends in stable isotope values are based on the principle that consumer protein reflects that of the prey they consume (Bergmann et al., 2009) and primary productivity where the consumer forages (Churchill et al., 2015) when considering tissue turnover rates. The ratio of nitrogen stable isotopes (^{15}N:^{14}N) has a stepwise enrichment of between 2‰ and 5‰ per trophic level (Bearhop et al., 2004) and is principally used to infer trophic position (Fry, 1988; Post, 2002) and food web length. The ratio of carbon stable isotopes (^{13}C:^{12}C) is indicative of habitat (Inger & Bearhop, 2008), distance to the primary carbon source (Bergmann et al., 2009) and undergoes a more conservative stepwise enrichment of 1‰ per trophic level (Mill et al., 2007). Caution is needed, however, when interpreting isotopic values because two distinct trophic pathways could be characterized by primary consumers with identical isotope values, leading to misinterpretation (Layman et al., 2011). Consequently, an integrated multi-method approach is often recommended (Christiansen et al. 2015; Churchill et al., 2015). Within deep-sea food webs, stable isotopes are now being used to address several key ecological questions with a recent review providing the first insights into macro- and megafauna in heterotrophic environments across a latitudinal gradient (Parzanini et al., 2019).

Here I review the state of knowledge on the application of stable isotopes to understand the structure and function of global deep-sea ecosystems including both chemosynthetic and heterotrophic environments. The review focuses on the following core topics: spatial variation, energy pathways, depth, temporal variation, feeding behaviour, trophic position, niche and body size.

2.0 Methods:

A systematic literature search was conducted using ‘Web of Science.’ Studies were identified using the key words “stable isotopes” and “food webs” and one of the following terms: “deep-water” or “deep-sea.” References within identified papers but not identified through the systematic search were also considered. All studies focusing on deep-sea food webs and applying stable isotopes to examine species interactions and trends published before January 2018 were included.

For each study, the following information was extracted: location, biome classification (based on Sutton et al., 2017), environment type (i.e. canyon, slope, vent, etc.), depth, species studied (phylum), study purpose, how stable isotopes were used and key findings. All studies were subsequently categorized according to the identified topics in Table 1.

3.0 Results and Discussion:

A total of 53 stable isotope studies focused on global deep-sea ecosystems were published from 1992 – 2017 (Figure 1) with the majority of studies in the northern hemisphere (Figure 2). The mesopelagic zone (200-1000m) is lower in the deep-sea and can be divided into four biomes based on primary productivity patterns, seasonal fluxes, stratification, and irradiance which play dominant roles in defining the structure of ecosystems (Sutton et al., 2017). Deep-sea food webs have been most frequently studied in the westerly winds biome (n=26; 46%), followed by the polar biome (n=14; 25%), distant neritic biome (n=8, 14 %) and trade wind biome (n=8, 14%) (Figure 3). Each biome can be further subdivided by ecoregions (number of ecoregions: westerly winds =10, polar =3, distant neritic=13, trade wind=7), which are defined based on water masses, oxygen minimum zones, temperature extremes, surface water productivity, biotic partitioning and caveats (e.g. data deficient areas; Sutton et al., 2017). The most well studied ecoregion is the Mediterranean with 21.4% of studies (n=12); the next most popular study hot spots are located in the Northwest Atlantic Subarctic ecoregion (n=7, 12.5%) and North Atlantic Drift ecoregion (n=6, 10.7%) (Figure 3). Areas that have not been studied and should be considered for future research include: the Arabian Sea, Bay of Bengal, Northern Indian Ocean, Mid-Indian Ocean, Mauritania / Cape Verde, Benguela upwelling, Coral Sea, Tasman sea, Southern Indian Ocean and the South Atlantic (Figure 3).

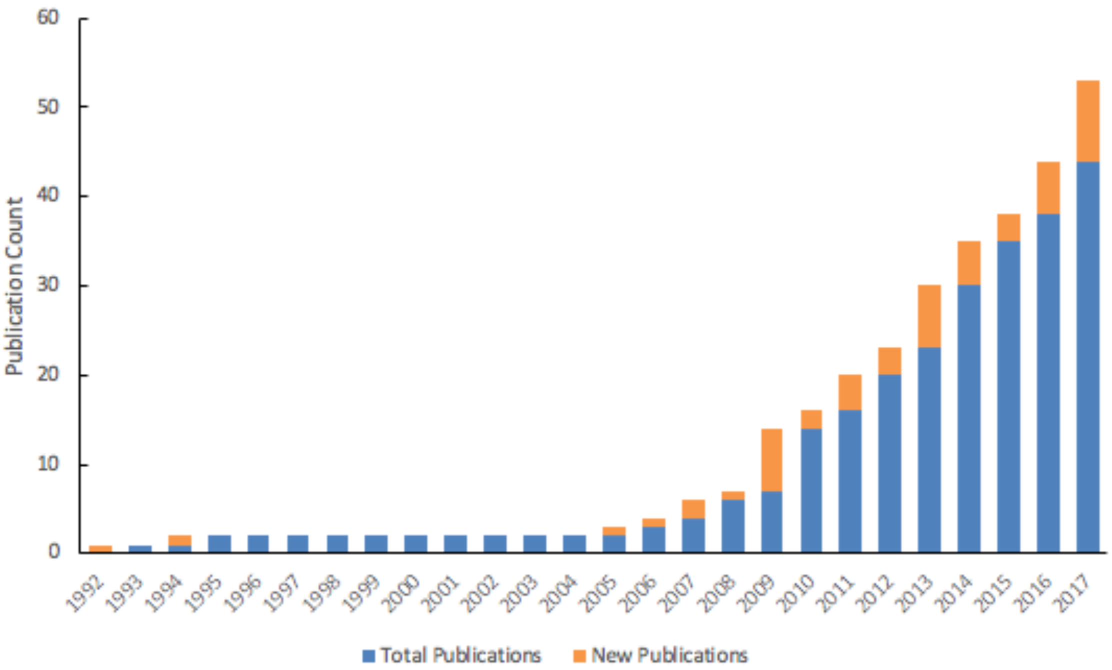

Figure 1: Count of deep-sea ecosystem studies by publication year (1992 - 2017). Bar length reflects publications in orange for the current year and cumulative publications to date from previous years are in blue.

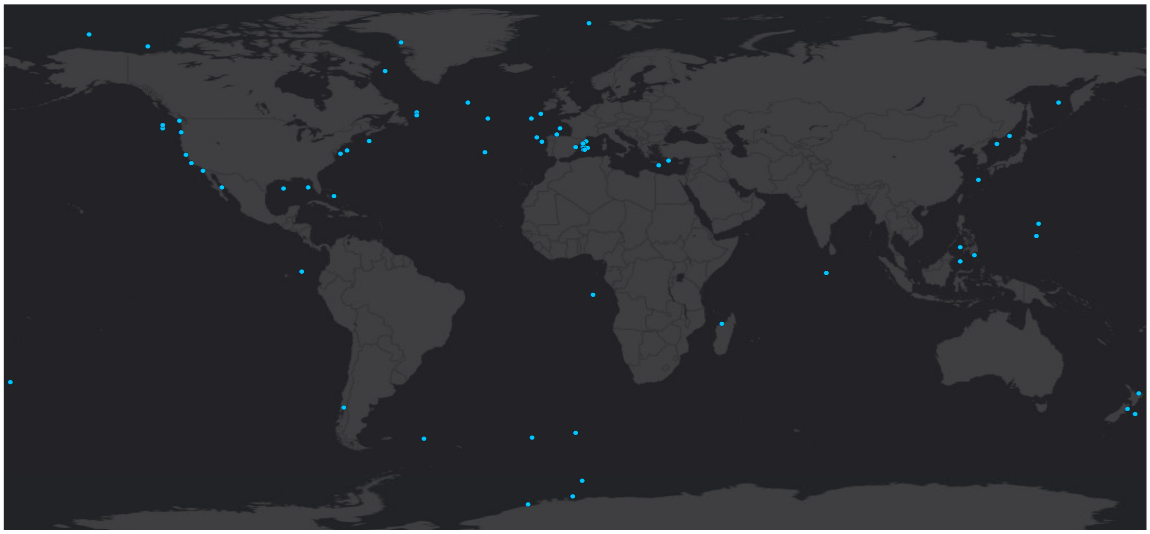

Figure 2: Locations of studies using stable isotopes to examine deep-sea ecosystems globally. Each dot represents a relevant identified study. For studies undertaken in two or more distinct locations, one dot was added for each relevant location.

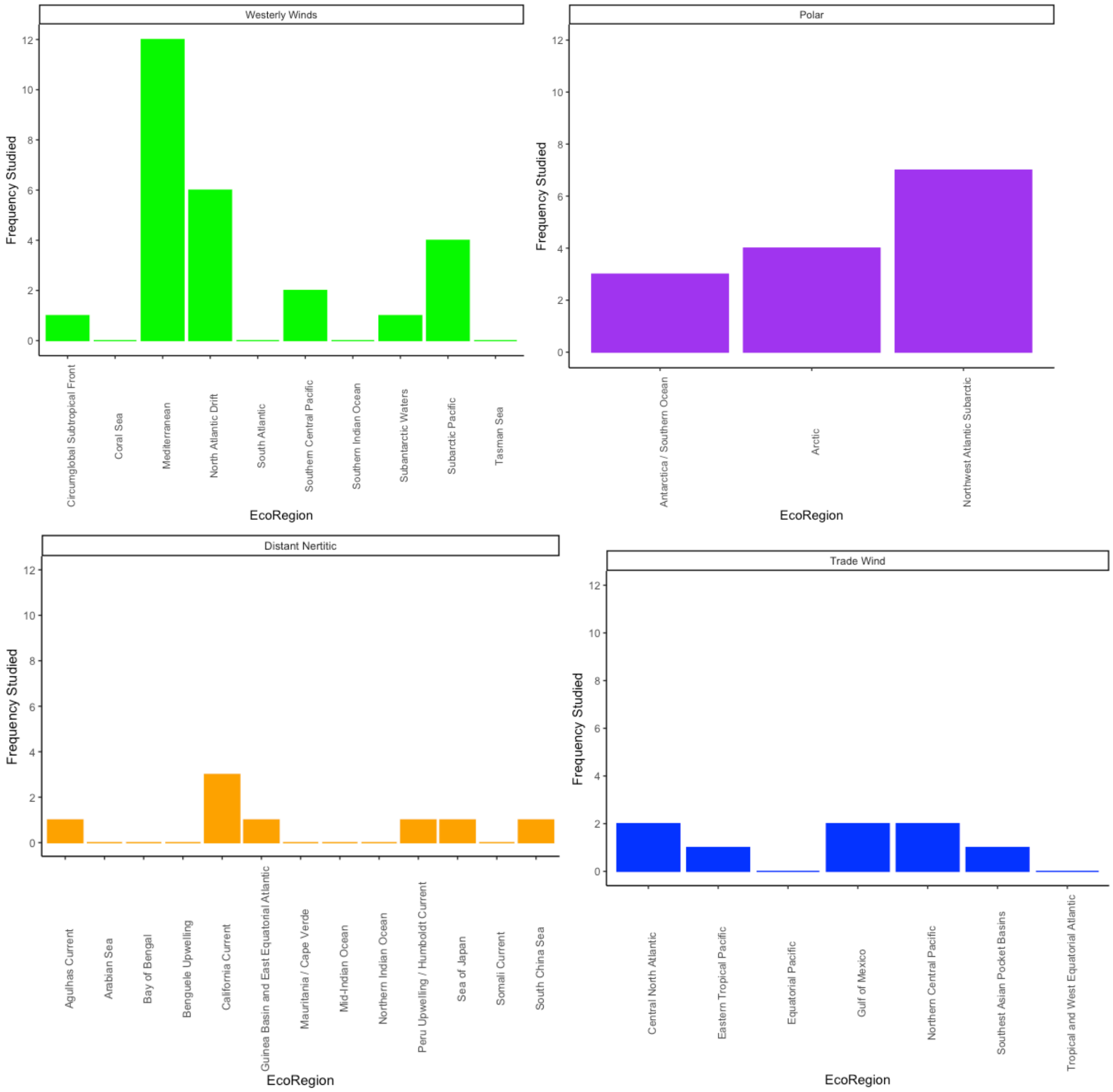

Figure 3: Count of studies published by biome and ecoregion. The count is a reflection of ecoregions which are studied but some studies occurred in more than one ecoregion which was therefore counted in each relevant region. Blue represents the distant neritic biome (n=8), purple is the polar biome (n=14), orange is the trade wind biome (n=7), and green is the westerly winds biome (n=26).

Table 1: All studies examining bulk stable isotope (δ^{15}N and δ^{13}C) in deep-sea food webs from 1992 – 2017 identified from 'Web of Science' standard literature searches.

#	Reference	Location	Environment type	Year(s)	Ocean	δ^{15}N	δ^{13}C	Species studied	Depth (m)	Key themes discussed
1	Asante et al., 2008	East China Sea	NR	2001-2002	Pacific	Y	Y	Chordate, mollusca, coelenterata, echinodermata, arthropoda	91 - 500	Depth, trophic position
2	Asante et al., 2010	Sulu and Celeb Sea, Philippines	Basin	2002	Pacific	Y	Y	Chordate	0 - 1488	Body size, spatial
3	Bergmann et al., 2009	Hausgarten station, East of Greenland	Upper slope	2005	Arctic	Y	Y	Chordate, retaria, porifera, cnidaria, nemertea	1300 - 5600	Depth, trophic position, energy, spatial
4	Boyle et al., 2012	Cape Flattery, Washington to the US - Mexico boarder	Continental slope	2007, 2008	Pacific	Y	Y	Chordate, cnidaria, echinodermata, gastropoda, arthropoda, annelida	1000 -1200	Body size, trophic position, feeding
5	Colaço et al., 2013	Condor seamount, located 18.5 km southwest of Faial Island in the Azores	Seamount	2010	Atlantic	Y	Y	Porifera, cnidaria, ctenophora, bryozoa, mollusca, annelida, echinodermata, chaetognatha, chordate	50 - 500	Trophic position, energy
6	Chambers, 2009	Baffin Island region, Nunavut, Canada	NR	2000-2004	Arctic	Y	Y	Chordate	401 - 1500	Body size, feeding, trophic position
7	Chouvelon et al., 2012	Bay of Biscay	Shelf, canyon	2001-2010	Atlantic	Y	Y	Chordate, mollusca, arthropoda,	0 - >2000	Trophic position, temporal, spatial
8	Churchill et al., 2015	Gulf of Mexico	Slope	2011, 2012	Atlantic	Y	Y	Elasmobranch	200 - 1100	Body size, depth, trophic position, temporal, feeding, energy, niche, ontogenetic, spatial
9	Demopoulos et al., 2017	Baltimore Canyon, NE United States in mid-Atlantic Ocean	Canyon, slope	2011 - 2013	Atlantic	Y	Y	Annelida, arthropoda, chordate, cnidaria, echinodermata, mollusca, porifera, sediments	200 - > 900	Depth, temporal, energy, niche, spatial
10	Denda et al., 2011	Rhodes Basin and Anaximenes Mountain	Seamount, basin	2006	Atlantic	Y	Y	Chordate, arthropoda,	50 - 4487	Depth, spatial

11	Fanelli et al., 2016	Balearic Basin, Mediterranean Sea	Slope, basin	1985-1989, 2007-2011	Atlantic	Y	Y	Chordate, arthropoda, echinodermata, porifera, sipuncula	1000, 2250	Temporal
12	Fanelli et al., 2013	Balearic Basin, NW Mediterranean	Slope, basin	2010	Atlantic	Y	Y	Chordate, arthropoda	445 - 2198	Depth, trophic, feeding, niche, spatial
13	Fanelli et al., 2009	Cabrera Archipelago - Balearic Islands, Western Mediterranean	Slope, basin	2003-2004	Atlantic	Y	Y	Arthropoda	650, 780	Trophic, temporal
14	Fanelli et al., 2011a	Barcelona, Span middle slope	Slope, basin	2007-2008	Atlantic	Y	Y	Arthropoda	650, 800	Trophic, temporal, feeding
15	Fanelli et al., 2011b	Continental slope of Catalan Sea	Slope, basin	2007-2008	Atlantic	Y	Y	Nemertea, annelida, sipuncula, mollusca, arthropoda, echinodermata	651 - 1694	Depth, trophic position, temporal, feeding, energy
16	Fisher et al., 1994	Galapagos Rift	Vent, rift	1988	Pacific	Y	Y	Echinodermata, cnidaria, arthropoda, annelida, mollusca, chordate	NR	
17	Fontanier et al., 2016	Madagascar Mozambique Channel	Slope, basin	2014	Indian	N	Y	Retaria	527 – 789	Ontogenetic
18	Gale et al., 2013	North-eastern continental shelf and slope of Newfoundland and Labrador (Canada)	Continental shelf	2005-2011	Atlantic	Y	Y	Echinodermata	258 - 1418	Trophic position, temporal, feeding
19	Gerringer et al., 2017	Mariana trench, Kermadec trench	Trench	2014	Pacific	Y	N	Chordate	3569 - 7966	Trophic position, feeding, energy
20	Gorbatenko et al., 2014	Sea of Okhotsk	Shelf, open water	2003-2013	Pacific	Y	Y	Arthropoda, cnidaria, chaetognatha, chordate, mollusca,	0 - 200	Trophic position, temporal, spatial
21	Hill et al., 2014	California margin (6 seamounts and Monterey Canyon)	Margin, seamount	2004, 2007	Pacific	Y	Y	Cnidaria	792 - 2136	Depth, trophic position, temporal, energy, spatial
22	Iken et al., 2005	Canada Basin	Gulf/Basin	2002	Arctic	Y	Y	Retaria, arthropoda, echinodermata	625 - 3398	Depth, trophic position, energy, spatial

23	Jeffreys et al., 2010	Iberian margin (Northern Atlantic)	Margin	2008, 2009	Atlantic	Y	Y	Chordate, sediment, POM, zooplankton	3000	Feeding
24	Kiyashko et al., 2014	Sea of Japan	Basin	2010	Pacific	Y	Y	Chordate, arthropoda, echinodermata, molluscs	2481 - 3666	Body size, trophic position, ontogenetic, energy, spatial
25	Kopp et al., 2017	Celtic Sea	Upper continental slope	2014	Atlantic	Y	Y	Chordate	415, 516	Trophic position, feeding, energy, niche
26	Koppelmann et al., 2009	Levantine Basin of the eastern Mediterranean	Basin	2001	Atlantic	Y	Y	Mesozooplankton	0 - 4200	Body size, depth, trophic position, temporal
27	Laakmann and Auel., 2009	Southern Ocean - Atlantic Sector	Strait, shelf	2006	Atlantic	Y	Y	Arthropoda	2097 - 4841	Depth, ontogenetic
28	Laakmann et al., 2009	Fram Strait, Arctic Ocean	Strait	2006	Arctic	Y	Y	Arthropoda	105 - 2000	Depth, trophic position, ontogenetic
29	Leduc et al., 2015	Chatham Rise, New Zealand (South Island).	Submarine ridge	2011	Pacific	Y	Y	Arthropoda, echinodermata, nematoda	566 - 1026	Spatial, trophic position
30	Levesque et al., 2006	Juan de Fuca Ridge : NE Pacific (Seattle, Washington)	Hydrothermal vents, volcano	1998-2000	Pacific	Y	Y	Annelida, mollusca, pogonophora	~1500	Spatial, temporal
31	Limen et al., 2007	Juan de Fuca Ridge : NE Pacific	Hydrothermal vents	2002	Pacific	Y	Y	Arthropoda, nematoda, pogonophora, mollusca, annelids	~1500	Feeding
32	Louzao et al., 2016	Iberian continental shelf and slope	Continental shelf, slope, oceanographic features, basin	2004	Atlantic	Y	Y	Chordate	256 +/- 219	Body size, spatial
33	McClain-Counts et al., 2017	North-Central Gulf of Mexico	Cold seep	2007	Atlantic	Y	Y	Chordate, arthropoda, mollusca, chaetognatha, cnidaria, gastropods, zooplankton	45 - 1503	Body size, depth, trophic position, feeding, energy, ontogenetic, spatial
34	Mintenbeck et al., 2007	Weddell Sea Shelf	Shelf, slope	1996, 1998, 2003	Southern	Y	N	Arthropoda, cnidaria, chordate, mollusca, bryozoa, echinodermata, hemichordata, porifera, sipuncula, annelids	50 - 1500	Depth, trophic position
35	Navarro et al., 2014	Catalan Sea and Gulf of Lions	NR	2011-2013	Atlantic	Y	Y	Chordate	350 - 1200	Trophic position, temporal, feeding
36	Papiol et al., 2013	NW Mediterranean	Continental slope, canyon, basin	2007, 2008	Atlantic	Y	Y	Arthropoda, chordate	423 - 1175	Body size, temporal

37	Parzanini et al., 2017	Northwest Atlantic, Newfoundland	NR	2016	Atlantic	Y	Y	Chordate	310 - 1413	Body size, depth, trophic position, feeding, energy
38	Portail et al., 2016	Guaymas Basin	Hydrothermal vents, cold seeps, basin	2010	Pacific	Y	Y	Mollusca, annelida, proteobacteria, arthropoda, nematoda, cnidaria, echinodermata	1500	Energy, niche, spatial
39	Preciado et al., 2017	Galicia Bank (Lusitanian)	Seamount	2009-2011	Atlantic	Y	Y	Chordate	749, 1809	Trophic position, feeding, spatial, body size
40	Pruski et al., 2017	Congo deep-sea fan	Fan	2011	Atlantic	Y	Y	Annelida, echinodermata, arthropoda, cnidaria, porifera, mollusca	3200 - 4950	Feeding, energy
41	Reid et al., 2012	Mid-Atlantic Ridge	Ridge	2007, 2009	Atlantic	Y	Y	Cnidaria, echinodermata, chordate, arthropoda	2405 - 2720	Temporal, energy, spatial
42	Reid et al., 2013	Mid-Atlantic Ridge	Ridge	2007, 2009	Atlantic	Y	Y	Chordate	2400 - 2750	Body size, trophic position, temporal, ontogenetic, spatial
43	Romero et al., 2016	Cantabrian Sea, Southern Bay of Biscay	Submarine canyon	2012-2013	Atlantic	Y	N	Mollusca, arthropoda, chordate, cnidaria, echinodermata, annelida, sipuncula, branchiopoda, porifera	128 - 4766	Body size, trophic position, temporal
44	Sherwood et al., 2011	Nova scotia	Continental slope	2002	Atlantic	Y	N	Cnidaria	275 - 450	Trophic position, temporal,
45	Shipley et al., 2017	Exuma Sound, Bahamas	Slope	2013-2014	Atlantic	Y	Y	Chordata, arthropoda	462 - 923	Body size, depth, ontogenetic
46	Stevens et al., 2015	Mariana Arc submarine volcano East Diamante	Hydrothermal vent, submarine volcano	2004	Pacific	Y	Y	Arthropoda, gastropoda, annelid, porifera, echinoderm, cnidaria	179 - 461	Depth, energy
47	Stowasser et al., 2009	Porcupine Seabight of the NE Atlantic	Seabight and plain	2001-2002	Atlantic	Y	Y	Chordate	785 - 4814	Body size, depth, trophic position, feeding, ontogenetic, temporal
48	Valls et al., 2017	Balearic Sea, Western Mediterranean	NR	2007-2016	Atlantic	Y	Y	Mollusca, chordate	50 - 755	Body size, trophic position, feeding, energy, niche, ontogenetic, spatial
49	Valls et al., 2014	Mallorca, Balearic Islands, western Mediterranean	Continental shelf, slope	2009-2010	Atlantic	Y	Y	POM, zooplankton, arthropoda, chordate, brachiopod, echinoderms, gastropoda, molluscs	250 - 850	Depth, trophic position, energy
50	Van Dover et al., 1992	New Jersey coast	Dumpsite	1989-1990	Atlantic	Y	Y	Cnidaria, echinodermata, chordate	2500	Energy

51	Veit-Köhler et al., 2013	Atlantic, Southern Ocean (southern Polar front, Central Weddell Sea, seamount Maud Rise, Lazarev Sea).	Seamount, continental slope	2007-2008	Southern / Pacific	Y	Y	Arthropoda, nematoda, sediment	1935 - 5323	Depth, spatial
52	Zapata-Hernández et al., 2016	Interior Sea of Chiloé in Northern Patagonia	Fjord, basin	2013-2014	Pacific	Y	Y	Porifera, cnidaria, nemertea, sipuncula, mollusca, annelida, arthropoda, bryozoa, brachiopoda, echinodermata, chordate, algae, OM	200 - 461	Trophic position, feeding, energy, niche
53	Zintzen et al., 2013	White Island and Kaikoura, NZ	NR	2009-2010	Pacific	Y	Y	Seagrass, mollusca, chordate	50 - 900	Depth, trophic position

Literature was identified from Web of Science standard searches using the search terms “stable isotopes” and “food webs” and one of the following terms: “deep-water” or “deep-sea” conducted January 2018. NR refers to not recorded. δ^{15}N and δ^{13}C columns identify studies that did (y) and did not (n) discuss δ^{15}N and/or δ^{13}C.

3.1 Spatial variation:

Spatial variation refers to variation in the isotopic composition of consumers related to different environments or locations where they reside. Spatial patterns are principally denoted by the $\delta^{13}C$ value which indicates habitat usage related to baseline carbon sources and processes (Peterson & Fry, 1987), whereby higher $\delta^{13}C$ values are associated with benthic habitats and more negative $\delta^{13}C$ values are associated with pelagic environments (Watt, 2013). Isotopic variation can occur at fine spatial scales, such as over hundreds of meters between mangrove and seagrass beds (Duarte et al., 2018), to broad spatial scales such as across a latitudinal gradient (Ruiz-Cooley & Gerrodette, 2012).

3.1.2 Latitudinal Gradients:

A synthesis of the Isotopic composition of consumers in deep-sea heterotrophic environments across a global latitudinal gradient was conducted by Parzanini et al. (2019). The authors indicated that lower isotopic values ($\delta^{13}C$ and $\delta^{15}N$) are present in deep-sea temperate and polar species compared to tropical counterparts (Parzanini et al., 2019), matching trends observed across all marine ecosystems (Newsome et al. 2007), phytoplankton (Laakmann & Auel, 2010) and meiofauna (Veit-Köhler et al., 2013) at a regional latitudinal scale in polar deep-sea environments. Declining isotope values near the poles is attributed to water temperature whereby higher fractionation rates are linked with colder temperatures (Sackett et al., 1965) and thus lower $\delta^{13}C$ values (Lara et al., 2010) as well as denitrification related to lower productivity (Hetherington et al., 2017). Additional studies undertaken at regional latitudinal scales, however, have identified that stable isotope values increased at higher latitudes in the deep-sea (e.g. Chouvelon et al., 2012; Louzao et al., 2017), linking this increase in $\delta^{15}N$ with latitude to less dissolved organic nitrogen in the food web being unable to meet the demand for nutrients needed thus driving higher $\delta^{15}N$ values in primary producers (Chouvelon et al., 2012), and the influence of oceanographic conditions (Louzao et al., 2017). Studies undertaken at smaller latitudinal scales reinforce that there are additional factors besides latitude driving variation in consumer isotope values including chlorophyll-A concentrations, bathymetry and localized oceanographic processes (Louzao et al., 2017).

3.2 Energy pathways within the deep-sea: Consideration of habitat types

Carbon plays an essential role in providing energy for the growth, development and survival of organisms. The deep-sea is generally considered to be an energy limited environment, yet multiple pathways deliver energy to the deep-sea including: sinking particulate organic matter (e.g. marine snow; Stevens et al., 2015; Gerringer et al., 2017; Bergmann et al., 2009), sea ice (-18.4‰, -18.7‰; Hobson et al., 1995; Nurnberg et al., 1994), photosynthetic material including phytoplankton (range $\delta^{13}C$ is -18 to -24 ‰; Fry & Sherr, 1984; Churchill et al., 2015; Demopoulos et al., 2017; Reid et al., 2012; Stevens et al., 2015; Iken et al., 2004; Zapata-Hernández et al., 2016), seaweed (e.g. *Sargassum species*; -16.6 ‰ to -16.2‰; Wells & Rooker, 2009), terrestrial organic matter (−22.5‰; Kumar et al., 2016; Fanelli, Cartes, & Papiol, 2011a; Pruski et al., 2017), whale falls (-32‰ to -20‰; Smith & Baco, 2003), macroalgae (-8 ‰ to -27 ‰; Fry & Sherr, 1984) and chemosynthetic sources (-65‰ to -25 ‰; MacAvoy et al., 2008). The reported relative contributions of these various carbon sources vary depending on the type of environment a species or community inhabits. Deep-sea environments are not all equally represented in literature (Figure 4) which may be because some habitats are less accessible or have a higher proximity from land. For example, slope and basin environments are studied more frequently, whereas trenches are more difficult to access and are therefore less studied (Figure 4).

Benthic pelagic coupling refers to the connection between surface water inputs via the water column to benthic taxa through trophic interactions that exchange energy, mass or nutrients (Valls et al., 2014). Large variation in $\delta^{13}C$ of deep sea consumers is used as an indicator of benthic-pelagic coupling and has identified this process providing energy pathways to deep-sea bamboo corals (Hill et al., 2014) and cephalopods in the Mediterranean (Valls et al., 2017). In Arctic deep-sea environments species utilize carbon from surface-derived particulate organic matter, refractory bottom sediments, particles trickling downslope, sea ice and photosynthetic pathways (Bergmann et al., 2009; Iken et al., 2004) which highlights the connection between the surface and deep-sea environments.

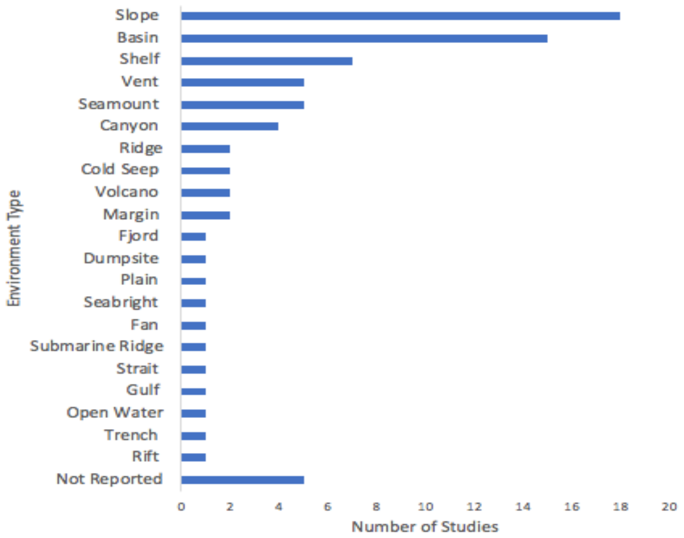

Figure 4: Count of published studies from 1992-2017 examining deep-sea ecosystems by environment type.

Slopes, the most studied environment in the deep-sea to date (n=18) extend out from the shelf and have varying steepness, but are typically divided into upper, lower, middle and continental (Table 1, Figure 4). Slope communities receive energy from photosynthetic carbon (e.g. -22.9 to -15.5 ‰; Demopoulos et al., 2017) and terrestrial inputs (Fanelli et al., 2011a). Isotopic enrichment (^{13}C and ^{15}N) on the Catalan slope compared to the Balearic slope occurred because of differences in physical variables (e.g. temperature, salinity, oxygen, direction was not reported) and higher chlorophyll-A concentration from vertical inputs (Fanelli et al., 2013) which impact the energy available to species in slope environments.

Fluvial environments are created and modified through erosion, transport and sediment deposition (Evans, 2018), often in the form of deltas and estuaries (Savoye et al., 2009). Deep-sea fans are unique in their size, structure and morphology and are usually located at the mouth of fluvial environments (Savoye et al., 2009). Both chemosynthetic and terrestrial energy in the form of organic matter transferred by bacteria through turbidity currents are important to deep-sea fans (Pruski et al., 2017). Chemosynthetic environments (e.g. seeps, vents) rely on microbes which use sulphur and methane to create organic material (Levin et al., 2016; Van Dover et al., 2012; Priede, 2017; Portail et al., 2016; Stevens et al., 2015). Chemosynthetic environments are different from heterotrophic environments because they do not utilize photosynthesis to generate primary productivity (Van Dover et al., 2012) and despite harsh conditions there are many chemosynthetic endemic species (Erickson et al., 2009). In a deep-sea fan, chemosynthetic derived energy for vesicomyid bivalves and heterotrophs was indicated by more negative $\delta^{13}C$ values (Pruski et al., 2017).

Cold seeps are a chemosynthetic environment present in continental areas where fluids seep out of the seafloor (Portail et al., 2016) with methane and hydrogen sulphide (Torres & Bohrmann, 2014). Although often found near volcanic environments where species rely on chemosynthetic and photosynthetic derived energy (Stevens et al., 2015), cold seeps are not directly reliant on volcanic activity (Priede, 2017). For example, weak $\delta^{13}C$ and $\delta^{15}N$ relationships among cold seep fauna in the Gulf of Mexico indicated that the fauna relied on a variety of trophic pathways for energy (McClain-Counts et al., 2018). These pathways included basal sources, endogenous microbial production (Portail et al., 2016), benthic sources for suspension feeders (*Pseudamussium peslutrae*) and the pelagic pathway for planktivorous fish (*Micromesistius poutassou*, indicated by lower $\delta^{13}C$, Kopp et al., 2018).

Hydrothermal vents are a geothermal feature characterized by the presence of buoyant hot water plumes (Priede, 2017) and emissions rising from seafloor cracks (Portail et al., 2016) which are a chemosynthetic environment. Energy access in hydrothermal vents is linked to location as species that live closest to the vent have access to greater primary productivity (Levesque et al., 2016) and species in high flow environments utilize more chemoautotrophic bacteria (70%) compared to lower flow environments (Limen et al., 2007). Additionally, vent species obtain energy from basal sources, and endogenous microbial production (Portail et al., 2016; Limen et al., 2007).

Seamounts are undersea mountains (Denda & Christiansen, 2011), often originating as volcanoes containing magma and hydrothermals (Staudigel & Clague, 2010) and are exposed in summits, slopes and cliffs (Priede, 2017). In seamounts, SIA has revealed that energy is provided to fauna through lateral advection of non-migrating organisms, inputs from the pelagic food web (Colaço et al., 2013) and allochthonous inputs of organic material (Clark et al., 2010). A further study examining zooplankton at seamount and basin locations indicated similar diets and food web structure, and thus energy transfer, among basins and seamounts in the Eastern Mediterranean (Denda & Christiansen, 2011).

Trenches, specifically in the hadal zone (>6,000 m), are one of the world's least studied environments (Jamieson et al., 2010). Trenches are formed by the collision of tectonic plates (Stern, 2002) and have a V-shape cross-section that is relatively narrow (2-5 km wide), flat bottomed, extremely long (usually < 2000 km) and generally run parallel to continental landmasses or island arc systems (Jamieson et al., 2010). Trenches are the deepest places on earth; at nearly 11,000 m below the surface, the Mariana Trench is the deepest part of the ocean (Kato et al., 1998). Within the hadal zone trenches, two major $\delta^{15}N$ deep-sea pathways occur (i) slowly sinking particles and organic matter from downslope (higher $\delta^{15}N$ in consumer tissues due to ^{15}N enrichment with depth) and (2) larger dead organisms that sink and reflect the isotopic composition of the habitat from where they died (e.g. euphotic zone with lower $\delta^{15}N$; Gerringer et al., 2017).

Isotopic studies have revealed that anthropogenically produced carbon is also found in the deep-sea. For example, sewage-derived organic matter identified by lower $\delta^{15}N$ values relative to plankton derived organic matter reference trawls were found in sea urchins (*Echinus affinus)* and sea cucumbers (*Benthodytes sanguinolenta*). The sea urchins and seas cucumbers were sampled within the benthic food web 185 km off the coast of New Jersey, United States at depths of 2500 m (Van Dover et al., 1992).

Overall, energy contributions to the deep-sea are variable and dependent on habitat type and taxa. Variations in energy contribution suggests complexity and multiple pathways present within deep-sea environments which are primarily derived from photosynthetic, chemosynthetic or anthropogenically produced energy. These energy sources are a reflection of the importance of surface to deep-sea connectivity.

3.3 Stable isotopes and depth:

The relationship between consumer isotopic composition and depth has received considerable attention when compared to remaining topics, with the majority of studies examining $\delta^{15}N$ versus $\delta^{13}C$ (Table 2).

Table 2: Relationship between $\delta^{15}N$ and $\delta^{13}C$ values of distinct trophic levels or functional groups with depth.

Functional Group	**Reference**
$\delta^{15}N$ increases with depth	
Copepods	Laakmann & Auel, 2009 ; Laakmann et al., 2009
Zooplankton	Koppelmann et al., 2009; Leduc et al., 2015; Denda & Christiansen, 2010
Invertebrates	Stevens et al., 2015
Coral	Hill et al., 2015
Fishes	Zintzen et al., 2013; McClain-Counts et al., 2017; Asante et al., 2008
Pelagic feeders	Demopoulos et al., 2017
Benthic feeders	Fanelli et al., 2013; Demopoulos et al., 2017
Suspension feeders	Bergmann et al., 2009; Mintenbeck et al., 2007
Entire food web (POM to large fish)	Valls et al., 2014
$\delta^{15}N$ decreases with depth	
Fishes	Zintzen et al., 2013; Churchill et al., 2015
Deposit feeders	Bergmann et al., 2009
Copepods	Laakmann et al., 2009
Sediment	Bergmann et al., 2009
$\delta^{15}N$ no clear relationship with depth	
Fishes	Shipley et al., 2017; Parzanini et al., 2017
Invertebrates	Bergmann et al., 2009; Iken et al., 2005; Veit-Köhler et al., 2013
Deposit feeders	Mintenbeck et al., 2007
Sediment	Fanelli et al., 2011b
$\delta^{13}C$ increases with depth	
Fishes	Parzanini et al., 2017; Zintzen et al., 2013
Invertebrates	Fontanier et al., 2016
$\delta^{13}C$ decreases with depth	
Fish	Shipley et al., 2017; Churchill et al., 2015
Invertebrates	Shipley et al., 2017
$\delta^{13}C$ no clear relationship with depth	
Fishes	Stowasser et al., 2009
Sediment	Fanelli et al., 2011b
Invertebrates	Iken et al., 2005; Veit-Köhler et al., 2013

3.3.1 δ^{15}N and depth:

A recent review reported that δ^{15}N values of deep-sea consumers in general increased with depth at a global scale (Parzanini et al., 2019). This trend of increasing δ^{15}N values with depth was reported for several environments from the poles to the tropics and across several taxa (Table 2). For example, deep-sea copepods in the Arctic had δ^{15}N values of 6.3 - 6.9‰ from the surface to 200 m with values increasing to 8.9 - 9.9‰ below 2000 m (Laakmann et al., 2009). Equally, δ^{15}N values of particulate organic matter in the Mediterranean increased from 1.3 – 5.5‰ at 50 m to 9.3 – 15.6‰ below 1000 m (Denda & Christiansen, 2010). Potential explanations for increased consumer δ^{15}N values with depth in the deep-sea include: longer food webs with more trophic links (Polunin et al., 2001; Denda & Christiansen, 2010), increased consumption rates of higher trophic level species (Zintzen et al., 2013) due to the lower abundance of phytoplankton in deeper regions (e.g. more carnivory; Auel & Hagen, 2002), nutritional stress and associated fasting due to food limitation (Zintzen et al., 2013; Hobson et al., 1993). Species at depth also consume sinking particles / marine snow consisting of aggregated phytoplankton, phytodetrital materials, fecal pellets, and other particles (Turner, 2015) which are absent in the diet of surface primary producers (Denda & Christiansen, 2011; Mintenbeck et al., 2007). Overall, the δ^{15}N values of deep-sea consumers are expected to be higher because particles often contain organic material originating from higher trophic level organisms.

In contrast to the overarching patterns reported by Parzanini et al. (2019), decreasing δ^{15}N values with depth are widely reported for both vertebrates and invertebrates. Elasmobranchs in the Gulf of Mexico (Churchill et al., 2015), hagfish (range of *Eptatretus cirrhatus* is ~15.0‰-15.4‰ at 48 m and ~14.4‰ at 912 m; Zintzen et al., 2013), deposit feeders (Bergmann et al., 2009), and copepods (Laakmann et al., 2009) all followed this trend. Sediment sampled along a depth gradient in the Arctic also indicated that $\delta^{15}N$ values decreased with depth although the effect was weak (1292 m; 5.28‰, 5586 m; 5.41‰; Bergmann et al., 2009). It was suggested that the decrease in $\delta^{15}N$ values occurred because less and smaller particulate organic matter (with lower $\delta^{15}N$ values; Rau et al., 1990) reaches deeper depths, resulting in lower microorganism turnover rates and a more food limited environment for deposit feeders (Bergmann et al., 2009). Other potential factors are less well examined, but the decrease in $\delta^{15}N$ with depth could be due to diet shifts, such as individuals consuming lower trophic level prey (Churchill et al., 2015; Zintzen et al., 2013), and productivity differences (Churchill et al., 2015). Clearly, a positive or negative relationship between $\delta^{15}N$ and depth is not ubiquitous across deep-sea food webs and the trophic level of a species and depth are not always linked (Shipley et al., 2017).

Despite most studies indicating a clear positive or negative trend between $\delta^{15}N$ and depth, several studies reported no clear relationship. For example, $\delta^{15}N$ values of several elasmobranches (Shipley et al., 2017), teleosts (Shipley et al., 2007; Parzanini et al., 2017[demersal]), invertebrate species (Shipley et al., 2017), pelagic particulate organic matter (Iken et al., 2005), predators, scavengers (Bergmann et al., 2009) and deposit feeders (Mintenbeck et al., 2007) were not correlated with depth (Table 2). The rationale for the lack of a relationships is not well explained and is often overlooked.

3.3.2 δ^{13}C relationships in the deep-sea

The relationship between depth and δ^{13}C values of consumers has received less attention when compared to δ^{15}N. Parzanini et al. (2019) indicated that in the deep-sea, δ^{13}C values typically increased with depth when examined at a global scale (Table 2). Moreover, more positive δ^{13}C values are associated with benthic habitat use and more negative δ^{13}C values tied with feeding in pelagic habitats (Watt, 2013; Zintzen et al., 2013), similar to trends observed in the photic zone. There is less photosynthesis and phytoplankton at deeper depths, resulting in more ^{12}C, and therefore less negative δ^{13}C. An increase in δ^{13}C values with depth has been observed in fishes (Parzanini et al., 2017; Zintzen et al., 2013) and invertebrates (Fontanier et al., 2016), likely a result of particle fractionation and degradation (Altabet et al., 1999) which consumers feed on.

In contrast to the above trends, three shark species in the Gulf of Mexico (Churchill et al., 2015) and several functional groups examined in Exuma Sound, Bahamas (6 elasmobranchs, 7 teleosts, 3 invertebrates; Shipley et al., 2017) showed decreasing δ^{13}C values with depth. These trends are not well understood but may be linked to diet shifts, productivity in the deep sea (Churchill et al., 2015) and/or changes in community composition associated with depth strata (Trueman et al., 2014). Similarly, studies of fishes in the North East Atlantic (Stowasser et al., 2009) and pelagic particulate organic matter in the Canadian High Arctic (Iken et al., 2005) suggested no clear relationship between δ^{13}C and depth. These contrasting findings indicate that the relationship between δ^{13}C and depth may not be clear cut in the deep-sea.

3.4 Temporal variation in isotopic profiles in the deep-sea:

Temporal variation in isotope values considers how an ecosystem changes both physically and chemically through time. This variation can occur seasonally (intra-annual) or between years (inter-annual) as a result of environmental or anthropogenic influences. Understanding how the isotopic profiles of species, communities and ecosystems change temporally is important to understand how species interactions and energy flow vary within and among years.

3.4.1 Intra-annual variation: Seasonal

Limited research has been undertaken to understand seasonal isotopic variation within the deep-sea, but available data indicates that it may be dependent on the functional group examined. For example, zooplankton and suprabenthos in the Western Mediterranean had more positive $\delta^{13}C$ values in late autumn through late winter which is likely due to higher chlorophyll-a surface concentrations before sampling (Fanelli, et al., 2009). Similarly, seasonal isotopic shifts in zooplankton that feed on particulate organic matter and decapods feeding on migratory macroplankton were observed with lower $\delta^{13}C$ values in late winter and spring (Papiol et al., 2013). The authors proposed that these lower zooplankton/decapod $\delta^{13}C$ values were related to the food web becoming more reliant on pelagic productivity and/or ontogenetic migrations of individuals from mid water habitats to the benthic zone (Papiol et al., 2013).

During summer and fall, $\delta^{13}C$ patterns were not uniform across all habitats and functional groups among studies examined. For example, $\delta^{13}C$ liver values were 2‰ more negative in August compared to October because of different organic matter reaching the seafloor for deep-sea fish (Abyssal Grenadier*, Coryphaenoides armatus* and

Blue Antimora, *Antimora rostrata*) in the North East Atlantic (Stowasser et al., 2009). Contrary to deep-sea fish, plankton $\delta^{13}C$ were 2‰ higher (less negative) in the summer in the Sea of Okhotsk, reflecting diets composed of spring phytoplankton bloom species, such as diatom algae and plankton foraging on the shelf zone (Gorbatenko et al., 2015). These studies suggest that seasonal $\delta^{13}C$ shifts among consumers is not straight forward but indicate that there may be some habitat switching seasonally among consumers.

Generally, lower $\delta^{15}N$ in spring for consumers across studies was linked to phytoplankton blooms, but this pattern is not uniform across all taxa. For example, $\delta^{15}N$ values of pelagic and benthic submarine canyon species (Romero-Romero et al., 2016) and plankton (Gorbatenko et al., 2015) decreased during the spring (March – May) potentially a result of the spring phytoplankton bloom (Romero-Romero et al., 2016; Gorbatenko et al., 2015), plankton feeding behaviour (Raymont, 1983) and particulate organic matter reflecting the previous season (Sorokin, 1997) all of which contribute to lower $\delta^{15}N$ values. Whereas during the fall, $\delta^{15}N$ values for benthic and pelagic consumers were higher due to stratification as well as consumption of suprabenthic prey and macroplankton-micronekton availability (Papiol et al., 2013; Cartes, 2010; Romero-Romero et al., 2016). For example, $\delta^{15}N$ of the benthic feeding fish, Longsnout grenadier, *Trachyrhynchus scabrus* was 10.71 ± 0.60‰ in October which was higher than 9.77 ± 0.55‰ in February (Papiol et al., 2013). These results suggest that generally consumers with access to abundant phytoplankton had lower $\delta^{15}N$ values (e.g. during spring) and when phytoplankton was not as abundant (e.g. fall) species had higher $\delta^{15}N$ values.

In the Mediterranean, strong correlations occurred between $\delta^{15}N$ and $\delta^{13}C$ values of species (invertebrates, decapods, fishes) during the spring when peak surface primary production occurs. In contrast, weaker δ^{15}N vs δ^{13}C relationships were recorded in the summer/ fall when surface primary production was lower and multiple carbon sources (i.e. river discharge particulate organic matter) were available to species (Papiol et al., 2013; Fanelli et al., 2011a; Fanelli et al., 2009). Despite, indications of seasonal isotopic patterns for several taxa, no seasonal δ^{15}N variation occurred in the European pilchard, *Sardina pilchardus*, between the spring and fall (Chouvelon et al., 2012) and there was no pattern for δ^{15}N for deep-sea fish in the North Atlantic (Stowasser et al., 2009). Overall, these results indicate deep-sea environments experience seasonal differences but that that this is variable within the deep-sea.

3.4.2 Inter-annual variation: Less than a decade

Food webs in the deep-sea experience inter-annual variation in isotope values as a result of changing environmental conditions and prey availability, but the trends to date are variable and species dependent. Over a three year period (2007-2009), the δ^{13}C values declined for a Holothuroidea species (*Benthothuria funebris*) and fish species (*Coryphaenoides brevibarbis*), while an increase in δ^{13}C values was observed for a cnidaria species (*Anthomastus agaricus*) in the Mid-Atlantic Ridge (Reid et al., 2012). Similarly, δ^{13}C values increased by 3.5‰ between 2005-2006 for the starfish, *Novodinia Americana* likely because of variation in phytodetritus inputs (Gale et al., 2013). In contrast, a second starfish species, *Mediaster bairdi*, had lower δ^{13}C values in 2011 compared to 2006 (Gale et al., 2013). No consistent inter-annual patterns in δ^{15}N values of cephalopods and fish were observed in the Bay of Biscay, indicating that inter-annual variation may be the result of changes in food supply rather than a baseline isotopic shift, or a combination of the two (Chouvelon et al., 2012). In summary, this suggests that there are no consistent short term (less than a decade) inter-annual temporal trends in the isotopic composition of deep-sea species.

3.4.3 Inter-annual variation: More than a decade

Studies examining inter-annual variation in the deep-sea over more than a decade indicate that generally $\delta^{15}N$ and $\delta^{13}C$ has declined. This has been observed in benthopelagic fish , benthic invertebrates and pelagic organisms in the Mediterranean between the 1980's and 2000's (mean decrease of 1.5, 1.1 and 0.8‰, respectively; Fanelli et al., 2016) and in cold-water coral, *Primnoa resedaeformis*, since 1926, with the strongest decline recorded in the 1970's (Sherwood et al., 2011). These studies indicate that the decline in $\delta^{15}N$ was linked to increased temperature and salinity, reduced O_2 in deep-sea water masses driven by climate change and river damming (Fanelli et al., 2016) as well as changes to the North Atlantic Oscillation (NAO) (Sherwood et al., 2011). Decadal change in $\delta^{13}C$ is not as well studied, but the $\delta^{13}C$ values for benthic invertebrates and pelagic species in the Mediterranean, with the exception of benthopelagic fishes, was more negative in the 2000's than the 1980's (Fanelli et al., 2016), which is attributed to increased consumption of zooplankton (Conversi et al., 2010; Fanelli et al., 2016) that have lower $\delta^{13}C$, changes in the North Atlantic Oscillation and increased bottom temperature which reduced available benthic biomass in the area (Cartes et al., 2015; Fanelli et al., 2016). These examples indicate that there has been isotopic composition shifts within the deep-sea over recent decades due to changes in foraging and environmental changes.

3.4.4 Inter-annual variation: Century

Only one study has examined stable isotope trends in the deep sea over a century. Deep-sea bamboo corals (*Isididae* family) can live up to 400 years (Thresher et al., 2004) and grow their calcite skeleton in rings which when analyzed, similar to trees and ice cores, provide inferences on past oceanographic conditions from decades to centuries (Hill et al., 2014). The $\delta^{15}N$ and $\delta^{13}C$ of deep-sea bamboo corals have remained relatively stable on a centennial scale in the California current (Hill et al., 2014). However, the ocean quahog, *Arctica islandica*, shell was examined to reconstruct $\delta^{13}C$ values in the northern North Sea from 1551 to 2005 revealing a depletion in ^{13}C in the 1850's (Estrella-Martinez et al., 2019). The point at which ^{13}C became depleted was correlated with fossil fuel burning, a trend termed the '*Suess Effect'* (Keeling, 1979). This suggests that the major shift in $\delta^{13}C$ may have occurred before the deep-sea bamboo corals were studied.

3.5 Feeding behaviour:

3.5.1 Seasonal diet estimates: Comparing stomach content and SIA

Combining stomach content analysis (SCA) and SIA can provide insight into recent and long-term diet (Post et al., 2002; Pinnegar & Polunin, 1999). Seasonal variation in diets in deep-sea food webs is considered to be minimal, however recent work is starting to identify more variable diets on a species by species basis. For example, similar SCA and SIA results indicated consistent diets in 13 of 17 deep-water sharks from the Gulf of Mexico (Churchill et al., 2015), kitefin shark (*Dalatias licha*) in the Mediterranean (Navarro et al., 2014) and the roughtail skate (*Bathyraja trachura*), in the Eastern North Pacific (Boyle et al., 2012), suggesting similarity in the short term versus long term diet. In contrast, SCA and muscle SIA results for five deep-sea sharks and rays (*Etmopterus spinax, Galeus melastomus, Scyliorhinus canicula, Dipturus oxyrhinchus, Raja clavate*) in the Mediterranean did not align (Valls et al., 2017). SCA suggested that deep-sea sharks consumed mesopelagic prey such as cephalopods and, pelagic crustaceans and teleosts whereas SIA indicated consumption of benthic prey (Valls et al., 2017). These differences between methods may be because of contrasting prey isotopic signatures (Valls et al., 2017). Few comparisons of SIA and SCA to determine diet in teleost fish have been undertaken. However, results of SCA and SIA aligned for the teleost, Gunther's grenadier [*Coryphaenoides guentheri*] suggesting a primarily benthic diet in the Northeast Atlantic (Stowasser et la., 2009) and hadal liparids rely heavily on benthic inputs (identified by high $\delta^{15}N$ values) and crustaceans (Gerringer et al., 2013). Combining SIA and SCA provides insight into seasonal variation in diet by examining recent dietary snapshots and average longer diet history, with results indicating that there are inconsistencies in seasonal variation of diet in the deep-sea. More research is needed to clearly understand taxa specific patterns in the deep-sea in seasonal diet variation.

3.5.2 Feeding behaviour: Mixing models

Four studies have used stable isotope mixing models to estimate prey proportions in the diet of deep-sea species which include: megabenthic fauna in the Interior Sea of Chiloé (Zapata-Hernández et al., 2016), roughtail skates (*Bathyraja trachura*) along the Pacific coast of the United States (Boyle et al., 2012), mesopelagic fishes in the North-Central Gulf of Mexico (McClain-Counts et al., 2017) and kitefin sharks in the Mediterranean (Navarro et al., 2014). These studies indicated the need for more research in the deep-sea as stable isotope mixing models do not always align with SCA. For example, a mixing model using the package Stable Isotope Analysis in R (SIAR) for roughtail skates estimated six prey groups whereas SCA estimated 86 prey groups (Boyle et al., 2012). Due to low sample availability and similar isotopic composition among sampled prey, the SIA mixing model underestimated the importance of euphausiids and overestimated the importance of tanner crabs (*Chionoecetes tanneri*) to the diet of rough tail skates compared to SCA (Boyle et al., 2012). The MixSIAR output suggested that the diet of one of the lanternfish, *Myctophum affine* could potentially be supplemented with chemosynthetic pathways (18.6% of diet) (McClain-Counts et al., 2017). It is unclear whether mixing model parameters led to the inference that chemosynthetic pathways are utilized directly or if variation in particulate organic matter with more negative $\delta^{13}C$ may have lowered the contribution of chemosynthetic materials to the diet of mesopelagic fish in the mixing model (McClain-Counts et al., 2017). These mesopelagic fish may also aggregate in the benthos where they could potentially utilize chemosynthetic pathways, but samples were not taken in the benthic zone to understand if this occurred (McClain-Counts et al., 2017). However, another example indicated that mixing models and SCA both agreed. Small demersal sharks as well as teleosts, crustaceans and cephalopods were found to be major contributors to the diet of kitefin sharks (Navarro et al., 2014). These mixed results demonstrate that the successful application of stable isotope mixing models is dependent on several factors including data quality, study design, previous knowledge of a species diet, temporal scale of samples collected, diet tissue discrimination factors and the inclusion of relevant food sources to avoid bias (Phillips et al., 2014).

3.5.3 Feeding behaviour: Remotely operated vehicles and in-situ

Remotely operated vehicles and video are gaining popularity as tools to understand food web dynamics (Sward et al., 2019). Two studies used video footage in combination with stable isotope analysis and indicated variation in feeding behaviours among deep-sea species (e.g. Gale et al., 2013; Jeffreys et al., 2010). Gale et al. (2013) used a remotely operated vehicle, which observed Asteroidea predating on corals (*Hippasteria phrygiana, Tremaster mirabilis*) and other species (*Ceramaster granularis, Mediaster Bairdi)* in Newfoundland and Labrador (Gale et al., 2013). Feeding experiments on Asteroidea (*Ceramaster granularis*) in a laboratory indicated a generalist sponge feeding behaviour and the species that were observed being consumed by Asteroidea in the wild were located near sponges and corals (Gale et al., 2013). All Asteroidea in the video that were analyzed for δ^{13}C and δ^{15}N (i.e. excludes *Tremaster mirabilis*) had higher δ^{15}N (16.4 ± 0.9 ‰, n=15) and similar δ^{13}C compared to the other species in the video *(Ctenodiscus crispatus, Leptychaster arcticus, Novodinia americana, Zoroaster fulgens*; Gale et al. 2013). This indicated that the Asteroidea are either predators or scavengers and fed at a higher trophic level than the other species (Gale et al., 2013). For teleosts, plant-based material (i.e. seagrass, macrophyte debris, terrestrial plant material) could be an important dietary contributor in the deep-sea based on the first in-situ documentation which captured grenadiers (*Coryphaenoides mediterraneus)* and cusk-eels (*Spectrunculus sp.)* consuming spinach (Jeffreys et al., 2010), but the study did not capture this fish for SIA as a longer temporal scale is needed to show the reflection of spinach in fish diet. This study highlights that deep-sea fishes are variable in their scavenging and could be linked to photic zone productivity if the resources are available in the deep-sea (Jeffreys et al., 2010). However, Kiyashko et al. (2014) reported that despite plant material being available for polychaetes in the Sea of Japan, this was not reflected in stable isotope signatures. Video provides the opportunity to observe deep-sea environments in real time (similar to SCA) and used in combination with SIA gives scientists a better understanding of species behaviour and how diet varies temporally in deep-sea environments.

3.6 Estimating trophic position in the deep-sea:

Trophic position is a measure of the energy pathway to a consumer and is used to quantify a species' position within a food web (Vander Zanden & Rasmussen, 1999). Trophic position is commonly calculated with stable isotopes (Post, 2002) and is used to group species into categories or functional groups including: primary producers, primary consumers, secondary consumers, and predators, etc. (Lindeman, 1942).

Trophic position using $\delta^{15}N$ is estimated based on known stepwise fractionation between consumers relative to a known baseline species (MacNeil, Drouillard & Fisk, 2016; Post, 2002; Peterson & Fry, 1987). Baseline data, although difficult to obtain, is necessary to accurately estimate trophic positions and to determine whether isotopic variation is the result of changes at the base of a food web or structural changes within a food web (Post, 2002). Most deep-sea studies estimating trophic position used a standard fractionation value of 3.4‰ (Post, 2002; Vander Zanden et al., 1999; Cabana & Rasmussen, 1996; Vander Zanden et al., 2001), but also values of 3.8‰ (Bergmann et al., 2009; Iken, Bluhm, & Gradinger, 2004) and 2.54‰ (Fanelli et al., 2009). The latter value of 2.54‰ was used to ensure that trophic positions were distinguished because of high $\delta^{15}N$ overlap among all trophic levels in the deep-water food web in the Algerian

Basin (Fanelli et al., 2009). To date, only one deep-sea study (e.g. Churchill et al., 2015) has discussed trophic position using the scaled fractionation approach of Hussey et al. (2014). Fourteen studies did not calculate absolute trophic position using a fractionation factor, but instead inferred relative trophic position from δ^{15}N values, based on the premise that a larger δ^{15}N implies higher trophic position (Fry, 1988).

Deep-sea food webs typically contained four to five trophic levels; with data available for the Arctic (Bergmann et al., 2009; Iken et al., 2004), canyon (Demopoulos et al., 2017), as well as column and shelf ground environments (Valls et al., 2014). Low trophic levels (~1) typically contained invertebrate species such as, mesozooplankton (Koppelmann et al., 2009), cumaceans (deposit feeders), amphipoda (deposit feeders), and hydrozoans (suspension feeder; Bergmann et al., 2009). Deep-sea skate species generally occupied trophic position 3 including: roughtail skate, (3.5 ± 0.2: Boyle, Ebert, & Cailliet, 2012), shorttail skate, *Amblyraja jenseni* (3.0), smooth skate, *Malacoraja senta* (3.3), and round skate, *Rajella fyllae* (3.4 ± 0.1: Parzanini et al., 2017). Most teleost species were found at approximately the third and forth trophic level: the banded whiptail, *Coelorinchus fasciatus* (3.6 : Zapata-Hernández et al., 2016)*,* Angler, *Lophius piscatorius* (4.9), rockfish, *Trachyscorpia cristulata* (4.9; Preciado et al., 2017), bristlemouth species, *Cyclothone sp.,* (zooplanktivore, 2.6; Colaço et al., 2013a). Higher level trophic species include: kitefin shark, *Dalatias licha,* (4.3 to 5.5; Navarro et al., 2014) and Greenland shark, *Somniosus microcephalus* (4 -7 ; Hussey et al., 2014).

Trophic position can be determined using traditional SCA and compared to SIA to understand temporal variation. For example, the SCA-derived trophic positions of mesopelagic fishes in the Gulf of Mexico were higher than those calculated with stable isotopes, with the exception of constellation fish (*Valenciennellus tripunctulatus),* tan bristlemouth (*Cyclothone pallida*)*,* lovely hatchetfish *(Argyropelecus aculeatus)* and half-naked hatchetfish (*Argyropelecus hemigymnus*) (McClain-Counts et al., 2017). This indicates that trophic position of mesopelagic fish in the Gulf of Mexico may vary seasonally because trophic position derived from SCA (i.e. recent dietary history) was than SIA (i.e. long term average dietary history). However, the opposite was observed in bentho-pelagic fishes on the Galicia Bank, where SIA predictions for trophic level were higher than SCA trophic position estimates (Preciado et al., 2017). This may have occurred because they used the pelagic organism (amphipod, *Phronima sedentaria*) as a baseline suggesting that there may be bias in the benthic feeder trophic position estimates (Preciado et al., 2017) or that species were consuming species of lower trophic level compared to the average trophic position that they consume.

Due to the unique environment of deep-sea ecosystems, several factors can influence and drive variation in the trophic position of deep-sea species' when compared to pelagic species. Given the deep-sea is typically resource limited environment (no available sunlight), species rely on food obtained from: (i) sinking surface particulate organic matter which falls as marine snow through the water column known as the 'biological pump,' (ii) food falling to the seafloor (macrocarrion, mesocarrion, nanocarrion, ultracarrion) and (iii) seafloor predation (Priede, 2017). Deep-water species of a similar body size and functional group can therefore have enriched ^{15}N values relative to shallow-water counterparts due to the consumption (directly or indirectly) of sinking organic matter derived from higher trophic level species (e.g. carrion falls; Boyle et al., 2012; Gerringer et al., 2017; Koppelmann et al., 2009) which has been observed in zooplankton that are highly reliant on suspended particles (Koppelmann et al., 2009). A higher estimated trophic position than expected may also indicate species are nutritionally stressed (i.e. fasting; Bergmann et al., 2009). Nutritional stress elevates ^{15}N values because the lighter ^{14}N is not replenished through the species' diet (Bergmann et al., 2009). In addition, scavenging (Churchill et al., 2015) and continual recycling of food in benthic environments instead of consuming fresh phytodetritus available in pelagic ecosystems (Iken et al., 2004) and the choice of baseline species (e.g. using a pelagic species instead of benthic; Preciado et al., 2017) all influence the trophic positions estimated for deep-sea species.

3.7 Niche and community metrics in the deep-sea:

Limited research has been undertaken to understand species' niche in the deep-sea. Dietary niche is traditionally characterized using stomach content data, but the isotopic niche now provides a complementary approach (Bearhop et al., 2004; Newsome et al., 2007). The isotopic niche considers the area in δ-space with δ^{13}C on the X-axis and δ^{15}N on the Y-axis providing a link between prey resources and foraging location (Newsome et al., 2007). Moreover, aspects of isotopic community structure can be inferred using standardized metrics (e.g. δ^{15}N nitrogen range, δ^{13}C carbon range, total area of the convex hull, distance to the centroid, mean nearest neighbor distance, standard deviation of the nearest neighbor distance; Layman et al., 2007). In total 6/7 studies that examined niche in the deep-sea food web used a combination of metrics by Layman et al. (2007; convex hull, and associated community metrics; n = 5) and Jackson et al. (2011; corrected standard ellipse area, SEA_C, n=6 ; Bayesian standard ellipse area, SEA_B n=4).

Niche overlap occurs in the deep-sea environment (e.g. Demopoulos et al., 2017; Kopp et al., 2017; Zapata-Hernández et al., 2016). Within deep-sea environments, the most comprehensive study to quantify an entire community estimated niche overlap (SEA_c) for 140 species from invertebrates to sharks in three basins of the Sea of Chiloé (Zapata-Hernández et al., 2016). The high incidence of overlapping niche among the three basins (range: 52% to 79%,) indicated that habitat usage, trophic position and species interactions were similar among communities (Zapata-Hernández et al., 2016). A high degree of isotopic niche overlap was also observed among benthic slope species in the Celtic Sea (Kopp et al., 2017). Along the upper continental slope, three of the five studied fish species had overlapping niches (SEA_c, overlapping niche area: 1 to 44%), as predicted given that all species were benthopelagic consumers (Kopp et al., 2017). The overlap observed by Kopp et al. (2017) is thought to be due to larger organisms having higher search times for food (Dayton & Hessler, 1972) and revealed that these species are highly linked to benthic species (Kopp et al., 2017). Within a community, niche overlap can also indicate prey abundance (Pettitt-Wade et al., 2015), productivity in an ecosystem (Linnebjerg et al., 2016), invasive species (Guzzo et al., 2013), and / or competition (Bolnick, 2001).

Contrary to the previously mentioned findings, no niche overlap occurred for suspension, epibenthic and unknown feeders in canyon and slope environments (Demopoulos et al., 2017), invertebrate species within some cold seep and vent sites despite overlap not being quantitatively estimated (Portail et al., 2016), corals and anemones in a canyon environment despite both being suspension feeders (Demopoulos et al., 2017), and secondary consumers (benthic and a benthopelagic fishes) in the Celtic

Sea (Kopp et al., 2017). Distinct niches indicated variability in the location of foraging, carbon sources and trophic level of prey being consumed.

To understand niche diversification at the base of the food web and determine if species are foraging in a single habitat or on the same primary consumers, the carbon (δ^{13}C) range is often examined (Layman et al. 2007) because δ^{13}C provides inference on the number of basal carbon resources species are using (Demopoulos et al., 2017). Through this approach it was found that canyon species (Layman metric δ^{13}C carbon range: 4.33) had significantly higher δ^{13}C range compared to slope species (Layman metric δ^{13}C carbon range: 1.25) and wider isotopic niches estimated using the standard ellipse area corrected approach (Demopoulos et al., 2017). A larger δ^{13}C range was also observed for lower fluid environments (characterized by having lower sulphide and methane concentrations as well as being less enriched in compounds that promote microbial activity) compared to higher ones, with seeps (generally less fluid) having larger δ^{13}C ranges comparable to vents (generally more fluid) at some locations due to variable basal carbon sources such as endogenous microbial production, thiotrophs, methanotrophy, and petroleum-derived organic matter (Portail et al., 2016).

Trophic level diversity within an ecosystem and chemosynthetic δ^{15}N baselines can be inferred using the nitrogen isotope range (Layman et al., 2007; Portail et al., 2016). Fishes in Mediterranean slope environments generally had wider δ^{15}N ranges (6.1 to 12.63‰) compared to decapods (4.19 to 10.53 ‰; Fanelli et al., 2013), indicating that fishes have more trophic diversity. Similarly, seep ecosystems had higher δ^{15}N ranges (~7 to 14 ‰) compared to vent ecosystems (~5 to 7 ‰; Portail et al., 2016) and canyon ecosystems had significantly higher δ^{15}N range (Layman metric δ^{15}N nitrogen range:

6.26) compared to slope ecosystems (Layman metric δ^{15}N nitrogen range: 3.35, $p < 0.01$). The larger δ^{15}N range could be attributed to the presence of deep-sea corals, which have lower δ^{15}N values in the canyon (Demopoulos et al., 2017). The low δ^{15}N values in corals could be due to consumption of bacteria or symbiotic nitrogen fixation, whereby N_2 is converted to NH_4 (ammonium; Demopoulos et al., 2017; Mueller et al., 2013; Middelburg et al., 2015).

Overall, trends in niche overlap were diverse between habitats and among functional groups, suggesting variability in trophic resources in deep-sea environments. There is a need for additional studies to examine niche in the deep-sea and potential distinction of overlapping niches in shelf, canyon and chemosynthetic environments to further understand deep-sea niche spatial and temporal variation. There is also a need for more comprehensive niche studies to ensure that the entire food web is captured. Further research in different environments will aid in identifying more clearly whether there are patterns in niche related to environment and species type in deep-sea environments.

3.8 Body size in the deep-sea:

Table 3: Relationship between body size and isotopic composition in the deep-sea.

Phylum	**Species**	**Area(s)**	**Reference**
δ^{15}N Increases with increasing body size			
Chordata	22 fish species	Celebes Sea, Sulu Sea, Philippine Sea	Asante et al., 2010
Chordata	*A. rostrate, C. brevibarbis, H. macrochir*	Mid Atlantic Ridge	Reid et al., 2013
Chordata	19/20 mesopelagic fish	Gulf of Mexico	McClain-Counts, Demopoulos & Ross, 2017
Chordata	Pelagic and benthic fish	Cantabrian Sea	Romero-Romero et al., 2016
Chordata	*Lampanyctus crocodilus, Gadiculus argenteus, Micromesistius poutassou*	Mediterranean Iberian Shelf	Louzao et al., 2017
Chordata	*Hymenocephalus italicus, Cataetyx alleni, Galeus melastomus*	Catalan Sea	Papiol et al., 2013
Chordata	Sculpin Species	Arctic	Chambers et al., 2005
Chordata	*A. rostrate, C. armatus*	Porcupine Seabight	Reid et al., 2013
Chordata	giant squid (*Architeuthis dux*)	Cantabrian Sea	Romero-Romero et al., 2016
Chordata	cetaceans (*Delphinus delphis, Stenella coeruleoalba, Physeter microcephalus*)	Cantabrian Sea	Romero-Romero et al., 2016
Chordata	*Squalus cf. mitsukurii*	Gulf of Mexico	Churchill et al., 2015
Chordata	*Squalus cubensis*	Exuma Sound, Bahamas	Shipley et al., 2017
Chordata	Deep-sea fish	NE Atlantic	Parzanini et al., 2017
Chordata	*Antimora rostrate and Coryphaenoides armatus*	NE Atlantic	Stowasser et al., 2009

Arthropoda	Decapods	Catalan Sea	Papiol et al., 2013
Zooplankton	Zooplankton	Submarine Canyon	Romero-Romero et al., 2016
Arthropoda	Zooplankton	Eastern Mediterranean	Koppelmann et al., 2009
δ^{15}N decreases with body size			
Chordata	*Mustelus canis*	Gulf of Mexico	Churchill et al., 2015
δ^{15}N no relationship with body size			
Chordata	8 deep-sea shark species	Gulf of Mexico	Churchill et al., 2015
Chordata	Spiny skates	Western United States and Mexican Border	Boyle et al., 2012
Chordata	Bentho-pelagic fish	Galicia bank	Preciado et al., 2017
Annelida	Polychaeta, *Harmothoe derjugini*	Sea of Japan	Kiyashko et al., 2014
Chordata	Deep-sea fish	Baffin Region, Nunavut	Chambers, 2008
δ^{13}C Increases with increasing body size			
Chordata	*Lampanyctus crocodiles, Gadiculus argenteus, Micromesistius*	Mediterranean	Louzao et al., 2017
Chordata	*A. rostrate, H. macrochir, C. armatus, C. brevibarbis* – not all stations indicated this trend	Mid Atlantic Ridge	Reid et al., 2013
Chordata	*Hymenocephalus italicus, Cataetyx alleni, Galeus melastomus*	Catalan Sea	Papiol et al., 2013
Chordata	*Lampanyctus crocodilus*	Mediterranean	Valls et al., 2017
Chordata	18 deep-sea fish	NE Atlantic	Parzanini et al., 2017
δ^{13}C decreases with increasing body size			
Chordata	*C. armatus*	Mid-Atlantic Ridge	Reid et al., 2013

$\delta^{13}C$ no relationship with increasing body size			
Chordata	5 sharks	Gulf of Mexico	Churchill et al., 2015
Chordata	4 species	Galicia Bank	Preciado et al., 2017
Chordata	*Antimora rostrate and Coryphaenoides armatus*	NE Atlantic	Stowasser et al., 2009
Chordata	Demersal and Pelagic fish	Sulu Sea, Philippines Sea, Celebes Sea	Asante et al., 2010
Chordata	18 deep-sea fish	Baffin Region, Nunavut	Chambers, 2008

Table 4: Studies that specifically used the term ontogenetic variation.

Species	Ontogenetic pattern	Reference
Fish: Abyssal grenadier (*C. armatus*)	Switched from a benthic to pelagic prey ($\delta^{13}C$ lowered with body size)	Reid et al., 2013
Mesopelagic fish	Increase $\delta^{15}N$ with body size, suggesting ontogenetic shifts in diet	McClain-Counts et al., 2017
Copepods	Diet shift from juveniles to adults where $\delta^{15}N$ was lower in adults due to more carnivorous predation occurring in juveniles and herbivory/ omnivory occurs in adults.	Laakmann et al., 2009
Fish: A. rostrate and *C. armatus*	Shift from active predation to scavenging with the increase in body size	Stowasser et al., 2009
Sharks*: M. canis, S. cubensis and S. cf. mitsukurii*	Altering prey types or foraging locations	Churchill et al., 2015
Cephalopods, elasmobranchs	As species grow, they are consuming the same prey but at different ontogenetic stages	Valls et al., 2017
Fish and polychaete	No dietary ontogenetic shift due to no relationship between body size and $\delta^{15}N$	Kiyashko et al., 2014
Elasmobranch: Cuban dogfish, *Squalus cubensis*	Switched to higher trophic level prey with ontogeny	Shipley et al., 2017

3.8.1 Effect of body size on $\delta^{15}N$:

Larger organisms typically had higher $\delta^{15}N$ values due to consumption of larger and higher trophic level prey, linked to ontogenetic changes (Table 3; Table 4; McClain-Counts et al., 2017; Stowasser et al., 2009), switching foraging locations to areas that have different prey isotopic signatures (Churchill et al., 2015), temporal variation in prey isotope values (Matthews & Mazumder, 2005), and increased levels of scavenging (Churchill et al., 2015). The majority of studies indicated that as body size increased, $\delta^{15}N$ values were higher in fishes (Table 3), giant squid (*Architeuthis dux*) and cetaceans in the Cantabrian Sea (Romero-Romero, 2016), shortspine spurdog (*Squalus cf. mitsukurii*) in the Gulf of Mexico (Churchill et al., 2015), Cuban dogfish (*Squalus cubensis*) in Exuma Sound, Bahamas (Shipley et al., 2017) and decapods in the Catalan Sea (Papiol et al., 2013). Smaller species also increased in $\delta^{15}N$ with body size, which was observed in zooplankton and invertebrates in a submarine canyon (Romero-Romero, 2016) and in the Eastern Mediterranean (Koppelmann, et al., 2009).

Despite the majority of studies suggesting that $\delta^{15}N$ increases with body size in the deep-sea, some research contradicts this pattern (Table 3). For example, in the dog shark, *Mustelus canis*, $\delta^{15}N$ values declined with increasing body size in the Gulf of Mexico, potentially in response to changes in both foraging habitat and prey (Churchill et al., 2015). Moreover, several studies have not found a relationship between $\delta^{15}N$ and body size, in particular this trend has been observed in some sharks (*Centrophorus cf. granulosus, Etmopterus bigelowi, Galeocerdo cuvier, Hexanchus griseus, Squalus cf. mitsukurii, Centrophorus cf. niaukang*), some bentho-pelagic fish, and polychaeta, *Harmothoe derjugini* (Table 3). The lack of relationship in sharks may be due to reduced resource pathways such as starvation (Hussey et al., 2012) or scavenging (Churchill et al., 2015), whereas in polychaeta the relationship indicates similarity among trophic status and diet (Kiyashko et al., 2014). The other studies did not provide a rationale for why a trend between δ^{15}N and body size is absent. Overall, the majority of studies indicated that with increasing body size, δ^{15}N also increased, but this was not consistent among species suggesting that foraging strategies, among other factors impacts trophic dynamics in the deep-sea environment.

3.8.2 Effect of body size on δ^{13}C:

Higher δ^{13}C values with increasing body size have been observed in fishes (Table 3) and may be a result of ontogenetic changes from pelagic to benthic prey, which are more enriched in ^{13}C relative to their pelagic counterparts (Table 3; Reid et al., 2013; Papiol et al., 2013). In contrast, δ^{13}C decreased with body size in the abyssal grenadier in the Mid-Atlantic Ridge, (Reid et al., 2013) which the authors attributed to spatial differences in the isotopic composition of benthic prey items (Reid et al., 2013). As with δ^{15}N, several studies reported no relationship between body size and δ^{13}C values for some sharks (*Centrophorus cf. granulosus, Etmopterus bigelowi, Galeocerdo cuvier, Hexanchus griseus, Squalus cf. mitsukurii, Centrophorus cf. niaukang, Mustelus canis*) and demersal, pelagic and deep-sea fish (Table 3). These studies suggest that the relationship between δ^{13}C and body size is variable among species, and that more in depth research is needed to understand this pattern.

4.0 Future directions:

Since the first deep-sea expedition by the British Navy in 1857, the deep-sea has gained considerable popularity among scientists, explorers and extractive industries (e.g.

deep-sea mining, fishing, tourism; Miller et al., 2018; Danovaro et al., 2014). Advances in fishing gear, sampling techniques and methodological approaches to understand species interactions (e.g. chemical tracer analysis) within recent decades has granted access to further reaches of the deep-sea, providing new opportunities to understand this environment. Despite the progress to date, there is still much to be understood about deep-sea ecosystems.

At present our understanding of spatial isotopic variation within the deep-sea and characterization of isotopic patterns across entire deep-sea habitats is lacking. Deep-sea ecosystems are complex and the harsh conditions bring ecological challenges. A meta-analysis of species' isotopic compositions is recommended to understand how isotopes vary depending on environment type (e.g. slope versus trench, seamount versus basin) and by phylum to determine the influence of habitat to ecological traits (e.g. energy pathways, trophic position, feeding behaviour) in the deep sea. However, in order for this to be completed more data needs to be collected in specific environments (e.g. canyon, ridge, cold seep, volcano, among others in Figure 4 are all particularly understudied).

It is critical that dedicated work focuses on deep-sea environments to establish baseline data to understand how the deep-sea is being altered due to physical, chemical and biological modifications (Thresher et al., 2015). Emerging stressors facing the deep-sea include: climate change (Ramirez-Llodra et al., 2011; Sweetman et al., 2017), invasive species (Galil et al., 2019), changes to nutrient recycling (Levin & Le Bris, 2015), ocean acidification (Kunz et al. 2016; Sweetman et al., 2017), mineral exploitation (Weaver et al., 2018), fishing (Norse et al., 2012; Victorero et al., 2018), waste disposal (Ramirez-Llodra et al., 2011), and biogeochemical changes (Danovaro et al., 2016).

Direct climate change impacts to the deep sea include: temperature increases of up to 4.4°C in the Atlantic Ocean (Sweetman et al., 2017), carbon dioxide more readily dissolving in colder waters than warmer waters (Chen et al., 2017), release of methane from continental margins (Levin & Le Bris, 2015) which may exceed the capacity for organisms to oxidize methane (Marlow et al., 2014), and acidification because it is predicted the pH will be lowered by 0.29 to 0.37 pH units (Sweetman et al., 2017). SIA will address the impact of climate change in the deep-sea because the burning of fossil fuels has led to the release of more ^{12}C and less ^{13}C, known as the '*Suess effect'* (Keeling et al., 1979), this δ^{13}C decline has been observed in tuna globally from 2000-2015 (Lorrain et al., 2020). By monitoring δ^{13}C over long time periods in the deep-sea, it is possible to detect that anthropogenic induced emissions are reaching the deep-sea. Long term studies utilizing SIA will also provide ecological insight into how species may respond to stressors described above by detecting top down and bottom up effects as well as how species' habitat, physiology and trophic position may be affected pre- and post-stressor.

Accessibility has been a barrier to study deep-sea environments in the past. However, the rise of technology in the form of remotely operated vehicles, fishing technology, tracer analysis, sampling equipment, as well as communication and sensor advancements has improved accessibility for both scientists and industry. The deep-sea remains largely inaccessible for humans to directly experience, although visits are increasing (Lutz & Falkowski, 2012). The remoteness of the deep-sea environment incurs large challenges and limitations on potential sampling gear. For example, it is difficult to encapsulate the entire deep-sea food web from primary producers to predators using current methods. Some sampling gear, such as trawls with larger mesh sizes, can selectively exclude smaller prey items that pass through the mesh and are not captured. In contrast, larger predatory species can alter behaviour to avoid being captured by the trawl. Researchers are encouraged to undertake a multi-method approach to sample several trophic levels within the deep-sea and reduce associated limitations with each method when gathering samples for SIA.

It is recommended that SIA be used in combination with other metrics including telemetry (e.g. Matich & Heithaus, 2014), fatty acids (e.g. Leduc et al., 2015; Kiyashko et al., 2014), highly branched isoprenoid lipid biomarkers (e.g. Brown et al., 2017), and respirometry. An multi-method approach (e.g. combination of SIA with another metric) could provide more confidence in the trends observed. Using a multi-method approach by combining SIA with another metric adds confidence in observed trends and provides an opportunity to make inferences on the ecological characteristics of deep-sea food webs without constant monitoring and having to be physically present. Additionally, future work needs to be undertaken to better understand the isotopic turnover rates of deep-sea species; this will aid in advancing understanding of temporal variability in ecological characteristics that can be inferred from SIA such as feeding behaviour, trophic dynamics, and ecological characteristics.

Overall, SIA is a powerful tool which can be used to understand deep-sea species' ecological characteristics and how they may respond to stressors. This review acts as a baseline and summary for future research directions by synthesizing available literature. Additional research involving SIA in combination with other metrics is needed to fully understand observed patterns. By understanding key ecological trends in deep-sea environments through a multiple species approach, this information can be used for management to understand how several species interact.

5.0 Summary of findings:

- Deep-sea environments are highly complex and variable in isotopic patterns among taxa and the type of habitat. The general trend is that generally $\delta^{13}C$ and $\delta^{15}N$ decrease with latitude towards the poles, however this is not uniform across all deep-sea environments and taxa and additional factors besides latitude (e.g. environmental influences, localized conditions) drive isotopic composition.
- Deep-sea environments have been studied more frequently in the Northern hemisphere compared to the southern hemisphere with data hotspots occurring in Western Europe, North America, Eastern Asia and the Southern Ocean.
- The most well studied environment types include: slope, basin and shelf. Rift, trench, margin, strait, ridge, volcano, cold seep, fan, sea bright, plain and fjord are not as well studied.
- Energy pathways in the deep-sea are variable depending on the type of habitat and (e.g. trench, seamount, etc.) species present suggesting multiple $\delta^{13}C$ pathways including: sinking particulate organic matter, anthropogenic sources, sea ice, phytoplankton, terrestrial organic matter and sinking particles. Additionally, some habitats rely on energy derived from chemosynthetic pathways which rely on microbial activity, sulphur and methane for primary productivity instead of photosynthesis.

- The relationship between depth and $\delta^{15}N$ is not ubiquitous across deep-sea food webs, but the majority of studies indicate that $\delta^{15}N$ increases with depth. The pattern for $\delta^{13}C$ and depth is not as clear because of data deficiency.
- Deep-sea food webs experience temporal variation both intra- and inter- annually. Generally, lower $\delta^{15}N$ correlates to spring phytoplankton blooms and higher $\delta^{15}N$ is present when phytoplankton may not be as abundant in an environment. Studies examining temporal scales less than ten years did not indicate that there are consistent changes in stable isotopes. However, studies examining more than ten years of data suggest that overtime $\delta^{15}N$ and $\delta^{13}C$ has decreased due to environmental changes, development and plankton consumption. At a centennial scale, isotopic composition has remained relatively stable except for decreases in $\delta^{13}C$ with the onset of fossil fuel burning.
- There is variation in some species feeding between the average dietary history (e.g. SIA) and recent diet (e.g. SCA). More research is needed to determine mixing models which encapsulate and best predict deep-sea species diet. The introduction of video is a novel approach to understand feeding behaviour in the deep-sea alongside SIA.
- There are typically 4 to 5 trophic levels in the deep-sea. Trophic position in the deep-sea is dependent on sinking particulate organic matter (marine snow), falling food (macro – and meso- carrion falls) and prey consumption on the seafloor. Isotope derived estimates of trophic position are impacted by prey choice, biological conditions, baseline data, tissue type and scavenging. Trophic level is not standardized in the deep-sea which makes cross study comparisons difficult.

- Niche is highly variable dependent on functional groups and variability in the base of the food web. Species within the deep-sea have inconsistent overlapping and non-overlapping niches.
- Larger organisms typically have higher $\delta^{15}N$ due to shifts in feeding behaviour. The relationship with $\delta^{13}C$ is not as well studied, but higher $\delta^{13}C$ does occur with increasing body size for some species suggesting changes in foraging behaviour.
- It is critical that baseline research is undertaken to understand how deep-sea environments will respond to future environmental perturbations and aid in conservation measures.

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Chapter 3: Trophic ecology of five deep-sea teleosts and two decapod species with different functional roles across an Arctic latitudinal gradient.

1.0 Introduction:

Globally, marine food web structure varies along environmental gradients, however, limited studies have examined these relationships in poorly sampled Arctic waters. Environmental conditions in the Arctic are rapidly changing and marine food webs face several emerging stressors which may impact local functional ecology including: climate change (Beaugrand & Kirby, 2018), resource extraction (Reeves et al., 2014), increased shipping (Halliday et al., 2017) and tourism (Palma et al., 2019), north-ward shift of species ranges (Chan et al., 2019), and plastic pollution (Halsband & Herzke, 2019). Within the Barents Sea, food webs have been shown to be more distinct (e.g. fewer links per species, low connectivity) at sites with cooler waters and higher seasonal ice coverage compared to lower latitude areas (Kortsch et al., 2018). Sea ice and temperature influence species' ecological and biological traits (Frainer et al., 2017), interactions (Post et al., 2013), movements (Hussey et al., 2017), abundance (Szymanski & Gradinger, 2016), and distributions (David et al., 2016). These interacting traits suggest that Arctic marine food webs are particularly vulnerable to emerging stressors, especially climate change.

Stable isotope analysis ($\delta^{15}N$ and $\delta^{13}C$) is a proven tool to examine food web dynamics in marine environments. The ratio of nitrogen stable isotopes ($\delta^{15}N$) is commonly used to make inferences on trophic position (Post, 2002), whereas the ratio of carbon stable isotopes ($\delta^{13}C$) reflects a species' foraging habitat (Inger & Bearhop, 2008). Inference based on these isotopic patterns centres on the distinct and relatively conservative enrichment of ^{15}N and ^{13}C, respectively in food webs and the incorporation of these signals into animals' tissues following consumption. These methods can be particularly valuable for resolving trophic relationships in physically challenging environments such as the deep-sea, which is light limited (Danovaro et al., 2014), and generally considered to be low energy (Woolley et al., 2016), high pressure (Rogers, 2015) and host highly *k*-selected species (Victorero et al., 2018). At the global level, $\delta^{13}C$ values in deep-sea fauna (specifically pelagic and demersal species) and squid (*Dosidicus gigas* and *Sthenoteuthis oualaniensis*) were shown to decrease from low to high latitudes (Parzanini et al., 2019; Ruiz-Cooley & Gerrodette, 2012). In contrast, benthic species showed no latitudinal relationships with $\delta^{13}C$ (Parzanini et al., 2019). Squid sampled at higher latitudes had higher $\delta^{15}N$ values compared to those at the equator (Ruiz-Cooley & Gerrodette, 2012) whereas in deep-sea fauna $\delta^{15}N$ at the poles was lower compared to the equator (Parzanini et al., 2019). Aside from the synthesis of data by Parzanini et al. (2019), limited research has been undertaken to understand isotopic latitudinal trends, especially in poorly sampled and potentially vulnerable ecosystems such as the deep-sea and Arctic regions.

Niche breadth is one metric which can be used to understand how food web structure is influenced by environmental gradients. The concept of niche was first used to describe species in an environmental context by examining environmental factors and non-interactive variables (e.g. solar radiation, precipitation; Turner et al., 2003) to look at biotic and abiotic species properties (Grinnell, 1917). Hutchinson then expanded on this concept in the mid-1900's defining the ecological niche as a hypervolume of n-dimensions in space occupied by a species in relation to resource use (Hutchinson, 1957;

Bearhop et al., 2004; Colwell et al., 2009). While, Hutchinson's approach is considered the most rigorous for quantifying niche, the n-dimension concept is inherently complex to estimate because the calculation requires a robust understanding of the effects of multiple biotic and abiotic variables on the life history characteristics of the species in question (Holt, 2009).

Building on the seminal work of Hutchinson, MacArthur's 'Latitudinal Niche Breadth Hypothesis' (MacArthur, 1972) states that species at the poles will occupy wider niches compared to tropical environments due to a lack of tropical seasonality (Vázquez & Stevens, 2004). Moreover, narrower niches are predicted in the tropics due to higher resource diversity, promoting intraspecific niche variation among species (Araújo & Costa-Pereira, 2013). The 'Latitudinal Niche Breadth Hypothesis' has been tested at large scales from the poles to the tropics (e.g. Vázquez & Stevens, 2004; Cirtwill et al., 2015) and at smaller scales spanning < 10 ° (e.g. 5°: Lappalainen & Soininen, 2006). Recent studies examining niche breadth in the Arctic, suggest the Latitudinal Niche Breadth Hypothesis may not hold true. Fishes were observed to have smaller niche widths in more northern colder waters compared to warmer waters in the Chukchi Sea (Marsh et al., 2017) and niche size decreased with increasing latitude for beluga whales and ringed seals in the Canadian Arctic (Yurkowski et al., 2016).

The isotopic niche (combined $\delta^{15}N$ and $\delta^{13}C$) considers the n-dimensional δ-space of a species (or community) and can provide insight into links among a species' bionomic resource use (resource consumption, prey trophic level, prey abundance), scenopoetic (habitat, depth), as well as inter- and intraspecific variation (Newsome et al., 2007). Isotopic niche can also be used to understand how species biotic (e.g. prey consumption) and abiotic (e.g. habitat) traits interact with each other. For example, inferences based upon isotopic niche can be used to understand species co-existence (Shipley et al., 2019), interspecies interactions (Bison et al., 2015), feeding behaviours (Clavel et al., 2011), long term persistence (Shipley et al., 2019), and responses to environmental stressors (Clavel et al., 2011; Weisse et al., 2013; White et al., 2015) to aid in species conservation and management (Shipley et al., 2019). In the deep-sea, niche is highly variable and is considered to be dependent on species' functional roles and the environment they inhabit, dependent on basal carbon sources and trophic diversity in the environment (Kopp et al., 2017; Zapata-Hernández et al., 2016; Demopoulos et al., 2017; Portail et al., 2016; Valls et al., 2017). While previous work has examined niche across Arctic shallow water ecosystems, including polar bears (*Ursus maritimus;* Johnson et al., 2019), narwhals (*Monodon Monoceros;* Watt et al., 2013), walrus (*Odobenus rosmarus ;* Linnebjerg et al., 2016), seals (*Pusa hispida, Pagophilus groenlandicus;* Ogloff et al., 2019), seabirds (*Rissa tridactyla, Uria aalge, Uria lomvia*; Will & Kitaysky, 2018), and fish (*Boreogadus saida, Eleginus gracilis, Gadus ogac;* Brewster et al., 2016), little work has been undertaken to understand niche in the deep-sea, particularly across a latitudinal gradient in the Eastern Canadian Arctic.

The overall objective of the current study is to test whether MacArthur's 'Latitudinal Niche Breadth Hypothesis' holds true on a relatively small latitudinal scale in the Eastern Canadian Arctic. To examine this hypothesis, I quantify and compare the niches of five fish and two shrimp species that have diverse functional roles across a latitudinal gradient spanning 67°N to 72°N at three sampling sites in the Eastern Canadian Arctic deep-sea. I also examine several biotic (e.g. morphometric, condition) and abiotic (e.g. air temperature, illumination, sea ice) factors to investigate potential drivers of differences in niche breadth other than latitude. Specifically, I address key aspects of niche across an Arctic latitudinal gradient through (i) characterizing the environmental conditions at each study location to determine variation in sea ice, air temperature and illuminance, (ii) quantifying species' morphometric and condition characteristics (e.g. hepatosomatic index, fork or carapace length, body mass), (iii) estimating isotopic niche for each species to compare and contrast niche size/overlap within each study site and among sites, (iv) calculating isotopic community metrics at each site using methods developed by Layman et al. (2007) (nitrogen range, carbon range, mean distance to the centroid, nearest neighbour distance, standard deviation to the nearest neighbour), and (v) determining whether fish length, hepatosomatic index, latitude and sampling depth are factors that explain variation in isotopic composition among species and sites.

Based on MacArthur's 'Latitudinal Niche Breadth Hypothesis', I predict that: 1) species will have narrower niches at lower latitudes compared to higher latitudes as a result of lower productivity and biodiversity at the most northern site; 2) there will be positive relationships between latitude and overlap, niche breadth and morphometric characteristics (i.e. length), as well as niche breadth and condition (i.e. hepatosomatic index); and 3) latitude will have an overriding effect because environmental conditions (i.e. elevated temperatures and less sea ice, i.e. shorter duration of land fast ice) and energy pathways (i.e. dominance of pelagic vs. sympagic derived carbon) will contribute to smaller isotopic niches at lower latitudes.

2.0 Materials and Methods:

2.1 Study Sites and Environmental Conditions

Sampling took place in three deep-sea channels near the communities of Pond Inlet (~72°N), Scott Inlet (~71°N) near Clyde River and Qikiqtarjuaq (~67°N), Nunavut, located on Eastern Baffin Island in the Canadian Arctic (Figure 5).

Daily air temperature (°C) was obtained for Pond Inlet, Clyde River and Qikiqtarjuaq. Data was obtained for the years 2018, 2013, 2018 respectively from the Environment Canada historical database. Daily hours of illumination (both daylight and sky) were obtained for all sites from the sunrise and sunset calendar published by the National Research Council of Canada (https://app.hia-iha.nrc-cnrc.gc.ca/cgi-bin/sun-soleil.pl, November 2019). Daylight hours are defined as the period of light from sunrise to sunset whereas sky illumination is the amount of time during civil twilight (NRCC, 2019). Weekly sea ice data were obtained from the Canadian Ice Survey (https://iceweb1.cis.ec.gc.ca/, December 2019) and a spatially weighted average was obtained for a 25-kilometer zone around all sampling locations at each of the three sites. Sea ice data were categorized into three types, formation defined as >50% sea ice concentration when the sea ice concentration is increasing, break up between 10% and 50% when the sea ice concentration is decreasing and the open water period as <10%.

Environmental data were subdivided into meteorological seasons (winter: December-February, spring: March-May, summer: June-August, fall: September-November). This was selected to avoid sampling bias by selecting dates that best fit the unique seasonal conditions of the Arctic. Data did not fit a normal distribution (Shapiro-

Wilk Test), consequently differences among sites were tested using Kruskal-Wallis and Dunn’s post hoc tests.

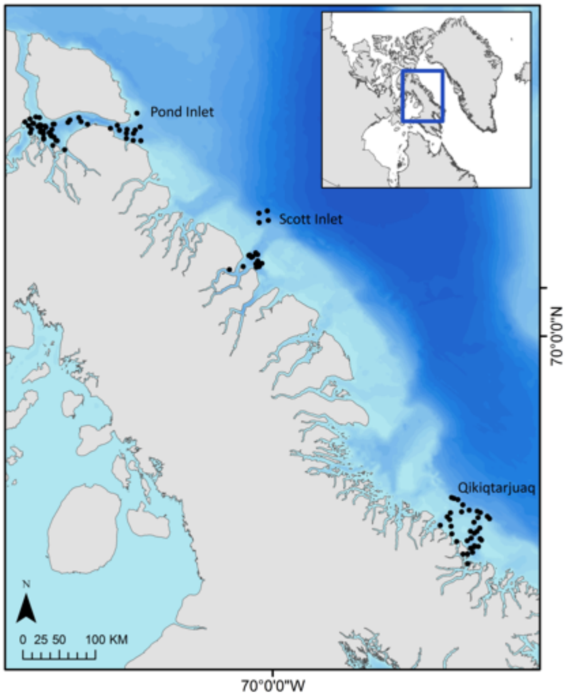


Figure 5: Locations of scientific bottom trawl surveys and longline surveys conducted along the Eastern Coast of Baffin Island in 2013 (Scott Inlet) and 2018 (Pond Inlet, Qikiqtarjuaq). The distance between Pond Inlet and Scott Inlet is ~300km; the distance between Scott Inlet and Qikiqtarjuaq is 500km; the full geographic range was ~800km.

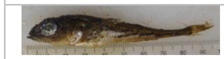
2.2 Sample collection and morphometric characteristics

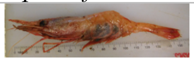
The M.V. Nuliajuk, a fisheries research vessel owned by the Government of Nunavut, was used for all sampling. Longline and trawl surveys were completed during the fall in 2013 in Scott Inlet near the community of Clyde River (~71°N, 14 trawls, depth range 224 - 800 m). During the late summer and early fall of 2018, trawl surveys were completed near Pond Inlet (~72°N, 51 trawls, depth range 67 – 844 m) and in the Qikiqtarjuaq area (~67°N, 35 trawls, depth range 67 - 732 m) (Figure 5). Target species include 5 fishes and 2 shrimp that were selected based on functional roles (Table 5).

Upon retrieval of fishing gear, samples were sorted and immediately frozen onboard in a -20°C freezer and transported back to the University of Windsor. During dissection, a ~5 g sample of muscle tissue was excised form the dorsal side of each fish and from the abdomen of each shrimp. Muscle was chosen because it is considered to have a relatively slow turnover rate (MacNeil et al., 2006; Matich et al., 2006; Xia et al., 2013), which provides inferences on integrated average dietary history over a long time period.

Morphometric characteristics including body mass (g), liver mass (g), fork length (cm) (Greenland Halibut [*Reinhardtius hippoglossoides*], Arctic Cod [*Boreogadus saida*]), total length (cm) (Gelatinous Snailfish [*Liparis fabricii*], Atlantic Poacher [*Leptagonus decagonus*], Bigeye Sculpin [*Triglops nybelini*]) and carapace length (cm) (Northern Shrimp [*Pandalus borealis*], *Sclerocrangon ferox*) were recorded. The hepatosomatic index (HSI) was calculated ($HSI = \frac{liver\ mass}{body\ mass}\ x\ 100$) and used as a proxy for fish health and condition (Hussey et al., 2009) because higher HSI indicate that fish are well fed and not in a period of nutritional stress (Plante et al., 2005). HSI was chosen because of all condition metrics, it is sensitive to short term variations (Hussey et al., 2009). Greenland Halibut was removed from morphometric and condition data comparisons because we did not have complete measurements across all locations.

Table 5: Ecological characteristics of deep-sea Arctic species collected in Scott Inlet (2013), Qikiqtarjuaq (2018) and Pond Inlet (2017, 2018) (Christie, 2019).

	Depth Range (m)	**Maximum Length (cm)**	**Age of maturity**	**Stomach Contents Frequency of Occurrence (%)**	**Economically Significant**	**References**
 Arctic Cod, *Boreogadus saida*	Surface – 1390 m Benthopelagic / pelagic	40	2-3 years (males) 3-4 years (females) Offshore fish reach 2.0 cm in their first year	Polychaeta (0-1.82%) Crustacea (12.7-23.6%) Copepods (53.5-63.6%) Mysidae (0-10.5%) Cumacea (0-8.9) Amphipoda (30-37.6%) Euphausiids (0-17.1%) Decapods (4.1-15.0%) Echiuroidea (0-2.3%) Chaetognatha (0-15.4%) Thaliacea (2.9-4.1%) Copelata (23.6-52.9%) Teleostei (6.44-23.18%) Unidentified (5.7-11.7%)	Yes	Coad & Reist, 2017; Vollen et al., 2004
 Greenland Halibut, *Reinhardtius hippoglossoides*	14 – 2000 m Benthopelagic	130	50% maturity 9.5-10 years (females) and 8.2-11.6 years (males)	Mollusca (23.3%) Crustacea (38.7% - 47.6%) Teleostei (44.7% - 78.8 %) Offal (9.3%) Cephalopoda (1.2%) Echinodermata (2.5%) Other (2.35-3.4%)	Yes	Coad & Reist, 2017; Fish base, n.d.d.; Hovde et al., 2002; Vollen et al., 2004
 Bigeye Sculpin, *Triglops nybelini*	135-1279 m Bathydemersal Juveniles can be found >37 m	17	Not available	Hydrozoa (0-1.3%) Copepoda (0-1.4%) Mysididacea (0-12.8%) Gammaridae (0-5.7%) *Parathemisto libellula* (0-30%) *Hyperia galba* (0-18.5%) Pandalus sp. (0-1.4%) Cructacea (unidentifiable) (4.1 - 30%) Animal remains (50-95.8%)	No	Coad & Reist, 2017; Fish base, n.d.b.; Ottesen, 2004
 Atlantic Poacher,	2 – 968 m	25	Females larger than males	*Bradyidius similis* (87%) Amphipoda (23%) Calanus species (23%)	No	Coad & Reist, 2017; Fish base, n.d.a. Heggland et al., 2015

Leptagonus decagonus	Benthic – Bathypelagic, Demersal			Isopoda (17%) Mysida (13%) OstraCoda (10%) Cumacea (7%) Decapoda (7%) Euphasiacea (7%)		
 Gelatinous Snailfish, *Liparis fabricii*	6 – 1880 m Southeastern Baffin Island depth is 146-409 m Bathydemersal	19.4	Not available	Stomach content data is not available. Prey include: Crustaceans (pelagic hyperiid amphipods, mysids, euphausiids, gammarids, gastropods, polychaete worms, calanoid copepods	No	Coad & Reist, 2017; Fish base, n.d.c.
 Northern Shrimp, *Pandalus borealis*	20-1330 m Benthic	16.5	2.4 cm	Shells (2.5 – 16.9%) Cructaceans (4.5 – 18.4 %) (Gulf of Maine) Additional prey items include: zooplankton, detritus, phytoplankton, euphausiids, chaetognaths, amphipods, mysids, jellyfish, copepods, tunicates, ichthyoplankton	Yes	McLeod et al., n.d. Fisheries and Oceans Canada, 2003; Savenkoff et al., 2006; Sea Life, n.d.; Apollonio et al., 1986
 *Sclerocrangon ferox*	90 – 1000 m	Carapace length : 3.1	Males mature at 1.5cm and females 2.4 cm	Stomach content is not available. Prey include: phytobenthos, amphipods, polychaetes, ophiuroids, gastropods, bivalves, spong spinicles	No	McLeod et al., n.d.; Squires, 1990; Squires, 1996; Squires, 1965

2.2 Sample preparation for stable isotope analysis

To prepare fish and shrimp muscle tissue for stable isotope analysis (SIA), samples were freeze dried using a Labconco freeze drier at -53°C for 48 hours and then homogenized. Lipids were removed using a modified Bligh and Dyer (1959) method with a 2:1 chloroform methanol solution. The chemical extraction method was chosen given inadequate mathematical lipid correction models for deep-sea fish (Hoffman & Sutton, 2010). Tissue samples were first vortexed in 2:1 chloroform methanol and then placed in a 30°C water bath for 24 hours. Samples were then centrifuged for 5 minutes; the chloroform methanol was discarded and the remaining supernatant was retained in a vial. A second dose of 2:1 chloroform methanol was then added and the sample was vortexed again. After the 2:1 chloroform methanol was discarded, the remaining supernatant and samples were placed with the lid off in a fume hood for 24 – 48 h to allow the sample to dry by evaporation. This process was completed once for all species except Greenland Halibut (Pond Inlet, Qikiqtarjuaq) which were lipid extracted twice due to high C:N ratios in previously analysed samples from a different location (N. Hussey, personal communication, July 2019). The C:N ratios in this study range from 2.8 to 5.3 (1 Arctic Cod from Scott Inlet > 5, 21 Greenland Halibut from Scott Inlet 4-5), with the majority of samples having a C:N ratio between 2.8 and 4.0 (n=315).

Homogenized lipid-extracted muscle samples were weighed out (400-600 um) in tin capsules using a Sartorius microgram balance. All samples were then analyzed using a continuous flow Thermofinnigan Delta Plus mass spectrometer coupled with an elemental analyzer. Scott Inlet fish were analyzed at the Great Lakes Institute for Environmental Research (GLIER, Windsor). Pond Inlet and Qikiqtarjuaq fish and all shrimp were analyzed at the chemical tracer lab in Fisheries and Oceans Canada Freshwater Institute (FWI, Winnipeg). Stable isotope ratios were obtained (^{15}N:^{14}N and ^{13}C:^{12}C) and referenced to internal standards ($\delta^{13}C$: Pee Dee Belemnite carbonate derived from cretaceous cephalopods, $\delta^{15}N$: Atmospheric nitrogen as well as USGS40 and 41a) at GLIER and the FWI (Christie, 2018; Newton, 2001; Pinnegar & Polunin, 1999; Rosenberg, personal communications). The ratio of stable isotopes was then calculated in parts per thousand (‰) compared to the internal standard references using the formula:

$$\delta X = (\frac{R_{sample}}{R_{standard}} - 1) \text{ x } 10^3,$$

where δ is quantifying the measure of heavy to light isotope, X representing the heavier isotope (^{15}N or ^{13}C), R_{sample} the sample isotope ratio (^{15}N:^{14}N or ^{13}C:^{12}C) and $R_{standard}$ representing the isotope ratio in the standard reference (Pinnegar & Polunin, 1999 ; McMeans et al., 2010) to assess accuracy and precision. The averages among runs were -26.4‰ ± 0.02 and -4.5‰ ± 0.1 for USGS 40 for $\delta^{13}C$ and $\delta^{15}N$, respectively, and -36.6‰ ± 0.1 and 47.6‰ ± 0.2 for USGS 41a for $\delta^{13}C$ and $\delta^{15}N$, respectively .

2.3 Data Analysis

2.3.1 Isotopic Niche

Isotopic niche was determined using Stable Isotope Bayesian Ellipses in R (SIBER) to account for differences in sample size and to facilitate comparisons across sites (Jackson et al., 2011). Standard ellipse areas corrected (SEA_c) were estimated that account for 40% of the true data, which is a conservative estimate of true niche core area (Jackson et al., 2011). One degree of freedom is added to account for bivariate data (SEA_c) to adjust for differences in sample sizes (Jackson et al., 2011). Bayesian statistics (SEA_B) were then used to run the simulation (i.e. 10000 iterations), providing unbiased

40% ellipses that account for different sample sizes among species and populations (Jackson et al., 2011). Niche overlap was determined to understand niche similarities between and among species across a latitudinal gradient using SEA_B. An overlap of >60% was considered significant and 100% indicated complete overlap (Schoener, 1971). Overlap was determined using the following equation:

$$\%\, overlap\ of\ niche\ A = \frac{Total\ Overlapping\ Area\ of Ellipse\ A\ and\ Ellipse\ B}{Total\ Ellipse\ Area\ of\ A} \text{ x } 100$$

To test parametric assumptions before performing statistical tests on isotope data, Levine's Test was used to determine if sample variances were equal and the Shapiro-Wilk Test was used to determine if the data were normally distributed. Data (length, $\delta^{15}N$, $\delta^{13}C$) was mostly normal and heteroscedastic. A MANOVA was first undertaken to test for differences in combined $\delta^{15}N$ and $\delta^{13}C$ values among species at each location. ANOVA was then used to test for significant differences in isotopic composition among species at each site for $\delta^{15}N$ and $\delta^{13}C$ independently where the MANOVA indicated a significant difference. Tukey-Post Hoc tests were used for pairwise comparisons when the ANOVA results showed a statistically significant difference. All statistical analyses were conducted in R v.1.1.383. Unless otherwise stated the significance level was $p < 0.05$.

2.3.2 Layman Metrics

Layman niche metrics (Table 12) were calculated to understand species and community metrics across a latitudinal gradient. Layman metrics provide estimates of isotopic variation across an entire community (i.e. at one study location) by examining the $\delta^{15}N$ range, $\delta^{13}C$ range, mean nearest neighbour distance, standard deviation of the mean nearest neighbour distance, distance to the centroid and the total area of the convex hull (Layman et al., 2007, Jackson et al., 2011, Table 12).

2.3.3 Linear Model

Linear models were used to examine isotopic variation (either $\delta^{15}N$ or $\delta^{13}C$) in relation to location, sampling depth, and length (fork or carapace) for species at each site. Species (Atlantic Poacher, Arctic Cod, Greenland Halibut, Bigeye Sculpin, Gelatinous Snailfish, *Sclerocrangon ferox*, Northern Shrimp) and location (numerical value given for each site: Pond Inlet, Scott Inlet, Qikiqtarjuaq) were categorical fixed factors, while length was included as a continuous fixed factor.

3.0 Results:

3.1 Environmental characteristics of the three study sites

Of the three study sites on Baffin Island, Pond Inlet had significantly colder mean air temperatures in the winter and spring compared to Scott Inlet and Qikiqtarjuaq (winter: Kruskal-Wallis chi-squared = 44.7, df=2, $p < 0.001$; spring: Kruskal-Wallis chi-squared = 15.1, df=2, $p < 0.001$; Figure 6). Mean air temperatures were not significantly different between Pond Inlet and Scott Inlet During the summer and fall (Dunn's-test, $p > 0.05$), or between Qikiqtarjuaq and Scott Inlet in the winter and spring (Dunn's-test, $p < 0.001$).

Pond Inlet had the shortest open water period (7 weeks), followed by Qikiqtarjuaq (10 weeks) and Scott Inlet (13 weeks) (Figure 7). There were no significant differences in weekly ice concentration during the summer months (Kruskal-Wallis chi-squared = 1.6, df=2, $p > 0.05$) but Pond Inlet had significantly higher ice concentration in the winter compared to Qikiqtarjuaq and Scott Inlet (Kruskal-Wallis chi-squared = 20.6, df=2, p <

0.0001). Pond Inlet was also ice covered (>50% ice coverage) for 42 weeks, when compared to Qikiqtarjuaq (40 weeks) and Scott Inlet (36 weeks) (Figure 7). Freeze up in Pond Inlet occurred earlier than Qikiqtarjuaq and Scott Inlet (Figure 7).

As expected for this latitudinal gradient, Pond Inlet had the longest period of 24-hour sunlight (93 days) and darkness (75 days) compared to Scott Inlet (sunlight: 78 days, darkness: 57 days) and Qikiqtarjuaq (daylight: 51 days, darkness: 21 days) (Figure 8). There were no significant differences in daylight hours of illumination and sky hours of illumination during the spring (daylight: Kruskal-Wallis chi-squared = 3.4012, df = 2, p-value > 0.05; sky: Kruskal-Wallis chi-squared = 0.74514, df = 2, p-value = 0.689). During the summer, Pond Inlet and Scott Inlet had more daylight hours of illumination than Qikiqtarjuaq (Dunn's test $p<0.05$). All three sites were significantly different in hours of illumination in the fall (Kruskal-Wallis chi-squared =92.033, df=2, $p < 0.001$).

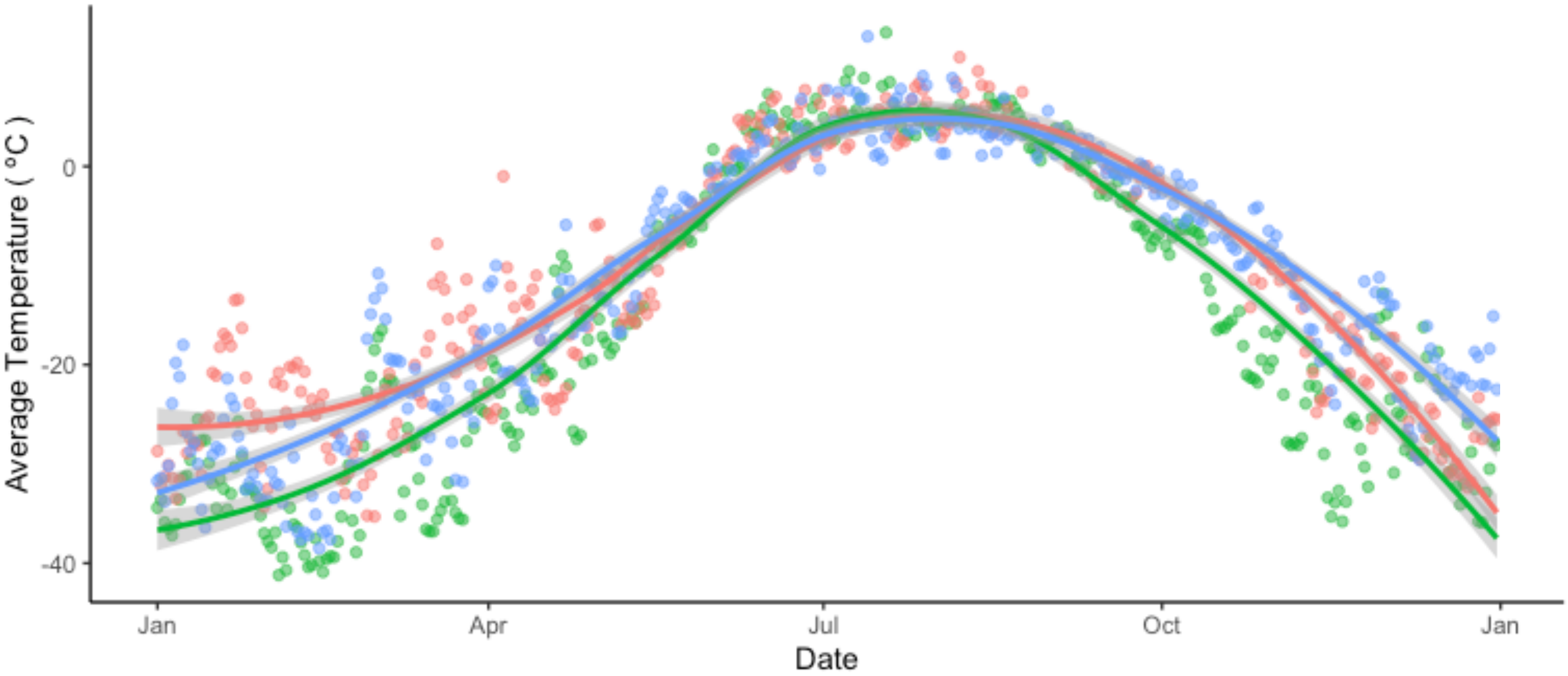


Figure 6: Average air temperature (°C) for the three locations**:** Pond Inlet (green), Clyde River near Scott Inlet (red), and Qikiqtarjuaq (blue), Nunavut. Points represent daily mean air temperature data which was obtained from Environment Canada. Data was smoothed using a smoothed conditional means and the grey represents standard error bounds.

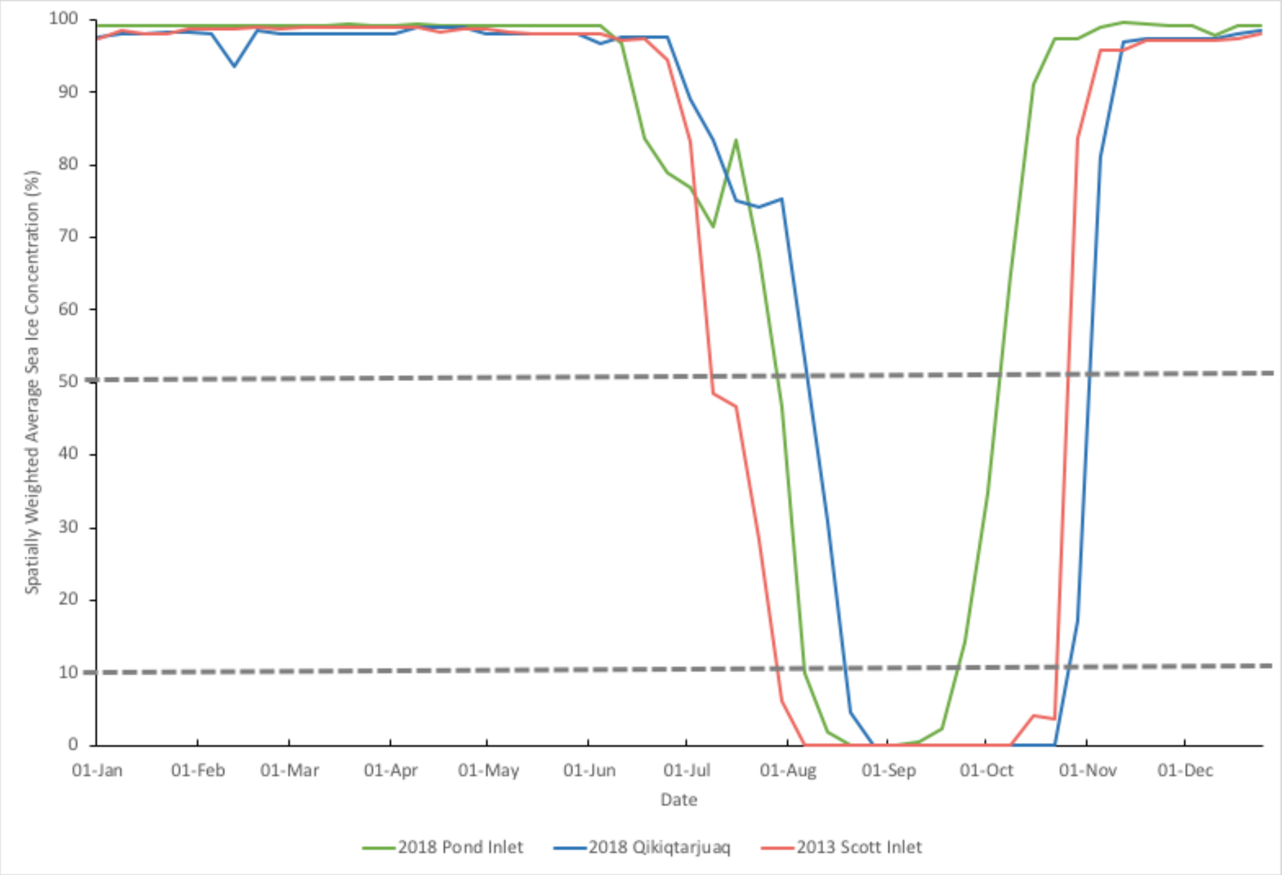


Figure 7: Mean spatially weighted sea ice concentration for Pond Inlet (2018), Scott Inlet (2013), and Qikiqtarjuaq (2018). Sea ice data obtained from the Canadian Ice Survey weekly ice charts. Sea ice concentration >50% is considered formation when the ice concentration is increasing (i.e. fall), <50% is considered sea ice break up when the sea ice concentration is decreasing (i.e. spring) and <10% is considered ice free / open water (i.e. summer period) (Canadian Ice Service, 2019). Pond Inlet (green), Clyde River near Scott Inlet (red), and Qikiqtarjuaq (blue), Nunavut.

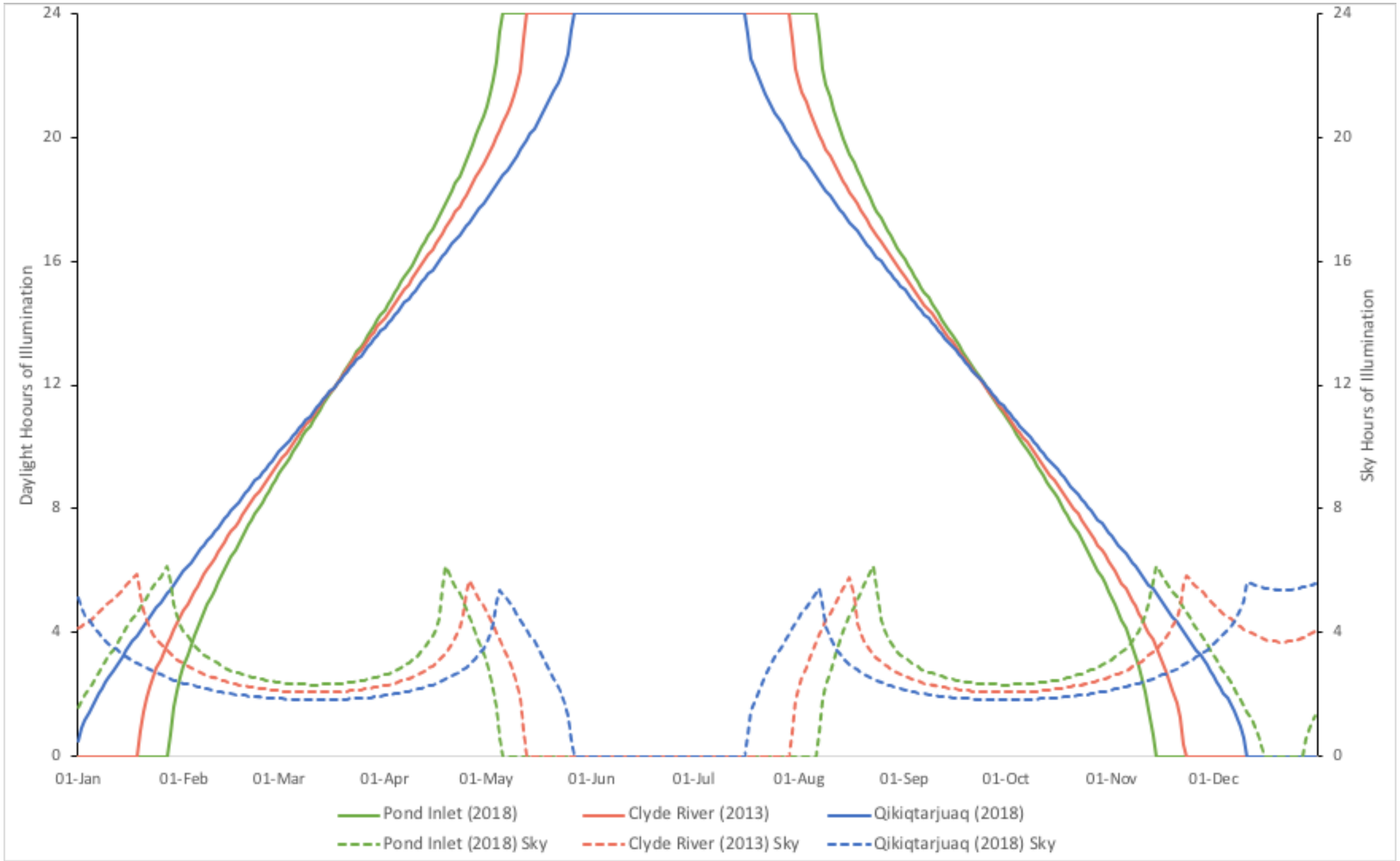


Figure 8: Hours of daylight illumination (solid) and sky hours of illumination (dashed) at three locations: Pond Inlet (green), Clyde River near Scott Inlet (red) Qikiqtarjuaq (blue). Data obtained from sunrise and sunset calendar from the National Research Council of Canada (https://app.hia-iha.nrc-cnrc.gc.ca/cgi-bin/sun-soleil.pl, September 2019).

3.2 Morphometric Data

Across sampling years, a total of 448 individuals of the two shrimp and five fish species were sampled (Table 6). Fish fork/total length ranged from 3.1 to 58 cm across all locations and taxa, whereas shrimp carapace length ranged from 1.6 to 4.2 cm (Table 6, Figure 9). Average lengths (mean ± S.D.) of fish species across all three sites were the highest for Greenland Halibut (44.9 ± 7.66 cm) and the lowest for Bigeye Sculpin (10.8 ± 1.35 cm) (Table 6, Figure 9). Northern Shrimp had a higher carapace length (3.21 ± 0.57 cm) than *Sclerocrangon ferox* (2.32 ± 0.45 cm, Table 6, Figure 9).

The length of Bigeye Sculpin increased in length from high to lower latitudes (Table 6, Figure 9). Across all three sites the species that had the highest body mass (mean ± S.D.) was Greenland Halibut (850 ± 455 g) followed by Arctic Cod (30 ± 25.8 g) (Table 6). *Sclerocrangon ferox*, Northern Shrimp, Gelatinous Snailfish, Bigeye Sculpin and Atlantic Poacher had similar lower masses (Table 6).

HSI varied across species and sites (Figure 10, Table 13 in supplemental). HSI was the highest at mid-latitude (Scott Inlet) for Arctic Cod (Figure 10, Table 13 in supplemental). There was a decline in mean HSI with increasing latitude between Qikiqtarjuaq and Pond Inlet for Bigeye Sculpin (i.e. Qikiqtarjuaq was highest in HSI, Figure 10, Table 13 in supplemental).

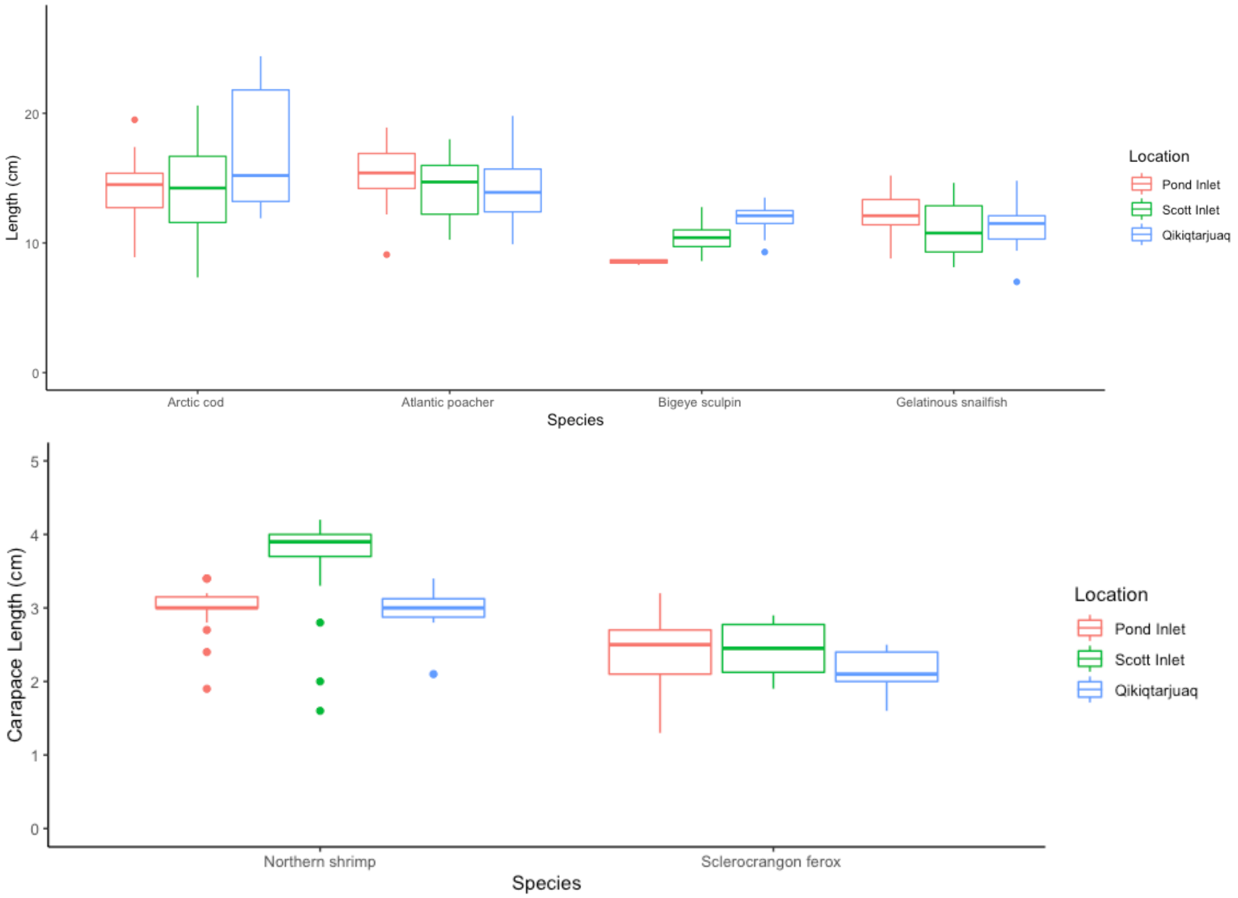


Figure 9: (A) Boxplot representing the distribution of fork length in cm (Arctic Cod), total length (Gelatinous Snailfish, Atlantic Poacher, Bigeye Sculpin) and (B) Carapace length in (Northern Shrimp, *Sclerocrangon ferox*) for each species at the three locations. Boxes represent the interquartile range (first quartile, median and third quartile), whiskers representing approximately the 95% confidence interval and outliers.

Table 6: Stable isotope (white muscle $\delta^{13}C$ and $\delta^{15}N$; ‰) and body size data (all mean ± SD) for five deep-sea fish and two shrimp species across three sites on Baffin Island, Nunavut collected in 2013 (Scott Inlet) and 2018 (Pond Inlet, Qikiqtarjuaq).

	Pond Inlet						**Scott Inlet**						**Qikiqtarjuaq**					
Species	**n_1**	**Length (cm)**	**Mass (g)**	**n_2**	**$\delta^{13}C$**	**$\delta^{15}N$**	**n_1**	**Length (cm)**	**Mass (g)**	**n_2**	**$\delta^{13}C$**	**$\delta^{15}N$**	**n_1**	**Length (cm)**	**Mass (g)**	**n_2**	**$\delta^{13}C$**	**$\delta^{15}N$**
AC	22	14.1 ± 2.5	23.7 ± 16.8	22	-20.4 ± 0.4	14.4 ± 0.60	30	13.8 ± 3.4	23.7 ± 16.3	30	-20.5 ± 0.4	14.8 ± 0.7	20	17.3 ± 4.6	46.5 ± 37.0	20	-20.3 ± 0.5	15.3 ± 1.0
AP	20	15.3 ± 2.4	13.0 ± 5.8	20	-18.8 ± 0.3	17.3 ± 0.33	10	14.2 ± 2.8	10.3 ± 6.3	10	-19.6 ± 0.2	17.4 ± 0.3	27	14.0 ± 2.4	9.5 ± 5.7	27	-19.8 ± 0.3	17.1 ± 0.5
GH	0	NA	NA	6	-19.6 ± 0.1	16.7 ± 0.41	0	N/A	NA	56	-20.7 ± 0.7	15.0 ± 0.4	20	44.9 ± 7.7	849.7 ± 454.8	20	-19.6 ± 0.2	15.9 ± 0.3
SC	4	8.6 ± 0.2	5.0 ± 1.4	4	-21.0 ± 0.3	14.1 ± 0.21	28	10.4 ± 1.0	10.2 ± 3.7	28	-20.5 ± 0.1	14.6 ± 0.3	19	11.8 ± 1.1	15.2 ± 4.5	19	-20.9 ± 0.3	13.9 ± 0.3
GSF	31	12.3 ± 1.4	16.0 ± 6.7	31	-20.5 ± 0.3	14.5 ± 0.36	22	11.0 ± 2.0	12.9 ± 9.3	22	-20.4 ± 0.3	14.6 ± 0.6	23	11.38 ± 1.7	12.6 ± 6.5	23	-20.8 ± 0.2	14.2 ± 0.5
NS	19	3.0 ± 0.4	15.0 ± 4.4	19	-17.9 ± 0.3	15.4 ± 0.62	20	3.6 ± 0.7	9.3 ± 8.9	20	-19.6 ± 0.3	15.1 ± 0.4	20	3.00 ± 0.3	14.2 ± 3.4	20	-18.3 ± 0.6	15.5 ± 0.5
SCF	6	2.4 ± 0.5	18.7 ± 10.2	20	-16.1 ± 0.5	16.6 ± 0.88	19	2.4 ± 0.4	11.5 ± 5.0	17	-17.5 ± 2.0	17.9 ± 0.6	11	2.11 ± 0.3	9.6 ± 4.3	11	-16.6 ± 0.5	16.4 ± 0.6

Arctic Cod (AC), Atlantic Poacher (AP), Greenland Halibut (GH), Bigeye Sculpin (SC), Gelatinous Snailfish (GSF), Northern Shrimp (NS), *Sclerocrangon ferox Shrimp* (SCF). Length (cm) refers to fork length (AC, GH), total length (AP, SC, GSF) or carapace length (NS SCF). N_1 refers to the number of individuals measured for length and mass and n_2 refers to the number of individuals used for stable isotope analysis. The following lists the overall mean $\delta^{15}N$ and $\delta^{13}C$ ± SD of each species across all sites: Arctic Cod (14.8 ± 0.9 and -20.4 ± 0.4), Atlantic Poacher (17.2 ± 0.4 and -19.4 ± 0.5), Bigeye Sculpin (14.3 ± 0.5 and -20.7 ± 0.3), Gelatinous Snailfish (14.4 ± 0.5 and -20.6 ± 0.3), Greenland Halibut (15.3 ± 0.7 and -20.4 ± 0.8), Northern Shrimp (15.3 ± 0.5 and -18.6 ± 0.8), and *Sclerocrangon ferox* shrimp (17.0 ± 1.0 and -16.6 ± 0.7).

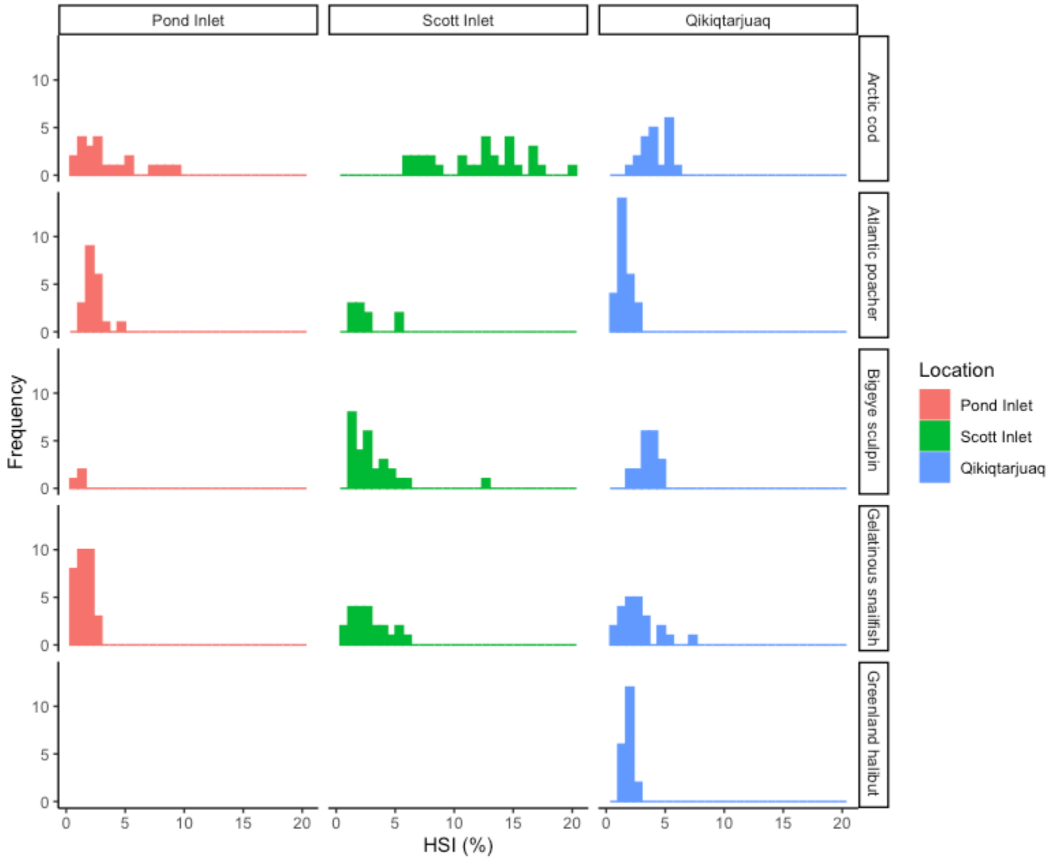


Figure 10: Frequency distribution of Hepatosomatic Index (HSI) (%) for Arctic Cod, Atlantic Poacher, Bigeye Sculpin, Gelatinous Snailfish, and Greenland Halibut at three sites: Pond Inlet, Scott Inlet and Qikiqtarjuaq. Greenland Halibut HSI is unavailable for Pond Inlet and Scott Inlet. The maximum, minimum, mean and standard deviation are in the supplemental material (Table 13).

3.3 Stable Isotope Data:

Variation in δ^{13}C and δ^{15}N values was observed across Arctic deep-sea food webs (-21.4‰ to -15.4‰ and 13.0‰ to 18.8‰, respectively). For all three sites, maximum and minimum δ^{13}C values were nearly identical; Pond Inlet: -21.4 to -15.4‰, Scott Inlet: -22.0 to -16.3 ‰, Qikiqtarjuaq: -21.6 to -16.0 ‰ (Table 6). Trophic diversity, measured using the range of δ^{15}N values, was also similar across the three sites; Pond Inlet: 13.0 to 18.1‰, Scott Inlet: 13.0 to 18.8‰, and Qikiqtarjuaq: 13.2 to 18.4‰, Table 6). The highest δ^{15}N value recorded in the study was for *Sclerocrangon ferox* (Pond Inlet; 17.7‰) and the lowest was for Arctic Cod (Pond Inlet; 13.0‰; Table 6). Arctic Cod also had the lowest $\delta^{13}C$ value (Scott Inlet; -21.4‰) while Atlantic Poacher had the highest $\delta^{13}C$ value (Scott Inlet; -19.3‰; Table 6).

Greenland Halibut had higher mean $\delta^{15}N$ at Pond Inlet compared to Scott Inlet and Qikiqtarjuaq (Table 6, Figure 11). The mean $\delta^{15}N$ was lowest for Bigeye Sculpin in Qikiqtarjuaq compared to the other sites (Table 6, Figure 11). For two species (Atlantic Poacher and Northern Shrimp) the mean $\delta^{13}C$ was higher in Pond Inlet than the other sites (Table 6, Figure 11).

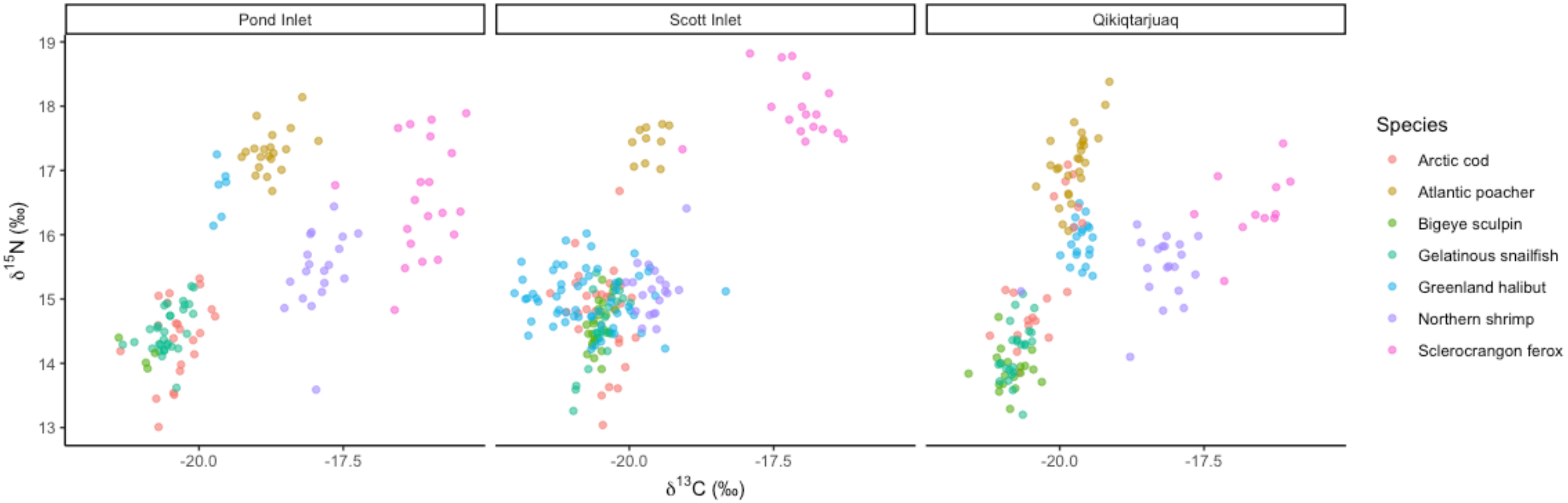


Figure 11: Isotopic biplot ($\delta^{13}C$ versus $\delta^{15}N$) of Arctic Cod, Atlantic Poacher, Bigeye Sculpin, Gelatinous Snailfish, Greenland Halibut, Northern Shrimp and *Sclerocrangon ferox* collected from three locations in the Canadian Arctic: Pond Inlet, Scott Inlet, and Qikiqtarjuaq.

There was a significant effect of species on combined $\delta^{13}C$ and $\delta^{15}N$ at all three sites (MANOVA, Table 7). Results from each ANOVA found that there were significant differences in $\delta^{13}C$ and $\delta^{15}N$ between species at each site (ANOVA, Table 7). *Sclerocrangon ferox* had significantly higher $\delta^{15}N$ and $\delta^{13}C$ than Arctic Cod, Northern Shrimp, Gelatinous Snailfish and Bigeye Sculpin at all locations (Tukey multiple comparison of means hereafter, $p < 0.05$, Table 8, Table 9). The $\delta^{15}N$ and $\delta^{13}C$ values for Arctic Cod and Gelatinous Snailfish were not significantly different from each other within each of the two high latitude sites (i.e. Pond Inlet and Scott Inlet, $p > 0.05$), but differed from those in Qikiqtarjuaq ($p < 0.05$; Table 8, Table 9). In contrast, Gelatinous Snailfish and Bigeye Sculpin were isotopically similar within Scott Inlet and Qikiqtarjuaq (Table 8, Table 9, $p > 0.05$). Atlantic Poacher was significantly higher in $\delta^{15}N$ compared to all other species within each site ($p < 0.05$) except Greenland Halibut in Pond Inlet and *Sclerocrangon ferox* in Scott Inlet and Qikiqtarjuaq ($p > 0.05$, Table 9).

Table 7: MANOVA and ANOVA results testing whether significant differences were present in $\delta^{15}N$ and $\delta^{13}C$ between species at each location. *** Indicates that there was a significant effect ($p < 0.05$).

	MANOVA	***df***	**Pillai trace**	**F**	**Num *df***	**P**
Pond Inlet	Species	5	1.67	115.29	10	p < 0.0001***
	Residuals	112				
Scott Inlet	Species	6	1.27	50.57	12	p < 0.0001***
	Residuals	176				
Qikiqtarjuaq	Species	1	0.63	117.72	2	p < 0.0001***
	Residuals	142				
	ANOVA ($\delta^{13}C$)	***df***	**Sum sq**	**Mean sq**	**F value**	**P**
Pond Inlet	Species	5	153	31	93.85	p < 0.0001***
	Residuals	112				
Scott Inlet	Species	6	196	33	127.5	p < 0.0001***
	Residuals	176				
Qikiqtarjuaq	Species	6	201	33	185.2	p < 0.0001***
	Residuals	137				
	ANOVA ($\delta^{15}N$)	***df***	**Sum sq**	**Mean sq**	**F value**	**P**
Pond Inlet	Species	5	153	31	93.85	p < 0.0001***
	Residuals	112				
Scott Inlet	Species	6	203	34	135.8	p < 0.0001***
	Residuals	176				
Qikiqtarjuaq	Species	6	164	27	57.39	p < 0.0001***
	Residuals	137				

Table 8: Tukey post hoc test results for δ^{13}C species comparisons within each location; Pond Inlet (PI), Scott Inlet (SI) and Qikiqtarjuaq (Qik). Species Codes are as follows: Atlantic Poacher (AP), Greenland Halibut (GH), Gelatinous Snailfish (GSF), Northern Shrimp (NS), Bigeye Sculpin (SC), and *Sclerocrangon ferox* (SFS). *** $p < 0.0001$, ** $p = 0.0001 - 0.009$, * $p = 0.01 – 0.049$. Dark grey area is for Bigeye Sculpin in Pond Inlet which had low sample size ($n < 5$) and therefore was not included in the comparisons.

	AC			AP			GH			GSF			NS			SC		
	PI	SI	Qik	PI	SI	Qik	PI	SI	Qik	PI	SI	Qik	PI	SI	Qik	PI	SI	Qik
AP	***	**	**	-	-	-	-	-	-	-	-	-	-	-	-		-	-
GH	**	0.2	***	***	1	1	-	-	-	-	-	-	-	-	-		-	-
GSF	0.5	1	*	***	**	***	***	0.3	***	-	-	-	-	-	-		-	-
NS	***	***	***	***	1	***	***	***	***	***	***	***	-	-	-		-	-
SC		***	**		***	***		***	***		1	1		***	***		-	-
SCF	***	**	***	***	***	***	***	1	***	***	***	***	***	***	***		***	***

Table 9: Tukey post hoc test results for δ^{15}N species comparisons within each location; Pond Inlet (PI), Scott Inlet (SI) and Qikiqtarjuaq (Qik). Species Codes are as follows: Atlantic Poacher (AP), Greenland Halibut (GH), Gelatinous Snailfish (GSF), Northern Shrimp (NS), Bigeye Sculpin (SC), and *Sclerocrangon ferox* shrimp (SFS). *** $p < 0.0001$, ** $p = 0.0001 - 0.009$, * $p = 0.01 – 0.049$. Dark grey area is for Bigeye Sculpin in Pond Inlet which had low sample size ($n < 5$) and was not included.

	AC			AP			GH			GSF			NS			SC		
	PI	SI	Qik	PI	SI	Qik	PI	SI	Qik	PI	SI	Qik	PI	SI	Qik	PI	SI	Qik
AP	***	***	***	-	-	-	-	-	-	-	-	-	-	-	-		-	-
GH	***	0.5	0.1	0.2	***	***	-	-	-	-	-	-	-	-	-		-	-
GSF	1	0.8	***	***	***	***	***	*	***	-	-	-	-	-	-		-	-
NS	***	0.2	1	**	***	***	***	1	0.5	***	*	***	-	-	-		-	-
SC		0.7	***		***	***		**	***		1	0.8		**	***		-	-
SCF	***	***	**	***	0.1	0.1	1	***	0.3	***	**	***	***	***	***		***	***

There was a significant positive relationship between length and δ^{15}N for Arctic Cod at all three locations (linear regression hereafter, Pond Inlet: R^2=0.6, $F_{1, 20}$= 29.4, $p < 0.0001$; Scott Inlet: R^2=0.8, $F_{1, 28}$= 110.3, $p < 0.0001$; Qikiqtarjuaq: R^2=0.9, $F_{1, 18}$=174.2, $p < 0.0001$). Equally, δ^{15}N values of Atlantic Poacher increased significantly with length in Pond Inlet (R^2=0.4, $F_{1, 18}$=13.3, $p < 0.01$) and Qikiqtarjuaq (R^2=0.3, $F_{1, 25}$=11.0, $p < 0.01$). No significant relationship between length and δ^{15}N were observed for remaining fish (n = 3) and shrimp (n = 2) species at any of the sites (Figure 12). Length data were not available for Greenland Halibut in Pond Inlet and Scott Inlet.

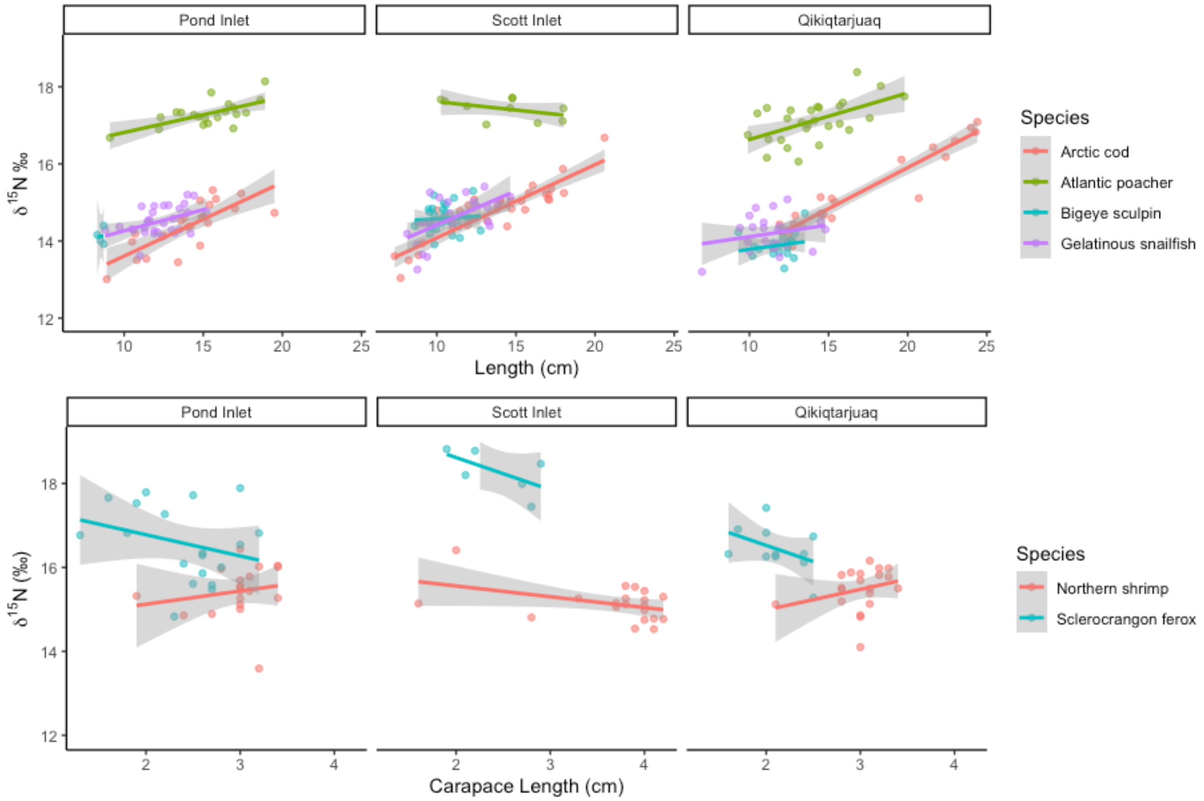


Figure 12: Linear regressions of length and δ^{15}N (‰) separated by site for (A) four deep-sea fish species separated and (B) two deep-sea shrimp species. Note the different scales on the x-axis between panels.

When examining HSI and δ^{15}N, there was a significant positive relationship for Arctic Cod in Scott Inlet (linear regression, hereafter, $R^2=0.2$, $F_{1,28}=10.2$, $p < 0.05$) and Atlantic Poacher in Qikiqtarjuaq ($R^2=0.1$, $F_{1,25}=5.0$, $p < 0.05$) (Figure 13). No relationships were observed for any other species at the three locations.

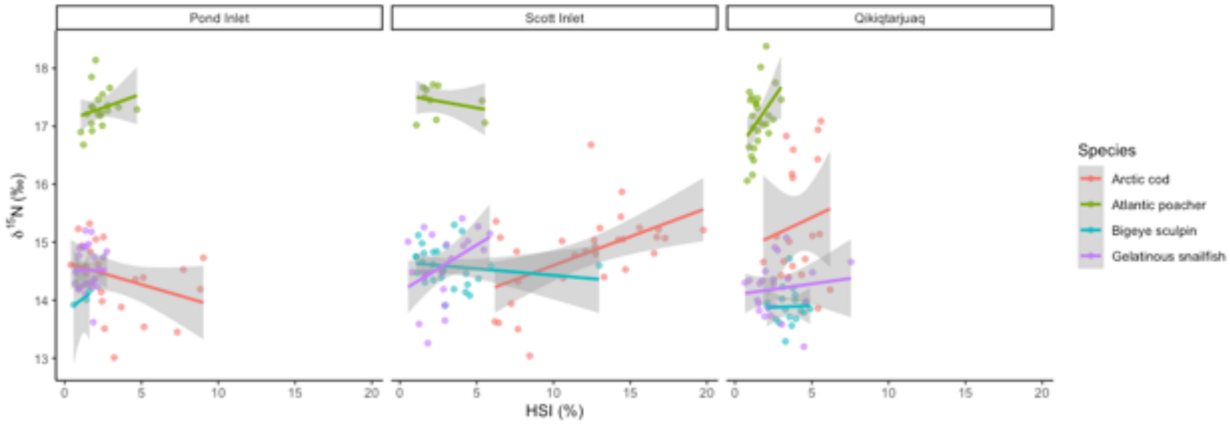


Figure 13: Linear regressions of hepatosomatic index (HSI) and δ^{15}N for five deep sea Arctic fish species separated by site.

Overall, for all species pooled in Pond Inlet and Qikiqtarjuaq, δ^{15}N decreased minimally with increasing depth (linear regression, hereafter, $R^2=0.02$, $F_{1,260}=5.2$, $p = 0.02$) and there was no relationship between depth and δ^{13}C ($R^2=0.0003$, $F_{1,260}=1.08$, $p = 0.30$). Examining each site (Pond Inlet and Qikiqtarjuaq) individually with the entire community combined, there were no significant relationships between δ^{15}N or δ^{13}C and depth (Pond Inlet δ^{15}N, $R^2=0.01$, $F_{1,120}=2.7$, $p=0.1$ and δ^{13}C, $R^2=0.01$, $F_{1,120}=2.2$, $p=0.1$; Qikiqtarjuaq δ^{15}N, $R^2=0.02$, $F_{1,137}=3.1$, $p=0.08$ and δ^{13}C, $R^2=0.01$, $F_{1,137}=3.03$, $p=0.08$). There was not enough depth data available for Scott Inlet. There was a weak significantly positive relationships between δ^{15}N and depth for Arctic Cod ($R^2=0.2$, $F_{1,18}=6.9$, $p < 0.05$) and Northern Shrimp ($R^2=0.3$, $F_{1,18}=10.2$, $p < 0.05$) at Qikiqtarjuaq (Figure 14). *Sclerocrangon ferox* ($R^2=-0.01$ $F_{1,9}=9.9$, $p < 0.05$) and Gelatinous Snailfish

(R^2=0.4, $F_{1, 21}$=15.1, $p < 0.001$) were the only species to show a significant relationship between depth and $\delta^{13}C$ at Qikiqtarjuaq (Figure 14).

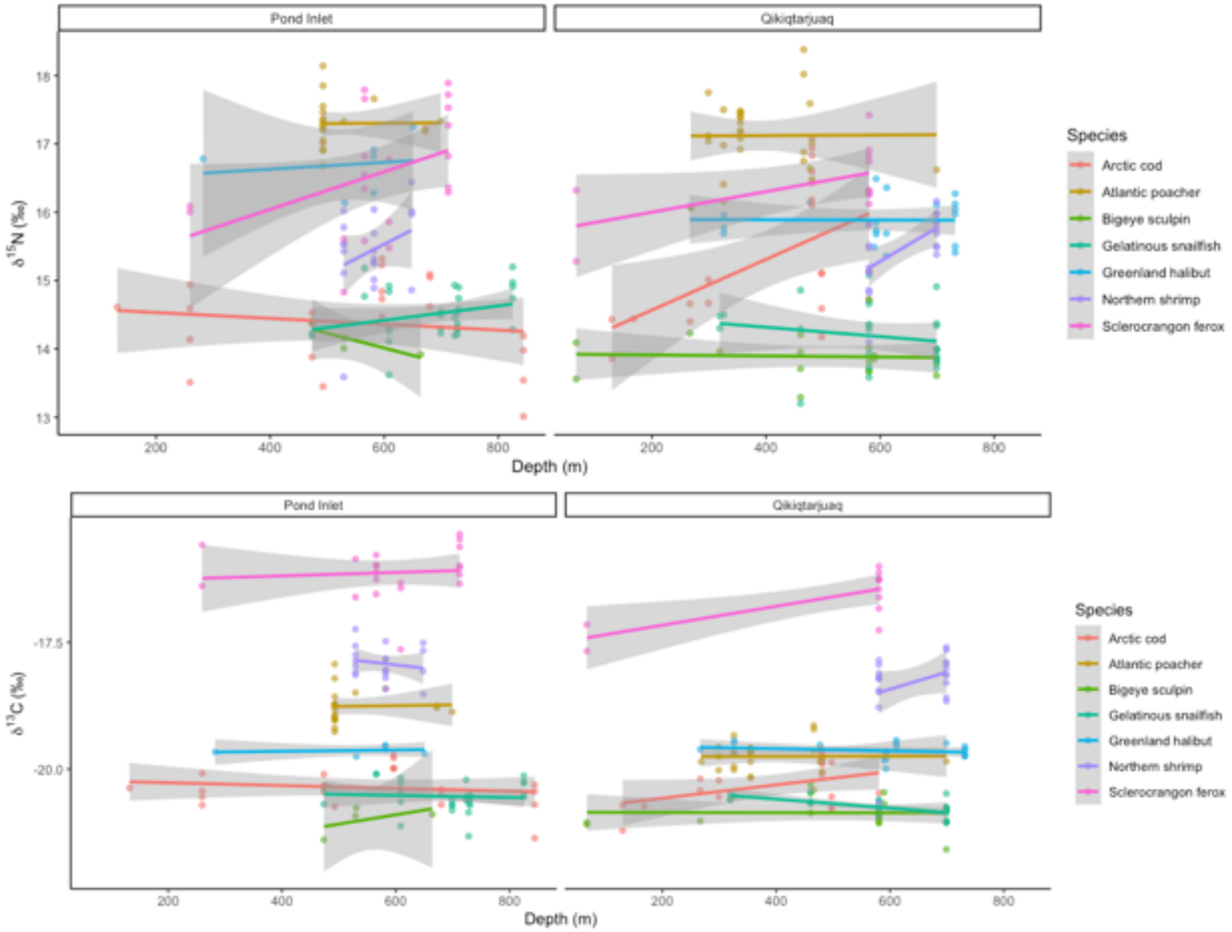


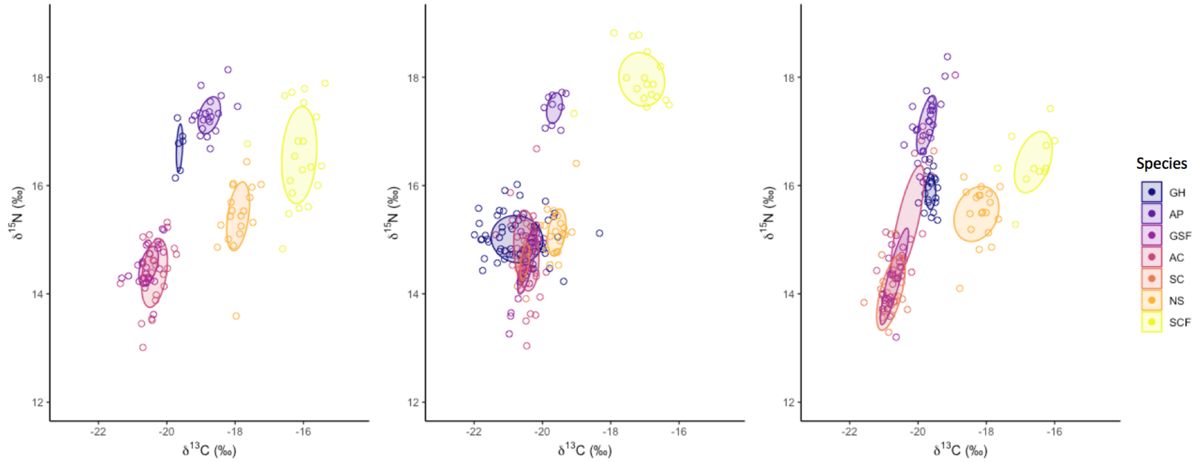
Figure 14: Isotopic composition and depth (m) for shrimp and fish in Pond Inlet and Qikiqtarjuaq (A) $\delta^{15}N$ (‰) and (B) $\delta^{13}C$ (‰). Not enough data were available to examine Scott Inlet.

3.3.2 Isotopic niche

Bayesian Standard Ellipse Areas (SEA_B) varied across species and locations with *Sclerocrangon ferox* having the highest SEA_B value at all locations except Qikiqtarjuaq, where Greenland Halibut was the highest (Table 10, Figure 15). Greenland Halibut (Pond Inlet and Qikiqtarjuaq) and Bigeye Sculpin (Scott Inlet) had the smallest SEA_B values (Table 10, Figure 15). Gelatinous Snailfish and Atlantic Poacher displayed similar SEA_B values across all sites (Table 10, Figure 15).

As hypothesized, niche breadth (i.e. SEA_B) increased with latitude for Gelatinous Snailfish and *Sclerocrangon ferox* (Table 10, Figure 15). However, for all other fishes (n=4) and shrimp (n=1) niche breadth either i) decreased with latitude, or ii) did not change with latitude, although these findings were not tested for significance (Table 10).

Across Bayesian 40% ellipses, the degree of overlap between ellipses was variable across sites and species (Table 11). We hypothesized that Pond Inlet would have the highest niche overlap, but the highest latitude location had the lowest species' niche overlap. Scott Inlet (mid-latitude) had the greatest amount of niche overlap among species (Figure 15, Table 11). The only significant overlap in Pond Inlet was for Gelatinous Snailfish (67.2%) with Arctic Cod (Figure 15, Table 11). Significant overlap in Scott Inlet included Gelatinous Snailfish (63.2%) with Arctic Cod and Bigeye Sculpin (75.2%) with Arctic Cod (Table 11, Figure 12). Arctic Cod and Gelatinous Snailfish overlapped at all three locations, but Gelatinous Snailfish was only significant in Pond Inlet (67.2%) and Scott Inlet (63.2%) (Figure 15, Table 11). There was no isotopic niche overlap between any species and either shrimp species (*Sclerocrangon ferox* and Northern Shrimp) or Atlantic Poacher (Figure 15, Table 11).



(A) High-Arctic Latitude (B) Mid-Arctic Latitude (C) Low-Arctic Latitude

Figure 15: Isotopic niches of five deep-sea fishes and two shrimp in Pond Inlet (A), Scott Inlet (B) and Qikiqtarjuaq (C), Nunavut generated from muscle tissue. Ellipses contain 40% of the data. Colours represent each species with codes: Arctic Cod (AC), Atlantic Poacher (AP), Greenland Halibut (GH), Gelatinous Snailfish (GSF), Bigeye Sculpin (SC) Northern Shrimp (NS), and *Sclerocrangon ferox* (SCF). Estimates were not available for Bigeye Sculpin in Pond Inlet because the sample size was small (n < 5).

Table 10: Bayesian standard ellipse areas (SEA_B mode, ‰^{2}) for five fish and two shrimp species in Pond Inlet, Scott Inlet and Qikiqtarjuaq, Nunavut. The sample size was not sufficient for Bigeye Sculpin in Pond Inlet to perform the analysis.

	Pond Inlet	Scott Inlet	Qikiqtarjuaq
Arctic Cod	0.6	0.8	1.3
Atlantic Poacher	0.3	0.2	0.4
Bigeye Sculpin	Not Available	0.1	0.2
Gelatinous Snailfish	0.3	0.3	0.2
Greenland Halibut	0.1	1.0	0.1
Northern Shrimp	0.6	0.3	1.0
***Sclerocrangon ferox* shrimp**	1.3	0.9	0.8

Table 11: Bayesian estimated isotopic niche overlap probability (%) determined from 40% Bayesian ellipses, separated by location (high to low Arctic: Pond Inlet, Scott Inlet, Qikiqtarjuaq). Overlap estimates are directional and presented based on the amount of species A's niche that overlaps with species B's niche. For example, in Scott Inlet 23.6% of Bigeye Sculpin niche overlaps with Gelatinous Snailfish niche, but only 9.3% of Gelatinous Snailfish niche overlaps with Bigeye Sculpin niche. Bigeye Sculpin is not available in Pond Inlet. * represents significant overlap which is defined as >60%. Species Codes are as follows: Arctic Cod (AC), Atlantic Poacher (AP), Gelatinous Snailfish (GSF), Bigeye Sculpin (BSC), Greenland Halibut (GH), Northern Shrimp (NS), *Sclerocrangon ferox* (SFS).

		Species B																				
		Pond Inlet							Scott Inlet							Qikiqtarjuaq						
		AC	AP	GSF	BSC	GH	NS	SFS	AC	AP	GSF	BSC	GH	NS	SFS	AC	AP	GSF	BSC	GH	NS	SFS
Species A	AC	■	0	27.5	NA	0	0	0	■	0	26.0	12.2	52.9	0	0	■	0	22.1	20.0	0	0	0
	AP	0	■	0	NA	0	0	0	0	■	0	0	0	0	0	0	■	0	0	0	0	0
	GSF	*67.2	0	■	NA	0	0	0	*63.2	0	■	9.3	39.8	0	0	23.3	0	■	52.4	0	0	0
	BSC	NA	NA	NA	NA	NA	NA	NA	*75.2	0	23.6	■	44.4	0	0	17.7	0	44.1	■	0	0	0
	GH	0	0	0	NA	■	0	0	43.9	0	13.6	6.0	■	0	0	0	0	0	0	■	0	0
	NS	0	0	0	NA	0	■	0	0	0	0	0	0	■	0	0	0	0	0	0	■	0
	SFS	0	0	0	NA	0	0	■	0	0	0	0	0	0	■	0	0	0	0	0	0	■

3.3.3 Layman Community Metrics:

Community-wide estimates varied depending on location. The $\delta^{13}C$ range (CR) was highest in Pond Inlet (4.4), indicating more variation in carbon sources compared to other sites (Scott Inlet: 3.7, Qikiqtarjuaq: 4.2, Table 12) which aligns with our hypothesis that niche breadth increases with latitude. The $\delta^{15}N$ range (NR) did not align with our hypothesis, indicating that trophic diversity was lowest in Pond Inlet (2.91), followed by Qikiqtarjuaq (3.09) and Scott Inlet (3.37) (Table 12). Total area (TA), distance to centroid (CD), and mean nearest neighbour distance (MNND) were highest in Pond Inlet. As hypothesized the results indicate that intraspecific variation is highest and there is less similar resource use in the highest latitude compared to lower counterparts (Table 12). These findings suggests that Pond Inlet may overall have a larger community niche breadth (Table 12). Qikiqtarjuaq (0.6) and Pond Inlet (0.8) had more even trophic distribution (SDNND) within their communities relative to Scott Inlet (1.1) (Table 12).

Table 12: Community-wide metrics (Layman et al., 2007) for 5 deep-sea fishes used to estimate variability in trophic structure for Pond Inlet, Scott Inlet, and Qikiqtarjuaq, Nunavut for white muscle tissue. Note: due to sample size (n=4), Bigeye Sculpin in Pond Inlet were not included.

Metric	Description	Interpretation at community level	Pond Inlet	Scott Inlet	Qikiqtarjuaq
δ^{15}N Range (NR), ‰	Range of δ^{15}N mean signatures from the most enriched (highest ^{15}N) to the most depleted (lowest ^{15}N).	Measure of trophic diversity, low NR indicates similar diet. Provides estimate of vertical length of the community food web.	2.9	3.4	3.1
δ^{13}C Range (CR), ‰	Range of δ^{13}C mean signatures from the minimum (^{13}C depleted, more negative) to maximum (^{13}C enriched, less negative).	Low values indicate uniform basal signatures at the base of the food web.	4.4	3.7	4.2
Total Area of the Convex Hull (TA), ‰^{2}	Total area containing all of the δ^{13}C and δ^{15}N of individuals being tested.	Low values indicate lack of intraspecific variation among niche and similar resource use.	5.9	4.6	5.2
Distance to the Centroid (CD)	Measure of trophic diversity in a food web to determine how similar species are in a food web by using the Euclidean distance between species means and centroid.	Consistent values of CD represent similar trophic diversity among all individuals and species examined indicating similar resource use.	1.8	1.5	1.5
Mean Nearest Neighbour Distance (MNND)	Indicates niche diversity and represents the average Euclidean distance between the species means.	Low nearest neighbour distance indicates more ecological similarities among and between species in a community.	1.1	0.9	1.0
Standard Deviation of Nearest Neighbour Distance (SDNND)	Measures evenness within a community. Not as impacted by sample size.	Lower values indicate more even trophic distribution within a food web and thus similar resource use in a community.	0.8	1.1	0.6

3.3.4 Linear model:

When examining variation in $\delta^{15}N$ and $\delta^{13}C$ across all three sites relative to the factors, species, length, and the species-length interaction, the linear model (location + species + length + species*length) suggested that there was no relationship with location (i.e. latitude) for $\delta^{15}N$, but there was a significant positive linear relationship between $\delta^{13}C$ and location (i.e. highest in Pond Inlet, $p < 0.0001$). The CR was higher at high latitudes than lower latitudes which may explain this relationship (Pond Inlet: 4.4, Scott Inlet: 3.7, Qikiqtarjuaq: 4.2). Additionally, the upper and lower values of $\delta^{13}C$ were the highest for Pond Inlet compared to Scott Inlet and Qikiqtarjuaq. There were significant linear relationships between both $\delta^{13}C$ and $\delta^{15}N$, and length ($p < 0.0001$).

4.0 Discussion:

To my knowledge, this study was the first to examine isotopic niche breadth of multiple deep-sea species in the Canadian Arctic along a latitudinal gradient. This includes both commercially significant species (i.e. Northern Shrimp, Arctic Cod, Greenland Halibut) and species that support these fisheries by being part of the benthopelagic food web (i.e. *Sclerocrangon ferox*, Bigeye Sculpin, Gelatinous Snailfish, Atlantic Poacher). This thesis examined isotopic niche at a localized scale (e.g. spanning 5°) in the Polar regions which is an extreme environment. Within the Polar regions there are large environmental shifts with latitude due to hours of daylight impacting productivity. Understanding how isotopic niche breadth changes with latitude provides insight into how species may respond to stressors in the future (e.g. increasing water temperature due to climate change, poleward shifts in species ranges). The current study found isotopic niche breadth had mixed patterns with latitude in deep-sea food webs in the Canadian Arctic. These mixed findings do not align or refute MacArthur's Latitudinal Niche Breadth Hypothesis which states that niche breadth increases with increasing latitude, i.e. species are more generalist and consequently would have broader niches at higher latitudes (MacArthur, 1972; Vázquez & Stevens, 2004).

My findings for Arctic Cod and the current literature on niche breadth, species richness and ecological characteristics of marine fauna indicates that decreasing niche breadth with latitude may be a common occurrence for the Arctic. Recent work in the Arctic reported that niche breadth decreased with latitude for beluga whales (Yurkowski et al., 2016) and for fish in more northern areas of the Chukchi Sea (Marsh et al., 2017). The findings from Yurkowski et al. (2016) and Marsh et al. (2017) match our findings for Arctic Cod with latitude. Decline in niche breadth with latitude may be due to reduced ecological opportunity (e.g. prey diversity), lower species density, and higher interspecific competition promoting narrower niche breadth (Yurkowski et al., 2016). Additionally, species richness may be driving differences in isotopic niche breadth, for example, globally fewer generalist species are needed to replace more specialists (Hayden et al., 2019) limiting diversity loss and functional redundancy decline (Rosenfeld et al., 2002). Both phytoplankton (Righetti et al., 2019) and zooplankton (Yasuhara et al., 2012) have lower species richness at the poles compared to the tropics.

In my study niche breadth was larger at higher latitudes for *Sclerocrangon ferox* and Gelatinous Snailfish. Few studies in the marine environment have supported MacArthur's "Latitudinal Niche Breadth Hypothesis." For example, temperate region brachyuran crab species had larger niche breadths at higher latitudes for temperate species whereas tropical species niche breadth was driven more by evolutionary life history traits instead of latitude (Papacostas & Freestone, 2015). Niche breadth increase with latitude may be linked to higher predation intensity at lower latitudes (Schemske et al., 2009) and species richness which is bimodal with latitude (Saeedi et al., 2019). At the poles, most species are generalist feeders by foraging on multiple trophic level prey with a wider niche breadth compared to tropical counterparts (Hayden et al., 2019).

Non-linear variation in isotopic niche with latitude in the Arctic deep-sea food webs studied here may be linked to the dominant influence of localized drivers (e.g. sea ice, sea surface temperature, chlorophyll-A) on species' isotopic niche trends. Local abiotic drivers may be particularly important for Arctic food webs over the latitudinal scale and time scale (i.e. tissue turnover rates) we examined. Localized environmental conditions, as discussed previously, demonstrate the importance of scale both temporally and spatially. Isotopic composition of species was examined on a geographical scale from 67°N to 72°N, yet localized conditions impacted isotopic composition more than latitude. Muscle integrates average dietary history over a long time period (Boecklen et al., 2011; Heady & Moore, 2012; Trueman, MacKenzie, & Palmer, 2012; Vander Zanden et al., 2015). Based on the equation for ectotherms by Vander Zanden et al. (2015), the average turnover rates (half-life) for each species across all sites were: Arctic Cod (53 ± 10 days), Atlantic Poacher (44 ± 6 days), Bigeye Sculpin (45 ± 4 days), Gelatinous Snailfish (46 ± 6 days), Greenland Halibut (114 ±15 days), Northern Shrimp (40 ± 3 days) and *Sclerocrangon ferox* (40 ± 6 days). This suggests that our niche assessment is a reflection of a 5° latitude difference across the late summer / early fall. Arctic ecosystems are highly seasonal, for example, sea ice spring melt drives phytoplankton blooms (Hoegh-Guldberg & Bruno, 2010). The highest latitude site in the current study, Pond Inlet is ~800 kilometers north of the most southern site, Qikiqtarjuaq. Pond Inlet had significantly colder mean air temperature from December to May, the shortest ice-free open water period and the longest period of 24-hour daylight. Environmental conditions (e.g. temperature) were quantified because they are a stronger regulator of food webs (Gilbert et al., 2019) and isotopic niche (Cirtwill et al., 2015) than latitude at localized scales, which could explain some niche breadth variability.

To my knowledge, this was the first time that the isotopic niche of Atlantic Poacher, Gelatinous Snailfish, Bigeye Sculpin and *Sclerocrangon ferox* was quantified, whereas previous studies have examined the isotopic niche of Arctic Cod, Greenland Halibut and Northern Shrimp (e.g. Linnebjerg et al., 2016; Marsh et al., 2017; McNicholl et al., 2018). Isotopic niche for invertebrates, including Northern Shrimp did not overlap with any species indicating that invertebrates in the Arctic may be specialized whereas fish species had higher overlap suggesting they are more generalists (Linnebjerg et al., 2016). In particular, little research examining isotopic niche has been completed on multiple species in Arctic food webs and no study has examined these particular species in the deep-sea.

Previous research has examined the $\delta^{15}N$ and $\delta^{13}C$ composition of species in the current study. Pooling samples within species across all sites for Arctic Cod (e.g. Marsh et al., 2017; Matley et al., 2013; Hansen et al., 2012), Bigeye Sculpin (e.g. Chambers, 2008; Hobson et al., 1995), Greenland Halibut (e.g. Linnebjerg et al., 2016; Hansen et al., 2012; Yurkowski et al., 2017) and Gelatinous Snailfish (Chambers, 2008) aligned in the mean ± standard deviation $\delta^{15}N$ and $\delta^{13}C$ composition in my study compared to other studies. For example, the mean pooled Greenland Halibut in my study was 15.3 ± 0.7‰

and in Cumberland Sound, Nunavut nearer to my locations, δ^{15}N was 16.4 ± 0.7‰ (Yurkowski et al., 2017), whereas in Greenland the δ^{15}N of Greenland Halibut was 14.5 ± 0.3‰ (Hansen et al., 2012) and 14.1 ± 1.1‰ (Linnebjerg et al., 2016). Compared to other studies Northern Shrimp (e.g. Hansen et al., 2012; Linnebjerg et al., 2016) and Atlantic Poacher (Källgren et al., 2015) had higher δ^{15}N and similar δ^{13}C in my study. This suggests that there are similarities in isotopic composition between my study and others, but that some regional variation exists which could be due to localized inputs such as glaciers. My samples were lipid extracted and without standardizing all isotopic values in the literature using baseline data it is difficult to quantitatively compare to other regions. However, the majority of my study species aligned with other published values suggesting similarity in isotopic composition.

In the current study, *Sclerocrangon ferox* and Atlantic Poacher had the highest δ^{15}N, indicating that they occupy the highest trophic levels in the Arctic deep-sea, despite not having the largest body size. Deep-sea species are generally thought to use various foraging strategies (e.g. benthic and benthopelagic) and have high diet overlap which makes classifying species into trophic levels and habitats challenging (Dayton & Hessler, 1972). *Sclerocrangon ferox* exhibited more positive δ^{13}C (-16.6 ± 0.7‰) and similar δ^{15}N (17.0 ± 1.0‰) in my study compared to previous studies (e.g. δ^{13}C: -23.3‰, δ^{15}N: 16.3‰; Hobson et al., 1995). *Sclerocrangon ferox* in a previous study also had higher δ^{15}N than decapods and fish in the Northeast Water Polynya food web and likely consumed small crustaceans and bivalves (Hobson et al., 1995). The δ^{15}N value of a species does not always reflect the actual trophic position in Arctic deep-sea species. For example, smaller species have been found to have higher δ^{15}N than larger counterparts due to the consumption of invertebrate detritivores and other benthic invertebrates (Chambers, 2008). Northern shrimp, *Sclerocrangon* ferox and Atlantic Poacher generally had higher $\delta^{13}C$ suggesting that they forage on more benthic prey compared to the other species.

I found a weak, although significant, positive relationship between $\delta^{13}C$ and latitude for pooled species which contrasts findings by Hansen et al. (2012) and Marsh et al. (2017). In the Chukchi Sea a decrease in $\delta^{13}C$ with latitude (Marsh et al., 2017) may be because CO_2 dissolves more easily at lower temperatures (and thus higher latitudes) and phytoplankton preferentially use more of the lighter isotope ($^{12}CO_2$) which results in lower $\delta^{13}C$ overall (reviewed in Fry & Sherr, 1984). The $\delta^{13}C$ of a species provides inferences on the habitat that a species is utilizing (e.g. benthic or pelagic prey; Inger & Bearhop, 2008). An increase in $\delta^{13}C$ with latitude suggests that species in Pond Inlet are foraging on more benthic prey than in Scott Inlet and Qikiqtarjuaq. Overall, species in my study from the Arctic deep-sea food web are likely reliant on a combination of phytoplankton, macroalgae and microphytobenthos derived $\delta^{13}C$ (Fry & Sherr, 1984) indicating a connection between the surface and the deep-sea. I found that Arctic Cod had similar $\delta^{13}C$ composition among sites (Pond Inlet: -20.4 ± 0.4 ‰, Scott Inlet: -20.5 ± 0.4 ‰, Qikiqtarjuaq: -20.3 ± 0.5 ‰) suggesting that their diet is sourced from phytoplankton (-24 to -18‰), macroalgae (-27 to -8 ‰), and microphytobenthos (-20 to -10 ‰, Fry & Sherr, 1984). Arctic Cod rely on sea ice algae for up to 54% of their diet in the European Basin of the Arctic (Kohlbach et al., 2017) and also use sea ice to provide protection from predators (Coad & Reist, 2017).

Previous research has indicated that depth can influence isotopic composition (e.g. Leduc et al., 2015; Denda & Christiansen, 2010; Laakmann et al., 2009). Across a latitudinal gradient in the deep-sea, δ^{15}N generally increases with depth (Parzanini et al., 2019). Findings from Parzanini et al. (2019) contrast findings from my study which suggested that there is a weak decrease in δ^{15}N with depth for deep-sea species. Similar to my study, decreasing δ^{15}N with depth has been reported in elasmobranchs (Churchill et al., 2015) and hagfish (Zintzen et al., 2013). Declining δ^{15}N with depth could be due to: a diet shift to consume lower trophic level prey (Zintzen et al., 2013), differences in productivity (Churchill et al., 2015), or smaller particulate matter with lower δ^{15}N being present in the deep-sea (Rau et al., 1990) originating from shallower waters. Globally, δ^{13}C increases with depth in the deep-sea (Parzanini et al., 2019) because more positive δ^{13}C signatures are generally associated with benthic habitats (Zintzen et al., 2013) due to less ^{13}C enrichment from phytoplankton (Hobson et al., 1995). Our findings indicate that depth did not influence δ^{13}C in the Arctic deep-sea, which is similar to other Arctic deep-sea food webs (e.g. Iken et al., 2004).

Bergmann's Rule states that species at higher latitudes with cooler temperatures have larger body sizes compared to their warmer and lower latitude counterparts (Bergmann, 1847). Highly seasonal environments whereby life history traits favour larger species predominate at higher latitudes (Hutchings, 2002). This rule generally applies to birds and several mammal species (Meiri & Dayan, 2003) including Canidae (Gohli & Voje, 2016). Niche breadth (specifically dietary) increased with maximum length in global fishes (2938 fishes) suggesting that the relationship is due to larger species being able to consume a wider array of prey sources (Hayden et al., 2019).

Results from my study suggested that there were mixed relationships with length and latitude (e.g. Atlantic Poacher increased length with latitude whereas Bigeye Sculpin decreased length with latitude), which is in contrast to fishes in the North Atlantic, South Pacific, Indian Ocean (Fisher et al., 2010) and deep-sea fishes in the East Atlantic (MacPherson and Duarte, 1994). In North America, cold freshwater fish followed Bergmann's Rule, suggesting that these patterns may be linked to a species niche (specifically thermal niche requirements and tolerances) (Rypel, 2014).

Around the world fish trophic position is most strongly predicted by species length, with fish at the poles generally consuming higher trophic level prey compared to similar length equatorial counterparts (Hayden et al., 2019). In Northeast Greenland, larger-bodied individuals within Arctic Cod and Polar Cod (*Arctogadus glacialis)* consumed higher trophic level prey because δ^{15}N increased with body size (Christiansen et al., 2012). In our study, Arctic Cod (across all three sites), Atlantic Poacher (Qikiqtarjuaq, Pond Inlet) and Gelatinous Snailfish (Scott Inlet, Pond Inlet) all showed increases in prey trophic level (higher δ^{15}N) with length. Larger bodied fishes are able to consume larger prey because they are gape limited consumers, and prey must fit into their mouth (Hayden et al., 2019). The other species in this study, which did not show positive relationships between species length and δ^{15}N, may have reduced resource pathways in the deep-sea, experience isotopic discrimination (Hussey et al., 2012) or utilize scavenging (Churchill et al., 2015).

Increasing δ^{13}C with length may explain the larger niche breadths observed for most of the species that had a positive relationship between δ^{13}C and length. Larger species/individuals have a greater ability to move between habitats for feeding or change their foraging locations with increasing body size. In our study, there was a positive relationship between length and $\delta^{13}C$ for Arctic Cod (Qikiqtarjuaq, Pond Inlet), Atlantic Poacher (Qikiqtarjuaq), Greenland Halibut (Qikiqtarjuaq), Northern shrimp (Qikiqtarjuaq) and *Sclerocrangon ferox* (Pond Inlet). Increases in $\delta^{13}C$ with length have been observed for the Jewel Lanternfish (*Lampanyctus crocodilus*) in the Mediterranean (Louzao et al., 2017), Glasshead Grenadier (*Hymenocephalus italicus*), *Cataetyx alleni*, and Blackmouth catshark (*Galeus melastomus*) in the Catalan Sea (Papiol et al., 2013) as well as Arctic Cod and Polar Cod in Northeast Greenland (Christiansen et al., 2012).

To my knowledge, there has been no work examining the effect of latitude on HSI. In my study, HSI did not show a clear pattern with latitude among fishes. Previous research has indicated that HSI is highest in July for American plaice (*Hippoglossoides platessoides;* Maddock & Burton, 1999) and in October and November for Atlantic Cod (*Gadus morhua;* Mello & Rose, 2005), suggesting that HSI for fish in my study may reflect the maximum in a year. Higher HSI has been recorded during periods of active feeding post spawning (Mello & Rose, 2005). Some fish sampled in this study contained eggs which may be an indication that they are in the post spawning phase. Isotopic niche breadth increased for species that are under physiological stress and have poor condition compared to their healthier counterparts (Karlson et al., 2018). Generally, species in our study with lower body condition levels did not have larger isotopic niches. This may be due to deep-sea fishes having variable and large livers accounting for up to 16% of total body mass (Drazen, 2007). Arctic Cod sampled in Svalbard ranged from 6.1– 24 cm, were 0 – 4 years old (Fey & Węsławski, 2017) and mature at ages 2-4 (Table 5), suggesting that many Arctic Cod in our study were juveniles. This suggests that the length of fish sampled may have a greater effect than latitude for HSI.

The highest latitude location, Pond Inlet had the lowest niche overlap whereas mid-latitude had the highest amount of niche overlap. Niche overlap provides insight into foraging and diet patterns for an entire community (Holt, 1987). Elton (1927) suggested that the same niche space could not be occupied by two different species, but more recent studies have indicated that similar species' niches can co-occur (e.g. Guzzo et al., 2013). The presence of high niche overlap in a community may indicate prey abundance (Pettitt-Wade et al., 2015), high productivity within an ecosystem (Linnebjerg et al., 2016) or species invasion (Guzzo et al., 2013). If prey are not abundant relative to the population in a community and there is high overlap, this could indicate that competition is occurring (Bolnick, 2001; Pettitt-Wade et al., 2018) and / or niche breadth is increasing because species have to find alternative resources (Bolnick, 2001). No overlap or non-significant overlap (>60%; Schoener, 1968) may indicate that species are consistently foraging in different locations and/or on different prey and/or at different times and thus not directly competing with other study species. Low niche overlap may suggest that there are multiple sources of abundant prey, the targeted study species may not be in direct competition for prey and/or we did not study all species in the food web. Low niche overlap may also indicate that the environment is nutrient poor and distinct niches reduce competition (Linnebjerg et al., 2016), as well as the presence of resource plasticity (Jackson & Britton, 2014). For example, Arctic Cod are primarily benthopelagic and also utilize sea ice whereas Gelatinous Snailfish are bathydemersal (Coad & Reist, 2017). Arctic Cod foraging behaviour depends on their life stage (pelagic and benthopelagic) (Majewski et al., 2015; Matley et al., 2013) which may explain the observed overlap.

The highest niche overlap occurred at the mid latitude site, Scott Inlet, suggesting that significantly overlapping species (Gelatinous Snailfish and Arctic Cod; Bigeye Sculpin and Arctic Cod) were foraging on the same prey (e.g. crustaceans) because prey may be abundant. High overlap in niche for multiple taxa of fish was also observed in West Greenland where fish adopted generalist feeding strategies (Linnebjerg et al., 2016). Overlap may also indicate the presence of multiple prey with similar isotopic signatures because it is difficult to taxonomically identify prey using stable isotopes (Newsome et al., 2007). Within Scott Inlet, the δ^{15}N value was similar among fishes, suggesting species were foraging on similar trophic level prey (e.g. crustaceans), but in different locations due to differences in δ^{13}C. Differences in δ^{13}C could also be attributed to Arctic cod using sea ice seasonally (Coad & Reist, 2017).

At the lowest latitude location, Qikiqtarjuaq, there was more overlap than at Pond Inlet but not as high as Scott Inlet. In Qikiqtarjuaq, δ^{13}C was similar among fishes suggesting species were feeding in similar locations, but δ^{15}N indicated that species were feeding at different trophic levels. In Qikiqtarjuaq, there was no significant overlap between fishes. Non-significant overlap suggests that some individuals could share the same prey but that the majority of each species fed on different prey.

Inconsistencies in niche overlap between sites in the current study suggests that there may be plasticity in feeding, foraging, competitive interactions and resource partitioning (Shiffman et al., 2019). In West Greenland, there was low overlap among mammals, fishes (including Greenland Halibut and Arctic Cod), seabirds and invertebrates (including Northern shrimp) when species were pooled together (Linnebjerg et al., 2016). In our study, Gelatinous Snailfish overlapped significantly with Arctic Cod at the two highest latitudes and Greenland Halibut overlapped with Arctic Cod, Bigeye Sculpin and Gelatinous Snailfish in the mid latitude. Greenland Halibut are good indicators for ecosystem change because they feed on the most abundant prey available (Dwyer et al., 2010) and also have isotopic niche overlap with Arctic Cod in West Greenland (Linnebjerg et al., 2016). Due to the opportunistic feeding behaviour of Greenland Halibut (Dwyer et al., 2010), it is likely that Arctic Cod, Gelatinous Snailfish and Bigeye Sculpin may be feeding on the same highly abundant prey in Scott Inlet. It also could indicate that Greenland Halibut are feeding on Arctic Cod, Gelatinous Snailfish, and Bigeye Sculpin. From stomach content analyses, Greenland Halibut are known to consume Arctic Cod, Gelatinous Snailfish (Giraldo et al., 2018) and Bigeye Sculpin (Chambers, 2008). Low sample sizes for Greenland Halibut (n=7) and Bigeye Sculpin (n=4) in Pond Inlet did not allow for accurate comparisons of isotopic niche at the highest latitude site.

Within the examination of the Eastern Baffin Island deep-sea food web, no isotopic niche overlap occurred for shrimp (Northern shrimp, *Sclerocrangon ferox*) or Atlantic Poacher. Findings for shrimp were similar to West Greenland where Northern shrimp did not overlap with any invertebrate species (squid, blue mussel, copepods, Iceland scallop, Northern krill and snow crab) suggesting a specialist feeding behaviour (Linnebjerg et al., 2016). However, I acknowledge in our study that there may be species that were not included that could be occupying similar isotopic niche space as the shrimp and Atlantic Poacher. However, when selecting sample species, the species' functional roles were considered to gain a more complete understanding of the Arctic deep-sea food web. An absence of niche overlap may also suggest that shrimp and Atlantic Poacher are seeking out different prey than other species.

Limitations exist when using stable isotopes to understand deep-sea organisms. Deep-sea fishes typically have variable and high lipid content (Hoffman & Sutton, 2010; Parzanini et al., 2018) and require lipid removal prior to SIA. The C:N ratio is used to understand lipid content as it represents a ratio of lipids to protein in tissues (Sweeting, Polunin, & Jennings, 2006). Fish store their lipids in skeletal muscle and liver tissue (Pinnegar & Polunin, 1999). Lipid removal is typically not necessary when the C:N ratio is < 3.5, accounting for approximately 5% lipid content in a tissue (Post et al., 2007) and a C:N ratio < 4 is considered low (Hoffman & Sutton, 2010). In this study, there was some variation, with C:N ratios ranging from 2.8 to 5.3 and most in the 2.8 to 4.0 range. However, lipid removal is necessary when tissues have high lipid content (or variable) and when the $\delta^{13}C$ difference among consumers or between a consumer and an end member (e.g. primary producer baseline) is less than 10-12‰ (Post et al., 2007). I acknowledge that differences in lipid removal methods (i.e. Greenland Halibut muscle was either lipid extracted once or twice) may have altered the isotopic composition, but I am confident that I captured the trophic dynamics within each community. It is also well recognised that physiology and non-dietary stressors (e.g. nutrient imbalance, anthropogenic stress, environmental drivers) can be falsely interpreted as dietary variation through isotopic niche (Karlson et al., 2018). Only prey species with contrasting isotopic compositions can be identified (Newsome et al., 2007; Bearhop et al., 2004) and diet derived macromolecules are constantly being rearranged in a species, which can alter the stable isotope values (Martinez del Rio & Wolf, 2005). In addition, there are factors that influence bulk isotopic turnover rate include maturity, metabolic rate (Sakano et al., 2005), growth rate (Miller, 2006) and amino acid composition (Xia et al., 2013), which alter isotopic composition. Differences in fish and shrimp isotopic composition could be a reflection of regional differences at the base of the food web (Layman et al., 2007) and comparisons between species at locations need to be interpreted with implicit assumptions. However, it is likely that the isotopic niche relationships observed between species at each location provide an indication of resource use patterns on a regional scale.

The current study advances our knowledge of little-known deep-sea ecosystems, which collectively represent the largest environment on earth (99% by volume; Norse et al., 2012). To date, little research has been completed using stable isotopes to understand Arctic deep-sea environments (e.g. Laakmann et al., 2009, Bergmann et al., 2009, Iken et al., 2005). By studying isotopic niches, inferences can be made on species co-existence and long-term persistence, which can help us understand vulnerability to stressors in the future (Shipley et al., 2019). Better understanding of species vulnerability to stressors will aid in conservation and management. The Arctic deep-sea is facing increasing stressors from anthropogenic sources (e.g. increasing pressure for fishing and mining, more transportation traffic due to increased open water periods) and climate scenarios indicate that the deep-sea will experience physical and chemical changes in the future (Thresher et al., 2015).

Environmental models suggest that by 2100, deep-sea (200 to > 3000 m) temperatures in the Arctic will rise by 0.1 - 3.7°C and the pH will be lowered by 0.01 to 0.37 pH units (Sweetman et al., 2017). Despite these predictions, it remains unclear how our study species will be impacted by these environmental changes. Temperature impacts studied on Greenland Halibut suggest that the age distribution and depth preference will be negatively impacted by climate change because younger fish inhabit shallower areas (warmer, more variable temperatures) whereas older fish prefer consistent temperatures in deeper waters (Wheeland & Morgan, 2020). Northern Shrimp have shown increases in mortality with pH declines (Dupont et al., 2014) and the movement and physiology of Arctic Cod are also predicted to be negatively impacted by climate change (Pettitt-Wade et al., 2020 – in press; Drost et al., 2014). Increased presence of boreal species expanding their ranges northward (e.g. Atlantic Cod and Haddock; Fossheim et al., 2015, Atlantic pipefish; Fleischer et al., 2007) is decreasing the abundances of northern species (e.g. Bigeye Sculpin, Snailfish species, Greenland Halibut) (Fossheim et al., 2015). The Arctic is expected to have increased precipitation, changes in snowfall timing and accumulation, decreased sea ice thickness (Bell & Brown, 2018), increased ocean stratification, and limited nutrient flow which may lead to less primary production (Carton et al., 2015).

Findings from this study will be useful for understanding how fishery food webs may be impacted by climate change. Here, I examined the same species at different latitudes and thus environmental conditions, which provided insight into how a species may respond to different environmental conditions (e.g. sea ice decline, temperature increase). Climate change impacts are an important consideration as the demand for the development of future test fisheries increases to bring economic, employment and food security (e.g. subsistence opportunities in the deep-sea: shrimp fisheries, grenadier; Christie, 2018) opportunities to northern communities. Ecosystem services and traditional foods are being compromised in the Eastern Arctic due to the area having some of the most accelerated warming in the North (Bell & Brown, 2018). Despite warming, offshore and inshore fisheries play an important role in Nunavut's economy; the Northern Shrimp, Arctic char and Greenland Halibut fisheries brought an estimated $86.3 million to the territory in 2015 (Government of Nunavut, 2016). There is currently only one Nunavut community-based Greenland Halibut fishery, in Pangnirtung (Coad & Reist, 2017); due to the success of the Pangnirtung fishery, other communities are interested in starting fisheries (Barkley et al., 2018). It is important to understand the isotopic niche of deep-sea food webs before the Arctic experiences its first ice free summer as this study will act as a baseline for future research as well as aid in monitoring and conservation efforts.

5.0 Conclusion:

Niche breadth did not consistently increase with latitude as was hypothesized in all species, suggesting that the Latitudinal Niche Breadth hypothesis may not hold true in the Canadian Arctic (67°N to 72°N). Isotopic niche overlap did not increase with latitude; the highest niche overlap occurred in Scott Inlet, suggesting that species in Scott Inlet may be consuming abundant prey or experiencing higher competition for prey compared to Pond Inlet and Qikiqtarjuaq. These trends could be linked to seasonal environmental conditions, such as sea ice and temperature or species-specific life histories (e.g. HSI). We found that HSI, an indicator of body condition, did not decrease with latitude in most fishes, the exception being Bigeye Sculpin. Intraspecific variation in isotopic niche among deep-sea species suggests flexibility in foraging and may provide insight into future trophic dynamics in an environment that is under increasing stress. Further research is needed to better understand the ecological traits of Arctic deep-sea species supporting economically important species to ensure the long-term sustainability and conservation of deep-sea food webs in a changing Arctic environment.

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Chapter 4: General Conclusions and Future Directions

Globally marine ecosystems face numerous stressors (e.g. climate change; Bruno et al., 2018) raising concerns about impacts on marine food webs and ecosystem services (Sandifer & Sutton-Grier, 2014). The structure and function of marine food webs is variable across a latitudinal gradient from the poles to the tropics in terms of species richness (Saeedi et al., 2019), feeding behaviour (generalist vs. specialist; Saupe et al., 2018), competition (Barnes & Neutel, 2016) and environmental conditions (e.g. water temperature; Priede, 2017). The deep-sea environment, defined as the area below 200 m is poorly understood, contains species with highly k-selected life history traits (Victorero et al., 2018) and conditions are generally harsh for inhabiting species (e.g. low light, high pressure, limited food availability; Clark, 2001; Rogers, 2015; Danovaro et al., 2014).

The principle objectives of this thesis were to first synthesize all available literature on the application of stable isotope analysis to understand deep-sea environments through a systematic review. I then, examined the isotopic niche for five deep-sea teleost and two decapod species across a localized latitudinal gradient in the Canadian Arctic to investigate if the "Latitudinal Niche Breadth Hypothesis", which states that species' niche breadth increases with latitude (MacArthur, 1972; Vázquez & Stevens, 2004), is supported on a regional scale in the Arctic. Globally, niche breadth is thought to increase with latitude due to species in the tropics being more specialized than polar counterparts (Saupe et al., 2018) as a result of increased availability of resources in the tropics (Araújo & Costa-Pereira, 2013). Testing of this theory in the marine environment has received minimal attention to date, but an initial study on crab (Papacostas & Freestone, 2016) found support.

Despite the deep-sea being the largest environment on the planet which faces increasing exploitation pressures, relatively little is known about deep-sea food webs. My results in Chapter 2 indicate patterns in spatial isotopic variation, energy pathways, trophic position, feeding behaviour, body size, temporal isotopic variation, and isotopic niche are highly variable within the deep-sea and there are inconsistencies across taxa and habitats. These reported results identify key future research directions and provide support for the inherent complexity within the little studied deep-sea environment. By acknowledging research gaps in the deep-sea, policy makers can make more informed management decisions, establish marine protected areas, and enact a conservative approach towards food web sustainability in the deep-sea.

To my knowledge, Chapter 3 provided the first estimation of niche for five teleost and two decapod species across a latitudinal gradient in the Canadian Arctic deep-sea. Studying the same species across a latitudinal gradient provides scientists and resource managers with insight into understanding how species may respond to environmental changes such as increasing water temperature and decreasing sea ice concentration. Isotopic niche breadth increased with latitude for Gelatinous Snailfish (*Liparis fabricii*) and *Sclerocrangon ferox* (shrimp), suggesting that more generalist feeding behaviours are present at higher latitudes for these two species. This provides some support for the "Latitudinal Niche Breadth Hypothesis" (MacArthur, 1972; Vázquez & Stevens, 2004). This trend of increasing niche with latitude, however, was not consistent for all Arctic deep-sea species, suggesting that localized changes (e.g. temperature, prey availability) may have a greater influence on driving niche diversification in the Arctic deep-sea in comparison with latitude. Examining the isotopic niche of Arctic deep-sea species over a latitudinal gradient indicates Arctic deep-sea species may be able to respond to some degree of environmental change as a result of high variation in niche among the three locations studied.

Findings from this thesis indicated that Arctic deep-sea species showed a weak $\delta^{15}N$ relationship with depth, which agrees with findings from global deep-sea food web reviews for fish (Zintzen et al., 2013; Churchill et al., 2015), deposit feeders (Bergmann et al., 2009), and copepods (Laakmann et al., 2009), but contrasted with the majority of studies that have found positive relationships between depth and $\delta^{15}N$ in the deep-sea (e.g. McClain-Counts et al., 2017; Parzanini et al., 2019). Arctic deep-sea species also did not show a relationship between $\delta^{13}C$ and depth, which was similar to particulate organic matter in the Arctic (Iken et al., 2005) and fish in the Northeast Atlantic (Stowasser et al., 2009). These findings contrast to those of Parzanini et al. (2019) who reported that $\delta^{13}C$ increased with depth in the deep-sea.

Species at higher latitudes typically have larger body sizes (and therefore higher $\delta^{15}N$) compared to lower latitude species (Bergmann, 1847) due to seasonal environments favouring larger body size life history traits (Hutchings, 2002). Larger organisms generally have higher $\delta^{15}N$ in the deep-sea, which was observed for a few species in the Arctic deep-sea food webs studied here (e.g. Arctic Cod, *Boreogadus saida*, at all three sites, Atlantic Poacher, *Leptagonus decagonus*, in Pond Inlet and Qikiqtarjuaq). The deep-sea review indicated that some deep-sea species have higher $\delta^{13}C$ values with increasing body size, which was observed in certain Arctic deep-sea species (Arctic Cod in Pond Inlet and Qikiqtarjuaq, Atlantic Poacher in Qikiqtarjuaq, Greenland Halibut, *Reinhardtius hippoglossoides* in Qikiqtarjuaq, Northern Shrimp, *Pandalus borealis* in

Qikiqtarjuaq and *Sclerocrangon ferox* in Pond Inlet), suggesting changes in foraging location with species growth.

Overall, more research is needed to fully understand Arctic deep-sea food webs. Due to time, sample availability, and finances this research focused on seven key species. Future research should examine additional invertebrates (e.g. Asteroidea, porifera, crustaceans, polychaetes, molluscs), fishes (e.g. Eelpout species, *Lycodes mcallisteri, L. rossi, L. eudipleurostictus,* Sea Tadpole, *Careproctus reinhardti,* American Plaice, *Hippoglossoides platessoides*), and elasmobranchs (e.g. Arctic skate, *Amblyraja hyperborea*) that have been collected at all three of the current study locations in the Canadian Arctic to gain a more complete understanding of these Arctic deep-sea food webs. This will aid in understanding trophic dynamics and species interactions and help inform resource allocations within deep-sea food webs for both commercial and non-targeted species.

Stable isotopes provide an integrated average dietary history of a species, but it is recommended that stomach content analysis (SCA) is completed as a complimentary method to understand recent diet (Pinnegar & Polunin, 1999). Frozen stomachs are available for my study specimens to identify dietary constituents (Vollen, Albert, & Nilssen, 2004; Woll & Gundersen, 2004) and can be compared to stable isotope results. In particular, it is recommended that SCA be undertaken on Gelatinous Snailfish, as there are no published SCA results to my knowledge for this species. SCA was not undertaken due to time constraints and small size of stomachs.

Arctic marine ecosystems experience seasonal differences in productivity between the open-water summer and ice-covered winter months. Highly branched isoprenoid

(HBI) lipids are secondary metabolites (Brown & Belt, 2017) originating from diatom species that form an index known as H-Print (Brown et al., 2014b) which can be used to quantify the amount of pelagic- and sympagic-derived carbon in food webs (Brown & Belt, 2017). This can provide an understanding of surface to deep-sea connectivity. Identifying HBIs and calculating the H-Print has been used previously to quantify carbon inputs of both sea ice and pelagic sources in primary consumers such as zooplankton (Brown & Belt, 2017; Brown & Belt, 2012)31 and particulate organic matter (Brown et al., 2016), fishes (Brown & Belt, 2017; Brown et al., 2017; Brown et al., 2015), beluga whales (Brown et al., 2017), ringed seals (Brown et al. 2014a), and polar bears (Brown et al., 2018) in the Arctic. Results from these studies show that species reliant on sea ice derived carbon include shallow water species such as polar bears (Brown et al., 2018), beluga whales (Brown et al., 2017), and ringed seals (Brown et al., 2017; Brown, et al., 2014a), as well as species that are known to utilize the deep-sea (e.g. alligator fish; Brown & Belt, 2011). Species that rely on phytoplankton (i.e. pelagic) derived carbon include capelin (Brown et al., 2017) and polar cod (Brown, Hegseth, & Belt, 2013). HBIs provide a complimentary tool to stable isotopes to understand food web dynamics and surface to deep-sea connectivity. In the future, it is recommended that deep-sea fish livers are analyzed for HBIs to understand the influence of sea ice to the deep-sea ecosystem across multiple sites spanning a latitudinal gradient.

There are several other tracers that may be useful for gaining a more complete understanding of deep-sea food webs. For example, fatty and amino acids have been used to understand trophic interactions in terrestrial and aquatic ecosystems (Ruess & Muller-Navarra, 2019) as well as the deep-sea (Parzanini et al., 2019). Fatty acids are required for optimum fitness and must be acquired from the consumption of food (e.g. primary producers; Kopprio et al., 2015; Parzanini et al., 2019). Fatty acids are impacted by temperature and by studying them in the deep-sea, this will aid in understanding how species will respond to changing temperatures with climate change (Parzanini et al., 2019).

Future work should also consider sampling multiple tissues with different metabolic turnover rates to gain a more complete understanding of seasonal diet dynamics. For example, muscle integrates average diet history over a long time period whereas liver integrates diets over shorter time periods (Boecklen et al., 2011; Heady & Moore, 2012; Trueman, MacKenzie, & Palmer, 2012; Vander Zanden et al., 2015). The 90% turnover rate of Arctic Sculpin (*Myoxocephalus scorpioides*) for muscle is 122 days and 58 days for liver (Barton et al., 2019). Fin tissue has been proposed as a non-lethal alternative to sampling a short turnover tissue because the 90% turnover rate is 56 days for Arctic Sculpin fin clips (Barton et al., 2019). By sampling tissues with different turnover rates, temporal variation in stable isotope signatures can be incorporated into analyses to provide insight into changes in diet over multiple time periods (i.e. seasonally).

Environmental data should be collected together with specimens to understand how sampling temperature, salinity, and dissolved oxygen may influence species isotopic composition in the Arctic, particularly with depth. Furthermore, chlorophyll-A concentration should be determined for study areas and analysed with niche breadth. This study used data that were collected in 2013 and 2018, and an ideal study would conduct a spatial comparison using data from the same year. By using the same year temporal variability would be reduced, strengthening spatial comparisons across the same year. It is difficult to compare isotopes across a latitudinal gradient because environmental conditions vary annually, and these changes can erroneously be attributed to latitude rather than inter-annual variation.

Undertaking research in the deep-sea and in particular the Arctic which is covered in sea ice for most of the year is challenging. High associated costs, limited accessibility and difficult working conditions (e.g. unpredictable weather) provide barriers to data collection in one of the harshest environments on the planet. Very few people have physically been present in the deep-sea and scientists rely on samples from bottom trawls, long-lining, dredges and tows as well as analysis from video footage and chemical tracers to understand these highly complex habitats.

The deep-sea contains abundant biotic and abiotic resources which could supplement natural resources that are depleting elsewhere in the world. Fishery development within deep-sea environments, in particular in the Arctic, may provide northern communities with opportunities for economic growth, employment, and food security. However, it is imperative that these resources and industries are developed with caution to ensure sustainability for future generations, especially in fragile ecosystems such as the Arctic, and given the typical life history traits of deep-sea species that make them sensitive to overexploitation (e.g. late maturing; Jennings et al., 1998, lower metabolic rates; Victorero et al., 2018). This thesis undertook a multiple species approach to food web ecology which will contribute to expanding baseline understanding of species that co-exist with already economic significant species such as Greenland Halibut, Northern Shrimp and Arctic Cod.

Effort was made to involve Inuit communities in this research, and future work should consider involving more community collaboration. Nunavut has the highest food insecurity rate (69%) and lowest high school graduation rate in Canada, and high suicide rates are prevalent across Nunavut (Bell & Brown, 2018). Inuit youth want to be involved in research and would like to see opportunities to be a "research apprentice" (Sadowsky, 2019), with studies indicating that engaging community members creates more integrative and inclusive research (Falardeau et al., 2019). By providing opportunities for northerners to further their education, this is one tool which can help improve well-being (Bell & Brown, 2018). This project worked closely with local Hunters and Trappers Associations to obtain support and receive input towards the project. Inuit research assistants were hired and trained in field sampling. These Inuit team members provided traditional knowledge and local insights to the project and sites. I also organized a community fisheries meeting in Qikiqtarjuaq and completed workshops in Nunavut high schools (Qikiqtarjuaq, Pangnirtung, Iqaluit) to explain project objectives, connect with northerners, and inspire them to be engaged in the research happening in their backyard. A poster was produced showcasing this project (available in English and Inuktitut) which is on display at the Nattivak Hunters and Trappers Association in Qikiqtarjuaq. While outreach activities and connections are helping to bridge the gap between the local and scientific communities to promote long-term collaboration, more activities are needed to further engagement and project ownership in northern communities.

In conclusion, this thesis provides an overview and fills a knowledge gap of how stable isotope analysis has been used to understand ecological dynamics in deep-sea food webs in different habitats around the globe. I concluded that niche breadth did not consistently increase with latitude, suggesting that environmental conditions or life history traits may contribute to variation in niche at localized scales. As climate change and other stressors continue to threaten deep-sea ecosystems, it is imperative that more research is undertaken to understand these ecosystems which will ensure sustainability and conservation within the changing deep-sea environment for future generations.

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Supplemental:

Table 13: Mean hepatosomatic index (HSI) in % for deep-sea fishes at three locations in the Eastern Arctic ± standard deviation, values in parentheses indicate the maximum and minimum HSI.

	Pond Inlet		**Scott Inlet**		**Qikiqtarjuaq**	
	n	HSI %	n	HSI %	n	HSI %
Arctic Cod	22	3.51 ± 2.62 (0.4 – 9.3)	30	12.0 ± 3.83 (6.8 – 19.8)	20	4.17 ± 1.16 (1.8 – 6.2)
Atlantic Poacher	20	2.26 ± 0.83 (1.1 – 4.7)	10	2.58 ± 1.57 (1.1 – 5.5)	27	1.55 ± 0.57 (0.8 – 3.0)
Bigeye Sculpin	3	1.20 ± 0.55 (0.6 – 1.6)	19	3.15 ± 2.35 (1.0 – 13.0)	28	3.52 ± 0.77 (2.1 – 4.9)
Gelatinous Snailfish	31	1.52 ± 0.55 (0.7 – 2.7)	23	2.81 ± 1.50 (0.5 – 5.9)	22	2.71 ± 1.54 (0.7 – 7.6)
Greenland Halibut	N/A	N/A	N/A	N/A	20	1.85 ± 0.4 (1.07 – 2.50)

The number of individuals examined is represented by n. Refer to methods for how to calculate HSI.

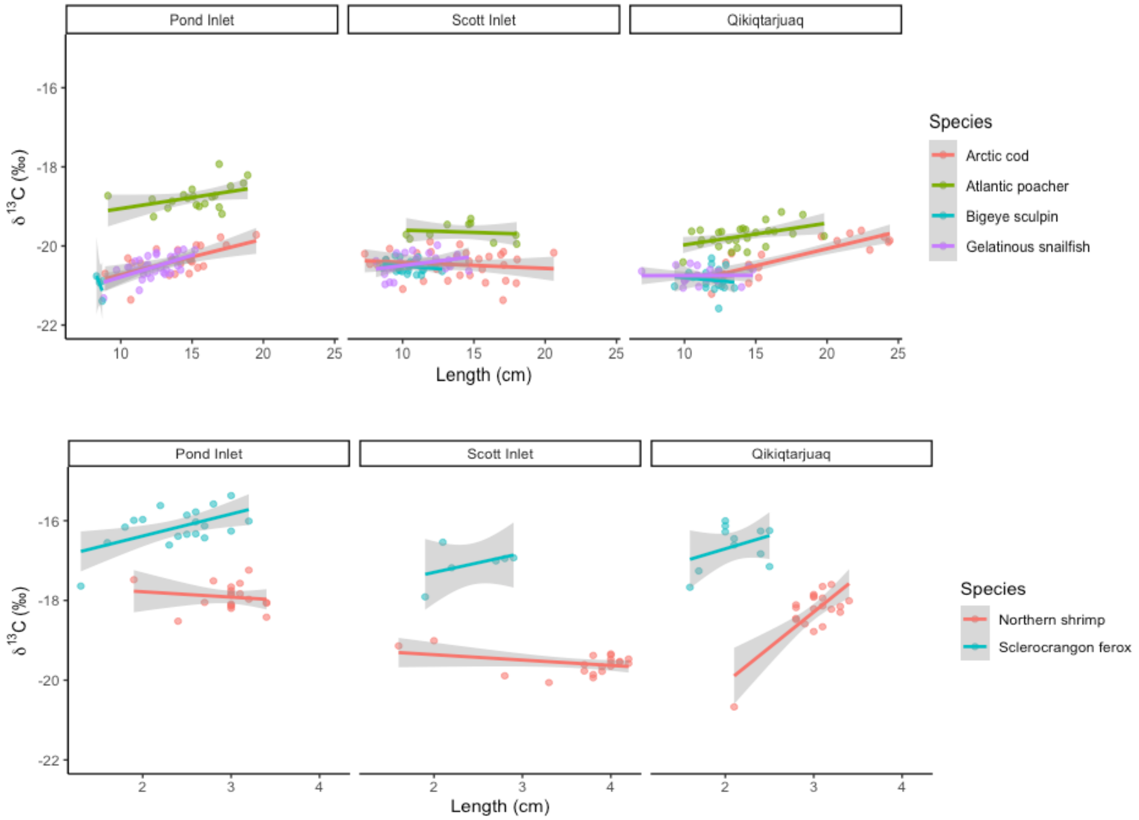

Figure 16: Linear regressions of length and $\delta^{13}C$ (‰) separated by site for (A) four deep-sea fish species separated and (B) two deep-sea shrimp species. Note the different scales on the y-axis between panels.

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