Exploring Trophic Dynamics and Fish Condition during Autumn to Understand the Lack of Recovery of Groundfish in Southern Newfoundland

by © Monica A. Sokolowski

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Land Acknowledgement

We respectfully acknowledge the territory in which we gather as the ancestral homelands of the Beothuk, and the island of Newfoundland as the ancestral homelands of the Mi'kmaq and Beothuk. We would also like to recognize the Inuit of Nunatsiavut and NunatuKavut and the Innu of Nitassinan, and their ancestors, as the original people of Labrador. We strive for respectful relationships with all the peoples of this province as we search for collective healing and true reconciliation and honour this beautiful land together.

Abstract

Following collapses in the 1990s, many Northwest Atlantic groundfish stocks have not recovered despite reduced fishing pressure. This leads to a key question in fisheries ecology today: Why do some stocks not recover? I address this question via analyses of condition, diet, and trophic dynamics of groundfish within Northwest Atlantic Fisheries Organization (NAFO) subdivision 3Ps. The first chapter introduces the research themes with seasonality highlighted and state of knowledge relevant to two subsequent research chapters. The second chapter uses diet and triple-stable isotope analysis ($\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$) to quantify seasonal differences in southern Newfoundland Atlantic Cod (*Gadus morhua*) diets and condition. I report differences in both seasonal and ontogenetic patterns within this southern Newfoundland stock in condition, diet, and stable isotope values. Chapter 3 incorporates a multispecies approach using similar methods to chapter 2 alongside stable isotope mixing models to identify pre-winter trophic interactions within the southern Newfoundland groundfish community. Ontogenetic isotopic niche overlap among various species indicates potential size dependent competition among southern Newfoundland species during the autumn. This research provided pre-winter physiological condition of Atlantic cod and the trophic interactions among the groundfish community within the autumn in southern Newfoundland and supports seasonal variation among the trophic structure within southern Newfoundland that may help identify oceanographic change related productivity shifts within the ecosystem.

General Summary

The lack of recovery of many species within Newfoundland and Labrador waters from over exploitation in the early 1980's and 1990's leads to questions of which factors limit species recovery. I address this question through the lenses of condition, diet, and transference of energy of groundfish, focusing on southern Newfoundland during the autumn season. I focus on the autumn season as condition during this time has the possibility to influence over-winter survival. I first do this through a single species lens, focusing on condition and diet of commercially important species Atlantic cod (*Gadus morhua*). Then I incorporate a multispecies approach to identify interactions among the groundfish community. Ultimately, this research provided physiological condition of Atlantic cod and the trophic interactions among the groundfish community within the autumn in southern Newfoundland. This study is the first to incorporate sulfur ($\delta^{34}S$), alongside nitrogen ($\delta^{15}N$), and carbon ($\delta^{13}C$) into analysis that occurs within the autumn of southern Newfoundland. The results from each chapter emphasize that to achieve a complete characterization of the southern Newfoundland ecosystem and its individuals, there is a need for repeated sampling over more than one season.

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Co-Authorship Statement

This manuscript-style thesis is comprised of 4 co-authored sections. I led the work including literature review, laboratory dissections, data analysis, and writing and editing of the manuscripts. Dr. Jonathan Fisher assisted with the conceptualization of the studies within this thesis, obtaining financial support, in addition to providing general supervisory support and manuscript editing. My committee members Laura Wheeland and Dr. Tyler Eddy assisted by providing helpful ideas and support during committee meetings as well as manuscript editing.

The first chapter of this thesis is designed as literature review, the second and third as research focused manuscript styles and the fourth as Conclusion and Future research Avenues. The first and final chapters are designed to link the ideas behind the two manuscripts together into a single thesis. Both the second and third chapters of this thesis are designed with intent to be submitted as independent peer-reviewed scientific journal articles, with all collaborators mentioned above as co-authors.

I was not involved in the collection of field samples for this study, as it was done two years before the start of this thesis. Samples were collected by CFER employee Wade Hiscock aboard the FV Nautical Legend. Wade also provided access to the CFER archive data set (2016) utilized in Chapter 2.

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Chapter 1: Condition and Trophic Interactions Within the Groundfish Community as Potential Drivers of Limited Stock Recovery Within Southern Newfoundland

1.0 Fish Ecology and Stock Recovery

Given the long, history of fisheries overexploitation (Longhurst 2010), marine resources are increasingly managed with the goal of sustainability of fisheries. To promote fisheries sustainability and positive economic outcomes, much focus has been put on single-species stock recovery. In Atlantic Canadian fisheries, Fisheries and Oceans Canada (hereafter 'DFO') has implemented fishery moratoria, continuously reduced the total allowable catch of various groundfish stocks (i.e. DFO, 2021a), and implemented formal rebuilding plans (Melnychuk, 2021; Hilborn et al., 2021) to reduce fishing pressures on various stocks. Although many Northwest Atlantic groundfish stocks have had reduced fishing pressure since multiple collapses in the 1990's, the biomass of most stocks still has not recovered, while in other jurisdictions they have (Hilborn et al., 2021). This leads to a key question in fisheries ecology today: Why do some stocks not recover?

There is increasing recognition of the impact that environmental changes have on fish population dynamics (Belkin er al., 2009; Gruber et al., 2011; Vert-pre et al., 2013; Boyce et al., 2014; Britten et al., 2016; Britten et al., 2017), and various drivers have been suggested to play more of a major role in the dynamics of stock collapse (Post et al., 2002; Dulvy et al., 2003) and contribute to poor recovering systems such as environmental conditions. Environmental conditions can both directly and indirectly affect reproductive conditions, occurrence of strong or weak cohorts and increased predator presence (Liermann and Hilborn 2001; Stachura et al., 2014). Helbig et al.

(1992) found that the Labrador Current can affect recruitment of various Newfoundland cod stocks (2J3KL, 3NO, 3Ps). While Mullowney (2016) found temperature to have a large impact on the trophic interactions of Newfoundland and Labrador marine shelf ecosystem (2J3KL, 3NO). Alterations in biological characteristics can lead to changes in biological reference points such as natural mortality, length-at-age, spawning stock biomass, etc., and ultimately the productivity of a stock (Klaer et al., 2015). Therefore, understanding the relationship between the effect these drivers have on fish productivity and their lack of recovery is important in addressing challenges in fisheries ecology.

1.1 Seasonality

Seasonal environmental variations influence marine fish life cycle events, and their intensity can vary with geographical area (Valiela, 1995; Cormon et al., 2014; Scranton and Amarasekare, 2017). These variations include, water temperature, salinity, sea ice, wind, etc. Mean temperature and temperature variability are consistently linked to productivity of a system through phytoplankton blooms (Martinez et al., 2011; Zhao et al., 2013), and the structure of a system through the dynamics of marine species' distributions (Tittensor et al., 2010). Increasing water temperature makes ecosystems susceptible to the introduction of new species that shift their distribution towards more thermally optimal habitats (e.g. Chen et al., 2011; Last et al., 2011; Perry, 2011; Hare et al., 2012; Nye et al., 2014; Rockwood, 2015), and alongside diminished ice coverage (Merkouriadi and Lep-päranta, 2014) which influences the timing of the spring bloom (Almén and Tamelander, 2020). Cyr et al., (2023) demonstrated for interannual variability, warmer ocean climates are associated with early spring blooms, and colder ocean climates to late blooms on the Newfoundland and Labrador shelf. These variations in environmental factors can induce further changes within marine ecosystems.

In North Atlantic Fisheries Organization (NAFO) Subdivision 3Ps (Referred to herafter as southern Newfoundland), water from the warm North Atlantic Current (Gulf Stream Extension) and a shallow cold shelf habitat covered in water derived from the Labrador Current (Pershing et al., 2001) characterize oceanographic influences on this region. The Labrador current is known to have interannual variations associated with salinity and temperature (Drinkwater, 1996; Han et al., 2008), providing southern Newfoundland with complex abiotic gradients each season (DFO, 2023a). The interaction between the Labrador Current and the Gulf Stream provides southern Newfoundland with the potential of high production due to possible upwelling of nutrient-rich water (Stenseth et al., 2002; Demarcq, 2009; Townsend et al., 2010).

In recent years, southern Newfoundland has shown an increase in bottom temperatures and reduced salinity in the spring (Cyr et al., 2020), with earlier, reduced-magnitude, phytoplankton spring blooms from 2014-2018 (Bélanger et al., 2021), indicating that the southern Newfoundland ecosystem continues to experience productivity changes. In southern Newfoundland, structural change has been characterized, for example, by the increased dominance of Silver hake (*Merluccius bilinearis*) (Rockwood, 2015; Koen-Alonso and Cuff, 2018; NAFO, 2021), but it is still unclear how these changes are affecting the productivity of the southern Newfoundland ecosystem as a whole. With the majority of fisheries survey data available from southern Newfoundland limited to the spring season due to the timing of annual DFO ecosystem surveys, assessments of the dynamics of higher trophic levels within this region do not consider potential seasonal variations.

This leaves a gap in knowledge and data involving both environmental conditions and trophic relationships among species for the autumn. Resolving this gap is important because the pre-winter condition of fish, determined by its diet and physiological condition in the autumn, can greatly influence over-wintering survival (Henderson et al., 1998; Dutil and Lambert, 2000). Having favourable condition in the autumn can allow fish to increase their energy reserves (Black and Love, 1986). With the close relationship between and individuals' diet and their condition (ex. Berard et al., 2020), identifying interactions among species during the autumn could clarify the changes occurring within the southern Newfoundland ecosystem. It is therefore important to quantify individual condition and interactions among groundfish species within the autumn of southern Newfoundland to better understand this changing ecosystem.

1.2 Single Species vs Ecosystem Assessment

Fish stocks have historically been managed as single species there has long been the assumption that quantifying population dynamics is sufficient to understand and forecast future population dynamics (Longhurst, 2010). Historically, single-species assessments were limited in their reliability due to strong assumptions on the stationarity of biological processes such as reproductive success, mortality, and growth, that affect the population (Britten et al., 2017; Vert-Pre et al., 2013). These processes are not stationary as the ecosystem impacts both abiotic (e.g., temperature) (Rice and Browman, 2014) and biotic (e.g. predation) (Longo et al., 2015) processes that affect biological processes. Murawski (2007) showed improved results over single species approaches that incorporated broader ecological processes than classical single species when reviewing several assessment models. Although it has been recognized that ecological processes have the potential to impact stock recovery (Link, 2002), the inclusion of environmental and ecological data in fishery assessments has been an ongoing issue for stock management (Beddington et al., 2007; Skern-Mauritzen et al., 2016; Pepin et al., 2022).

Shifting from only assessing single species to a broader ecosystem approach has the potential to conserve structure and function without degrading the ecosystem (Zhou et al., 2010). For Canadian stocks, Pepin et al., (2022) found 21% of the 178 Canadian stocks assessed include environmental factors quantitatively. DFO has historically incorporated limited ecological data in single species assessment, but has recently committed to the goal of incorporating more of an ecosystem approach as a part of their Sustainable Fisheries Framework (DFO, 2016). In more recent years, it has become recognized that the analysis of the ecosystem production potential should be incorporated into the assessment framework (e.g., Varkey et al., 2023). Aside from single species assessments, DFO has also implemented an Integrated Fisheries Management Plan (IFMP), (referenced as southern Newfoundland Ground Fish IFMP, 2016) which was used as a fisheries management tool for groundfish within southern Newfoundland. IFMP's are guides that support sustainable fisheries using both indigenous knowledge and scientific research. Currently, for individual species that are below their Limit Reference Point (LRP), DFO is in the process of implementing rebuilding plans (DFO, 2021b). These plans are species specific and contain performance metrics (PMs) that are used to track the stock's overall potential change in status. When it comes specifically to southern Newfoundland, there is a stock rebuilding plan for Atlantic cod only. However, there are also management regulations that encompass all commercial species within southern Newfoundland (Conservation Harvesting Plan (CHP)- https://www.dfo-mpo.gc.ca/fisheries-peches/decisions/fm-2023-gp/atl-25-eng.html). The shift towards ecosystem-based management tools occurred because of scientific evidence that broader ecosystem considerations were necessary for successful management.

1.3 Individual Fish Condition

The lack of recovery of various species has been hypothesized to be due to changes in ecosystem productivity (Frank et al., 2005; Hilborn and Litsinger, 2009; Rothschild, 2007). For example, Choi et al., (2004) suggested that the decline in groundfish productivity on the Scotian Shelf is exacerbated by variability in water temperature. It is widely recognized that growth and condition in individual fishes influence major components of a population's productivity through the levels of energy available for survival and reproduction (Lambert and Dutil 1997; Dutil and Lambert 2000; Rätz and Lloret, 2003; Rideout et al., 2006; Rideout and Morgan, 2010; Lloret et al., 2013; Morgan et al., 2014; Casini et al. 2016; Morgan et al., 2018) as individuals are the foundation from which population- and ecosystem-level traits emerge (Ward et al., 2016). More specifically, condition is a measure of the energy available for allocation to life-history decisions (Coops et al., 2004). Fulton's condition factor (K), calculated from the relationship between the weight of a fish and its length, is widely used in fisheries studies a measurement of condition (Nash et al., 2006), but is limited by its assumption of isometric growth. Another measurement of condition that has been used in fisheries science is relative condition (Kn) Le Cren (1951) where residuals from a regression of log gutted weight as a function of log length (Jakob et al., 1996). Although Kn doesn't share Fulton's K's limitation of the isometric growth assumption of individuals (Cone, 1989), Kn assumes that gutted weight is an appropriate physiological index and is only useful for comparisons within a single individual not between individuals (Cone, 1989) leading to the use of Fulton's K to measure condition in this thesis. Although both metrics have limitations, condition is still an important factor for understanding the factors affecting fish productivity.

Increased natural mortality is associated with declines in growth and condition when feeding opportunities are limited and can indicate reduced productivity (Lloret et al., 2013). For example, Regular et al. (2022) utilized a relative (and gutted weight) condition index to link changes in body size to model-derived natural mortality to investigate potential natural mortality contributions to Northern Cod's lack of recovery. Fully understanding natural mortality of fish is difficult as it represents the combined effects of multiple ecological processes (Johnson et al., 2015). Varkey et al., (2023) also suggested that assessing trends in body condition may therefore provide useful information on natural mortality for the southern Newfoundland Atlantic cod stock, but in terms of starvation-based mortality. Starvation has long been recognized as a factor that can induced mortality, and its role in regulating populations remains a central theme in ecology (McCue, 2010). Changes in body size may be linked to starvation as ontogenetic dietary shifts are common among different fish species as increased gape size allows for increased prey breadth (Werner and Gilliam 1984; Lomond et al.,1998; Woodward and Hildrew, 2002; Rose and O'Driscoll, 2002; Link and Garrison, 2002; Sherwood et al., 2007). Therefore, to better relate condition to starvation, it is important to highlight ontogenetic and seasonal variation in body condition within a population.

1.4 Changing Trophic Interactions

Ecosystems contain various components that are connected in a complex food web of evolving interactions (Cury et al., 2003). Trophic interactions relate to feeding and nutrition and can quantify the energy cycle through a system by nutrient transfer (Odum, 1969; Fennel and Neumann, 2014). Through examining energy flow between organisms and their environment, variation among individuals' responses to their environments can be identified (Carey, 2005). Aside from direct transfer through macroscopic consumption, pathways occur between different trophic levels though respiration, excretion, and detritus, with the microbial community driving elemental cycles (Burgin et al., 2011). Change among the structure of different trophic levels has also been found in food webs due to cannibalism, intraguild predation, as well as other predation events (Fath et al., 2007). The transfer of energy among different trophic levels can be considered at individual (Brown et al., 2004), population (Asch et al., 2019), and ecosystem scales (Ryther et al., 1969; Priyadarshi et al., 2019), and each scale together determines the trophic organization of an ecosystem. The complexity of marine ecosystems provides challenges in assessing not only energy transfer, but the various processes that control it (see Eddy et al., 2021).

There are two distinct trophic pathways that consumers on continental shelves rely on, either primary production or detritus (Moore et al., 2004). It has been suggested that the predators consuming pathways supported by both primary production and detritus can aid in stabilizing food webs (McCann et al., 2005; Blanchard et al. 2011) and may explain biogeographic patterns of groundfish dominance in some marine regions over others (van Denderen et al., 2018). Benthic-pelagic (B-P) coupling is an example of processes that connect these two different pathways through the exchange of energy, mass, and nutrients (Griffiths et al., 2017). This includes the deposition of nonliving organic material to benthic habitats (Hargrave, 1973; Suess, 1980; Smetacek, 1985; Graf, 1992), bioresuspension (Graf and Rosenberg, 1997), and the release of inorganic nutrients from the sediments (Raffaelli et al., 2003). Furthermore, there are various factors that can influence whether a consumer uses either pathway including ontogenetic and seasonal variations. For example, Woodland and Sector (2013) found interannual variation in plankton productivity affects the strength of B-P coupling and gape size limits small individuals and juveniles to favour the pelagic pathway. Larger individuals may rely on both pathways as they have fewer prey size constraints (Scharf et al., 2000; Woodland and Secor, 2013).

1.5 The Use of Stable Isotopes to Understand Community Ecology

Stable isotope analysis is a common tool used to study trophic relationships in marine ecosystems (Peterson and Fry, 1987, Carabel et al., 2006; Finlay and Kendall, 2007; Krumsick and Fisher, 2019). Stable isotopes are elemental tracers that circulate through natural systems reflecting the metabolic processes of an ecosystem (Peterson and

Fry, 1987). The stable isotopes Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) have been used most frequently in marine ecology, with the increased use of sulfur ($\delta^{34}S$) (Connolly et al., 2003; Finlay and Kendall, 2007; Barnes and Jennings, 2007). Elemental ratios change along a food web (Fagan et al., 2002; Fanin et al., 2013) due to metabolic retention of the heavier isotopes, known as fractionation of individual species tissue relative to their prey (Post, 2002; Fry, 2006). In marine environments, carbon ($\delta^{13}C$) variation among sources can be due to the photosynthesis pathway of plants and phytoplankton with little enrichment between prey and consumer (e.g C3 vs. C4; Rounick and Winterbourn, 1986; Peterson and Fry, 1987; Descolas-Gros et al., 1990; O'Leary et al. 1992; Post, 2002). $\delta^{15}N$ is enriched 3-4 ‰ from prey to consumer (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Peterson and Fry, 1987). The fractionation of $\delta^{34}S$ is often assumed to be negligible (Hesslein et al., 1991; McCarthy et al, 1997; Tomas et al., 2006; Barnes and Jennings, 2007), and $\delta^{34}S$ sources are heavily influenced by the presence of organic and inorganic Sulphur (Goldhaber and Kaplan, 1975; Chambers and Trudinger, 1979; Peterson and Fry, 1987; Barnes and Jennings, 2007). Connolly et al. (2003) found $\delta^{34}S$ to have less variance for source contributions, meaning $\delta^{34}S$ can identify sources indistinguishable by $\delta^{13}C$ and further clarify food web structure (Peterson et al., 1985; Lubetkin et al., 2004; Barnes and Jennings, 2007). Identifying food sources for a community can identify the production pathway that supports the energy flowing through that system.

Marine food webs rely on trophic pathways supported by primary production, detritus, or both (Moore et al., 2004). The two pathways represent pelagic and benthic origin with phytoplankton primary production commonly consumed in the water column and detritus accumulating on the seabed (Steele and Collie, 2005). Coupling between these two pathways may increase food web stability (Blanchard et al., 2011; Duffill Telsnig et al., 2019). Stable isotopes are also a useful tool for identifying if a consumer is feeding on pelagic or benthic sources (Kopp et al., 2015; Woodland and Secor, 2013). In comparison to pelagic feeding consumers, a diet with benthic sources can have relatively enriched $\delta^{13}C$ values (Kopp et al., 2015; Le Loc'h et al., 2008). Patterns in $\delta^{34}S$ are opposite; benthic sources would be reflected as depleted $\delta^{34}S$ values and pelagic sources as enriched (Thode, 1991; Connolly et al., 2004). Both Connolly et al. (2004) and Duffil Tesnig et al. (2019) found $\delta^{34}S$ led to more precise estimates of source contributions. With the SI ratios of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ in consumer tissue reflecting their diet, they provide further insight on predator/prey interactions over longer time periods than the more traditional stomach content (SC) analyses (Fry, 1988; Rau et al., 1992; Dalsgaard et al., 2003).

When the two methods of SI analysis and SC analysis can be used together through stable isotope mixing models (SIMM's), where SC can be used as priors to determine SI dietary contributions for a given consumer (Schwarcz, 1991; Phillips and Gregg, 2001). The exact proportion of prey present in the diet can be determined when three or less prey sources are present and iterative determination of contribution combinations utilizing SC priors when there are more than three sources (Stock et al., 2018). SIMM's have been used to better understand the different use of energy flow channels within ecosystems, and if pelagic or benthic sources are contributing more to the species diet (Duffill Telsnig et al., 2018; Krumsick, 2020). By identifying food web sources, I can further clarify trophic interactions within an ecosystem.

Stable isotopes have also been used as tool to explore ecological niches (See Bolnick et al., 2003; Bearhop et al., 2004; Newsome et al., 2007). An individual's trophic niche addresses the overall role a species has in the ecosystem (Leibold, 1995). The trophic niche has been defined as a species place within the biotic environment (Elton, 1927), and has been expanded to a species n-dimensional hypervolume of environmental resources (Hutchinson, 1957). SI ratios have been used to quantify the ecological niche space (Bearhop et al., 2004). With the relationship between SI values in consumer tissue to their diet, although not the exact same, the concept of isotopic niches is used to understand trophic niches and the trophic interactions between species in a community (Newsome er al., 2007).

Assessing isotopic niches of various species within a community can identify the general trophic structure within that community. Jackson et al. (2011) formulated SIBER (Stable Isotope Bayesian Ellipses in R) as a tool for measuring isotopic niches across communities. Assessing isotopic niche overlap can give details on competition among species in a community (Pianka, 1974), since niche overlap can show the degree to which species shared resources that regulate their population growth. If resources are not in unlimited supply, then the competitive exclusion principle (Hardin, 1960) may apply, where two different species' populations will not be able to coexist if they occupy the same ecological niche. Species have the potential to coexist because they have different resource use and do not interact, or they are equivalent in their competitive abilities and have partial shared unlimited resource use (Pastore et al., 2021). The latter is commonly known as niche partitioning, where competing species evolve different forms of resource use (Schoener 1974; Giller 1984; Ross, 1986). Identifying competition or resource partitioning of a system can clarify trophic interactions that may be influencing species recovery. To better understand the lack of recovery of Atlantic cod (*Gadus morhua*) within the coastal Newfoundland ecosystem, Knickle and Rose (2013) compared Bayesian metrics of isotopic niches for Atlantic cod and Greenland Cod (*Gadus ogac*). They showed niche partitioning between these two species and that they occupy similar trophic positions, suggesting Greenland cod are not limiting Atlantic cod recovery though competition for resources. This study only looked at two species within a community, potentially missing other species in the community that compete for similar resources.

1.6 Southern Newfoundland Fisheries

There are many different active groundfish fisheries within southern Newfoundland including, Atlantic cod, Redfish, Witch flounder, Greenland Halibut, Monkfish, Skates, Lumpfish, White Hake, and Atlantic Halibut (3Ps Ground Fish IFMP, 2016). Atlantic cod has been a primary fishery within southern Newfoundland and has had a reduction in the total allowable catch (TAC) since 1999 (DFO, 2022a). Although the TAC for Atlantic cod has consistently decreased, Redfish in Unit 2, southern Newfoundland Witch flounder, White hake, and Thorny skate have had constant TACs (DFO, 2022b; DFO, 2018; NAFO, 2023a; NAFO, 2023b). Many of these species are still in the critical zone (DFO, 2022a). Various commercially important species such as Redfish, American plaice, and White hake, are of special concern or worse in COSEWIC status (COSEWIC, 2009; COSEWIC, 2010; COSEWIC, 2013), and others are still unknown (DFO, 2022b). Some commercially important species are even still under moratorium within 3Ps including American plaice (*Hippoglossoides platessoides*) (Morgan et al., 2020), Haddock (*Melanogrammus aeglefinus*), Grenadier (*Macrouridae* sp.), and Pollock (*Pollachius pollachius*) (3Ps Ground Fish IFMP, 2016).

Even with multiple commercially important species having not achieved recovery, the majority of the focus on groundfish stock recovery and fish stock productivity has been on the Atlantic cod (Hutchings and Myers, 1994; Myers et al., 1997; Brander et al., 2006; Lilly, 2006; Schrank and Roy, 2013; Rice, 2018). However, the lack of recovery within southern Newfoundland is not isolated to Atlantic cod. There are still many unknowns when it comes to the effect of ecological process on numerous species in this region. The lack of seasonal diversity in data paired with the lack of recovery of many species shows the need for a better understanding of the entire southern Newfoundland marine community. The need of these different assessment tools may be a result of the various structural changes undergone within southern Newfoundland as demonstrated by the increase of silver hake presence (Rockwood, 2015; Koen-Alonso and Cuff, 2018; NAFO, 2021b; DFO, 2023b). The lack of recovery of various species and the increased dominance of piscivores such as silver hake show the need to further clarify ecosystem interactions within the southern Newfoundland community.

1.7 Present Research Objectives

The aim of the present study is to investigate seasonal influences on population recovery and trophic interactions within the southern Newfoundland groundfish community. To accomplish this, I first focus on filling the data and knowledge gap that occurs during the autumn months for Atlantic cod at both individual and community level. Specifically, in Chapter 2 I quantify seasonal differences (Spring vs. Autumn) in Atlantic cod diets and body condition. Then Chapter 3 expands on stock recovery themes from Chapter 2 to quantify trophic relationships that occur among various groundfish within southern Newfoundland during the autumn season. Finally, Chapter 4 synthesizes the findings, places them into context on how this research has demonstrated the importance of assessing ecosystems in a holistic approach, and suggests future research directions.

The broader scope of this study was to increase the understanding of species interactions during the autumn. This study is the first to quantify diet, and stable isotope values specifically for the autumn season in Southern Newfoundland of many of the species analyzed. These research results provide new information not only on trophic interactions for Atlantic cod, but also for other groundfish within the autumn of southern Newfoundland.

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Chapter 2: Seasonal Differences in Southern Newfoundland Atlantic Cod (*Gadus morhua*) Diets and Condition as Insight into Their Lack of Recovery.

2.1 Introduction

Since the collapse of Atlantic Canadian groundfish stocks in the early 1990s due to excessive fishing during a period of low productivity conditions (Lilly at al., 2008; Hilborn and Litzinger, 2009), many fishery restrictions have been put in place to reduce exploitation rates. However, even with these restrictions in place, key Atlantic Canadian groundfish stocks including Atlantic cod (*Gadus morhua*) have been unable to recover, leaving this region as anomalous within global patterns of exploitation reduction generally preceding stock recovery (Hilborn et al., 2020). Revealing and quantifying the mechanisms involved in recovering marine ecosystems is an important step towards improving the assessment and management of over-exploited and recovering fish stocks (e.g., Enberg et al., 2009; Neubauer et al., 2013; Wright, 2014; Audzijonyte et al., 2015).

Revealing the mechanistic basis underlying marine productivity is challenging, as there are many traits affected by threats/stressors that can determine the productivity of a fish population including rates of reproduction, growth and survival, and life history characteristics of the population (Randall et al., 2012). Traits proposed to explain lack of timely fish stock recovery include low reproductive rates at low population size (Myers et al., 1999), changes in size-age structure (Ohlberger et al., 2022), spawning behaviours (Brawn, 1961; Rowe, and Hutchings, 2003), and trophic interactions (Yodzis, 1998, 2000; Trzinski et al., 2006). A range of studies have been done to try to better understand the mechanisms that contributed to the collapses of Canadian Atlantic ground fish stocks.

More specifically for Atlantic cod (hereafter ‘cod’), time-varying life-history traits (Roff et al., 2002; Hutchings and Rangeley, 2011), and natural mortality (Shelton and Healey, 1999; Swain, 2011) including predation by seals (Trzcinski et al., 2006; O’Boyle and Sinclair, 2012) and starvation (Regular et al., 2022) and have been studied as potential mechanisms, with different suggested drivers among regions. Hammill et al., (2014), for example, suggested an increase in natural mortality of cod in the Cabot Strait region as a result from predation by grey seals. In contrast, Buren et al., (2014) found that harp seal predation did not limit recovery of other Newfoundland cod stocks.

Many of these studies have centered on assessing spatial and temporal components of natural mortality, often via indices of body condition. Lambert & Dutil, (2000) suggested that most natural mortality in adult cod occurs during the spring/summer period as a result of energy expenditure during the spawning season and only those that do not recover their body condition over their growth season may experience a higher level of natural mortality in the autumn. This includes cod depleting their energy reserves to near fatal levels if they are starved before the reproduction period, resulting also in reduced egg quality, quantity, and egg survival (Lambert and Dutil, 2000; Koen-Alonso et al., 2021). Overwintering fasting is sometimes found amongst fish (Shul’man, 1974; Love, 1958; Idler and Clemens, 1959; Beamish et al., 1979; Crawford, 1979; Holdway et al., 1984), and has been suggested for North Atlantic cod (2J3KL) in the months prior to spawning (Stanek, 1973; Ang et al., 1985, but see Krumsick and Rose, (2012)). There have also been instances where Northwest Atlantic cod stocks (3L) suppress their reproduction in times of poor nutritional condition to increase their chances of survival (Rideout and Rose, 2006). A recent study investigated the role of starvation as a driving mechanism for natural mortality of Atlantic cod on the Newfoundland and Labrador Shelf (2J3KL) (Regular et al., 2022). They used a gutted weight condition index of cod to form a time series of mortality associated with the availability of two key prey species, capelin (*Mallotus villosus*) and Northern shrimp (*Pandalus borealis*), and suggested prey availability as key to decadal scale trends in natural mortality.

While these studies have touched on many Canadian Atlantic cod stocks, there remain many questions surrounding the productivity dynamics of the south coast of Newfoundland, Canada, specifically in North Atlantic Fisheries Organization (NAFO) Subdivision 3Ps (southern Newfoundland) (Figure 2.6.1). Southern Newfoundland is known to have some of the most spatially variable and warmest water temperatures in Newfoundland (Colbourne et al., 2013), with high biomass of various species and primary production in general (Demarcq, 2009). However, DFO's (2020) stock assessment showed reduced production ("the potential sustained yield of a stock" DFO, 2019), and decreased length-at-age since the mid-2000s (DFO, 2022) within the southern Newfoundland stock with no clear explanation. The most recent state-space model for stock assessment of southern Newfoundland cod (Varkey et al., 2022), is expected to provide better insight into southern Newfoundland stock status by including mechanisms of natural mortality, more specifically, natural mortality as a function of fish condition. The model incorporates fish condition, since fish with low condition are more vulnerable to predation, disease, etc., which can lead to death. For individual fish, starvation from limited access to food can cause the body to use stored energy sources (Van Gils et al. 2004; Varkey et al., 2022).

Currently it is suggested that the food availability is highly variable, shown by the changes within prey compositions of southern Newfoundland cod diet over the last decade (DFO, 2021). In 2014, NAFO identified Atlantic cod was no longer the dominant piscivore by biomass, replaced by silver hake (Sacau-Cuadrado et al., 2015), and Rockwood, (2015) reported similar conclusions through diet analysis, yet quantified minimal interspecific competition in this region. However, Cadigan et al. (2022) showed southern Newfoundland cod sized 40–80 cm may be experiencing additional feeding deficiencies as indicated by decreased condition. These examples suggest mechanistic hypotheses related to the competition surrounding the diet of southern Newfoundland cod affecting their recovery. Feeding deficiencies, like those experienced through competition, could include both reduction in the amount of prey consumed and reduced quality of the prey consumed. Campanyà-Llovet et al., (2018) focused on nutritional value of essential compounds when studying properties contributing to total food quality in marine food webs. Benthic-based (detritus) and pelagic-based (primary) production cycles vary, and some essential compounds cannot be synthesized via the benthic-production pathway (Campanyà-Llovet et al., 2018). This results in continental shelf consumers relying on one or both of the pathways (Moore et al., 2004; Duffill Telsnig et al., 2019). Sherwood et al. (2007) reported benefits of a more pelagic diet in Atlantic cod and further suggested that in order for Newfoundland and Labrador cod stocks to rebuild, cod diet should consist of pelagic feeding (i.e., capelin) (Sherwood et al., 2007). Since then, it has been further suggested that stronger coupling between pelagic and benthic pathways may increase food web resilience more broadly (Blanchard et al., 2011; Duffill Telsnig et al., 2019) and may be a mechanism underlying the recovery and dominance of generalist groundfish species like Atlantic cod (van Denderen et al., 2018).

Investigating food web interactions, including pelagic-benthic coupling, through stomach contents only gives a snapshot of the diet of a species and can be biased towards some prey items. However, the nutrient cycling via predation affects the isotopic composition of individuals (Criss, 1999; Rubenstein and Hobson, 2004). This allows stable isotope analysis (SIA) to be used to assess diet data over longer periods through more integrative energy flow of past diet (Gannes et al., 1997, 1998; Fry, 1988; Lorrain et al., 2002; Schmidt et al., 2007). Therefore, SIA can provide insight on behaviours like migration, resource use, and trophic relationships in marine systems (McCarthy and Waldron, 2000; O'Reilly et al., 2002; Fry and Chumchal, 2011; Carr et al., 2017).

Carbon and nitrogen SIA have been heavily used in marine studies as they trace the productivity of an ecosystem (Finlay & Kendall, 2007). The metabolic changes in carbon ($\delta^{13}C$) of organic carbon usually do not exceed 1‰ at each trophic level (DeNiro et al., 1978; Hecky et al., 1995; McCutchan et al., 2003; Vander Zanden et al., 2005), however nitrogen ($\delta^{15}N$) increases by about 3.4‰ at each trophic level (Macko et al., 1982; Minagawa et al., 1984; Vander Zanden et al., 1997). These two isotopes tend to have co-linearity that has potential for bias in interpretation of results (Peterson et al., 1985). It can also be difficult to distinguish sources of organic matter when carbon isotope signatures overlap or are similar (Haines et al., 1979; Peterson and Howarth, 1987). Incorporating a third isotope, sulfur ($\delta^{34}S$) can help to improve the resolution of food web structure and to identify source materials (Peterson and Fry, 1987; Peterson and Howarth, 1987; Kwak and Zelder, 1997). The trophic shift for $\delta^{34}S$ has consistently been assumed negligible (Hesslein et al., 1991; McCarthy et al. 1997; Lubetkin and Simenstad, 2004), leading Barnes and Jennings, (2007), to show that $\delta^{34}S$ can be useful for source differentiation due to its greater range and minimal temperature effect, adding value to and carbon and nitrogen analysis.

Using condition, diet and SIA to identify and analyze seasonal patterns in cod is necessary as the southern Newfoundland cod stock is complex (DFO, 2022). Even with known seasonal fluctuations in condition (Varkey et al., 2022), past studies have focused largely on one season. Cadigan et al., (2022) used survey data from mainly February-April, while Rose and Rowe (2020) revealed the limited extent of autumn sampling in offshore areas of southern Newfoundland. Mello and Rose (2005a,b) showed biological seasonality in life history traits and behaviours for inshore cod within Placentia Bay, a small portion of southern Newfoundland, and more recent evidence in neighbouring populations of cod have shown seasonal variation and patterns in cod condition (Regular et al., 2022). Although, many studies have been done on the seasonal changes in diet (Turuk, 1968; Lilly, 1991; Hop et al.,1992), there are no diet studies published specifically for the autumn period of southern Newfoundland Cod. $\delta^{34}S$ has not been used in any SIA studies analyzing southern Newfoundland Atlantic cod and therefore can provide new insights into source differentiation and isotopic niche signatures (Barnes and Jennings, 2007; Duffill Telsnig et al., 2018) alongside any seasonal patterns. Spring surveys dominate southern Newfoundland cod data, but condition is expected to differ greatly before and after summer feeding season. Therefore, identifying seasonal change in condition, diet and SIA values is important when trying to analyze the recovery of Atlantic cod.

The goal of this thesis chapter is to quantify the seasonal differences (spring vs. autumn) in cod diets and condition. I consider these differences in the context of recovery to better understand the lack of recovery of Atlantic cod within southern Newfoundland. DFO's (2022) assessment that this stock has low productivity, therefore low individual fish conditions drives my hypothesis that cod are in a poor state before entering the winter season. This would be shown by all traits being analyzed being anomalous to traditional trends of condition by having a reduced condition relative to spring within each size class of the autumn cod samples. This would be reflected in lower overall biometrics such as Fulton's Condition (K), Hepatosomatic Index (HSI), and Gonadosomatic Index (GSI) when compared to spring samples. K is related to cod growth, and growth partially depends on the quality and quantity of feeding (Scott & Scott, 1988). Cod have been known to have a more generalist diet, further confirmed by Rockwood, (2015) who showed southern Newfoundland spring cod to have a the most varied generalist diet in the spring when compared to other gadoids. Although quality and quantity can heavily influence each other (Müller-Navarra, 2008), lower quality diet in the autumn would consist of cod consuming more of a benthic diet. I hypothesize that this low diversity and quality diet will be shown within each size class, with larger fish consuming a more prominent benthic diet. To better relate condition and diet, I hypothesize SIA results will also reflect a lower quality diet. When compared to spring samples, I hypothesize autumn samples will show depleted carbon isotope values as well as enriched sulfur isotope values. To test these predictions, I employ a variety of techniques, including size-aggregated stomach contents, a normalized Index of Relative Importance (%IRI), and stable isotope analyses involving C, N, S. Possible seasonal variations are assessed using SIA alongside length, K, HSI, and stomach content analysis.

2.2 Methods

2.2.1 Study Area & Sample Collection

Both inshore and offshore sites were sampled in two years off the southern coast of Newfoundland, within NAFO 3Ps. In October-November of 2018, 25 ecosystem survey trawls were completed aboard the *FV Nautical Legend* (mean depth 120 m, SD=45, range 31m-439m) (*Figure 2.6.1*). Sampling locations were identified to represent the same range of depths and areas of the spring trawl survey undertaken annually by DFO Newfoundland and Labrador Region (NL) (Rideout et al., 2018), but with reduced frequency of stations. Samples were collected using a Campelen 1800 shrimp trawl, as used currently in DFO surveys (Walsh and McCallum, 1997). Sets were then grouped into five overall regions (Halibut Channel, Hermitage Bay, Hermitage Channel, Placentia Bay, and St. Pierre Bank) for spatial comparisons. Similar methods were used aboard the *RV Celtic Explorer* in April-May of 2016 to provide a series of similar Spring samples (Wheeland, 2016). In 2016, 53 sets were sampled across the shelf slope (mean depth 189m, SD=108, range 107m-439m), but not at the two inshore regions Hermitage Bay and Placentia Bay (*Figure 2.6.1*). In the context of seasonal comparisons, the 2016 spring samples are considered despite sampling in different years, due to both similar methods and similar temperature anomalies for these months between the two years (Colbourne et al., 2017; Cyr et al., 2020).

2.2.2 Sub-Sampling

All trawl contents were separated and identified by species. Atlantic cod in the autumn survey were used for assessing the condition and diets and isotopes of the southern Newfoundland stock. To quantify any temporal and/or seasonal differences, random sub-samples of Atlantic cod from spring were then compared to the autumn samples for each type of analysis. To avoid sample size bias from the larger spring sampling, the same number of individual cod were used in each analysis based on the total number of autumn cod present in overlapping sampling locations (Hermitage Channel and St. Pierre Bank). Therefore, the number of individuals used in an analysis varied based on available autumn cod data for each analysis (Condition= 91/season, Diet=67/season). For the stable isotope analysis, no spring comparison was made due to insufficient data.

At sea, length sex, whole weight, gutted weight, and liver weight was recorded for all individuals caught; stomachs were also extracted at sea for the cod >25 cm. Smaller fish (generally <25 cm), with stomachs and muscle tissues difficult to sample at sea, were individually labelled, bagged, frozen whole, and later dissected in the laboratory (*n*=211). Individual cod from each sampling location were classified as immature (≤ 48.8 cm), or mature (> 48.8 cm), based on Atlantic cod's average size at maturity (Knickle and Rose, 2013). Although these categories are somewhat arbitrary, the categories account for anticipated ontogenetic variation in trophic interactions across sizes and is needed since the exact length of potential ontogenetic shifts remains unknown (Krumsick and Fisher, 2019). Individual stomach samples were accompanied by a unique identification tag, and frozen whole (-18 °C) for analysis in the laboratory. Muscle tissue (approximately 2 g) were taken from the anterior base of the dorsal fin, given a unique isotope identification code and individually stored and frozen (-18° C) for later stable isotope analyses.

2.2.3 Individual Fish Condition Indices

Fish energy reserves are often used to infer the overall condition of a fish, as they reflect the ability of an individual to find energy within their environment and store it. Energy sources for fish include proteins and lipids in which both liver and muscle tissue have been used (Brett and Groves, 1979; Dutil et al., 1995). Specifically, cod muscle is a lean tissue with proteins accounting roughly 75% of the muscle dry weight, and lipids being 80-90% of total energy stored in the liver (Lambert and Dutil, 1997a). To index the total muscle protein and liver lipid reserves of cod, Fulton's condition factor (K) (Equation 2.1) and hepatosomatic index (HSI) (Equation 2.2) were calculated for each individual fish, respectively, to indicate the condition of both autumn and spring cod, as follows:

$$K = (W/L^3)100 \qquad \text{[Equation 2.1]}$$

$$HSI = (W_{liver}/W_{body})100 \qquad \text{[Equation 2.2]}$$

These condition indices were selected because they are good indicators of the general energetic stores within cod (Jangaard et al., 1967; Holdway and Beamish, 1984; Pedersen and Jobling ,1989; Dos Santos et al., 1993; Foster et al., 1993; Lambert and Dutil, 1997b). By using these indices, I am assuming isometric growth in fish. If violated, problems of correlation between condition factor and length can arise (Lambert and Dutil, 1997a; Mommsen, 1998; Arnason et al., 2009). The results for HSI, K and length are presented together as means ± SD (standard deviation). As per Dutil & Lambert, (1997a), K values above 0.8 with HSI values of 6% indicate 'good' condition. Cod in 'excellent' condition have K values over 1 .00 and HSI values over 8%. However, K values of 0.4 and 0.6 and HSI values between 0.5 and 1.5 represent 'poor' condition overall for cod and the survival of cod with values at a higher risk of dying.

2.2.4 Stomach Content Analysis

Stomach contents were analyzed from a subsample of cod from both years to assess the magnitude of differences in cod diets within the autumn survey and between autumn and spring. In the laboratory, individual cod stomachs were dissected using stomach sampling protocols provided and overseen by trained technicians to ensure consistency in prey identification between survey years. Similar protocols are reviewed by Amundsen and Sánchez-Hernández, (2019). The stomachs containing content had prey items identified to the lowest taxonomic level possible, with otoliths being used to identify fish at the species level when it could not be determined otherwise. The mass and a count estimate of the prey were recorded, and in combination with their frequency of occurrence, the index of relative importance (IRI) was calculated for each prey taxa as follows:

$$IRI = (\%N + \%W)\%O \qquad \text{[Equation 2.3]}$$

Where %N is the percent contribution by number of a given prey item to stomach content, %W is its percent contribution by weight, and %O is the frequency of occurrence. To identify any regional dietary variations, stomach samples from all cod specimens examined in a single location were grouped together within the two size classes. To do this the percentage of the summation of the IRIs (%IRI) of all prey observed were calculated for all Atlantic cod sampled, excluding empty stomachs. By combining these different measures into a single index, then standardizing that index across all stomachs analyzed, it should reduce biases associated with each of the measures independently (Cortez, 1997). For considering the overall diet trends, prey items were categorized into seven groups: Pelagic Fish, Demersal Fish, Fish Other, Benthic Invertebrate, Benthopelagic Invertebrate, Invertebrate, and Other (*Table A.2.S1*).

2.2.5 Stable Isotope Analysis

Stable isotope analysis of carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$) and sulfur ($^{34}S/^{32}S$) were performed on a subsample of Atlantic cod from autumn 2018. In the laboratory, muscle tissue samples were oven dried at 75˚C for 48 hours and homogenized using an amalgamator. Lipids were not removed from samples to avoid the potential influence of derived products on isotopic signatures (Pinnegar and Polunin, 1999). The homogenized samples were sent to Cornell University Stable Isotope Laboratory (Ithaca, NY, USA). For the analysis of carbon and nitrogen, approximately 1 mg of each sample was placed into 7×7 mm tin capsules then introduced from the PN150 autosampler into the Carlo Erba NC2500 elemental analyzer for combustion analysis and analyzed using Thermo

Scientific Delta V Advantage Isotope Ratio Mass Spectrometer (IRMS) interfaced to a NC2500 elemental analyzer. Internationally accepted standards, animal (Deer) was used for δ^{13}C and δ^{15}N (overall SD: 0.07‰, 0.06‰), and feather (Goose Feather) for δ^{34}S (overall SD: 0.23‰) were used to derive delta values as follows (Peterson, 1999):

$$\delta^{15}N \ or \ \delta^{13}C \ or \ \delta^{34}S = \left(\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right) \times 1000 \qquad \text{[Equation 2.4]}$$

$$R = {}^{13}C/{}^{12}C \ or \ {}^{15}N/{}^{14}N \ or {}^{34}S/{}^{32}S$$

Based on the results of the samples, carbon and nitrogen delta values obtained between the amplitudes of 80mV and 8000mV for δ^{15}N have an error associated with linearity of 0.23‰ and between 60mV and 6000mV for δ^{13}C error is 0.27‰. Sulphur delta values obtained between the amplitudes of 100mV and 2700mV have an error associated with linearity of 0.26‰. Isotope corrections were performed using a two-point normalization (linear regression). δ^{15}N and δ^{13}C data used two additional in-house standards ('KCRN' - corn and 'CBT'- trout), while δ^{34}S data used NBS 127 and IEAE S3. To correct for lipids affecting the carbon values, the elemental carbon to nitrogen ratios (C:N) were used as a proxy of lipid content, and the mathematical correction for lipids proposed by Post et al., (2007) was applied to all samples since C:N ratios were higher than 3.5.

$$\delta^{13}C_{corrected} = \delta^{13}C_{uncorrected} - 3.32 + 0.99xC{:}N \qquad \text{[Equation 2.5]}$$

2.2.6 Statistical Analyses

All statistical analyses were performed in R-studio (2020; R Core Team, 2021) with significant values set at $p<0.05$ where appropriate. First, protocols in Zuur et al. (2010) were used in data exploration to determine which statistical tests would be appropriate to analyze samples from each year/season. Cod length, K, and HSI values were analyzed from all regions except Halibut Channel as only two cod were sampled there. The distributions of autumn cod samples differed significantly from normal across length, K, and HSI based on Shapiro-Wilks Normality Test ($W = 0.94$, *p-value* = 3.86e-13; $W = 0.96$, *p-value* = 3.24e-07; $W = 0.97$, *p-value* =0.0001). When grouped by the factor's region and size class, only K and HSI were analyzed across each size class, while length was added to the analysis for region. Between seasons, all variables were not normally distributed (Length [$W = 0.98$, *p-value* = 0.03], K [$W = 0.97$, *p-value* = 0.001], HSI [$W = 0.95$, *p-value* = 1.772e-05]). These results led to the application of non-parametric statistical tests for analysis of autumn cod condition and when comparing between seasons. Spearman's Rank Correlation method used along with Kruskal-Wallis test and Flinger-Killeen test to then analyze if differences exist between region, length-class, and season on each: length, K, and HSI. Post hoc pairwise comparisons using Wilcoxon rank sum test were then used to determine which factor of each variable (region, length-class, and season) contributed to differences. Boxplot graphs were also created with ggplot2 (Wickham, 2016) to visually show the variables analyzed.

For autumn cod diet, a data matrix of the %IRI for each individual fish was formed analyzed by season and size class. In analyzing stomach content, %IRI was not normally distributed for either season (p=<2.2e-16). This led to the use of non-parametric statistical tests (Kruskal-Wallis test and Flinger-Killeen test) for analysis of autumn cod and when comparing seasons to determine if there are differences in stomach content composition among the years/seasons and what factors (length class and location) contribute to those differences. A non-metric Multi-Dimensional Scaling (nMDS) ordination plot was created to show a visual configuration of all stomach samples based on rank similarities calculated from content composition. Bray-Curtis similarities (S) (Clarke and Gorley, 2006) were calculated between every pair of samples based on %IRI. Results can range between 0 (no prey in common) and 100 (all prey are the same between the two stomachs). Region was incorporated as a factor in this analysis because all autumn cod sampled within a region were not considered to be independent replicates. The data matrix was then used to run an Analysis of Similarities (ANOSIM) (Clarke and Gorley, 2006), to test the null hypothesis that there are no differences in stomach content composition among the three size classes and each region of Atlantic cod. For this study, a two-way nested ANOSIM was used to test for differences in prey composition among size classes grouped within regions and for differences among regions across all size classes caused by depth and/or seasonal effects. Then Similarity percentages (SIMPER) analysis (Clarke, 1993) was used to identify which assigned prey category contributed most to dissimilarities between diet among the different regions and size classes. Results presented include the average between-group dissimilarity contribution to average between-group dissimilarity, prey category/item contribution to average between-group dissimilarity, and the average abundances per group.

For the stable isotope analysis, Shapiro-Wilks Test was used to test for normal distribution, followed by Levene's test for homogeneity among variances. Multiple stable isotope biplots organized by size group were then created comparing each isotope. Pearson Correlation Coefficients were calculated and visualized for all Isotopes and length (cm). An ANOVA was then done on isotope data (Anderson et al., 2001) to identify trends or differences in each stable isotope (δ^{13}C, δ^{15}N, or δ^{34}S) across size class. Bayesian Ellipses and their corresponding metric areas (Standard Ellipses Area, Proportional Overlap, etc.) were then calculated for each size class with a confidence interval of 50% using Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson et al., 2011) for R. Standard ellipse areas(SEA) corrected for small sample sizes (SEAc) represents the core isotopic niche for each bivariate combination of isotope (δ^{13}C and δ^{15}N, δ^{13}C and δ^{34}S, δ^{34}S and δ^{15}N) (Jackson et al., 2011; Every et al., 2017; Shipley et al., 2019).

2.3 Results

2.3.1 Individual Fish Condition Indices

2.3.1.1 Autumn

When comparing autumn Cod length, K, and HSI, significant correlations were shown between most regions and within the immature size class (*Figure 2.6.2a,b*) when each factor was analyzed individually. Cod caught in the autumn had an average length of 32.58 cm +/- 12.63 cm with a range of 11cm to 71cm. The length of cod sampled in the autumn differed significantly (Kruskal-Wallis: p-value = <0.001) among regions. Pairwise comparison analysis using Wilcoxon rank sum test showed Hermitage Bay having significantly smaller cod than Hermitage Channel (p-value = <0.001), Placentia Bay (p-value = 0.007), and St. Pierre Bank (p-value = <0.001).

Autumn cod had an average K of 0.89+/- 0.15 and a range of 0.39 to 1.06 (Table 2.5.1a). Autumn cod showed significant differences in K across regions (*Kruskal-Wallis: p-value* =0.007). Further analysis showed Hermitage Bay having significantly lower K than Placentia Bay (*adjusted p-value* = 0.002) and St. Pierre Bank (*adjusted p-value* = 0.02), similar to the length results but excluding St. Pierre Bank. *Figure A.2.2.1a* shows St. Pierre Bank having the highest average condition, and Hermitage Bay having the lowest.

Autumn cod had an average HSI of 4.37 +/- 1.91 and range of 0.06 to 9.75 (*Table 2.6.1a*). Autumn cod showed significant differences in HSI for regions (*p*=<0.001) and size classes (*p*=<0.001). Unlike length and K results, Placentia Bay had significantly higher HSI values than Hermitage Bay (*p*=<0.001) and Hermitage Channel(*p*=0.05). *Figure A.2.2.1b* shows St. Pierre Bank having the lowest HSI. Similar to K, immature cod showed lower HSI values than mature cod (*p*=<0.001; *p*=<0.001).

2.3.1.2 Comparing Autumn to Spring

Seasonal comparison of spring and autumn Cod length, K, and HSI length revealed correlations between length and K, length and HSI, and K and HSI. When analyzed by seasons, *Figure 2.6.3* shows higher correlation within Spring samples than autumn samples. No significant differences were found between length of cod during the different seasons (*Kruskal-Wallis: p-value* = 0.98) (*Figure 2.6.3*). K was significantly higher in the autumn (*Kruskal-Wallis: p-value*= <0.001), and HSI was also significantly higher in the autumn (*Kruskal-Wallis: p-value* = <0.001). *Table 2.5.1b* shows average and range when comparing length, K, and HSI of autumn to spring cod.

2.3.1.3 Overall Condition

Using categorizations laid out in Dutil and Lambert (1997), *Table 2.6.2* shows most autumn cod are in fair condition or higher (*Figure 2.5.4a*) and have the highest percent in the good category overall. When seasons are compared, autumn cod had fewer cod in the poor and at-risk category for K, than Spring cod (*Figure 2.5.4b*). When categorizing the autumn HSI values, the majority were good or better (*Figure 2.5.4c*). More cod were in the poor category for HSI in the Spring (*Figure 2.4d*). When looking at seasons, *Table 2.5.1* shows cod have higher HSI values in the autumn.

2.3.2 Stomach Content Analysis

2.3.2.1 Autumn

Prey item categorization with %IRI for each category by region and size class can be found in *Appendix A, Table A.2.1*. Of the 211 stomachs analyzed, only 11 were empty (Immature= 9; Mature=2). *Figure 2.6.5a,b* shows autumn cod diet varied among regions and size classes. In analyzing autumn cod among size classes and regions, ANOSIM tests resulted in significant multivariate differences in stomach contents (R=0.06, p=<0.001) for region only. SIMPER analysis showed Hermitage Bay and St. Pierre Bank had the highest dissimilarity of 82.25%, with demersal fish contributing more to St. Pierre Bank cod diet, while Hermitage Bay consumed more prey in the other and benthopelagic invert categories. Hermitage Channel and St. Pierre Bank had the most similar diet but still had

56.69% dissimilarity, due to St. Pierre Bank being dominated by demersal fish (*Table A.2.1a*).

2.3.2.2 Comparing Autumn to Spring

In comparing autumn to spring cod, ANOSIM resulted in significant differences in diet when comparing prey category between seasons (R=0.09, p= <0.001), when looking at individual prey items these differences are still relevant (R= 0.12, p= <0.001). SIMPER results showed an 80.28 % seasonal dissimilarity between categorized Atlantic cod diets (*Table A.2.2*), but this value increased to 93.14% dissimilarity when analyzing individual prey items. Brittle Star (*Ophiuroidea*) being more dominant in the spring diet and Sand lance (*Ammodytidae*) contributing the most to the autumn diet. The Benthopelagic Inverts and Benthic Inverts prey categories differed significantly between seasons (p=0.005, p=0.007; respectively), and Pelagic prey were only present in autumn. *Figure A.2.2* shows the increase in fish in autumn cod diet when compared to spring. Of the 66 fish analyzed per season, autumn cod had less empty stomachs than spring cod (4.5%, 28.8%; respectively).

2.3.3 Stable Isotope Analysis

Stable isotope analysis revealed normal distribution across all isotope values. Pearson's correlation revealed significant results between length and isotopic values for all isotopes analyzed (*Figure 2.6.6*). ANOVA analysis also showed significant results for the difference of means of carbon corrected, nitrogen, and sulfur between Size Classes (p= <0.001, p= <0.001, p= <0.001; Respectively).

All isotopes increased when comparing immature cod to mature cod (*Table 2.5.3; Figure 2.6.6*). Although mature cod were shown to have larger isotopic values than immature cod, when length of mature cod increased, the isotopic values saw a decreasing trend (*Figure 2.6.6*). These results are also shown by Bayesian ellipses when comparing the different isotopic niches *Figure 2.6.8*. There is clear distinction between size classes for each isotopic comparison. Overlapping niches (*Figure 2.6.7*) were not present for any isotope comparison. Visualization of SEA confidence intervals for each ellipse and their SEA_C show mature cod expected at higher mean SEA for all isotopic comparisons (*Figure A.2.3*).

2.4 Discussion/Conclusion

In this study I was able to show seasonal and optogenetic patterns among southern Newfoundland cod. I used condition indices and complementary data, including stomach contents and stable isotope ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$) analyses, to quantify potential seasonal differences in condition and feeding. Importantly, I focused new data collections in the offshore area of southern Newfoundland during the autumn, a season largely unsampled in this stock area (Rose and Rowe, 2020; Cadigan et al. 2022). Although there was a larger shift in K than HSI of cod from spring to autumn, the larger end of mature cod appeared to have poorer condition and less enriched isotope values.

Different from my hypothesis of the autumn cod having poor condition overall, the results of this study reveal seasonal variations in K and HSI that are traditionally expected within cod, although exhibiting more variation than past studies in other regions. Lambert & Dutil (1997b) showed Gulf of St. Lawrence cod having maximum levels of K during the autumn. More recently, Regular et al.’s (2022) analyses of NAFO Divison 2J3KL cod also showed this same seasonal variation in condition using a different (residual-based on gutted weights) index of body condition. Our results also showed higher K in autumn cod, however, in Lambert and Dutil’s (1997b) experiment, the range of K for late summer (August-September) cod was approximately 0.86-0.90 and winter cod (January) was 0.80-0.95; only a 0.05 shift. Here I showed autumn cod had an approximate 0.24 shift in K from spring cod (Table 2.1b), and more fish are categorized in ‘poor’ condition in spring over autumn (Table 2.2). Also, when comparing increases in average K between seasons, our study showed a larger increase in from spring to autumn, 36%, than the average K increase of 24% found by Mello and Rose (2005b). The change in K averages and ranges indicates the increase of overall condition between spring and autumn, but interpretation of the overall magnitude of this change is confounded here by potential differences between 2016 and 2018. However, unlike K, HSI showed reduced rate of increase when compared to previous studies. Mello and Rose (2005b) showed an increase of 82% between spring and autumn average HSI (Placentia Bay cod), while our study only shows a 45% increase. This shows a more recent potential decrease in energy reserves for individuals within this stock. Although this is an improvement for K more than HSI, overall, the southern Newfoundland Cod stock is considered to be in critical condition (DFO, 2022).

Having a larger shift in K than HSI could imply the use of liver energy reserves over winter, leading to poor energy reserves in the spring. This is a time before the stressful spawning period. Atlantic cod energy reserves being maintained for gonad maturation are important before spawning (Lambert and Dutil, 1997a). Jørgensen et al., (2006) produced a model for Northeast Arctic stock (Baltic Sea) that showed mature cod having to trade-off reproduction, growth, and survival during the spring spawning period; Ohlberger et al. (2021) suggests a positive effect of an older spawning stock for Northeast Atlantic (NEA) Atlantic Cod stock; While Scott et al. (1999, 2006) used Icelandic cod as a model species to show large spawners that are in poor condition can lead to total reproductive failure for a population, but no such models have been used for analysis of southern Newfoundland cod. Dutil and Lambert (2000) suggested that in North Atlantic adult cod, natural mortality may start during the spawning period, but also occur later in the year for individuals that do not recover over the growing period. Southern Newfoundland cod are known to have significant interannual variation in their timing of spawning (Hutchings and Myers, 1994). They have traditionally been shown to start spawning around mid-May (Hutchings and Myers, 1994). Rose and Rowe (2020) suggested a protracted inshore spawning period that ranges from March to October. While more recently, the DFO (2022) southern Newfoundland Atlantic cod Stock Assessment states spawning cod are present in southern Newfoundland from March until August in some inshore areas (i.e., Placentia Bay), and in outshore areas (i.e., Halibut Channel) spawning may start in April. With the general size of spawning Newfoundland cod (48.8 (Knickle and Rose, 2013)), reflected in our mature cod category, and spring cod relating to the timing of spawning. Our results suggest that although overall there is increase in K and HSI from spring to autumn in mature cod (which suggests recovery to a degree during their growing period), the larger end of mature cod who may be spawning have poorer condition during the peak of the spawning period. To better understand the reduced condition in larger mature cod, and better relate spawning success to condition, more research incorporating the gonadosomatic index (GSI) alongside K and HSI is needed within southern Newfoundland.

With the incorporation of condition in present day stock assessments (Varkey et al., 2022) the importance of understanding the seasonal variation and patterns in cod condition is more important. The different trends that have been shown across Newfoundland waters (Mello and Rose, 2005b; Regular et al., 2022; Cadigan et al., 2022), have also been shown in this paper. However, when looking more closely at both K and HSI's relationship the larger of the mature cod seem to have slightly decreased values. This is also shown when focusing on each isotope's relation to fish length, even with mature cod having higher isotopic values overall, as length increases the values decrease. This leads to the question of why the larger mature cod seem to have reduced condition and are occupying a lower isotopic space. Cadigan et al., (2022) suggested a decrease in K of a larger size class could indicate feeding deficiencies. With no way to determine starvation directly, our only potential indicator is the number of empty stomachs. Our results did not show this. Only 5.5% of all autumn cod had empty stomachs and of these majority were immature cod. Spring cod were also shown to have more empty stomachs than autumn cod. Due to the limited data for larger sized cod in our analysis, starvation cannot be ruled out. Even with the possibility of diet deficiency of larger cod, the condition of cod was still higher in autumn than spring over-all. This does not prove starvation of southern Newfoundland cod entering the wintering season.

Diet is another key factor in understanding the lack of recovery of a stock. Atlantic cod are known to have a variable diet based on prey availability, and in this study, although limited by one year for each season, I showed a shift from a benthic dominated diet to a more benthopelagic/pelagic diet for autumn cod when compared to spring. This change in diet could be influence by many factors. Link et al., (2009) suggested low prey abundance may indicate an increase in competition among other species with Atlantic cod, as well as a decrease in quality of diet. Many studies (Mullowney and Rose, 2014; Rose and O'Driscoll, 2002; Sherwood et al., 2007; Morgan et al., 2018; Regular et al., 2022) have grouped the availability of capelin (*Mallotus villosus*) as prey to the growth and condition of northern cod. Litzow et al., (2006) showed capelin to be rich in essential fatty acids (EFAs) that can only be obtained by a fish through its diet. This suggests the requirement of capelin in the Atlantic cod diet for them to increase their productivity and recover. Although capelin is a high-quality prey type (Rose and O'Driscoll, 2002; Litzow et al. 2006; Sherwood et al. 2007; Mullowney and Rose 2014; Berard and Davoren, 2020), they were not present in spring cod stomach, and only had %IRI of 1.60% in autumn stomachs. Autumn cod did have an increase in finfish in their diet when compared to spring cod, however it was comprised mainly of sand lance (*Ammodytes dubius*) (Spring %IRI=9.10%; Autumn %IRI = 22.2%), supporting the Cadigan et al., (2022) finding of a positive correlation between southern Newfoundland Atlantic cod weight-at-length and Spring sand lance availability. Although sand lance only contain half the lipid content per unit mass of capelin, they contain double the lipid content of cod (Litzow et al., 2006) and could be considered another high-quality prey type for Atlantic cod, being more of a driver than capelin in this region (DFO, 2022).

Staudinger et al., (2020) conducted a review spanning US waters in the Northwest Atlantic Ocean neighbouring Southern Newfoundland; they showed Atlantic cod consumed more sand lance since the 1970's, and consumption in the spring was higher than both the summer and autumn combined. Our results are opposite as I showed an increased presence of sand lance in the autumn diet of Atlantic cod when compared to spring; I showed Cod having more than double %IRI of sand lance in their autumn diet than spring. The difference in seasonal pattern could suggest how important sand lance are to the diet and therefore recovery of southern Newfoundland cod. Sand-lance presence primarily depends on the substrate on the seabed (Auster and Stewart, 1986; Holland et al., 2005; Reay, 1970; Robards, Piatt, and Rose, 1999; Scott, 1968; Wright et al., 2000). Although most of their time is spent in the benthic zone, sand lance feed primarily on zooplankton in the water column (Gilman, 1994; Staudinger et al. 2020). This indicates Atlantic cod may be feeding on them in either the benthic zone or the water column/pelagic zone. With cod were feeding on the pelagic specie sand lance, our results would support Sherwood et al. (2007) suggestion that cod stocks will require a return to a system that supports mostly pelagic feeding in cod in order to recover. Within this study autumn cod have fed on more of a pelagic diet as well as having increased overall condition.

Atlantic cod feeding within the pelagic zone, and consuming prey that also feed in this zone, is a form of Pelagic-benthic coupling (P–B) (Boynton and Kemp, 1985; Dollar et al., 1991), that can create a positive feedback loop, enhancing productivity within the ecosystem (Malone & Chervin, 1979; Testa et al. 2020). It has been suggested that stronger coupling between these pathways may increase food web resilience (McCann et al., 2005; Blanchard et al., 2011; Duffill Telsnig et al., 2019). Through my stable isotope analysis of autumn cod, I was able to further support the hypothesis of more pelagic feeding in cod. The shift of mature autumn cod having higher isotope niches and therefore higher trophic level, yet reduced values for the largest sizes within the group is very different than the general trend of both size and trophic level increasing simultaneously found for other Atlantic cod in other areas (Krumsick and Fisher, 2019) and many other fish species (Werner and Gilliam, 1984; Woodward and Hildrew, 2002; Quevedo et al., 2009). The $\delta^{13}C$ signal shown to be depleted when compared to Sherwood et al., (2007) results from cod sampled in the same region. This could be another potential indicator that the southern Newfoundland stock is heading in a positive direction. The depleted $\delta^{13}C$ signal was also shown true for mature cod when compared to immature cod, indicative of a more pelagic diet for this size class (Sherwood et al., 2007). This is also confirmed by the $\delta^{34}S$ showing mature cod having more enriched values than the immature cod, indicating they may have had more long-term feeding within the water column (Thode, 1991; Connolley et al., 2004). To better understand the relationship between benthic-pelagic feeding and sulfur isotope analysis, further research into the sulfur isotopic signatures of other species in the ecosystem would be required. These results would also help to understand a more update trophic position of Atlantic cod within southern Newfoundland.

Aside from depleted/enriched isotope values, different from other studies (Sherwood and Rose, 2005; Krumsick and Fisher, 2019), our results showed a change in pattern relating isotope values to length. Although it was expected for mature cod to have enriched isotope levels when compared to the other size class, more specifically, I showed that the larger mature cod had less enriched isotope values. Although there were not enough individuals to make accurate assumptions for the larger mature cod only, the reduced K, HSI, and isotope values may indicate potential support of Cadigan et al., (2022) suggestion of feeding deficiencies of large size cod. In this study I was limited in making strong assumptions for the largest cod analyzed due to the small sample size of larger cod (only four cod > 51 cm available for stable isotope analysis). Being able to analyze more larger cod, along with better understanding of sulfur SIA in marine food webs would better fill this knowledge gap.

With this study I was able to include sulfur in addition to carbon and nitrogen for the isotope analysis, alongside complimentary stomach contents and condition indices analysis to gain insight into the lack of recovery of southern Newfoundland Cod. Focusing sampling during a period not normally sampled allowed me to show changes in both seasonal and ontogenetic patterns of this southern Newfoundland stock. However, through analyzing Atlantic cod alone I only get a slight look into how their overall condition is doing relative to their productivity in their community. Implementing more species from this ecosystem and identifying the food-web interactions is necessary to fully understand the role Atlantic cod within southern Newfoundland and their recovery processes.

2.5 Tables

Table 2.5.1: The number of cod sampled average length (cm), average Fulton's condition (K), and average hepatosomatic index (HSI) with +/- values representing standard deviation.

a) Autumn Cod by Size Class (Values indicated in parentheses represent cod in which stomach content data is also available)

Size Class	Number of Cod	Average Length (cm)	Range Length (cm)	Average K	Range K	Average HSI (%)	Range HSI
Immature	439(158)	28.91 +/- 9.49 (34.6+/- 9.2)	11-48	0.77+/-0.1 (0.76 +/- 0.1)	0.36-1.06 (0.35-1.03)	4.93 +/- 2.3 (5.14 +/- 1.86)	0.81-12.58 (0.81-12.58)
Mature	75(53)	54.08 +/- 4.48 (53.9 +/- 4.6)	49-71	0.79 +/- 0.09 (0.77 +/- 0.05)	0.66-0.97 (0.69-0.92)	5.90 +/- 2.5 (6.02 +/- 2.51)	0.08-11.58 (1.23-11.58)
Total	512(211)	32.58 +/- 12.63 (40.90 +/- 12.1)	11-71	0.89 +/- 0.15 (0.76 +/- 0.08)	0.39-1.06 (0.35-1.03)	5.20 +/- 2.4 (5.37 +/- 2.5)	0.08-12.58 (0.81-12.58)

b) Spring and Autumn Cod

Season	Number of Cod	Average Length (cm) +/- SD	Range Length (cm)	Average K +/- SD	Range K	Average HSI +/-SD	Range HSI
Autumn	93	43.0 ±9.7	20:71	0.81± 0.08	0.63:1.06	4.60 ± 1.9	0.81:9.41
Spring	93	43.9 ± 13.8	9:94	0.67 ± 0.1	0.45:0.82	2.40 ± 1.58	0.36:8.28
Total	186	43.47± 11.9	9:94	0.74 ± 0.1	0.45:1.06	3.34 ± 2.0	0.36:9.41

Table 2.5.2: Overall Cod Condition Seasonal Comparison. The percent of cod in each condition category for both autumn and spring.

Season	**# of Cod**	**Variable**	**% Excellent**	**% Good**	**% Fair**	**% Poor**	**% Critical**
Autumn	93	K	3.23	48.39	47.31	0.00	0.00
Spring	93	K	0.00	2.15	80.65	17.20	0.00
Autumn	93	HSI	21.51	40.86	6.45	3.23	0.00
Spring	93	HSI	4.30	31.18	31.18	27.96	2.15

Table 2.5.3: Isotope Summary: Number of Cod Analyzed per Size Class, Average and Range values for $\delta^{13}C_{Corr}$, $\delta^{15}N$, *and* $\delta^{34}S$

Size Class	**# Of Cod**	**Average $\delta^{13}C_{Corr}$**	**$\delta^{13}C_{Corr}$ Range**	**Average $\delta^{15}N$**	**$\delta^{15}N$ Range**	**Average $\delta^{34}S$**	**$\delta^{34}S$ Range**
Immature	28	-20.40 ± 0.40	-21.22: -19.75	14.15 ± 0.48	13.06:14.86	18.13 ± 0.54	16.46:19.03
Mature	13	-19.71 ± 0.24	-20.21: -19.35	15.27 ± 0.29	14.73:15.82	18.81 ± 0.42	18.13:19.68
Total	41	-20.18±0.48	-21.22: -19.35	14.50 ± 0.68	13.06: 15.82	18.35 ± 0.60	16.46: 19.68

2.6 Figures

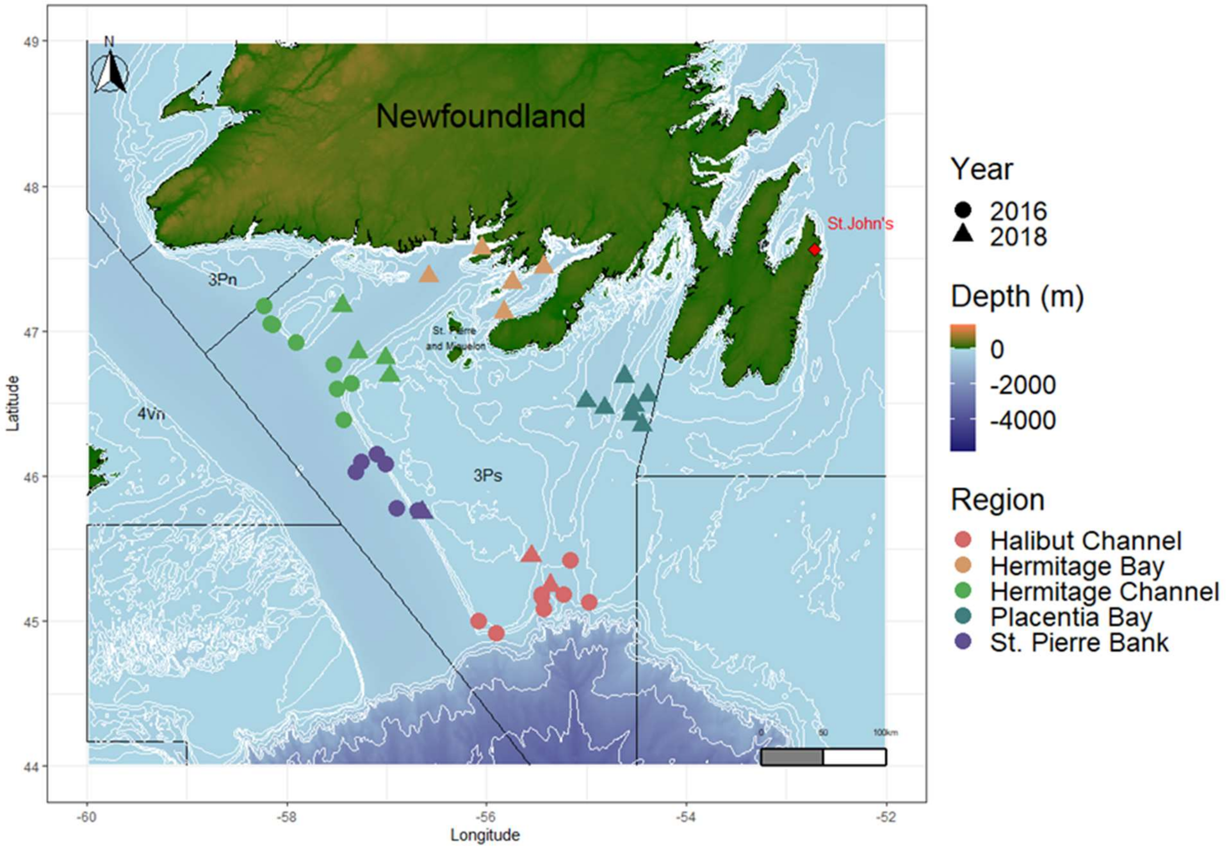

Figure 2.6.1: Southern Newfoundland Sampling Locations- Year is indicated by shape (●2016, ▲2018), Region by colour (● Halibut Channel ●Hermitage Bay ● Hermitage Channel ● Placentia Bay ● St. Pierre Bank) and Depth contours are shown at 100m intervals.

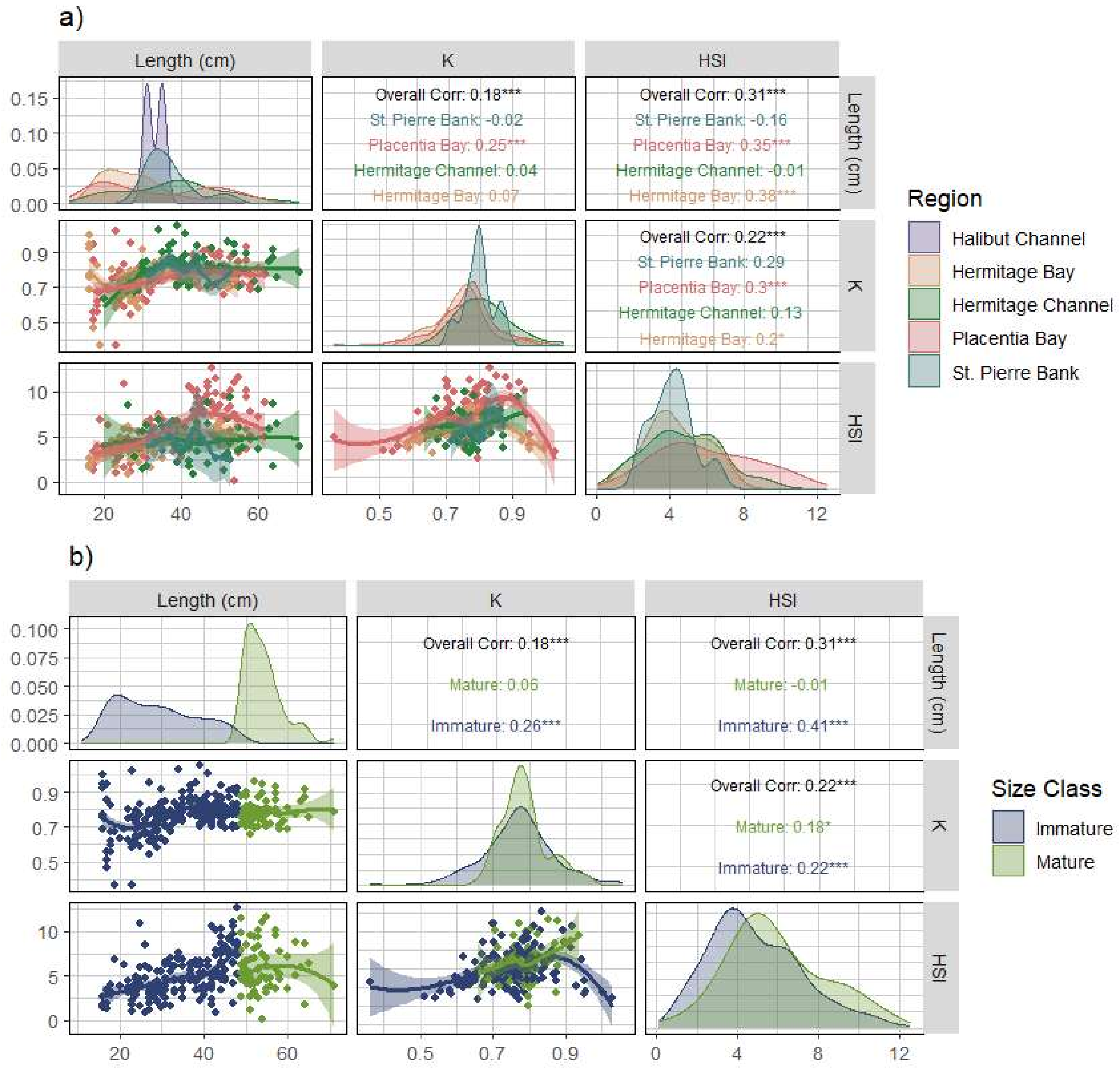

*Figure 2.6.2: Kendall Tau Rank Correlations of All Autumn Cod (n=514) for Length (cm), Condition (K), and Hepatosomatic Index (HSI). Correlations are analyzed by a) Region (Hermitage Bay [🟩], Hermitage Channel [🟧], Placentia Bay [🟥], & St. Pierre Bank [🟦]) and b) Size Class (Immature [🟦], Mature [🟩]). Correlation Panels consist of Kendal Tau's correlation coefficient and significance annotated by ('p>0.1, *p=0.05, **p=0.049-0.01, or ***p<0.009). Diagonal panels visualize the distribution of each variable and lower panels indicate loess regression with a 95% confidence interval.*

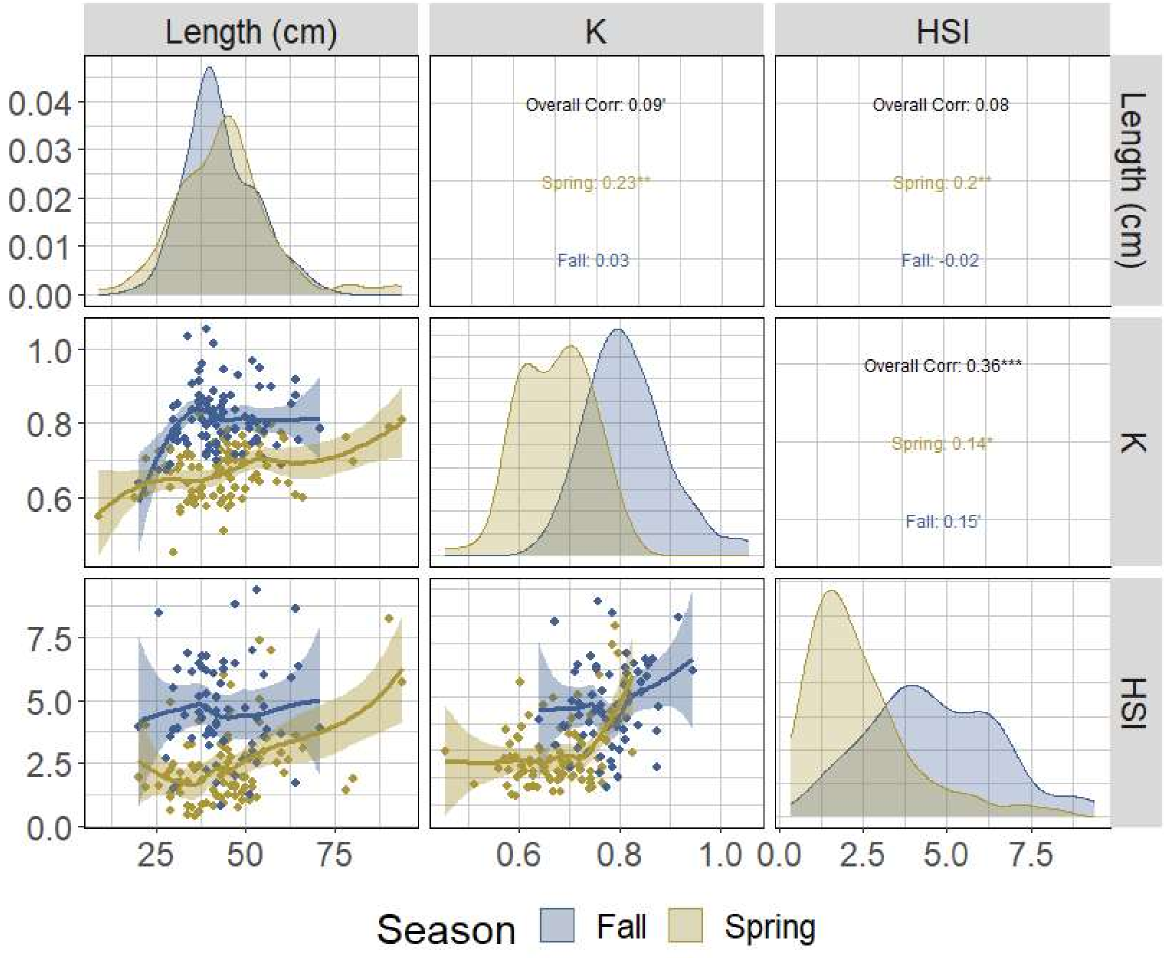

*Figure 2.6.3: Spearman's Rank Correlation of Autumn (n=91, 🟦) and Spring Cod (n=91, 🟨) comparing length(cm), condition (K), and hepatosomatic Index (HSI). Significance annotated by ('$p>0.1$, *$p=0.05$, **$p=0.049$-0.01, or ***$p<0.009$). Diagonal panels visualize the distribution of each variable and lower panels indicate loess regression with a 95% confidence interval.*

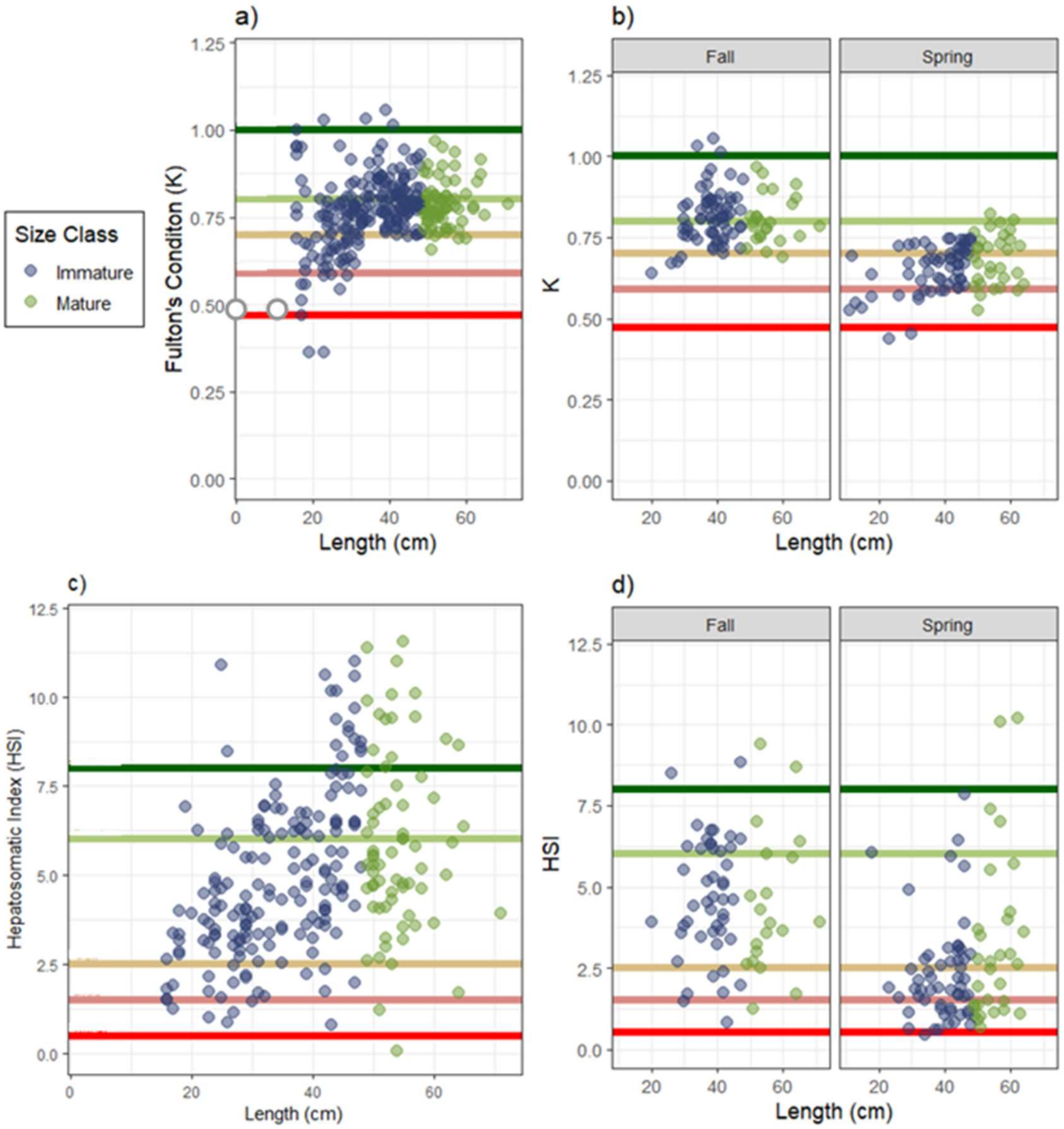

Figure 2.6.4: Atlantic Overall Condition Categorization. Categorization is analyzed by a) Autumn Condition (n=280) (K), b) Spring (n=93) and Autumn (n=93) Condition (K), c) Autumn (n=243) Hepatosomatic Index (HSI), & d) Spring (n=91) and Autumn (n=91) Hepatosomatic Index (HSI). Categorization is visualized within the coloured lines (Excellent [🟩], Good [🟩], Fair [🟨], Poor [🟥], Critical [🟥]). Individual size class is also identified as Immature [🟦], Mature [🟩].

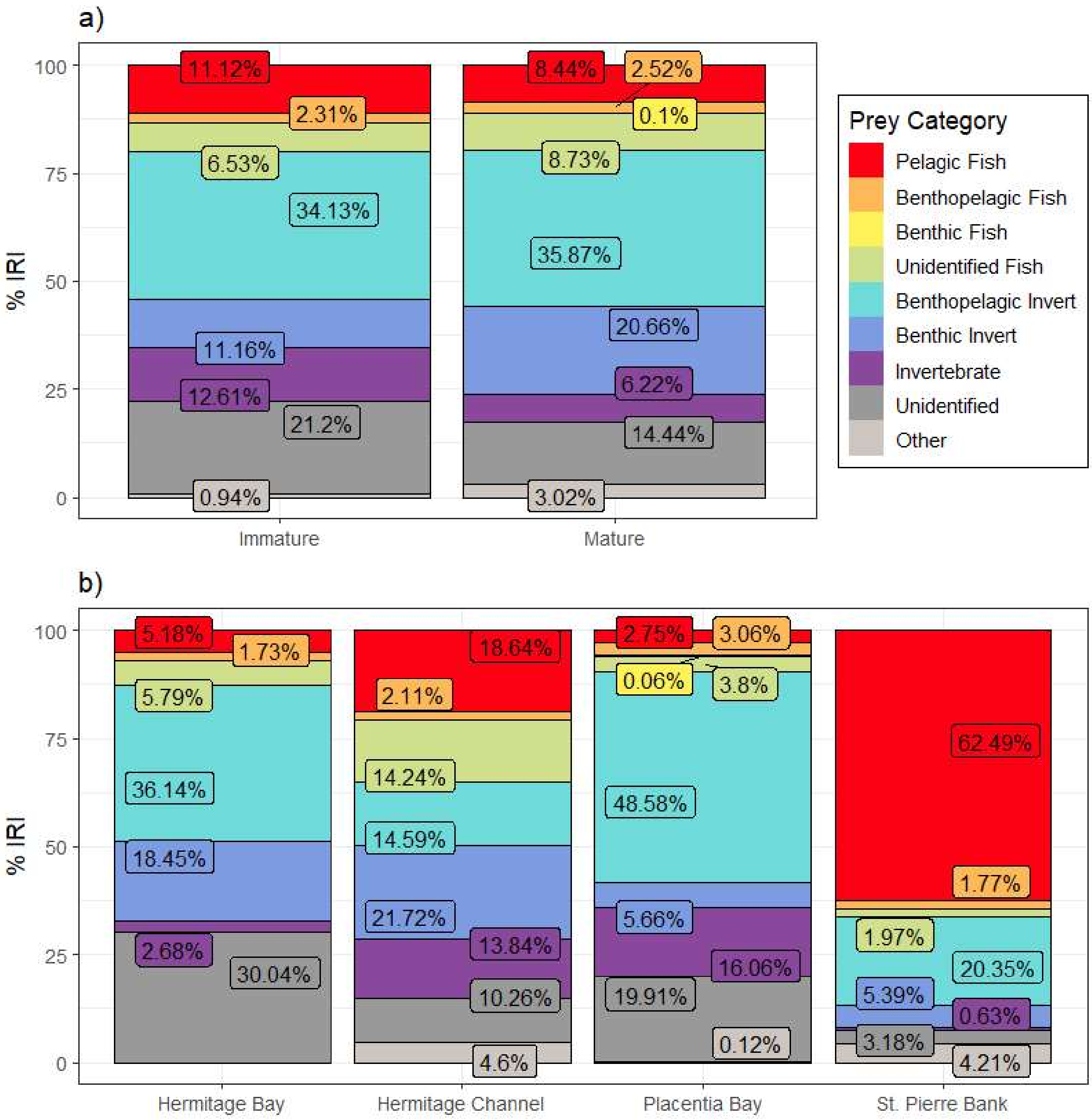

Figure 2.6.5: Autumn Atlantic Cod Diet by %Index of Relative Importance (%IRI): 211 Cod samples analyzed by a) Size class and b) Region, showing the total %IRI contribution to diet of each prey category (Pelagic Fish (🟥), Benthopelagic Fish (🟧), Benthic Fish (🟨), Fish Other (🟩), Benthopelagic Invert (🟦), Benthic Invert (🟦), Invertebrate (🟪), Unidentified (⬛), & Other (⬜).

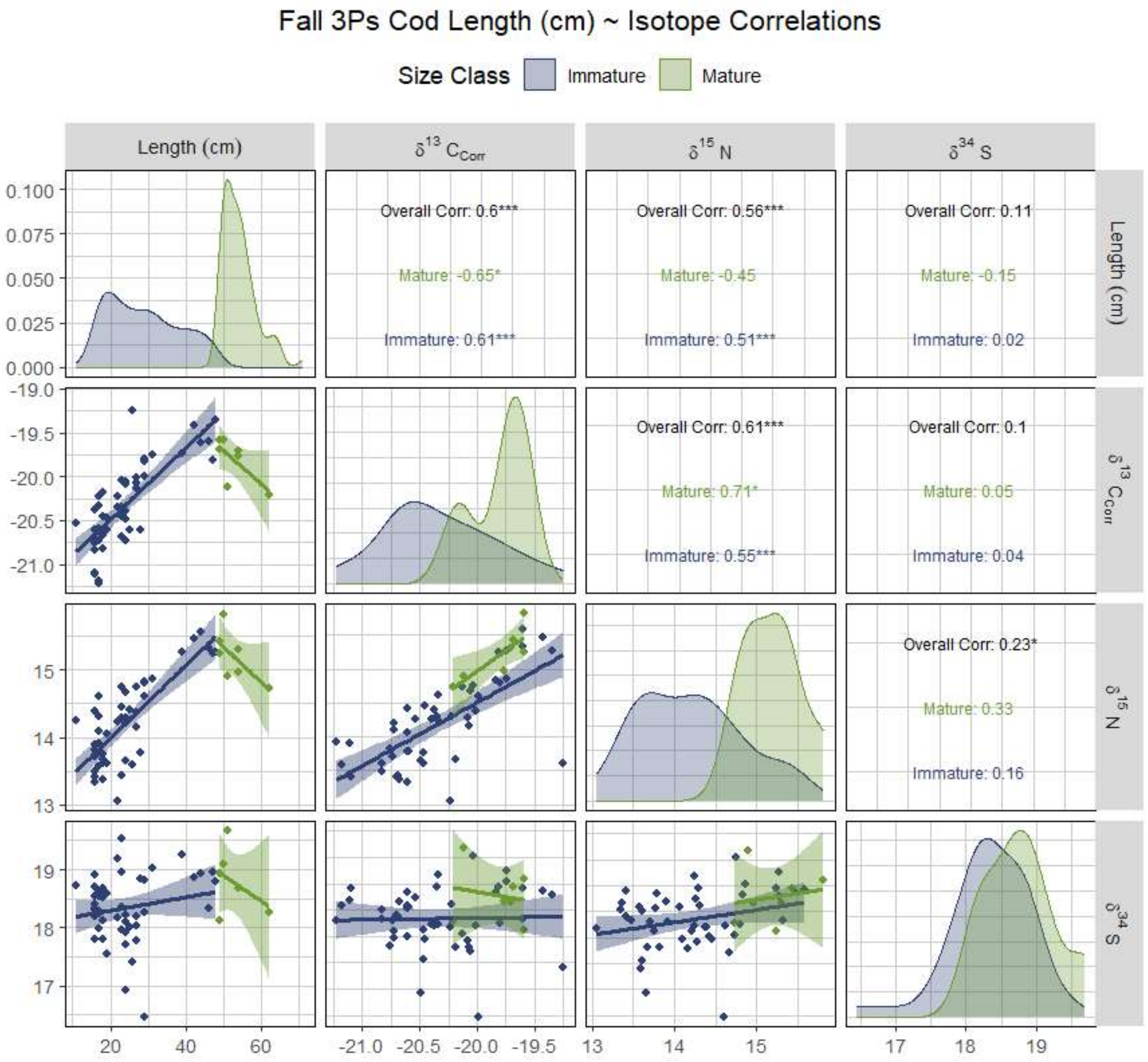

*Figure 2.6.6: Pearson Correlations Coefficient of All Autumn Cod (n=41) for Length (cm), Corrected Carbon ($\delta^{13}C_{Corr}$), Nitrogen ($\delta^{15}N$), and Sulfur ($\delta^{34}S$). Correlations are analyzed by Size Class (Immature [🟦], Mature [🟩]). Correlation Panels consist of Spearman's correlation coefficient and significance annotated by ('p>0.1, *p=0.05, **p=0.049-0.01, or ***p<0.009).*

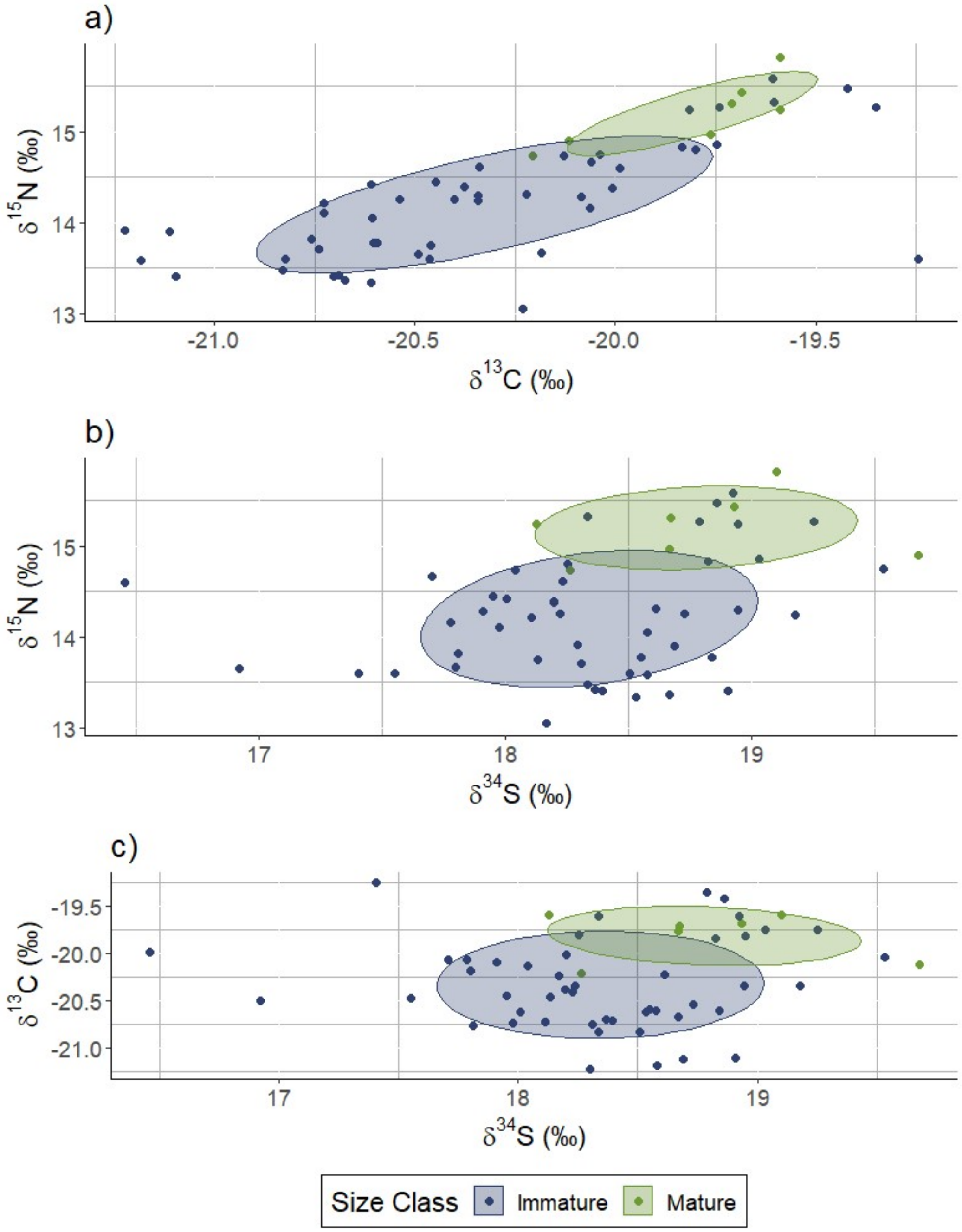

Figure 2.6.7: Bayesian ellipses for all three size classes for Autumn southern Newfoundland Atlantic Cod. Immature cod are represented by ●, and mature cod by ●. a) $\delta^{15}N$ n and $\delta^{13}C_{Corr}$. b) $\delta^{15}N$ and $\delta^{34}S$ c) $\delta^{13}C_{Corr}$ and $\delta^{34}S$.

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Chapter 3: A Multispecies Approach to Understanding Changing Dynamics of the Southern Newfoundland Marine Ecosystem.

3.1 Introduction

The anomalously slow recoveries of multiple Northwest Atlantic marine ecosystems in response to reductions in fisheries exploitation (e.g., Hilborn et al., 2021), have led to renewed efforts to expand the suite of potential drivers of single-species to include potential community (Levin et al., 2009) and ecosystem-level factors (Link, 2010). For example, only 27% of Canadian fisheries assessment advice includes knowledge of climate, oceanographic, and/or ecological considerations (Pepin et al., 2022); with demersal fisheries assessments at even lower rates (Pepin et al., 2022). This gap persists despite fishery collapses and ecosystem changes being linked to various trophic interactions that also affect fishery production including reductions in prey availability, competition, predation, and mortality (Hollowed et al., 2000; Christensen and Walters, 2004; Garrison et al., 2010; Audzijonyte et al., 2019).

In Newfoundland and Labrador, commercial groundfish fish stocks collapsed in the 1990's due to excessive fishing and for some stocks environmental influences that have continued to show low productivity alongside slow recovery (Hutchings, 2000; Hutchings and Reynolds, 2004; Krumsick and Fisher, 2020; 2022). With the decline of Newfoundland groundfish populations reducing the influence of dominant top predators including Atlantic cod (*Gadus morhua*) (Lilly et al., 2000), these species dynamics can alter interactions among species both directly and indirectly through competition, predation, density-mediated interactions, trophic cascades and migration (Menge, 1995;

Windle et al., 2012; Estes et al., 2013). Understanding these interactions within fish populations and their ecosystem is therefore necessary for effective fisheries management.

In recent decades, models and empirical evaluations have highlighted the likely importance of predator-prey interactions to recovery of ecosystems. Bundy, (2001) reported that in models of Newfoundland ecosystem dynamics, top-down control produced the slowest stock recovery for various species. Similarly, Worm and Myers, (2003) interpreted the predator-prey interaction of Newfoundland cod populations can have strong effects on their prey northern shrimp (*Pandalus borealis*), indicating the need to understand the changing relationships between consumers and their prey. Such relationships have been evaluated less thoroughly along the south coast of Newfoundland, within North American Fisheries Organization (NAFO) Subdivision 3Ps (referred to now on as "southern Newfoundland"). The recent levels of phytoplankton blooms have been normal (DFO, 2022a; DFO, 2021b), which give southern Newfoundland the potential for high productivity (Demarcq, 2009). However, due to low productivity, there are management plan in place such as southern Newfoundland Atlantic cod (*Gadus morhua*) Reubuilding Plan (DFO, 2021a; DFO, 2022a). Rebuilding plans are a result of DFO decision-making framework that requires that removals from all sources must be kept at the lowest possible level until the stock clears the Critical Zone (DFO, 2022a). Southern Newfoundland also remains under a Conservation Harvesting Plan (CHP) for groundfish. These plans are put in place to reduce fishing pressure on species without completely closing the fishery. The southern Newfoundland CHP incorporates different regions and time frames that are specific to the ground fish's biological and ecological habits (See Section 5 of the 3Ps 23-24 CHP).

Currently there are many different commercial groundfish fisheries within southern Newfoundland (See DFO's Groundfish Division 3Ps Integrated Fisheries Management Plan (IFMP), referenced now on as 3Ps Ground Fish IFMP, 2016), including Atlantic cod (*Gadus morhua*), Atlantic Halibut (*Hippoglossus hippoglossus*), Greenland Halibut (*Reinhardtius hippoglossoides*), Redfish (*Sebastes* spp.), Skate (*Raja* spp.), and Witch Flounder (*Glyptocephalus cynoglossus*). Although some of these species do have Total Allowable Catch (TAC) allocated by DFO to reduce the effects of fishing on these species, many are still in the critical zone (DFO, 2022a), or status is unknown (DFO, 2022b). Many species within southern Newfoundland are also still under moratorium including American plaice (*Hippoglossoides platessoides*) since 1993 (Morgan et al., 2020), Haddock (*Melanogrammus aeglefinus*), Grenadier (*Macrouridae* sp.), and Pollock (*Pollachius pollachius*) (3Ps Ground Fish IFMP, 2016).

Despite many of these species exhibiting seasonally variable biotic interactions, the majority of southern Newfoundland ecosystem surveys that contribute information to stock assessments are completed during the spring, leaving knowledge gaps about the ecology of these species within southern Newfoundland during the autumn (DFO, 2018a; DFO, 2020; DFO, 2022a; DFO, 2022b). A common theme within various southern Newfoundland stock assessments is that there is change within the fish community structure (DFO, 2022a, 2020, 2018). Silver hake (*Merluccius bilinearis*) has replaced Atlantic cod (*Gadus morhua*) as the dominant piscivorous fish within southern

Newfoundland (DFO 2015; Rockwood, 2016; Koen-Alonso et al., 2020), and more recently there has been an increase in Redfish (*Sebastes* spp.) (DFO, 2020). Each of the above-mentioned species are known to have seasonal influences on biological processes. Redfish within southern Newfoundland have been found to have seasonal trends in sexual maturity factor (Ni and Templeman, 1985) with copulation occurring in the autumn (DFO, 2022b). Atlantic cod have been shown to have seasonal fluctuations in condition (Varkey et al., 2022, Chapter 1 results), and silver hake's seasonal migrations cause them to have variations in diet (Garrison and Link, 2000a,b; Lock and Packer, 2004) with southern Newfoundland silver hake consuming mostly finfish during the spring (Rockwood, 2016). This changing ecosystem allows for potential increase in competition for the same resources influences by season, as it is suggested that food availability within southern Newfoundland is highly variable (DFO, 2021). With the known overlap in diet of Redfish, Atlantic cod and silver hake ranging from benthic inverts like brittle stars, to both demersal and pelagic fish such as capelin (Pérez-Rodríguez & Saborido-Rey, 2012; Bowman et al., 1987; Helser et al., 1995, Rockwood, 2016). Silver hake have also been shown to feed on both Atlantic cod and Redfish (Zhu, 2020). These few examples demonstrate the complexity the changing system within southern Newfoundland, and the need to further understand seasonal effects of trophic relationships among species.

With the energetics of individual species largely driving shifts in their trophic interactions (Rosenblatt et al., 2016), carbon and nitrogen have traditionally been used to form isotopic niches as a proxy for trophic niches (Bearhop et al., 2004; Newsome et al., 2007). Analyzing the trophic niche of a species is an essential component in understanding predatory and competitive interactions within their ecological niche (Leibold, 1995; Newsome et al., 2007; Jackson et al., 2011). Various techniques have been used to quantify trophic interactions including fatty acid analysis (Kiyashko et al., 1998; Parrish et al., 2000), pyrosequencing of prey DNA from stomach contents or feces (Symondson, 2002; King et al., 2008; Deagle et al., 2009), stomach content analysis (Hynes, 1950; Hyslop, 1980), and stable isotope analyses (Post, 2002). Stable isotope analysis identifies a more long-term diet when compared to stomach content analysis. Carbon ($\delta^{13}C$) and Nitrogen ($\delta^{15}N$) have been used to analyze marine trophic ecology in other Newfoundland regions (e.g., Sherwood and Rose, 2005; Krumsick and Fisher, 2019). $\delta^{15}N$ provides information on tropic levels as the stable nitrogen isotope signature typically becomes enriched by approximately 3 ‰ for fish species with each consumption (Minagawa and Wada, 1984; Vander Zanden et al., 1997; Post, 2002). While carbon fractionation between tropic levels is negligible (> 1.0‰ per trophic level; Vander Zanden and Rasmussen, 2001), $\delta^{13}C$ is beneficial in indicating habitat or a pelagic/benthic resource source (DeNiro and Epstein, 1978; Hecky and Hesslein, 1995). Benthic feeding would consist of enriched (more positive) $\delta^{13}C$ values, while a pelagic diet would consist of depleted (more negative) $\delta^{13}C$ values (Davenport and Bax, 2002; Sherwood and Rose, 2005; McMahon et al., 2013). However, in high trophic level consumers where $\delta^{13}C$ values may be misleading (Coltrain et al., 2004; Jaouen et al., 2016; Szpak et al., 2018), Szpak and Buckley, (2020) suggested a high potential for sulfur isotopes ($\delta^{34}S$) to differentiate between benthic and pelagic pathways when δ13C cannot (Barnes and Jennings, 2007). Fry & Chumchal, (2011) found enriched $\delta^{34}S$ values in more pelagic diets while and lower $\delta^{34}S$ values in more benthic-feeding species. Incorporation of all three isotopes allows for a more comprehensive analysis. Through incorporating the percent index of relative importance (%IRI) of prey in consumer diet alongside fractionation coefficient estimates, and additional prey isotopic values, isotope mixing models (SIMMs) can be used to approximate proportions of consumer diet (Phillips and Gregg, 2001). Here I utilize these techniques with the goal of characterizing trophic interactions that occur in the autumn within southern Newfoundland.

The shifts in community structure within southern Newfoundland (DFO, 2022a; 2020; 2018b), as well as the gap in data for community structure within southern Newfoundland during autumn drives the goals of this study. Expanding on Chapter 2 themes, this chapter aims to characterize and quantify multiple species' autumn diets and trophic interactions within southern Newfoundland. Barnes et al., (2018) proposed quantifying energy fluxes in food webs to measure ecosystem productivity. Therefore, using various techniques, including a normalized Index of Relative Importance (%IRI) of stomach contents, and stable isotope analyses involving C, N, and S, to inform SIMMs, I plan to identify ecosystem structure during the autumn in southern Newfoundland .

3.2 Methods

3.2.1 Study Area & Sample Collection

Sites were sampled off the southern coast of Newfoundland, within southern Newfoundland. In October-November of 2018, 25 ecosystem survey trawls were completed aboard the FV Nautical Legend (mean depth 120 m, SD=45, range 31m-439m, tow duration: 6-15 minutes; speed: 2.9- 3.2 kn) (*Figure 1*). Sampling locations were identified to represent the same range of depths and areas of the spring trawl survey undertaken annually by DFO Newfoundland and Labrador Region (NL) (Rideout et al., 2018), but with reduced frequency of stations. Samples were collected using a Campelen 1800 shrimp trawl, as used currently in DFO-NL surveys (Walsh and McCallum, 1997). Species were then grouped by length into three overall size classes (Small, Medium, and Large) for ontogenetic comparisons (*Table 3.5.1*).

3.2.2 Stomach Content Analysis

Frozen stomachs had their contents sampled to quantify diets within southern Newfoundland during the autumn. In the laboratory, individual stomachs were dissected using standard stomach sampling protocols similar to Amundsen and Sánchez-Hernández, (2019). Prey items were identified to the lowest taxonomic level possible, with otoliths being used to identify fish at the species level when other visual methods were insufficient. The mass and count estimates of prey were recorded, and in combination with their frequency of occurrence, the index of relative importance (IRI) was calculated for each prey taxa as follows:

$$IRI = (\%N + \%W)\%O \qquad \text{[Equation 1]}$$

Where %N is the percent contribution by number of a given prey item to stomach content, %W is its percent contribution by weight, and %O is the frequency of occurrence. To identify any dietary variations or links between species, stomach samples were first analyzed by species only, then grouped by each region. To do this the percentage of the summation of the IRIs (%IRI) of all prey observed were calculated for all individuals sampled per species, excluding empty stomachs. By combining these different measures into a single index, then standardizing that index across all stomachs analyzed, it should reduce biases associated with each of the measures independently (Cortez, 1997). For overall diet trends, prey items were categorized into seven groups: Pelagic Fish, Demersal Fish, Fish Other, Benthic Invert, Benthopelagic Invert, Invert, and Other (*Table S1*).

3.2.3 Stable Isotope Analyses

Stable isotope analysis of carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$) and sulfur ($^{34}S/^{32}S$) were performed on a subsample of the most frequently collected species. Muscle tissue samples were oven dried at 75˚C for 48 hours and homogenized using an amalgamator. Lipids were not removed from samples to avoid the potential influence of derived products on isotopic signatures (Pinnegar and Polunin, 1999). The homogenized samples were sent to Cornell University Stable Isotope Laboratory (Ithaca, NY, USA). For the analysis of carbon and nitrogen, approximately 1 mg of each sample was placed into 7×7 mm tin capsules then introduced from the PN150 autosampler into the Carlo Erba NC2500 elemental analyzer for combustion analysis and analyzed using Thermo Scientific Delta V Advantage Isotope Ratio Mass Spectrometer (IRMS) interfaced to a NC2500 elemental analyzer. Internationally accepted standards, animal (Deer) was used for $\delta^{13}C$ and $\delta^{15}N$ (overall SD: 0.07‰, 0.06‰), and feather (Goose Feather) for $\delta^{34}S$ (overall SD: 0.23‰) were used to derive delta values as follows (Peterson, 1999):

$$\delta^{15}N \text{ or } \delta^{13}C \text{ or } \delta^{34}S = \left(\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right) \times 1000 \qquad \text{[Equation 2]}$$

$$R = {}^{13}C/{}^{12}C \text{ or } {}^{15}N/{}^{14}N \text{ or } {}^{34}S/{}^{32}S$$

Based on the results of the samples, carbon and nitrogen delta values obtained between the amplitudes of 80mV and 8000mV for $\delta\ ^{15}N$ have an error associated with linearity of 0.23‰ and between 60mV and 6000mV for $\delta^{13}C$ error is 0.27‰. Sulphur delta values obtained between the amplitudes of 100mV and 2700mV have an error associated with linearity of 0.26‰. Isotope corrections were performed using a two-point normalization (linear regression). $\delta^{15}N$ and $\delta^{13}C$ data used two additional in-house standards ('KCRN' - corn and 'CBT'- trout), while $\delta^{34}S$ data used NBS 127 and IEAE S3.

3.2.4 Trophic Analyses

Trophic Position (TP) was calculated for each consumer twice using a single-source TP model (Equation 4; Post, 2002), with source data obtained from an adjacent Newfoundland region (Krumsick and Fisher, 2022), as there is currently none exclusively for southern Newfoundland that are publicly available.

$$TP_{Consumer} = TP_{Source} + \frac{\delta^{15}N_{Consumer} - \delta^{15}N_{Source}}{\Delta 15N} \qquad \text{[Equation 4]}$$

First a benthic feeding source (Brittlestar, Krumsick and Fisher, 2022; Amiraux et al., 2023b) was used, then a pelagic feeding source (Hyperiidae; Krumsick and Fisher, 2022), both with a constant source TP of 2 (Amiraux et al., 2023a) to identify potential differences in energy pathways and its effect on consumers. Both taxa are highly consumed by fish in southern Newfoundland waters (Krumsick, 2020). The fractionation coefficient of 3.4‰ for Nitrogen (Post, 2002) was used for all species. I designed Schematic 3.6A to be used for benthic/pelagic and trophic interpretation of stable isotope analysis results.

Although trophic position relates stable isotope values to long term diet, it doesn't identify the exact prey the consumer is feeding on. Therefore, I used Stable Isotope Mixing Models (SIMMS) to identify autumn diet and trophic relationships within southern Newfoundland from both stomach content and stable isotope results. For each consumer species analyzed, one stable isotope mixing model ($\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$) was preformed using the MixSIAR package in R (Stock et al., 2018) and the following equations (Equation 5, 6, 7, 8; Phillips & Koch, 2002):

$$(\delta^{13}C_i - \delta^{13}C_M)[C]_i f_{i,B} + (\delta^{13}C_{ii} - \delta^{13}C_M)[C]_{ii} f_{ii,B} + \cdots + (\delta^{13}C_n - \delta^{13}C_M)[C]_n f_{n,B} = 0$$

[Equation 5]

$$(\delta^{15}N_i - \delta^{15}N_M)[N]_i f_{i,B} + (\delta^{15}N_{ii} - \delta^{15}N_M)[N]_{ii} f_{ii,B} + \cdots + (\delta^{15}N_n - \delta^{15}N_M)[N]_n f_{n,B} = 0$$

[Equation 6]

$$(\delta^{34}S_i - \delta^{34}S_M)[S]_i f_{i,B} + (\delta^{34}S_{ii} - \delta^{34}S_M)[S]_{ii} f_{ii,B} + \cdots + (\delta^{34}S_n - \delta^{34}S_M)[S]_n f_{n,B} = 0$$

[Equation 7]

$$f_{i,B} + f_{ii,B} + \cdots + f_{n,B} = 0 \qquad \text{[Equation 8]}$$

Where $\delta^{13}C_n/\delta^{15}N_n/\delta^{34}S_n$ represent the tissue isotopic values for a given prey item, $\delta^{13}C_M/\delta^{15}N_M/\delta^{34}S_M$ the tissue isotopic values for the predator, $[C]n$ the carbon concentration of a given prey, $[N]_n$ the nitrogen concentration of a given prey, $[S]n$ the sulfur concentration of a given prey, and $f_{n,B}$ the proportion of the predator's diet represented by the given prey species. Mixing models were preformed using all individuals without influence of factors, then ran again using size class as a factor. The number of individual's data used can be found in Table.

Prey sources used for each consumer were determined by the %IRI of diet analyzed (*Table A.3.1.1*). Fractionation coefficient used for carbon was 0.4 (Post, 2002). For sulfur, the fractionation coefficient is assumed to be negligible with no agreed upon value (Peterson et al., 1986; Fry, 1988; Hesselein et al., 1991; Michener and Schell, 1994; McCarthy et al, 1997; McCutchan et al., 2003; Tomas et al., 2006; Barnes and Jennings, 2007) and therefore no value was used. Arostegui et al., (2019) showed lipid-correction can alter isotopic mixing model interpretation, and if different taxa contain different lipid concentrations it can further skew the mixing model outcome (Kiljunen et al., 2006; Tarroux et al., 2010). Although each species had mean carbon to nitrogen ratios (C:N) much higher than the 3.5 expected for marine fish (Ricklefs and Travis, 1980), $\delta^{13}C$ values were not corrected for lipids to reduce bias within our mixing model analysis.

3.2.5 Statistical Analyses

The main species chosen for analysis were determined primarily based on available samples, with a requirement for at least 10 individuals with isotope data along with stomach content data. Ten taxa within our sample set met this requirement: American plaice, Arctic cod, Argentine*,* Atlantic cod, Eelpout*,* Greenland halibut, Redfish, Silver hake, White hake, and Witch Flounder. Figure S1$_{\text{a-g}}$ identifies locations and abundances in which species were caught. All analyses were performed in R (R Core Team, 2021) with significance values set at $p<0.05$ where appropriate. Due to all individuals sampled within a region considered to be independent replicates, region was not incorporated as a factor in this analysis. Sampled individuals were classified as small, medium, or large, based on the species' observed length ranges, by dividing the observed range of sizes into three length categories of equal width (*Table 3.5.1*). White hake was the only exception in which the 3 largest fish were outliers and not included in the distribution calculation. These categories are recognized to be arbitrary, but as the exact timing of potential ontogenetic shifts was unknown, this division accounted for variation across the range of observed sizes.

To analyze southern Newfoundland diet, Bray-Curtis similarities (S) (Clarke and Gorley, 2006) were calculated between every pair of predator species based on %IRI. Results can range between 0 (no prey in common) and 100 (all prey are the same between the two species). An Analysis of Similarities (ANOSIM) (Clarke and Gorley, 2006) was then run-on individuals analyzed by individuals pooled by species to test the null hypothesis that there are no differences in stomach content composition among the different predator species. Then Similarity percentages (SIMPER) analysis (Clarke, 1993) was used to identify which assigned prey category contributed most to dissimilarities between diet among the different species. Results presented include the average between-group dissimilarity contribution to average between-group dissimilarity (*D*), prey category/item contribution to average between-group dissimilarity, and the average abundances per group.

To analyze stable isotopes across species, multiple stable isotope biplots were then created comparing each isotope. Pearson correlation coefficients were calculated and visualized for all isotopes and length (cm). Bayesian ellipses and their corresponding metric areas (Standard ellipses area, proportional overlap, mean distance to the nearest neighbour, etc.) were then calculated for each species with a confidence interval of 50% using Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson et al., 2011) for R.

3.3 Results

Of the species analyzed, Redfish was the most abundant species caught (*n*=1161) followed by American plaice (*n*=908), then Atlantic cod (*n*=514). Greenland halibut (*n*=35) and Eelpouts (*n*=58) were the least abundant species caught (*Table 3.5.2*). Witch flounder were the largest in mean length (47.68 ± 16.3 cm) and Arctic cod were the smallest (16.79 ± 4.0). Numbers of fish analyzed for stomach and isotope samples analyzed are also shown in *Table 2* and averaged 21% and 17% of numbers caught, respectively. Sample distribution among length is shown in Figure S2.

3.3.1 Diet Analysis

American plaice had the highest percent of empty stomachs (48%) while still containing a similar number of distinct prey items (n=11; A.3.1.1) to Eelpout, and Redfish. American plaice also had the largest %IRI of pelagic fish in their diet (Figure

3.6.2). Given the wide range of stomachs analyzed among species, there was a positive correlation between number of prey categories observed and number of stomachs analyzed (r = 0.79, p =0.01), Witch flounder had the highest %IRI of undetermined digested material (%IRI= 79.89; *Figure 3.6.2*). Analyzed by prey category identified in Figure 3.6.2, SIMPER results (*Table A.3.1.2*) revealed White hake and Argentine having the most similar diet (*D*= 0.776) with Benthopelagic Invert and Benthopelagic fish as two significant contributors to their difference. Greenland halibut had the least similar diet to White hake, Argentine, and Silver hake (*D*= 0.969, *D*= 0.966, *D*= 0.965), with significant difference in proportion of Polychaetas and Lanternfish. When analyzed by individual prey item, White hake and Argentine were the most similar (*D*=0.828), with unidentified material being the largest contributor to the difference. Supplementary *Figure S3* shows the large size classes of American plaice, Eelpout, and White hake having a greater %IRI of fish in their diet when each species diet was analyzed by size class.

3.3.2 Stable Isotopes

Stable isotope analysis showed Witch flounder having the largest mean δ^{15}N and δ^{13}C (15.86±1.1, -18.82±0.8; *Table 3.5.3*) but the lowest mean δ^{34}S (12.59±1.6; *Table 3.5.3*). Atlantic cod had the largest mean δ^{34}S (18.40±0.6) value and Greenland Halibut had the lowest mean δ^{13}C (-21.47±0.6; *Table 3.5.3*). Witch flounder, Atlantic cod, Arctic cod, Eelpout and American plaice all showed significant positive correlation between length and δ^{13}C (*Table A.3.1.3*). Significant positive correlations between length and δ^{15}N were shown for White hake, Redfish, Atlantic cod, and Arctic cod, with American plaice having a strong negative correlation (*Table A.3.1.3*). Correlations for length and δ^{34}S were mostly negative, as Atlantic cod and Eelpout had the only significant positive correlations; Silver hake, Redfish, and Arctic cod showed significant negative correlation (*Table A.3.1.3*).

Bayesian Ellipses for each pair of isotopes were analyzed by all species and by species' size class (*Figure 3.6.3a-c; Figure A.3.2.3a-c*). Nitrogen and carbon analysis by length showed larger Corrected Standard Ellipse Area (SEA$_{C}$) values for the smaller size class of Atlantic cod, Eelpout, and White hake (*Table A.3.1.2a*). The ellipse for medium Witch flounder had the highest SEAC overall, while Medium Atlantic cod had the smallest SEA$_{C}$ (*Table A.3.1.2a*). When size class was not included, White hake had the largest SEA$_{C}$, and Argentine had the smallest (*Table A.3.1.3a*). For nitrogen and sulfur, the medium followed by large size classes of Witch flounder occupied the largest isotopic space, and large Argentine has the smallest (*Table A.3.1.2b*); similar results emerged when length was not included in the analysis. For carbon and sulfur, species in which the smaller size class had larger SEA$_{C}$ values were Argentine, Atlantic cod, Eelpout, and White hake (*Table A.3.1.2c*). The medium and large size classes of Witch flounder had the biggest SEA*C*, while the large and medium size classes of Argentine had the smallest (*Table A.3.12c*). Witch flounder also had the largest SEA$_{C}$ when length was not included in the analysis; Silver hake and Argentine had the smallest (*Table A.3.1.3c*).

Proportion of overlap that occupied total combined isotopic space was used to identify possible competition between consumers (*Figure 3.5.3; Figure A.3.2.3*). For nitrogen and carbon, overall, White hake and American plaice shared the most isotopic space (30.48%), followed by Arctic cod and Atlantic cod (26.03%), and Arctic cod and

Redfish (25.83%). Incorporating length into the analysis resulted in Atlantic cod and Arctic cod have the highest proportional overlap for both the small and large size classes (34.72%; 23.02%). Nitrogen and carbon were the only analysis in which Witch flounder had small proportions of overlap. This included with American plaice, Eelpout, Redfish, and White hake (3.70%, 0.36%, 0.05%, 10.72%), but had no overlap with other species in the nitrogen and sulfur, or the sulfur and carbon analysis. For nitrogen and sulfur, Redfish and Arctic cod had the largest overlap (33.05%), followed by American plaice and White hake (30.62%). Including size into the analysis results small classes of Redfish and Arctic cod sharing 40.95%. Finally, for carbon and sulfur analysis, American plaice and White hake shared 36.44% of combined isotopic space. When size class was included, Redfish and Arctic cod shared the most for large size classes (25.78%).

3.3.3 Trophic Analysis

Trophic position (TP) calculations revealed a range of 3.24-4.05 when calculated based on benthic sources, and a range of 3.16-3.97 when calculated from pelagic sources. Witch flounder was found to have the highest TP, and Silver hake having the lowest when analyzed by both a benthic and pelagic source (*Table 3.5.4*). The two pelagic species (Arctic cod and Redfish) had the next highest TP. American plaice and White hake had the same mean TP when calculated from a benthic source, but American plaice had a slightly larger TP when calculated with the pelagic source (*Table 3.5.4*). This higher TP with benthic sourced prey was evident among all species (*Table 3.5.4*). TP further analyzed by size class is shown in Supplementary *Table 3.5.4*. Each species had a higher TP for their large size class when compared to small with American plaice and

Silver hake as exceptions. Both large and small size class of Witch flounder had the highest TP when analyzed by both categories of sources (*Table A.3.1.4*).

While mixing models were done for all consumers as a part of this study, American plaice, Redfish, Silver hake, White hake, and Witch flounder results are focused on in these results for their commercial interest. For details on the additional species analyzed, refer to *Table A.3.1.6*. Although Greenland halibut is also commercially important, there were not enough samples to run the analysis. To relate to the results found in Chapter 2, Atlantic cod results are shown in *Figure A.3.2.4* but are limited by two size classes. Redfish results are also limited by two size classes.

American plaice diet consisted of mainly Sand lance (*Ammodytes* spp.), with all other prey items comprising less than five percent total (*Figure 3.6.4a*). When analyzed by length, the amount of Sand lance increased with increasing size (*Figure 3.6.4b*). Redfish models results showed Euphausiids, followed by Pelagic fish as the two largest components of diet (*Figure 3.6.5a*). This was the same when length was included in the analysis, however large Redfish diet consisted of more pelagic fish and small Redfish consisted of more Euphausiids (*Figure 3.6.5b*). Euphausiids also comprised majority of silver hake diet (*Figure 3.6.6a*). There was an increase in pelagic fish in the diet of the larger size class of silver hake, but euphausiids still remained the most abundant in both size classes (*Figure 3.6.6b*). White hake diet primarily consisted of euphausiids (*Figure 3.6.7a*), but when analyzed by size class, large white hake had half the amount of euphausiids as small white hake (*Figure 3.6.7b*). The portion of fish in white hake diet also increased with increased size (*Figure 3.6.7b*). Witch flounder diet consisted of primarily polychaetes (*Figure 3.6.8a*), and had an increase in shrimp with increased length (*Figure 3.6.8b*).

3.4 Discussion/Conclusion

The ongoing community change within the southern Newfoundland marine ecosystem, paired with the lack of scientific survey data for this system during the autumn months (Rose and Rowe, 2020; Cadigan et al., 2022), leaves key gaps in knowledge of the structure and functioning of the southern Newfoundland ecosystem during the autumn season. To address these gaps, I characterized pre-winter trophic relationships and diet among various commercially important groundfish species within southern Newfoundland using isotope mixing models informed by both stomach contents and stable isotope analyses. Results revealed diet overlap among fish within southern Newfoundland which may contribute to competition for resources, as well as variation between size classes within species. Trophic analyses also indicated Atlantic cod was within the middle of groundfish ecosystem structure among the species analyzed during the autumn. Interspecific trophic interactions can greatly affect the timelines for stock recovery (Fung et al., 2013). By quantifying these interactions during the autumn, I characterize trophic relationships among species that may change seasonally, thereby affecting overall stock productivity, and in turn population, community, and ecosystem recovery.

Changes in trophic interactions and potentially prey abundances are identified through dietary habits of species (Garrison and Link, 2000a; Garrison and Link, 2000b; Worm and Myers, 2003; Link et al., 2008; Cook and Bundy, 2012), and energy and nutrient flow within ecosystems (Post, 2002; Fry, 2006, Parnell et al., 2013; Phillips et al., 2014; Pedersen et al., 2017). Quantifying stomach contents provide a high-resolution snapshot of what consumers eating (Atwell et al., 1998; Baker et al., 2013). Despite the expected biases among stomach content results in the measures of the diet composition caused by variable evacuation rates among prey types (Rindorf and Lewy, 2004), and uncertainty in the detectability of different prey types (Barnes et al., 2010; Baker et al., 2013), each proportion of prey item represented an indication of the relative importance of each prey item within this system (Phillips et al., 2014).

Combining stomach contents and stable isotope analyses also aids in the resolution of known biases in stomach content sampling, as shown by the resolution in diet composition with the SIMM results. In our study on average 29% of finfish diets were 'unidentified prey' (*Figure 2*) and perhaps the best example of this bias being resolved was shown by the Witch flounder SIMM. Although the vast majority of stomach contents for Witch flounder were undetermined digested material (79.89%, *Figure 2*), SIMM results revealed that the largest contributor to Witch flounder diet was polychaete marine worms. Polychaetes are a common prey item in Witch flounder diets, not only in southern Newfoundland, but in neighbouring divisions 2J3KLNO given the Witch founder's small mouth and benthic lifestyle (Scott, 1976; Link et al., 2002; Tam and Bundy, 2019; Krumsick, 2020).

The example of Witch flounder further illustrates the utility of sulphur (S) stable isotopes in resolving extreme benthic consumers, as has been demonstrated with dominant fishes of the North Sea (Duffill Telsnig et al., 2019b). In our study when looking at C and N isotope ellipses only, Witch flounder overlap with other species. However, given my further inclusion of S isotopes in the analysis, there is clear separation of Witch flounder from the other consumers analyzed based on their unique and consistently depleted S isotope signatures (*Figure 3a,b,c; S3a,b,c).* Since sedimentary sulfides are lighter isotopically (more depleted), and in contrast, enriched S values indicate feeding on sulfates in the water column (Connolly et al., 2004), our study further supports Witch flounder feeding more within the benthic food web on deposit feeding invertebrates rather than predatory invertebrates as similarly discussed by Wudrick (2023). In comparison to the S-isotope values among 15 species of North Sea fishes (Table S1 of Duffill Telsnig et al., 2019b).), southern Newfoundland Witch flounder are extremely depleted in sulphur isotopes, averaging 12.59±1.6 (present study) vs. 18.41±0.7 for North Sea species including the assumed North Sea benthic specialist flatfish (Lemon Sole-Microstomus kitt) (Duffill Telsnig et al., 2018). In addition to its S-isotope values, there is also clear separation between Witch flounder at the higher trophic end of our analysis when compared to the other species analyzed, perhaps characterized by the availability of microfauna and/or finfish deposit-feeding polychaetes to Witch flounder contributing to their apparent high trophic level. The high N values of Witch flounder may be due to high contribution of microbially processed organic matter and/or higher isotopic fractionation by polychaetes (Karlson et al., 2015). Clear isotopic niche separation also suggests limited competition for resources between Witch flounder and other consumers within southern Newfoundland.

In contrast to the distinct separation of Witch flounder, the majority of consumers analyzed had some degree of overlap in isotopic niche space of all three isotopes (*Figure 3a,b,c; S3a,b,c*), likely indicating shared resources among those species. Although interpretation of high isotopic niche overlap between species shouldn't be considered as equal trophic overlap due to uncertainties in basal isotopes values of the ecosystem (Hoeinghaus and Zeug, 2008), source differentiation is further clarified by incorporating a third isotope (S) into the analysis (Barnes and Jennings, 2007; Duffill Teslnig et al., 2018). Traditionally niche differentiation because of resource partitioning, has been known as the basis for coexistence within an ecosystem (Abrams, 1983). Shared resources shown by high isotopic niche overlap can imply competition within the ecosystem (Hutchinson, 1957; Alley, 1982), which in turn can limit recovery of various species. Overlapping isotopic niche space was also higher for the small size class when compared to large for all isotopic pairs (*Table S5*). This distinction among size classes could imply an ontogenetic bottleneck limiting the success of various species within southern Newfoundland. Specifically, within southern Newfoundland, cod weight-at-length has been below average in recent years, and the length at which southern Newfoundland cod mature has also been decreasing since the mid-1990's (Cadigan et al., 2022; DFO, 2021). Individuals that mature earlier allocate resources to reproduction rather than growth, and reduced size-at-age can increase predation on older age groups (Audzijonyte et al., 2015). Survival in the early life stages of gadoids have been found more important than age-at-maturity in terms of stock recovery (Wright, 2014), and competition among small fish within the autumn of southern Newfoundland could be a key factor in the limited recovery within this ecosystem. The present study indicates potential size dependent competition among southern Newfoundland species and cannot rule out limited food availability within this region during the autumn.

Changes in diet due to competition could include both reduction in the amount of prey consumed and reduced quality of the prey consumed. Recently it has been suggested that food availability is highly variable within southern Newfoundland (DFO, 2021). Of the species analyzed six contained some type of finfish in their diet, while all species analyzed consumed benthopelagic invertebrates. This could indicate that a group of species are feeding within the pelagic zone, while also consuming prey that also feed in this zone. This is a form of Pelagic-benthic coupling (Boynton and Kemp, 1985; Dollar et al., 1991), and is hypothesized to create a positive feedback loop that enhances productivity within the ecosystem (Malone **&** Chervin, 1979; Testa et al., 2020). With some essential compounds only being synthesized via the pelagic-production pathway (Campanyà-Llovet et al., 2018), stronger coupling between pelagic and benthic pathways may increase food web resilience more broadly (Blanchard et al., 2011; Duffill Telsnig et al., 2018), and be a mechanism underlying the recovery and dominance of generalist groundfish (van Denderen et al., 2018). In the first chapter, when only looking at Atlantic cod, I suggested this link could imply the system within southern Newfoundland is improving. However, the present chapter shows strong benthic-pelagic coupling among many species within southern Newfoundland and potential ontogenetic resource competition.

Diet analysis showed benthopelagic invertebrates being primary prey within this system, not only for forage species like capelin (Obradovich et al., 2014), but also for many predators within the system during the autumn. Obradovich et al., (2014) compared capelin diet in two neighbouring regions to southern Newfoundland, the eastern Scotian Shelf (ESS) and 2J3KL, and found ESS capelin to have higher condition and higher stomach fullness in an euphausiid dominated diet. Several studies have showed the importance of Euphausiids as a prey for capelin (Vesin et al., 1981; Panasenko, 1984; Gerasimova, 1994; Astthorsson and Gislason, 1997; Ozhigin et al., 2003; Orlova et al., 2002), and suggest full recovery of the species is linked to Euphausiid availability (Dalpadado and Mowbray, 2013). Although sand lance was more present in diets analyzed here than capelin (perhaps owing to seasonal migrations in capelin and predominance in demersal fish diets during summer, alongside an increased relative abundance of sand lance vs. capelin in southern Newfoundland), it is suggested that Sand lance abundance is regulated by prey abundance (Frederiksen et al., 2006; Lynam et al., 2017). With a dormancy period suggested for Sand lance during the winter months, Staudinger et al., (2020), vigorous feeding prior during the autumn may contribute to maturation and survival. Having active forage fish available to top predators during the autumn season may also lead to increased production of those predators. Historically, capelin is known to be a primary prey species of cod (Mello and Rose 2005; Link and Sherwood, 2019) and has been directly linked to Atlantic cod recovery (Mullowney and Rose, 2014) in neighbouring ecosystems. However, spring diet studies done by DFO in southern Newfoundland show capelin is not a large part of Atlantic cod diet, instead Sand lance is their primary piscivorous prey (See Figure 6.20 of NAFO, 2021). Robertson et al. (2021) found Atlantic cod consumed more sand lance and were more sensitive to changes in Sand lance population size within the Grand Bank area. Aside from Atlantic cod, Sand lance was present in American plaice and Silver hake diets of this study, while capelin were only found in Atlantic cod and White hake stomachs. This further implies capelin may not be a major factor in stock recovery within southern Newfoundland. Our study shows autumn diet among southern Newfoundland consumers contains not only Sand lance and capelin, but Euphausiids as well further supporting benthic-pelagic coupling potentially influencing recovery of groundfish within this system (van Denderen et al., 2018).

By quantifying trophic interactions during the autumn, this study shows the importance of seasonal considerations assessing species. In the spring of southern Newfoundland, Silver hake has been identified as a dominant species by biomass within southern Newfoundland (Sacau-Cuadrado et al., 2014; Rockwood, 2016). Although there was a low abundance of Silver hake caught in this study, I cannot conclude they are not a dominant species within southern Newfoundland in the autumn. Silver hake did have the lowest TP, and although stomach contents included finfish species, benthopelagic invertebrates were of larger proportion in the SIMM. Silver hake are known to have seasonal distributions (Alheit and Pitcher, 2012). During the autumn, Silver hake move onto shallower coastal bank areas (Bigelow and Schroeder, 1953; Edwards et al., 1962; Almeida, 1987; Waldron, 1988). Unlike silver hake, Redfish was abundantly caught in this study. Redfish within southern Newfoundland are managed by DFO as part of Unit 2, in which there is a less data that contributes to assessments in comparison its neighbouring region Unit 1 (DFO, 2022). Redfish were shown to have the most similar diet to American plaice and Greenland halibut of all species analyzed. In turn, Atlantic cod diet was also both similar to Greenland halibut and American plaice. These results could imply that during the autumn season, Redfish is a more dominant piscivorous predator, further indicating that not only may this region be undergoing structural change, but the relationship between species distribution and season may be influencing that change.

This study helps fill the knowledge gap on trophic dynamics within southern Newfoundland during the autumn. Through assessing various species within southern Newfoundland during the autumn, our results further show the seasonal influence on possible changing community structure. I also showed the importance of assessing this system in the autumn months as the results of this study indicate the use of similar resources with southern Newfoundland during this season. To improve bias related to diet composition, DNA meta barcoding of stomach content (Jakubavičiūtė et al., 2017; Siegenthaler et al., 2019; Riccioni et al., 2018), and capture of environmental DNA in water samples (Mychek-Londer, 2018; Briggs, 2020; Sevellec et al., 2021), can be used to further clarify the taxonomic resolution diet among all species within southern Newfoundland. Through the use of stomach contents and stable isotopes, I was able to identify possible competition among smaller size classes of fish. Although interpretations must take into consideration data limited still in terms of exact isotopic baselines for southern Newfoundland, such information is necessary to facilitate ecosystem productivity and recovery when looking at managing various fish stocks through an ecosystem’s framework within this region.

3.5 Tables

Table 3.5.1: Size Classes for Analysis: Species Length's (cm) organized into Small, Medium, and Large Size Classes based on individual species observed length distributions.

Species	Small	Medium	Large
American plaice (*Hippoglossoides platessoides*)	8.0 – 26.0	26.1 – 44.0	44.1 - 62.0
Arctic cod (*Boreogadus saida*)	11.0 - 16.3	16.4 - 21.7	21.8 – 27.0
Argentine (*Argentina spp.)*	10.0 – 21.3	21.4 – 32.7	32.8 – 44.0
Atlantic cod (*Gadus morhua*)	11.0 -31.0	31.1 - 51.0	51.1 – 71.0
Eelpout (*Lycodes spp.*)	19.0 – 30.0	30.1 – 41.0	41.1 – 52.0
Greenland halibut (*Reinhardtius hippoglossoides*)	14.0 -26.0	26.1 – 38.0	38.1 – 50.0
Redfish (*Sebastes spp.*)	4.0 – 18.7	18.8 – 33.3	33.4 – 48.0
Silver hake (*Merluccius bilinearis*)	12.0 -24.3	24.4 – 36.7	36.8 – 49.0
White hake (*Urophycis tenuis*)	21.0 -37.7	37.8 – 54.3	54.4 – 71.0
Witch Flounder (*Glyptocephalus cynoglossus*)	12.0 -24.7	24.8 – 37.3	37.4 – 50.0

Table 3.5.2: Length Summary of Species Analyzed. Mean ± sd Length (cm) and counts of consumers utilized for each type of analysis.

Species	**Total**		**Stomachs Analyzed**		**Isotopes Analyzed**	
	n	**Length (cm) mean ± sd**	**n**	**Length (cm) mean ± sd**	**n**	**Length (cm) mean ± sd**
American plaice	908	25.20±8.6	50	33.88±14.1	53	30.08±14.4
Arctic cod	136	16.79±4.0	20	16.95±6.0	30	18.53±5.5
Argentine	91	22.85 ± 5.6	15	24.67±6.6	17	25.24±7.7
Atlantic cod	514	32.58±12.6	212	37.90±12.8	55	27.64±13.0
Eelpout	58	31.19±8.4	17	33.00±7.0	16	32.00±5.8
Greenland halibut	35	25.49±7.2	13	26.62±9.5	17	28.94±8.7
	116		85	31.05±5.8	38	29.05±6.6
Redfish	1	24.34±6.5				
Silver hake	414	28.52±7.6	52	35.27±5.7	11	30.73±8.2
White hake	79	47.68±16.3	20	45.50±19.5	25	51.32±23.8
Witch flounder	268	32.19±7.1	28	33.93±9.6	26	33.23±9.6

Table 3.5.3: Stable Isotope Summary: Mean ± sd of Length (cm), $\delta^{13}C$, $\delta\ ^{15}N$, and $\delta\ ^{34}S$.

Species	***n***	***Length (cm)***				***$\delta^{13}C$***			
		Mean	**sd**	**min**	**max**	**Mean**	**sd**	**min**	**max**
American plaice	53	30.08	14.4	12	62	-19.61	0.9	-20.62	-17.60
Arctic cod	30	18.53	5.5	11	27	-20.58	0.5	-21.30	-19.20
Atlantic Cod	55	27.64	13.0	11	62	-20.86	0.4	-21.83	-19.88
Eelpout	16	32.00	5.8	19	39	-19.91	0.3	-20.42	-19.54
Greenland halibut	17	28.94	8.7	16	50	-21.47	0.6	-23.23	-20.85
Redfish	38	29.05	5.7	19	41	-20.27	0.5	-22.20	-19.52
Silver hake	11	30.73	8.2	16	47	-21.27	1.0	-23.17	-20.24
White hake	25	51.32	23.8	21	107	-19.67	0.6	-20.60	-17.56
Witch Flounder	26	33.23	9.6	17	44	-18.82	0.8	-21.08	-17.03

Table 3.5.3 Continued

	n	**$\delta\ ^{15}N$**				**$\delta\ ^{34}S$**			
		Mean	**sd**	**min**	**max**	**Mean**	**sd**	**min**	**max**
American plaice	53	14.25	0.6	12.92	16.48	17.65	0.8	14.94	19.35
Arctic cod	30	14.90	0.9	12.58	16.33	17.84	0.6	16.30	18.85
Atlantic Cod	55	14.33	0.7	13.06	15.82	18.40	0.6	16.46	19.68
Eelpout	16	14.37	0.4	13.88	15.25	17.95	0.8	16.34	18.80
Greenland halibut	17	13.47	0.6	12.46	14.72	17.17	0.6	16.23	18.41
Redfish	38	14.55	1.4	11.54	16.08	18.08	0.5	17.10	19.07
Silver hake	11	13.12	0.3	12.81	13.85	16.91	0.4	16.37	17.52
White hake	25	14.25	1.4	10.46	16.74	17.50	0.7	15.18	18.55
Witch Flounder	26	15.86	1.1	13.97	17.38	12.59	1.6	10.34	16.14

Table 3.5.4. Trophic Position (TP): TP of consumers analyzed using benthic and pelagic source.

Table 3.5.4: Trophic Position (TP)				
Species	**Benthic Source**		**Pelagic Source**	
	Mean	**sd**	**Mean**	**sd**
Witch Flounder	4.05	0.3	3.97	0.3
Arctic cod	3.77	0.3	3.69	0.3
Redfish	3.66	0.4	3.58	0.4
Eelpout	3.61	0.1	3.53	0.1
Atlantic Cod	3.60	0.2	3.52	0.2
American plaice	3.57	0.2	3.50	0.2
Argentine	3.53	0.1	3.45	0.1
White hake	3.49	0.4	3.41	0.4
Greenland halibut	3.34	0.2	3.26	0.2
Silver hake	3.24	0.1	3.16	0.1

Table 3.5.5: The number of individuals used for Stable Isotope Mixing Model Results. Species are categorized by small, medium, and large.

Species	***Large***	***Medium***	***Small***	***Total***
American plaice	5	6	6	17
Arctic cod	3	3	3	9
Argentine	2	2	2	6
Atlantic cod	9	9	9	27
Eelpout	-	8	8	16
Redfish	6	6	-	12
Silver hake	6	6	6	18
White hake	10	10	10	30
Witch flounder	5	5	5	15

Table 3.5.6: Stable Isotope Mixing Model Results. Consumer diet showing the total %IRI contribution to diet of each prey category as determined by SIMM.

Consumer/Prey	***%IRI***
American plaice	
Bivalve	1.6
Brittle star	0.4
Crustacean	0.1
Decapod	0.1
Hyperiid	1.7
Sand lance	96
Shrimp	0.1
Arctic cod	
Boreal red shrimp	0.2
Hyperiid	87.7
Shrimp	12.1
Argentine	100
Amphipod (Order)	81.7
Shrimp	18.3
Atlantic cod	
Amphipods	0.1
Benthic Fish	13.7
Benthic Invert	1
Benthopelagic Fish	0.1
Benthopelagic Invert	0.9
Crustacean	0.6
Hyperiid	21.7
Invert	0.3
Pelagic Fish	0.7
Sand lance	1
Toad Crab	59.9
Eelpout	
Amphipods	0.5
Brittle star	6.3
Decapod	3.4
Euphausiids	22.6
Polychaete	33.6
Sculpins	16.8
Shrimp	0.5
Toad Crab	16.3
Greenland halibut	

Amphipods	0.3
Brittle star	0.3
Crustacean	1
Hyperiid	69.9
Shrimp	28.5
Redfish	
Amphipods	0.1
Crustacean	0.3
Euphausiids	54.8
Hyperiid	3.6
Pelagic Fish	41
Shrimp	0.2
Silver hake	
Amphipods	0.1
Crustacean	0.7
Euphausiids	87.6
Hyperiid	0.1
Pelagic Fish	11.2
Sand lance	0.2
Shrimp	0.1
White hake	
Amphipods	0.5
Atlantic cod	1.3
Boreal red shrimp	0.7
Capelin	12.2
Codfish	0.7
Crustacean	7.5
Euphausiids	67.3
Lantern fish (Family)	
Redfish	3.8
Shrimp	6
Witch flounder	
Amphipods	0.1
Bivalve	0.4
Polychaete	82.1
Sea urchin	0.2
Shrimp	17.2

3.6 Figures

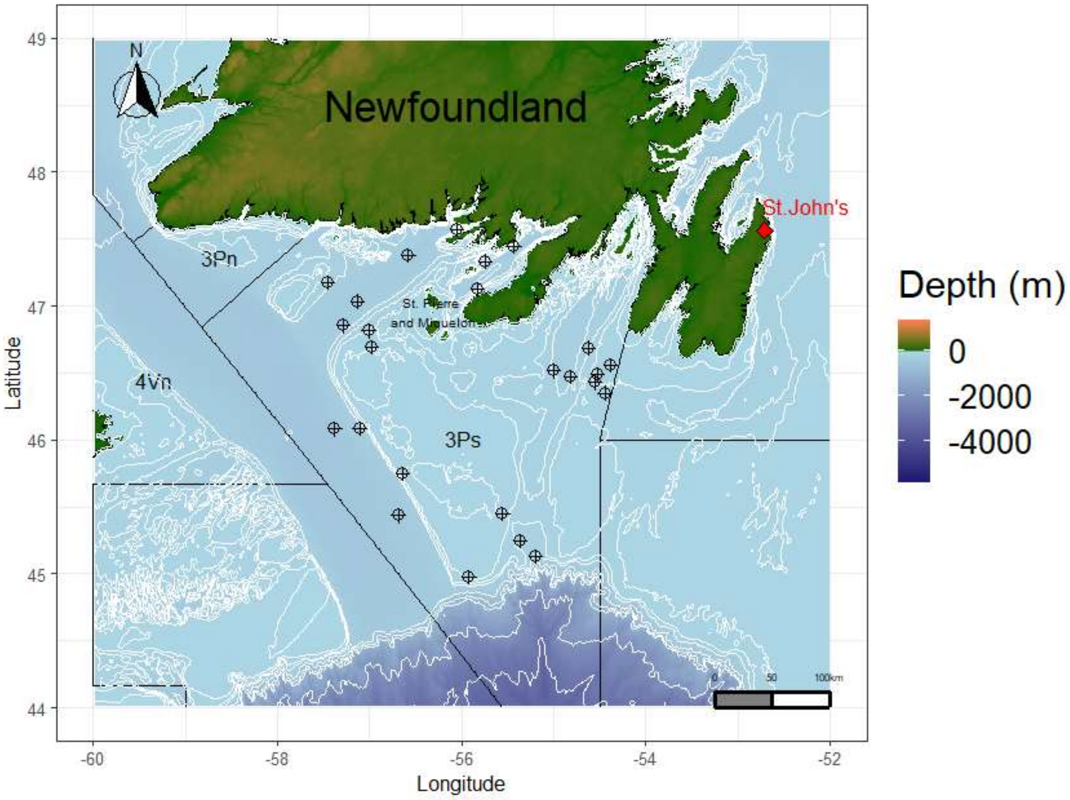
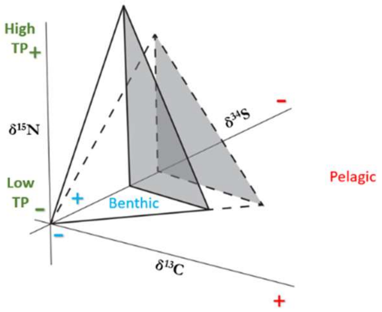


Figure 3.6.1: Southern Newfoundland Sampling Locations. Depth contours are shown at 100m intervals



Schematic 3.6.A: Trophic Position (TP) and Benthic/Pelagic Interpretation of Isotope Results.

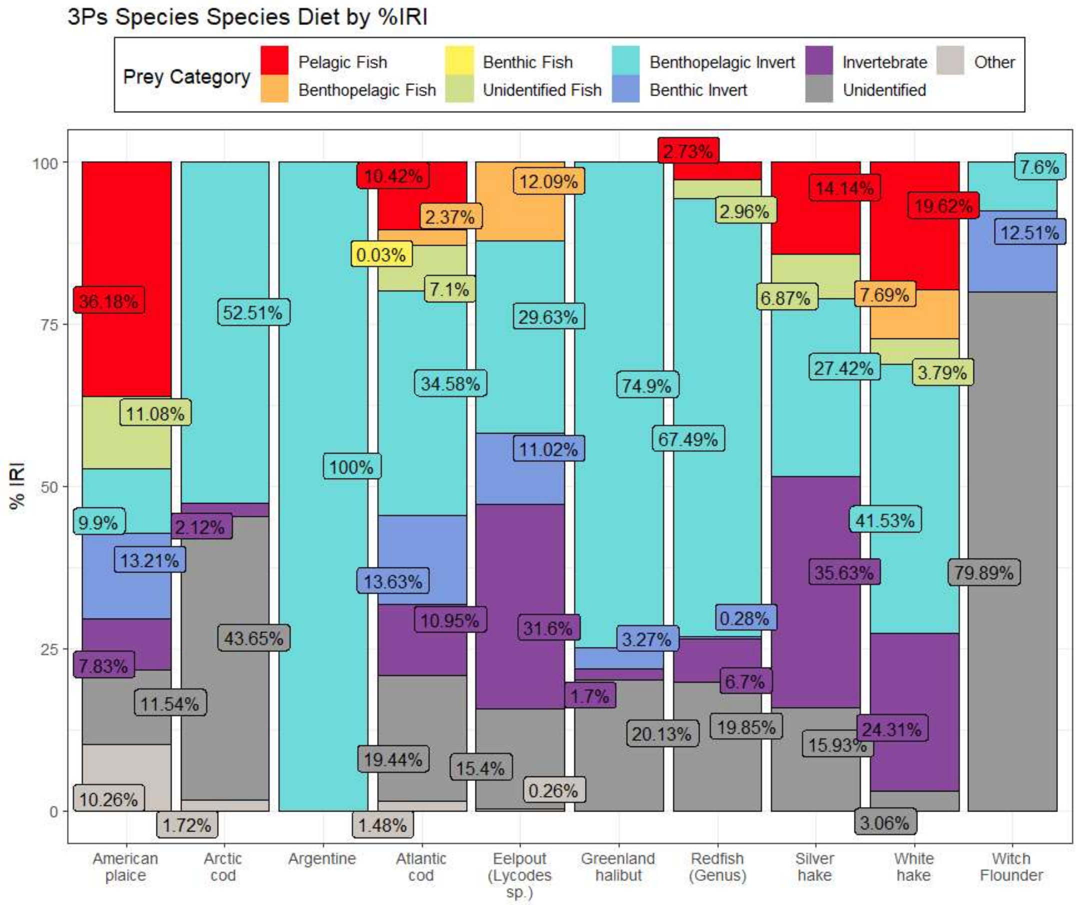
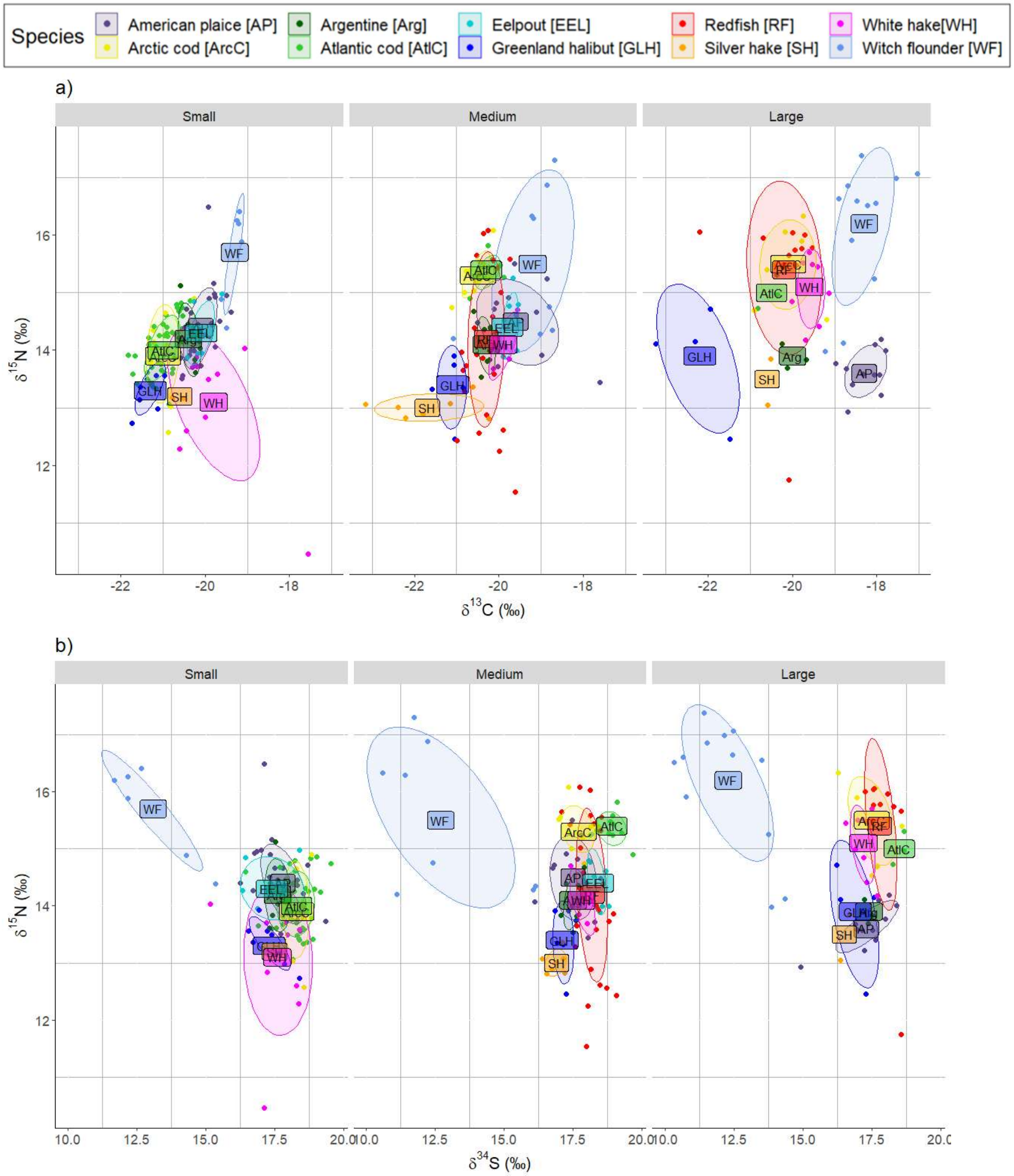


Figure 3.6.2: Consumer Diet by %Index of Relative Importance (%IRI): 10 southern Newfoundland Consumer diet showing the total %IRI contribution to diet of each prey category (Pelagic Fish (🟥), Benthopelagic Fish (🟧), Benthic Fish (🟨), Fish Other (🟩), Benthopelagic Invert (🟦), Benthic Invert (🟦), Invertebrate (🟪), Unidentified (⬛), & Other (⬜)).


Species
American plaice [AP]
Arctic cod [ArcC]
Argentine [Arg]
Atlantic cod [AtlC]
Eelpout [EEL]
Greenland halibut [GLH]
Redfish [RF]
Silver hake [SH]
White hake[WH]
Witch flounder [WF]
a)
Small
Medium
Large
δ^{15}N (‰)
16
14
12
-22
-20
-18
δ^{13}C (‰)
b)
Small
Medium
Large
δ^{15}N (‰)
16
14
12
10.0
12.5
15.0
17.5
20.0
δ^{34}S (‰)
WF
AtlC
ArcC
Arg
EEL
GLH
SH
WH
RF
AP

c)

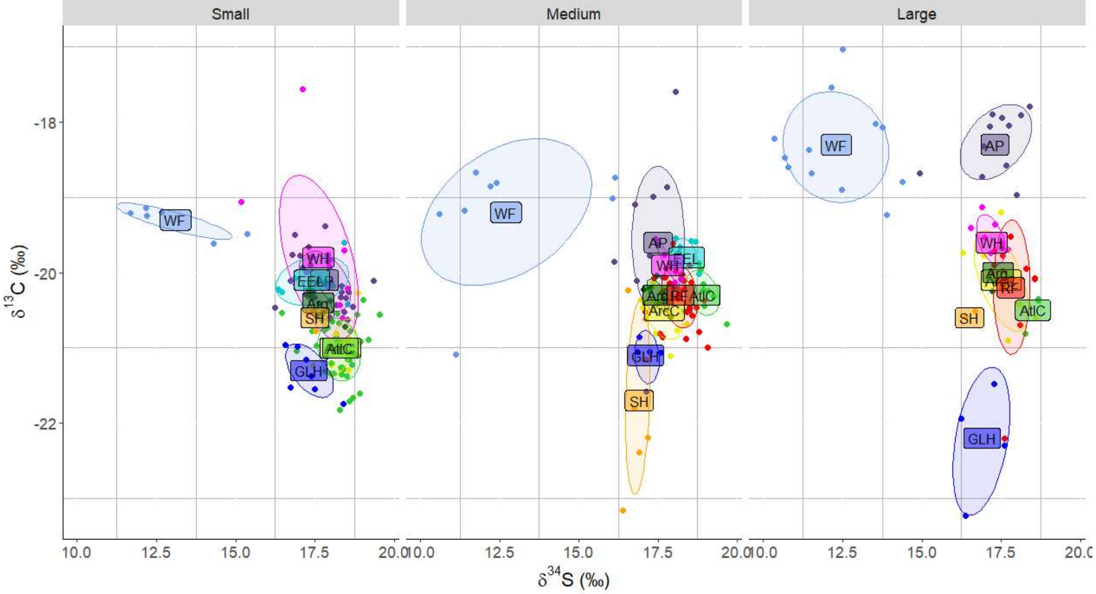
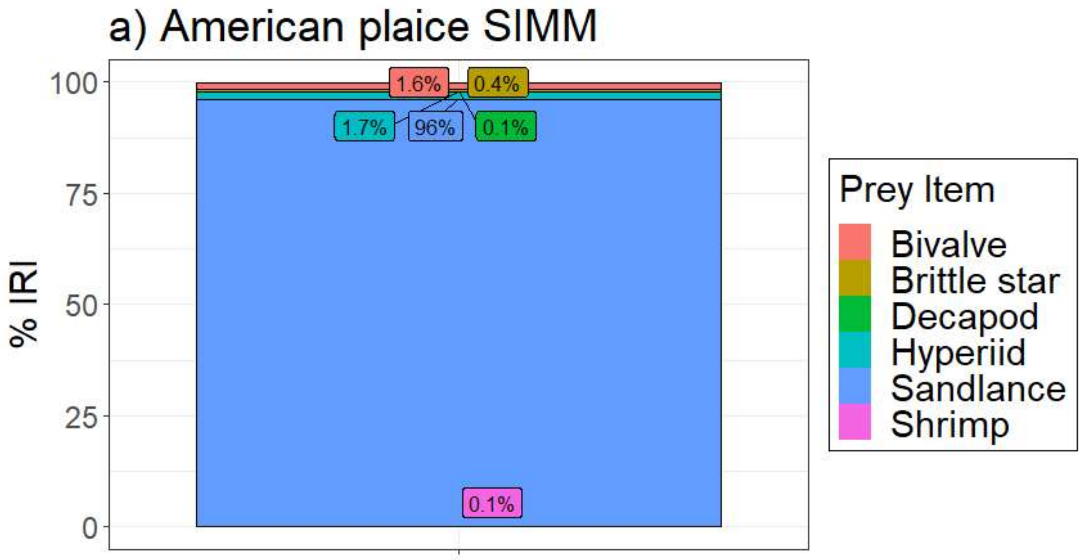


Figure 3.6.3: Bayesian ellipses for Consumers by Size Class. a) $\delta^{15}N$ and $\delta^{13}C$. b) $\delta^{15}N$ and $\delta^{34}S$ c) $\delta^{13}C$and $\delta^{34}S$. Ellipses are organized by consumer species and outlined in the legend.



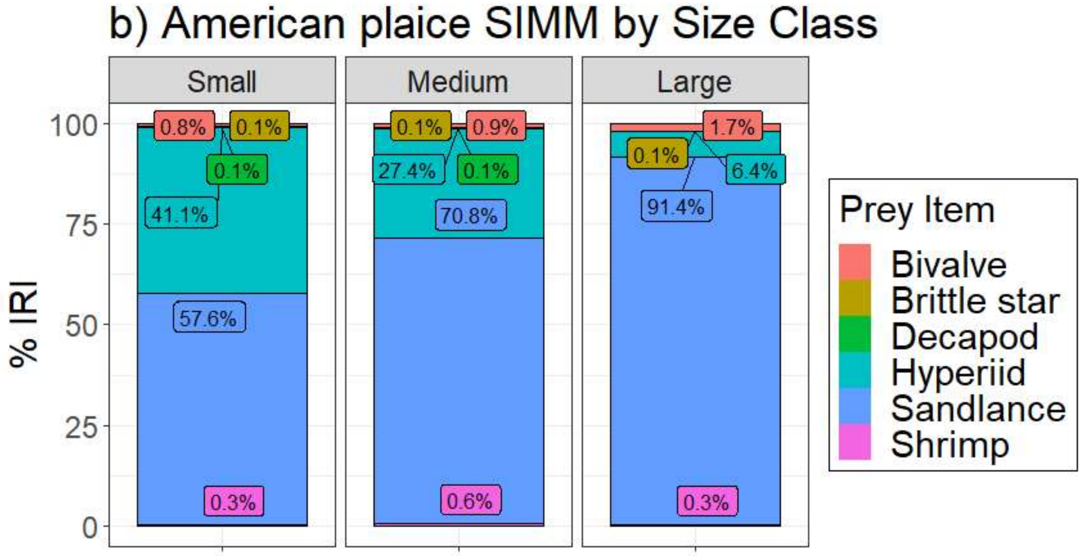


Figure 3.6.4: Stable Isotope Mixing Model Diet Composition Results. American plaice diet showing the total %IRI contribution to diet of each prey category. a) All Individuals, b) Organized by Small, Medium, and Large Length Classes.

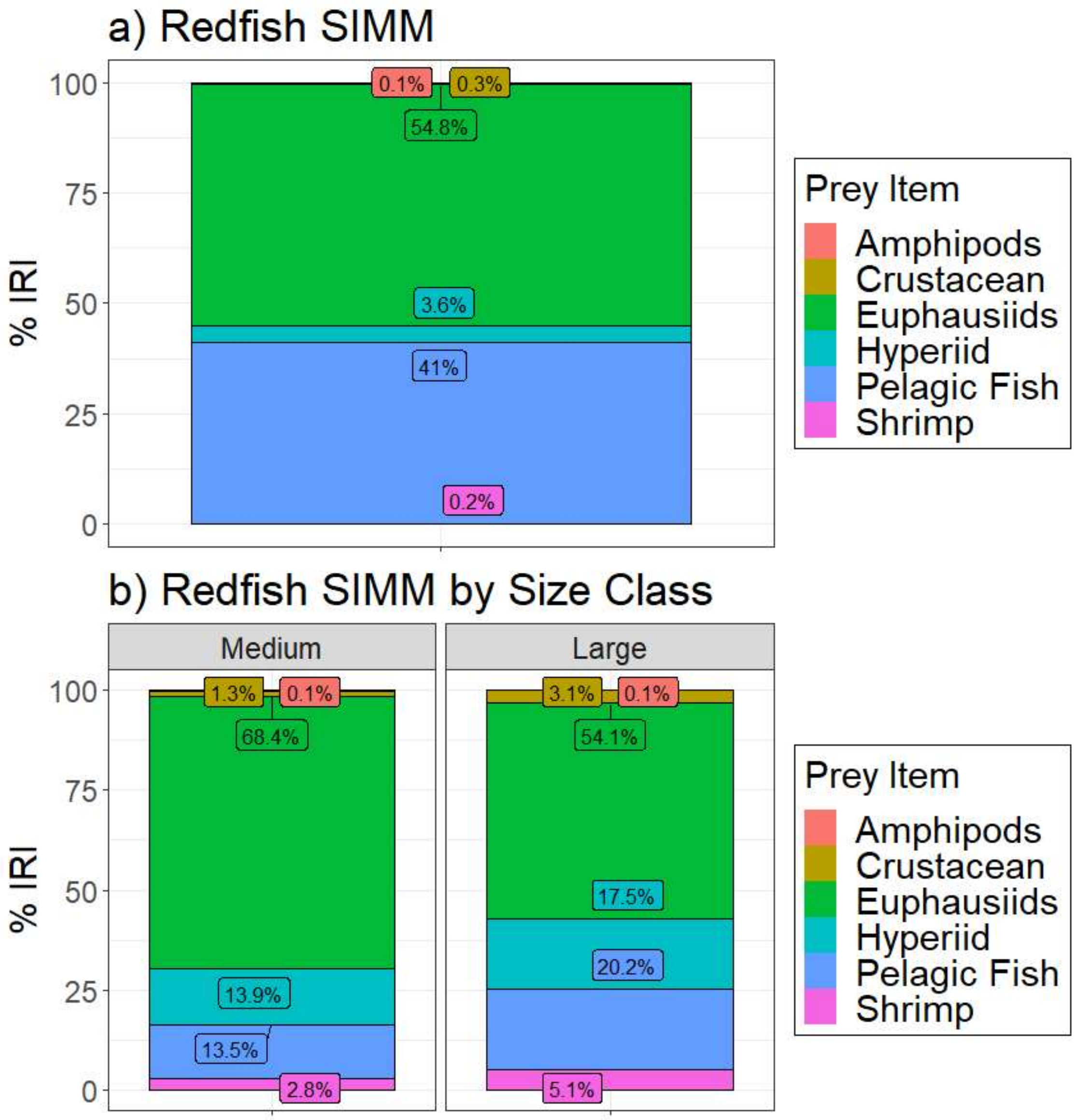


Figure 3.6.5: Stable Isotope Mixing Model Diet Composition Results. Redfish diet showing the total %IRI contribution to diet of each prey category. a) All Individuals, b) Organized by Medium, and Large Length Classes.

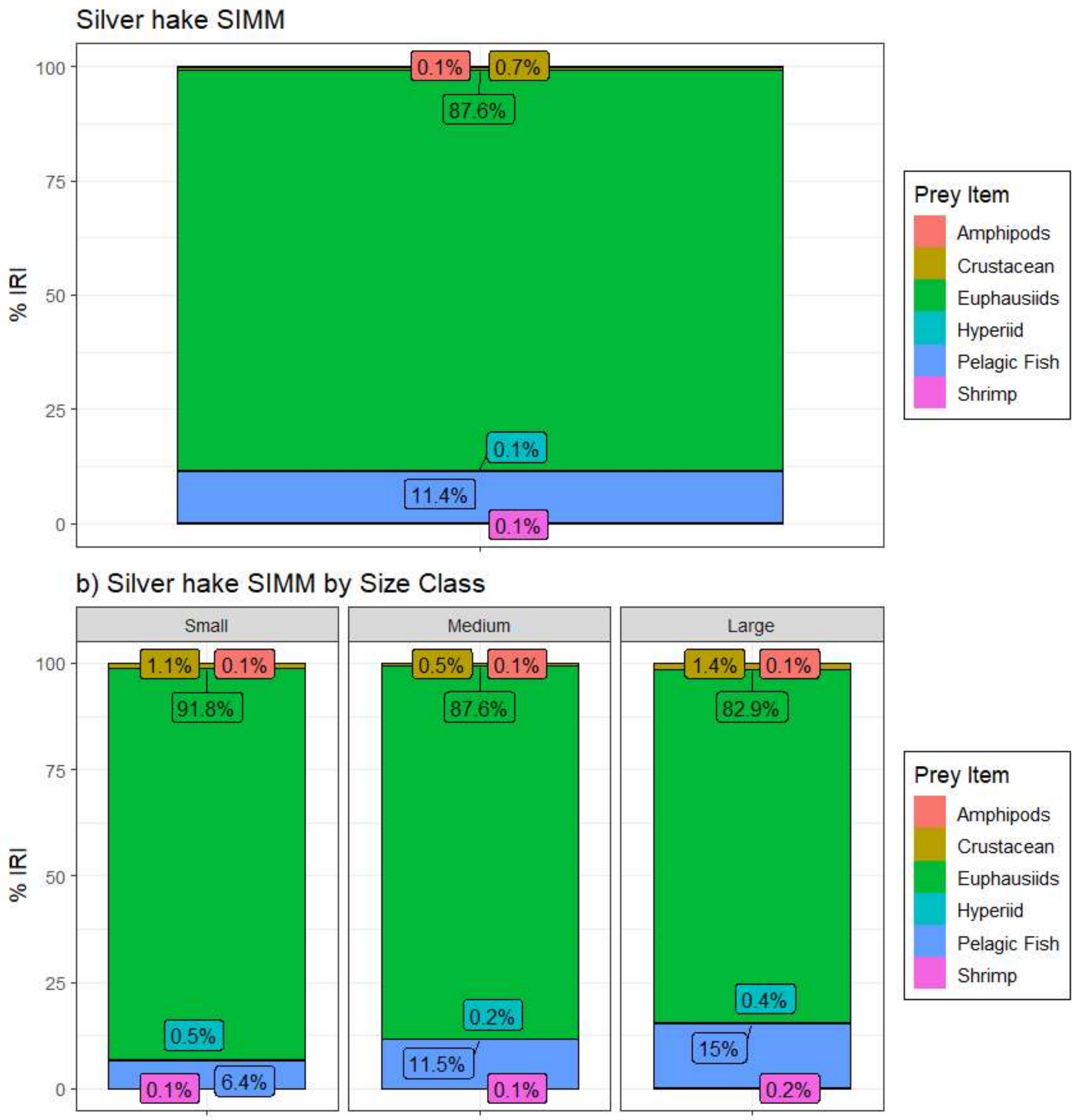
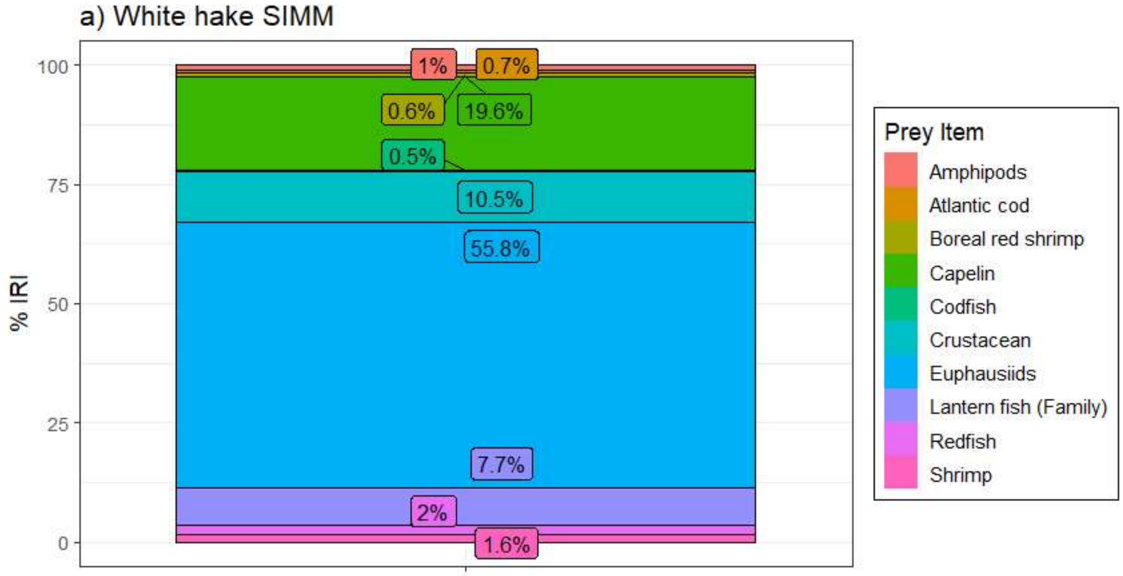


Figure 3.6.6: Stable Isotope Mixing Model Diet Composition Results. Silver hake diet showing the total %IRI contribution to diet of each prey category. a) All Individuals, b) Organized by Small, Medium, and Large Length Classes.



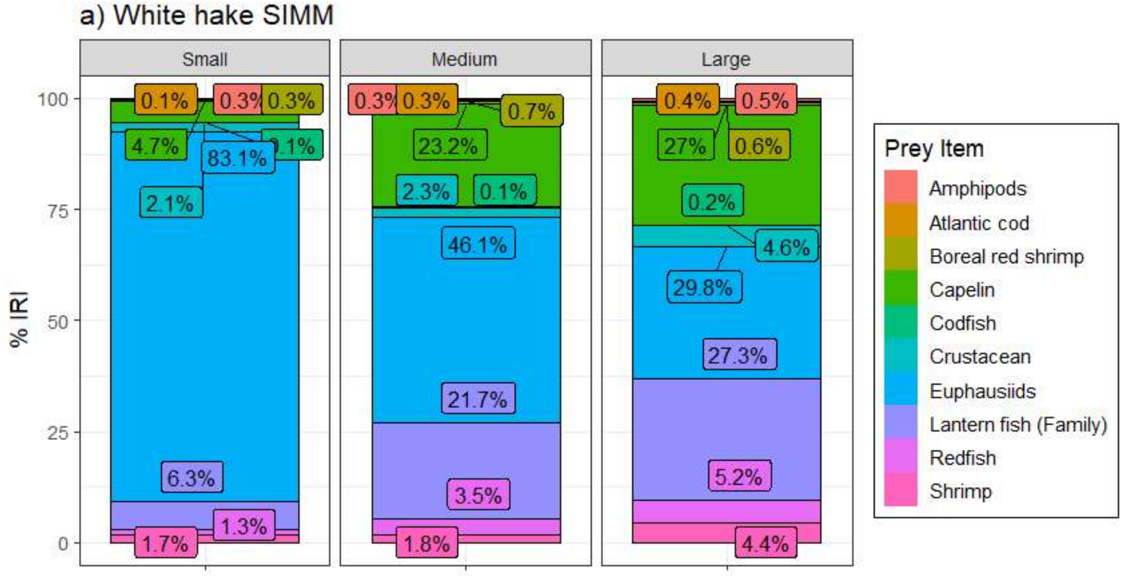


Figure 3.6.7: Stable Isotope Mixing Model Diet Composition Results. White hake diet showing the total %IRI contribution to diet of each prey category. a) All Individuals, b) Organized by Small, Medium, and Large Length Classes.

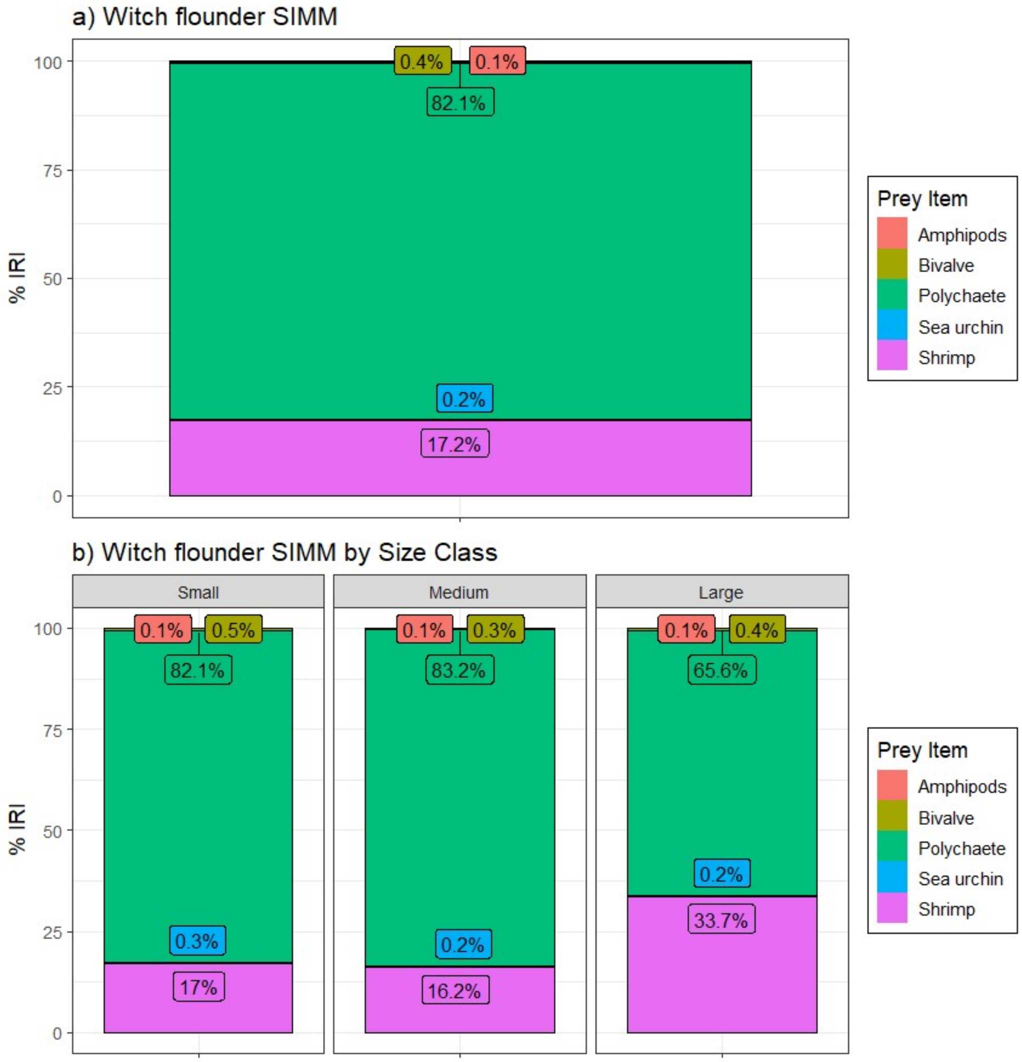


Figure 3.6.8: Stable Isotope Mixing Model Diet Composition Results. Witch flounder diet showing the total %IRI contribution to diet of each prey category. a) All Individuals, b) Organized by Small, Medium, and Large Length Classes.

3.7 References

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Chapter 4: Conclusion and Future Research Avenues

A key theme in fisheries ecology today is trying to understand the lack of recovery of various species. The southern Newfoundland ecosystem is experiencing structural change as the result of reduced productivity (DFO, 2023), and various ground fish stock have not recovered. Given the reliance too on spring survey data, the southern Newfoundland groundfish community is also data deficient for the autumn months. In neighbouring divisions 3KLNO where surveys occur in both spring and autumn, Pepin et al., (2011) found high persistence in seasonal distribution trends in the environment, including environment-related patterns in zooplankton community structure. Therefore, seasonal cycles on the magnitude and timing of annual temperature cycles directly affect resource availability and possibly predator abundance related to prey abundance. These factors can alter ecological processes that impact survival, reproduction, and fitness (McNamara and Houston, 2008; Varpe et al., 2009). The aim of this thesis was to investigate seasonal influences on population physiological condition and trophic interactions within the southern Newfoundland groundfish community to address potential drivers of population and ecosystem recovery or non-recovery. I did this by first providing an overview of challenges facing fisheries and literature review in Chapter 1. In Chapter 2 I assessed seasonal differences (spring vs. autumn) in Atlantic cod diets and body condition, then in Chapter 3 I quantified trophic relationships that occur among various groundfish. The results shown contribute to a better understanding of seasonal influences on trophic interactions that may be influencing the lack of productivity and recovery within this system.

The Atlantic cod has historically supported a large fishery in southern Newfoundland in the 1960's and early 1970's, until it collapsed (DFO, 2022) and was placed under a fishery moratorium between 1993 and 1997 (Council, F. R. C., 2011). Presently, the southern Newfoundland Atlantic cod stock is still in the critical zone (DFO, 2023) and their status has been a continuous topic in local public news (See Articles: Atlantic Groundfish Council, 2023; Dean-Simmons, 2021; Kelly, 2023). This shows the persistent social/economic importance of the southern Newfoundland Atlantic cod stock and the need to understand how the reduced productivity of the southern Newfoundland community is affecting Atlantic cod's lack of recovery. Chapter 2 of this thesis focuses on the autumn condition of Atlantic cod and identified seasonal variations in body condition (K) and hepatosomatic index (HSI) that are traditionally expected within cod, although exhibiting more variation than past studies in other regions (e.g. 0.05 shift in K, Lambert and Dutil, 1997; 24% shift in K, Mello and Rose, 2005). HSI results also showed a potential decrease in energy reserves during the autumn. This is of concern as the winter season can be a substantial period of energy deficit in individuals that utilize lipid stores to fuel metabolism (Biro et al., 2004), leading the larger sized mature cod (who may be spawning) to possibly have poorer condition post winter during the peak of the spawning period. More research is needed to clarify if the pre-winter condition of the spawning population of this stock is contributing to the lack of recovery. Chapter 2 also showed Atlantic cod diet during the autumn to address the hypothesis of potential starvation due to lack of prey in this stock contributing to its lack of recovery (Varkey et al., 2022; Cadigan et al., 2022), but starvation could not be supported within the analysis as I did not directly assess it. Cod are known to have a variable diet based on prey availability, and results of this Chapter further support their generalist diet in the autumn season.

One hypothesis directly related to diet was natural mortality due to starvation and Cadigan et al.'s (2022) suggestion of feeding deficiencies in the larger cod of this stock. The results of this thesis do not prove the starvation of southern Newfoundland cod entering the wintering season but does support decreased condition of Atlantic cod at the large end of the size range in this study. Having reduced condition and possibly reduced feeding in larger fish is one of the biggest concerns for the southern Newfoundland Cod stock, as there has been a decrease in mean length-at-age of Atlantic cod within southern Newfoundland over time (Varkey et al., 2022). While the effect of this change is not well understood for the southern Newfoundland stock, in the Barents Sea, Ohlberger et al., (2022) found evidence that a shift towards a smaller spawning size can negatively affect population productivity. The negative effect on reproductive potential has been suggested for various species before because of smaller females producing fewer and poorer quality offspring (Murawski et al., 2001; Berkeley et al., 2004; Hutchings, 2005). However, it is unknown whether the decreased length-at-age is isolated to Atlantic cod within southern Newfoundland, or if other species are experiencing the same biological shift. Within southern Newfoundland Witch flounder age data has not been available since 1994 (DFO, 2018), and American plaice have also not had recent aging done (DFO, 2020). Although witch flounder have had slightly increasing length (DFO, 2018), the most recent DFO survey for American plaice found few fish greater than 30 cm (DFO, 2020). I was unable to find length-at-age for other species within southern Newfoundland, as both the White hake and Thorny skate stock managed by NAFO have very little biological reference points identified (Sosebee et al., 2022; Sosebee et al., 2023). This shows that drawing community- or ecosystem-level conclusions from this single species assessment is difficult as it isolates the Atlantic cod productivity and diet from the productivity and potential competition within southern Newfoundland. Chapter 3 addresses these limitations by incorporating multiple species into my analyses.

Chapter 3 visualized the pre-winter relationships among species that have the possibility to impact over wintering survival. This chapter is the first time a community level analysis has been done for southern Newfoundland during the autumn season that incorporates both diet, and three different stable isotopes ($\delta^{13}C$, $\delta^{15}N$, & $\delta^{34}S$). Results of Chapter 3 indicate potential size dependence competition among southern Newfoundland species and therefore the potential of limited food availability within this region during the autumn cannot be ruled out. The higher competition among smaller size classes compared to large is of concern. Smaller fish tend to utilize their energy reserves more rapidly than larger fish during winter (Hurst, 2007). Therefore, competition during the autumn for smaller fish could increase their likelihood of starvation during the winter. With the effect temperature has on prey and predator life history traits such as migration (Lewis et al., 2001; Davoren and Montevecchi, 2003), further research into temperature associated movement in prey items could further indicate whether or not there is sufficient prey among southern Newfoundland during the autumn.

One aspect of this thesis that makes it novel is the inclusion of $\delta^{34}S$ in stable isotople analyses (SIA) for ecosystem level analysis within southern Newfoundland. This study identified trophic structure within southern Newfoundland that was not previously assessed but was limited in confidence of base-line isotopic values due to this being the first study including sulfur stable isotopes for various species specifically within southern Newfoundland. The organisms within the sediment can interact with the dynamics of organism food webs through recycling organic matter, including different microbes, rooting plants, and burrowing animals (de Ruiter et al., 1995; Meysman et al., 2006; Rooney et al., 2006). Further research into the stable isotope baselines, including those found in the environment (sediment, benthic flora, zooplankton, etc.) would greatly reduce bias within SIA and strengthen the confidence of spatial associations between species and possible prey.

This study provided population and ecosystem level data for southern Newfoundland during the autumn season, alongside some spring comparisons. Even though I was able to visualize pre-winter relationships within the southern Newfoundland groundfish community, there are still many questions on the impact these seasonal relationships have on the recovery of species within southern Newfoundland. A major assumption made in this thesis was that the temperature of autumn 2018 was representative of the autumn season (Chapter 2 & 3) and the temperature of spring 2016 was representative of the spring season (Chapter 2). However, even with limited autumn data for southern Newfoundland, similar temperature anomalies for these months between the two years have been recorded (Colbourne et al., 2017; Cyr et al., 2020). I was unable to directly associated potential temperature effects of southern Newfoundland to trophic interactions due to equipment malfunction during sampling. Further research into seasonal variation among the trophic structure within southern Newfoundland that includes temperature may help identify oceanographic change related productivity shifts within the ecosystem.

Ultimately, the results from each chapter emphasizes that in order for a complete characterization of the southern Newfoundland ecosystem and individuals within them, there is a need for repeated sampling over more than one season. This thesis also supports inclusion of dynamics among different species in the ecosystem in the framework of species assessments (Holsman et al. 2012; Varkey et al., 2023).

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Appendices

Appendix A: Chapter 2 Supplementary Files

A.2.1 Tables

Table A.2.1.1: Prey Item Categorization showing percent of stomachs analyzed containing each prey category and item[1].

Prey Category/Item	***Sum of % of Stomachs with Prey Category/Item***	***Sum of %IRI***
Immature		
Benthic Invert	**26.74**	**7.71**
Isopod (Order) [Isopoda]	1.16	0.22
Polychaete (Class) [Polychaeta]	9.30	2.32
Sea mice (Family) [Aphroditidae]	1.16	0.44
Striped pink shrimp [Pandalus montagui]	1.16	0.42
Toad crab [Hyas sp.]	13.95	4.31
Benthopelagic Invert	**80.23**	**36.40**
Amphipod (Order) [Amphipoda]	33.72	16.45
Boreal red shrimp [Pandalus sp]	9.30	3.53
Copepod (Class) [Copepoda]	1.16	0.13
Euphausiids [Euphausiacea]	11.63	3.98
Gammarid [Rhachotropis aculeata]	2.33	0.33
Hyperiid (Suborder) [Hyperiidae]	17.44	10.75
Lebbeus sp. [Lebbeid]	1.16	0.21
Shrimp (generic) [Dendrobranchiata/Caridea]	3.49	1.02
Demersal Fish	**39.53**	**16.53**
Lantern fish (Family) [Myctophidae]	1.16	0.65
Sand lance [Ammodytidae]	5.81	3.66
Sculpins (Family) [Cottidae]	1.16	0.43
Snailfish (Family) [Liparidae]	1.16	0.56
Snakeblenny [Lumpenus lampretaeformis]	2.33	0.77
Fish Other	**13.95**	**5.23**
Unidentified Fish	13.95	5.23

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[1] Prey Species and Categorization Derived from Stasko, A. D., et al. 2018, and Sea Life Base Trophic Ecology Table (https://www.sealifebase.ca/TrophicEco/FishEcoList.php?ve_code=1205)

Invertebrate	**26.74**	**12.14**
Crustacean (Subphylum) [Crustacea]	18.60	10.20
Crustacean decapod [Decapoda]	8.14	1.95
Other	**53.49**	**28.92**
Stone	5.81	1.42
Unidentified digested material	46.51	27.05
Unidentified egg	1.16	0.45
Pelagic Fish	**5.81**	**3.53**
Barracudina (Family) [Paralepididae]	1.16	0.80
Capelin [Mallotus villosus]	4.65	2.73
Mature		
Benthic Invert	**54.39**	**18.10**
Anemone (Order) [Actiniaria]	2.63	0.77
Anthozoan [Anthozoa]	0.88	0.02
Bivalve (Class) [Bivalvia]	5.26	1.12
Brittle star [Ophiuroidea]	11.40	5.27
Polychaete (Class) [Polychaeta]	7.02	2.29
Sea cucumber [Holothuroidea]	1.75	0.54
Striped pink shrimp [Pandalus montagui]	4.39	0.59
Toad crab [Hyas sp.]	21.05	7.51
Benthopelagic Invert	**100.00**	**33.21**
Amphipod (Order) [Amphipoda]	29.82	8.47
Arctic argid [Argis dentata]	0.88	0.01
Boreal red shrimp [Pandalus sp]	24.56	5.70
Cephalopod (Class) [Cephalopoda]	1.75	0.74
Euphausiids [Euphausiacea]	9.65	0.68
Gammarid [Stegocephalus inflatus]	1.75	0.56
Gastropod (Class) [Gastropoda]	0.88	0.10
Hyperiid (Suborder) [Hyperiidae]	25.44	11.65
Lebbeus sp. [Lebbeid]	3.51	0.71
Northern shrimp [Pandalus borealis]	6.14	1.92
Shrimp (generic) [Dendrobranchiata/Caridea]	7.02	2.65
Demersal Fish	**28.95**	**12.94**
Atlantic cod [Gadus morhua]	5.26	1.16
Codfish (Family) [Gadidae]	0.88	0.25

Grenadier (Family) [Macrouridae]	0.88	0.05
Poachers (Family) [Agonidae]	0.88	0.23
Sand lance [Ammodytidae]	15.79	10.07
Sculpins (Family) [Cottidae]	2.63	0.77
Snakeblenny [Lumpenus lampretaeformis]	0.88	0.11
Spotted hake [Urophycis regia]	0.88	0.22
White hake [Urophycis tenuis]	0.88	0.09
Fish Other	**23.68**	**8.51**
Unidentified Fish	23.68	8.51
Invertebrate	**32.46**	**10.05**
Crustacean (Subphylum) [Crustacea]	20.18	5.35
Crustacean decapod [Decapoda]	12.28	4.70
Other	**53.51**	**14.89**
Plant/Wood/Algae	1.75	0.16
Stone	5.26	1.37
Unidentified digested material	45.61	13.17
Unidentified egg	0.88	0.19
Pelagic Fish	**7.02**	**2.30**
Barracudina (Family) [Paralepididae]	1.75	0.63
Capelin [Mallotus villosus]	4.39	1.60
Redfish (Genus) [Sebastes]	0.88	0.07
Hermitage Bay		
Benthic Invert	**41.27**	**18.45**
Bivalve (Class) [Bivalvia]	1.59	0.34
Brittle star [Ophiuroidea]	7.94	2.77
Isopod (Order) [Isopoda]	1.59	0.33
Polychaete (Class) [Polychaeta]	6.35	2.66
Sea cucumber [Holothuroidea]	1.59	0.59
Toad crab [Hyas sp.]	22.22	11.77
Benthopelagic Invert	**68.25**	**36.14**
Amphipod (Order) [Amphipoda]	19.05	10.76
Boreal red shrimp [Pandalus sp]	11.11	4.40
Euphausiids [Euphausiacea]	9.52	2.76
Gammarid [Rhachotropis aculeata]	1.59	0.33
Gammarid [Stegocephalus inflatus]	3.17	1.12
Hyperiid (Suborder) [Hyperiidae]	20.63	14.72

Shrimp (generic) [Dendrobranchiata/Caridea]	3.17	2.05
Demersal Fish	**4.76**	**2.90**
Sand lance [Ammodytidae]	1.59	1.17
Snailfish (Family) [Liparidae]	1.59	0.85
Snakeblenny [Lumpenus lampretaeformis]	1.59	0.88
Fish Other	**14.29**	**5.79**
Unidentified Fish	14.29	5.79
Invertebrate	**6.35**	**2.68**
Crustacean (Subphylum) [Crustacea]	3.17	0.80
Crustacean decapod [Decapoda]	3.17	1.88
Other	**46.03**	**30.04**
Unidentified digested material	44.44	29.37
Unidentified egg	1.59	0.68
Pelagic Fish	**4.76**	**4.01**
Barracudina (Family) [Paralepididae]	1.59	1.21
Capelin [Mallotus villosus]	3.17	2.80
Hermitage Channel		
Benthic Invert	**49.12**	**21.72**
Anemone (Order) [Actiniaria]	3.51	1.26
Bivalve (Class) [Bivalvia]	3.51	0.96
Brittle star [Ophiuroidea]	12.28	7.94
Polychaete (Class) [Polychaeta]	12.28	4.98
Sea mouse [Aphrodita hastata]	1.75	0.70
Toad crab [Hyas sp.]	15.79	5.89
Benthopelagic Invert	**52.63**	**14.59**
Amphipod (Order) [Amphipoda]	28.07	8.57
Boreal red shrimp [Pandalus sp]	7.02	1.64
Cephalopod (Class) [Cephalopoda]	1.75	0.64
Euphausiids [Euphausiacea]	3.51	0.79
Hyperiid (Suborder) [Hyperiidae]	5.26	0.88
Lebbeus sp. [Lebbeid]	1.75	0.87
Shrimp (generic) [Dendrobranchiata/Caridea]	5.26	1.20
Demersal Fish	**26.32**	**17.56**
Atlantic cod [Gadus morhua]	3.51	2.11
Sand lance [Ammodytidae]	22.81	15.45
Fish Other	**28.07**	**14.24**

Unidentified Fish	28.07	14.24
Invertebrate	**26.32**	**13.84**
Crustacean (Subphylum) [Crustacea]	14.04	7.80
Crustacean decapod [Decapoda]	12.28	6.04
Other	**43.86**	**14.85**
Plant/Wood/Algae	3.51	0.33
Stone	10.53	4.27
Unidentified digested material	29.82	10.26
Pelagic Fish	**10.53**	**3.19**
Barracudina (Family) [Paralepididae]	3.51	1.32
Capelin [Mallotus villosus]	7.02	1.87
Placentia Bay		
Benthic Invert	**34.15**	**5.66**
Anthozoan [Anthozoa]	1.22	0.02
Bivalve (Class) [Bivalvia]	3.66	0.71
Polychaete (Class) [Polychaeta]	4.88	0.31
Sea cucumber [Holothuroidea]	1.22	0.35
Striped pink shrimp [Pandalus montagui]	7.32	1.29
Toad crab [Hyas sp.]	15.85	2.98
Benthopelagic Invert	**100.00**	**48.58**
Amphipod (Order) [Amphipoda]	37.80	15.51
Arctic argid [Argis dentata]	1.22	0.02
Boreal red shrimp [Pandalus sp]	29.27	7.59
Copepod (Class) [Copepoda]	1.22	0.14
Euphausiids [Euphausiacea]	15.85	2.75
Gammarid [Rhachotropis aculeata]	1.22	0.12
Gastropod (Class) [Gastropoda]	1.22	0.14
Hyperiid (Suborder) [Hyperiidae]	31.71	16.52
Lebbeus sp. [Lebbeid]	3.66	0.43
Northern shrimp [Pandalus borealis]	8.54	2.74
Shrimp (generic) [Dendrobranchiata/Caridea]	7.32	2.61
Demersal Fish	**18.29**	**3.82**
Atlantic cod [Gadus morhua]	4.88	0.22
Codfish (Family) [Gadidae]	1.22	0.36
Grenadier (Family) [Macrouridae]	1.22	0.06

Lantern fish (Family) [Myctophidae]	1.22	0.69
Poachers (Family) [Agonidae]	1.22	0.33
Sculpins (Family) [Cottidae]	4.88	1.56
Snakeblenny [Lumpenus lampretaeformis]	1.22	0.16
Spotted hake [Urophycis regia]	1.22	0.31
White hake [Urophycis tenuis]	1.22	0.12
Fish Other	**15.85**	**3.80**
Unidentified Fish	15.85	3.80
Invertebrate	**48.78**	**16.06**
Crustacean (Subphylum) [Crustacea]	34.15	12.68
Crustacean decapod [Decapoda]	14.63	3.38
Other	**56.10**	**20.03**
Stone	1.22	0.12
Unidentified digested material	53.66	19.64
Unidentified egg	1.22	0.27
Pelagic Fish	**4.88**	**2.05**
Capelin [Mallotus villosus]	3.66	1.95
Redfish (Genus) [Sebastes]	1.22	0.10
St. Pierre Bank		
Benthic Invert	**33.33**	**5.39**
Anemone (Order) [Actiniaria]	11.11	2.14
Brittle star [Ophiuroidea]	11.11	1.64
Polychaete (Class) [Polychaeta]	11.11	1.62
Benthopelagic Invert	100.00	20.35
Amphipod (Order) [Amphipoda]	44.44	7.14
Boreal red shrimp [Pandalus sp]	11.11	0.75
Cephalopod (Class) [Cephalopoda]	11.11	5.56
Hyperiid (Suborder) [Hyperiidae]	22.22	4.93
Lebbeus sp. [Lebbeid]	11.11	1.97
Demersal Fish	**100.00**	**64.26**
Sand lance [Ammodytidae]	100.00	62.49
Snakeblenny [Lumpenus lampretaeformis]	11.11	1.77
Fish Other	**11.11**	**1.97**
Unidentified Fish	11.11	1.97
Invertebrate	**11.11**	**0.63**
Crustacean (Subphylum) [Crustacea]	11.11	0.63

Other	**77.78**	**7.39**
Stone	44.44	4.21
Unidentified digested material	33.33	3.18
Autumn		
Benthic Invert	**46.97**	**19.39**
Anemone (Order) [Actiniaria]	4.55	1.38
Bivalve (Class) [Bivalvia]	3.03	0.82
Brittle star [Ophiuroidea]	12.12	7.04
Polychaete (Class) [Polychaeta]	12.12	4.50
Sea mice (Family) [Aphroditidae]	1.52	0.60
Toad crab [Hyas sp.]	13.64	5.05
Benthopelagic Invert	**59.09**	**15.41**
Amphipod (Order) [Amphipoda]	30.30	8.37
Boreal red shrimp [Pandalus sp]	7.58	1.51
Cephalopod (Class) [Cephalopoda]	3.03	1.34
Euphausiids [Euphausiacea]	3.03	0.68
Hyperiid (Suborder) [Hyperiidae]	7.58	1.46
Lebbeus sp. [Lebbeid]	3.03	1.03
Shrimp (generic) [Dendrobranchiata/Caridea]	4.55	1.03
Demersal Fish	**37.88**	**24.23**
Atlantic cod [Gadus morhua]	3.03	1.81
Sand lance [Ammodytidae]	33.33	22.17
Snakeblenny [Lumpenus lampretaeformis]	1.52	0.25
Fish Other	**25.76**	**12.49**
Unidentified Fish	25.76	12.49
Invertebrate	**24.24**	**11.96**
Crustacean (Subphylum) [Crustacea]	13.64	6.78
Crustacean decapod [Decapoda]	10.61	5.18
Other	**48.48**	**13.79**
Plant/Wood/Algae	3.03	0.28
Stone	15.15	4.26
Unidentified digested material	30.30	9.25
Pelagic Fish	**9.09**	**2.74**
Barracudina (Family) [Paralepididae]	3.03	1.13
Capelin [Mallotus villosus]	6.06	1.60
Spring		
Benthic Invert	**50.00**	**38.30**

Anemone (Order) [Actiniaria]	4.55	2.36
Brittle star [Ophiuroidea]	24.24	23.48
Caprellid [Aeginina longicornis]	1.52	0.46
Polychaete (Class) [Polychaeta]	12.12	4.60
Scarlet psolus [Psolus fabricii]	3.03	2.60
Sea cucumber [Holothuroidea]	4.55	4.80
Benthopelagic Invert	**34.85**	**19.37**
Amphipod (Order) [Amphipoda]	7.58	3.36
Boreal red shrimp [Pandalus sp]	1.52	1.33
Copepod (Class) [Copepoda]	1.52	1.09
Euphausiids [Euphausiacea]	1.52	0.80
Friendly blade shrimp [Spirontocaris liljeborgii]	1.52	0.57
Gammarid (Anonyx sp.) [Anonyx sp.]	1.52	0.37
Hyperiid (Suborder) [Hyperiidae]	16.67	8.92
Shrimp (generic) [Dendrobranchiata/Caridea]	3.03	2.93
Demersal Fish	**12.12**	**9.88**
Codfish (Order) [Gadiformes]	1.52	1.59
Lantern fish (Family) [Myctophidae]	4.55	0.51
Sand lance [Ammodytidae]	6.06	7.79
Fish Other	**6.06**	**2.53**
Unidentified Fish	6.06	2.53
Invertebrate	**10.61**	**9.98**
Crustacean (Subphylum) [Crustacea]	9.09	7.86
Invertebrate [Invertebrata]	1.52	2.13
Other	**27.27**	**19.93**
Plant/Wood/Algae	6.06	3.60
Sand	3.03	1.68
Stone	7.58	4.72
Unidentified digested material	9.09	8.89
Unidentified egg	1.52	1.04

Table A.2.2: Average interspecific diet dissimilarity based on Bray-Curtis and prey species in descending order of contribution to diet dissimilarity between Seasons

Factors: Spring and Autumn
Average Dissimilarity= 80.28%

Prey Category	**Spring Av. Abundance**	**Autumn Av. Abundance**	**Av. Diss**	**Diss/SD**	**p**
Benthic.Invert	0.87	0.31	0.23	1.15	0.001
Pelagic.Fish	0.25	0.40	0.14	0.82	0.630
Benthopelagic.Invert	0.46	0.25	0.14	0.86	0.012
Invertebrate	0.21	0.19	0.10	0.57	0.640
Unidentified.Fish	0.07	0.20	0.07	0.51	1.000
Other	0.18	0.07	0.06	0.49	0.062
Unidentified	0.08	0.15	0.06	0.48	0.996
Benthopelagic.Fish	0.000	0.03	0.01	0.16	1.000

A.2.2Figures

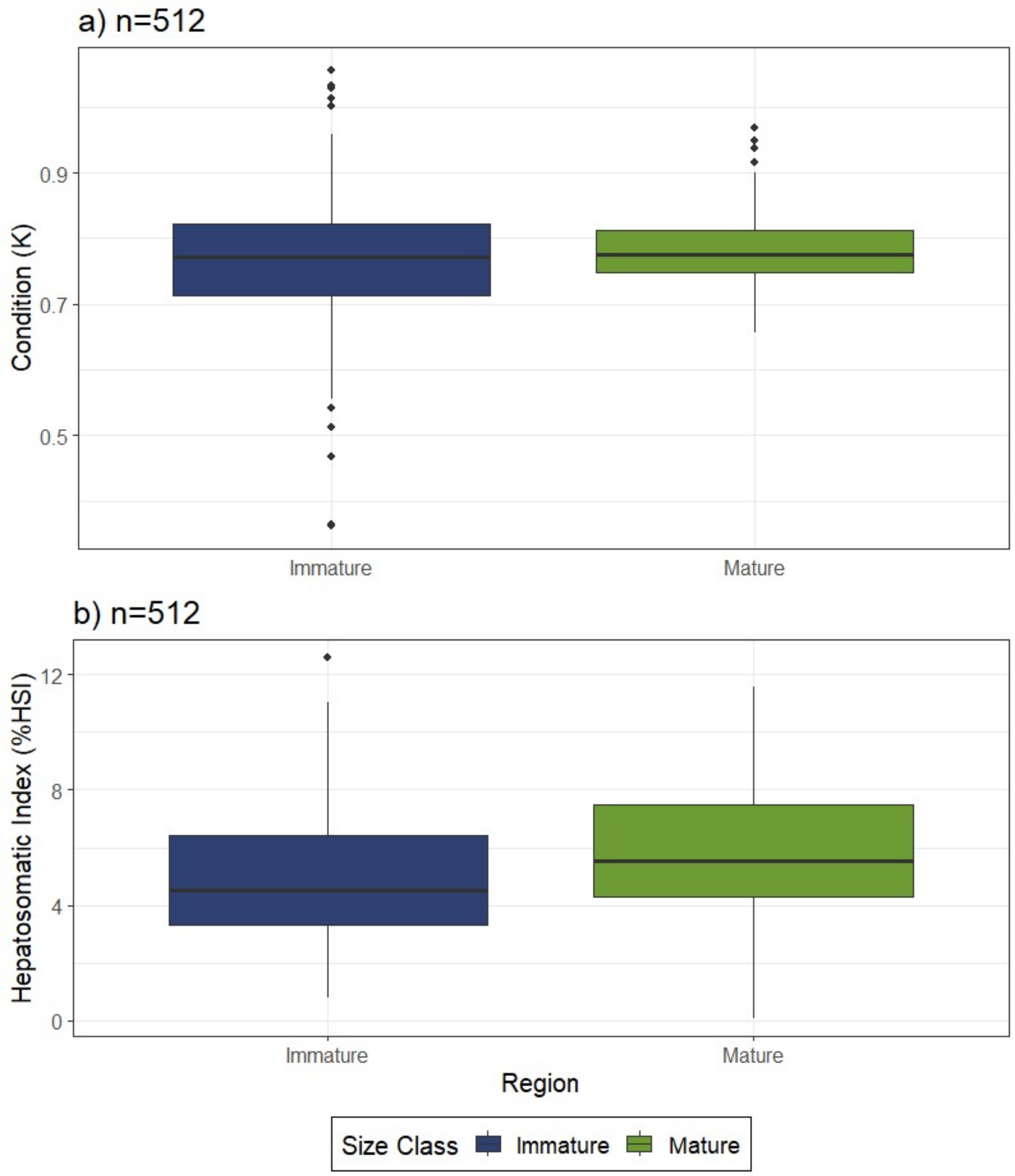

Figure A1: Autumn Cod a) Condition (K) and b) Hepatosomatic index (HSI) represented by Size Class (Immature [🟦], Mature [🟩]). Average values are indicated by the black line (━).

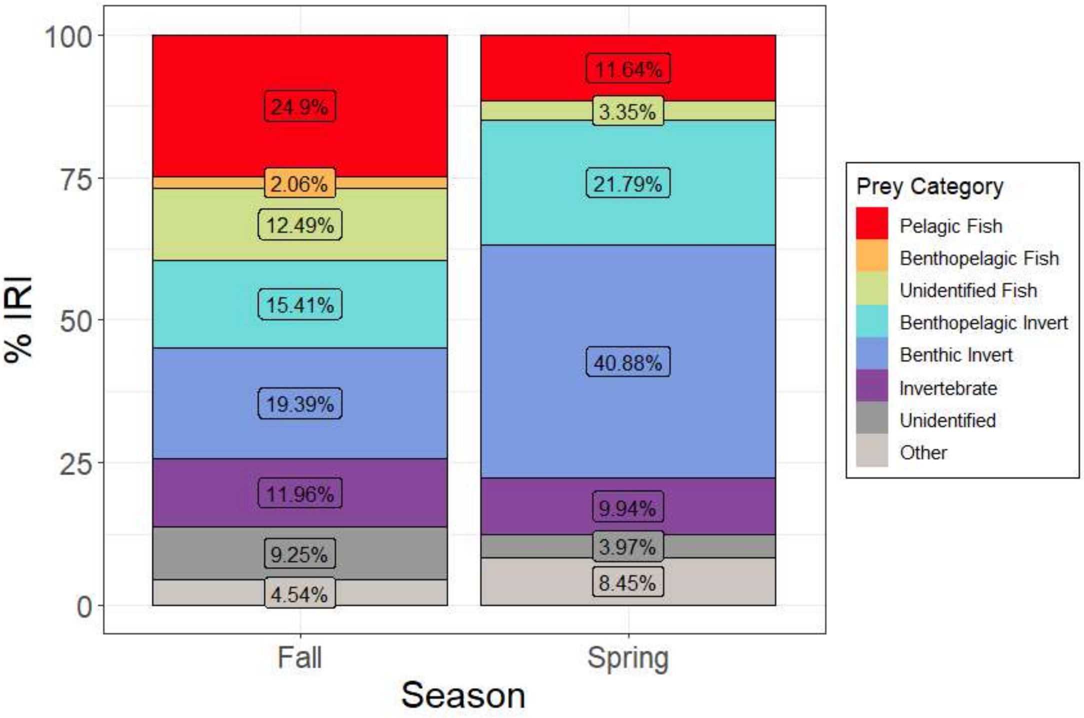

Figure A.2.2: Percent Index of Relative Importance (%IRI) of Prey Categories. Organized by season, prey categories are identified as Pelagic Fish (🟥), Benthopelagic Fish (🟧), Benthic Fish (🟨), Fish Other (🟩), Benthopelagic Invert (🟦), Benthic Invert (🟦), Invertebrate (🟪), Unidentified (⬛), & Other (⬜). Supporting Data found in Supplementary Table S1c.

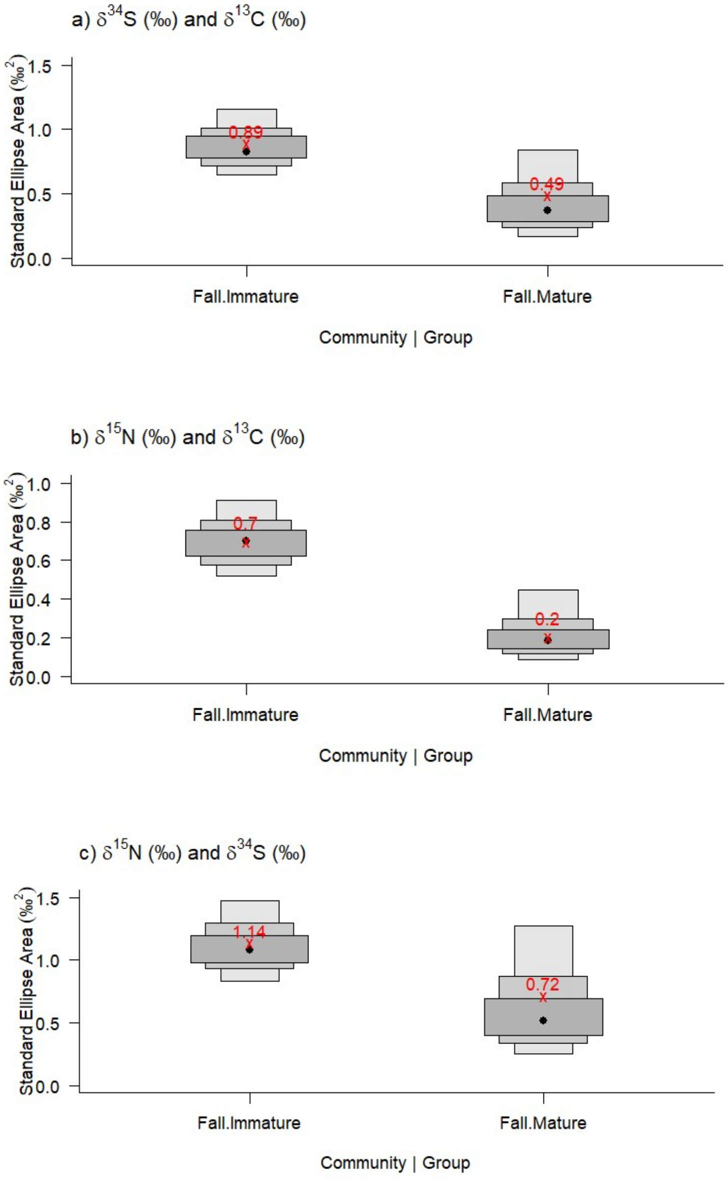

*Figure A.2.3: SIBER density plots of the standard ellipse areas computed with δ^{13}C, δ^{15}N, and δ^{34}S values [a) δ^{13}C & δ^{34}S, b) δ^{15}N & δ^{13}C, c) δ^{15}N & δ^{34}S] estimated with Bayesian analysis. The standard ellipse areas corrected for sample size (SEAc) are represented by (**x**). Black dots represent the mode of SEA. Shaded boxes represent the 50 %, 75 % and 95 % confidence intervals, from dark to light grey.*

Appendix B. Chapter 3 Supplementary Files

A.3.1 Tables

Table A.3.1.1: Consumer Diet by Prey %IRI. Consumer diet is organized by size class (Large, Small). Prey items are organized by category (Pelagic Fish, Demersal Fish, Fish Other, Benthic Invert, Benthopelagic Invert, Invert, and Other[2]).

Species Diet by Length	***%IRI***
American plaice	
Large	
Benthic Invert	*4.32*
Ophiuroidea (Brittle star)	4.32
Benthopelagic Invert	*2.78*
Hyperiidae (Hyperiid (Suborder))	2.78
Invertebrate	*4.66*
Crustacean (Subphylum) (Crustacean (Subphylum))	4.66
Other	*24.25*
Sand (Sand)	4.77
Stone (Stone)	19.48
Pelagic Fish	*55.97*
Ammodytes dubius (Sand lance)	55.97
Unidentified Fish	*8.02*
Unidentified Fish (Unidentified Fish)	8.02
Medium	
Benthic Invert	*29.19*
Ophiuroidea (Brittle star)	29.19
Pelagic Fish	*54.15*
Ammodytes dubius (Sand lance)	54.15
Unidentified Fish	*16.67*
Unidentified Fish (Unidentified Fish)	16.67
Small	
Benthic Invert	*13.44*
Bivalvia sp. (Bivalve (Class))	13.44
Benthopelagic Invert	*25.20*
Caridea sp. (Shrimp (generic))	19.90
Hyperiidae (Hyperiid (Suborder))	5.30
Invertebrate	*16.92*
Crustacean decapod (Crustacean decapod)	16.92

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[2] Prey Species and Categorization Derived from Stasko, A. D., et al. 2018, and Sea Life Base Trophic Ecology Table (https://www.sealifebase.ca/TrophicEco/FishEcoList.php?ve_code=1205

Table A.3.1.1: Consumer Diet by Prey %IRI. Consumer diet is organized by size class (Large, Small). Prey items are organized by category (Pelagic Fish, Demersal Fish, Fish Other, Benthic Invert, Benthopelagic Invert, Invert, and Other[3]*).*

Unidentified	*33.33*
Unidentified digested material (Unidentified digested material)	33.33
Unidentified Fish	11.11
Unidentified Fish (Unidentified Fish)	11.11
Arctic cod	
Large	
Benthopelagic Invert	*58.68*
Caridea sp. (Shrimp (generic))	8.68
Hyperiidae (Hyperiid (Suborder))	25.00
Pandalus sp. (Boreal red shrimp)	25.00
Invertebrate	*8.99*
Crustacean (Subphylum) (Crustacean (Subphylum))	8.99
Other	*7.33*
Stone (Stone)	7.33
Unidentified	*25.00*
Unidentified digested material (Unidentified digested material)	25.00
Medium	
Benthopelagic Invert	*11.60*
Hyperiidae (Hyperiid (Suborder))	11.60
Unidentified	*88.40*
Unidentified digested material (Unidentified digested material)	88.40
Small	
Benthopelagic Invert	*75.00*
Caridea sp. (Shrimp (generic))	12.50
Hyperiidae (Hyperiid (Suborder))	62.50
Unidentified	*25.00*
Unidentified digested material (Unidentified digested material)	25.00
Argentine	
Medium	
Benthopelagic Invert	*100.00*
Amphipoda sp. (Amphipod (Order))	100.00

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[3] Prey Species and Categorization Derived from Stasko, A. D., et al. 2018, and Sea Life Base Trophic Ecology Table (https://www.sealifebase.ca/TrophicEco/FishEcoList.php?ve_code=1205

Table A.3.1.1: Consumer Diet by Prey %IRI. Consumer diet is organized by size class (Large, Small). Prey items are organized by category (Pelagic Fish, Demersal Fish, Fish Other, Benthic Invert, Benthopelagic Invert, Invert, and Other).

Small	
Benthopelagic Invert	*100.00*
Caridea sp. (Shrimp (generic))	100.00
Atlantic cod	
Large	
Benthic Fish	*0.15*
Macrouridae (Grenadier (Family))	0.15
Benthic Invert	*19.18*
Bivalvia sp. (Bivalve (Class))	0.72
Holothuroidea sp. (Sea cucumber)	0.83
Hyas sp. (Toad crab)	7.35
Ophiuroidea (Brittle star)	9.32
Pandalus montagui (Aesop prawn)	0.60
Polychaete (Class) (Polychaete (Class))	0.38
Benthopelagic Fish	*1.41*
Gadus morhua (Atlantic cod)	0.68
Urophycis regia (Spotted hake)	0.72
Benthopelagic Invert	*35.15*
Amphipoda sp. (Amphipod (Order))	10.35
Argis dentata (Arctic argid)	0.04
Caridea sp. (Shrimp (generic))	0.77
Euphausiacea (Krill)	0.58
Hyperiidae (Hyperiid (Suborder))	16.23
Pandalus borealis (Northern shrimp)	1.25
Pandalus sp. (Boreal red shrimp)	5.93
Invertebrate	*5.46*
Crustacean (Subphylum) (Crustacean (Subphylum))	3.13
Crustacean decapod (Crustacean decapod)	2.34
Other	*3.43*
Plant/Wood/Algae (Plant/Wood/Algae)	0.25
Stone (Stone)	3.19
Pelagic Fish	*10.44*
Ammodytes dubius (Sand lance)	10.19
Barracudina sp. (Barracudina)	0.25
Unidentified	*13.79*
Unidentified digested material (Unidentified digested material)	13.79
Unidentified Fish	*10.99*

Table A.3.1.1: Consumer Diet by Prey %IRI. Consumer diet is organized by size class (Large, Small). Prey items are organized by category (Pelagic Fish, Demersal Fish, Fish Other, Benthic Invert, Benthopelagic Invert, Invert, and Other).

Unidentified Fish (Unidentified Fish)	10.99
Medium	
Benthic Invert	*15.55*
Anthozoan (Coral Sp.)	0.02
Bivalvia sp. (Bivalve (Class))	1.07
Holothuroidea sp. (Sea cucumber)	0.35
Hyas sp. (Toad crab)	6.73
Ophiuroidea (Brittle star)	2.96
Pandalus montagui (Aesop prawn)	0.49
Polychaete (Class) (Polychaete (Class))	3.03
Sea Anemone (Sea Anemone (Order))	0.91
Benthopelagic Fish	*3.38*
Agonidae sp. (Poachers (Family))	0.27
Gadus morhua (Atlantic cod)	1.13
Gadus sp. (Codfish (Family))	0.30
Lumpenus lampretaeformis (Snakeblenny)	0.65
Myoxocephalus sp. (Sculpins (Family))	0.92
Urophycis tenuis (White hake)	0.10
Benthopelagic Invert	*31.97*
Amphipoda sp. (Amphipod (Order))	9.41
Caridea sp. (Shrimp (generic))	3.34
Cephalopoda sp. (Squid)	0.88
Copepoda sp. (Copepod (Class))	0.12
Euphausiacea (Krill)	0.82
Gastropoda sp. (Gastropod (Class))	0.12
Hyperiidae (Hyperiid (Suborder))	8.93
Lebbeus sp. (Lebbeus sp.)	0.85
Pandalus borealis (Northern shrimp)	1.84
Pandalus sp. (Boreal red shrimp)	5.00
Stegocephalus inflatus (Gammarid (Stegocephalus inflatus))	0.66
Invertebrate	*12.87*
Crustacean (Subphylum) (Crustacean (Subphylum))	8.11
Crustacean decapod (Crustacean decapod)	4.76
Other	*0.60*
Plant/Wood/Algae (Plant/Wood/Algae)	0.10
Stone (Stone)	0.50

Table A.3.1.1: Consumer Diet by Prey %IRI. Consumer diet is organized by size class (Large, Small). Prey items are organized by category (Pelagic Fish, Demersal Fish, Fish Other, Benthic Invert, Benthopelagic Invert, Invert, and Other).

Pelagic Fish	*13.23*
Ammodytes dubius (Sand lance)	9.39
Barracudina sp. (Barracudina)	0.66
Mallotus villosus (Capelin)	2.52
Myctophum (Lantern fish (Family))	0.58
Sebastes sp. (Redfish (Genus))	0.09
Unidentified	*14.20*
Unidentified digested material (Unidentified digested material)	13.98
Unidentified egg (Unidentified egg)	0.23
Unidentified Fish	*8.20*
Unidentified Fish (Unidentified Fish)	8.20
Small	
Benthic Invert	*8.31*
Aphrodita sp. (Sea mice (Family))	0.54
Hyas sp. (Toad crab)	4.73
Isopoda (Isopod (Order))	0.27
Pandalus montagui (Aesop prawn)	0.52
Polychaete (Class) (Polychaete (Class))	2.24
Benthopelagic Fish	*1.44*
Liparidae Sp. (Snailfish (Family))	0.69
Lumpenus lampretaeformis (Snakeblenny)	0.23
Myoxocephalus sp. (Sculpins (Family))	0.52
Benthopelagic Invert	*37.90*
Amphipoda sp. (Amphipod (Order))	16.08
Caridea sp. (Shrimp (generic))	0.62
Euphausiacea (Krill)	4.60
Hyperiidae (Hyperiid (Suborder))	12.04
Lebbeus sp. (Lebbeus sp.)	0.25
Pandalus sp. (Boreal red shrimp)	3.89
Rhachotropis aculeata (Gammarid (Rhachotropis aculeata))	0.41
Invertebrate	*10.99*
Crustacean (Subphylum) (Crustacean (Subphylum))	8.60
Crustacean decapod (Crustacean decapod)	2.39
Other	*1.74*
Stone (Stone)	1.74
Pelagic Fish	*6.56*

Table A.3.1.1: Consumer Diet by Prey %IRI. Consumer diet is organized by size class (Large, Small). Prey items are organized by category (Pelagic Fish, Demersal Fish, Fish Other, Benthic Invert, Benthopelagic Invert, Invert, and Other).

Ammodytes dubius (Sand lance)	3.07
Barracudina sp. (Barracudina)	0.98
Mallotus villosus (Capelin)	2.50
Unidentified	*29.37*
Unidentified digested material (Unidentified digested material)	28.81
Unidentified egg (Unidentified egg)	0.55
Unidentified Fish	*3.70*
Unidentified Fish (Unidentified Fish)	3.70
Eelpout (Lycodes sp.)	
Large	
Benthopelagic Fish	*61.01*
Myoxocephalus sp. (Sculpins (Family))	61.01
Benthopelagic Invert	*7.93*
Euphausiacea (Krill)	7.93
Invertebrate	*21.95*
Crustacean decapod (Crustacean decapod)	21.95
Unidentified	*9.11*
Unidentified digested material (Unidentified digested material)	9.11
Medium	
Benthic Invert	*10.57*
Eusirus cuspidatus (Gammarid (Eusirus cuspidatus))	2.15
Hyas sp. (Toad crab)	4.58
Ophiuroidea (Brittle star)	1.33
Polychaete (Class) (Polychaete (Class))	2.51
Benthopelagic Fish	*7.63*
Myoxocephalus sp. (Sculpins (Family))	7.63
Benthopelagic Invert	*33.99*
Amphipoda sp. (Amphipod (Order))	22.96
Caridea sp. (Shrimp (generic))	10.04
Euphausiacea (Krill)	0.99
Invertebrate	*30.62*
Crustacean decapod (Crustacean decapod)	30.62
Unidentified	*17.19*
Unidentified digested material (Unidentified digested material)	17.19
Small	

Table A.3.1.1: Consumer Diet by Prey %IRI. Consumer diet is organized by size class (Large, Small). Prey items are organized by category (Pelagic Fish, Demersal Fish, Fish Other, Benthic Invert, Benthopelagic Invert, Invert, and Other).

Benthic Invert	*14.67*
Hyas sp. (Toad crab)	6.06
Ophiuroidea (Brittle star)	8.61
Benthopelagic Fish	*8.80*
Myoxocephalus sp. (Sculpins (Family))	8.80
Benthopelagic Invert	*26.34*
Amphipoda sp. (Amphipod (Order))	22.42
Caridea sp. (Shrimp (generic))	3.91
Invertebrate	*35.97*
Crustacean decapod (Crustacean decapod)	35.97
Other	*0.84*
Plant/Wood/Algae (Plant/Wood/Algae)	0.84
Unidentified	*13.39*
Unidentified digested material (Unidentified digested material)	13.39
Greenland halibut	
Large	
Benthic Invert	*29.45*
Ophiuroidea (Brittle star)	29.45
Benthopelagic Invert	*55.30*
Caridea sp. (Shrimp (generic))	55.30
Invertebrate	*15.26*
Crustacean (Subphylum) (Crustacean (Subphylum))	15.26
Medium	
Benthopelagic Invert	*70.00*
Amphipoda sp. (Amphipod (Order))	31.25
Hyperiidae (Hyperiid (Suborder))	38.75
Unidentified	*30.00*
Unidentified digested material (Unidentified digested material)	30.00
Small	
Benthopelagic Invert	*78.41*
Amphipoda sp. (Amphipod (Order))	14.29
Caridea sp. (Shrimp (generic))	18.39
Hyperiidae (Hyperiid (Suborder))	45.73
Unidentified	*21.59*
Unidentified digested material (Unidentified digested material)	21.59

Table A.3.1.1: Consumer Diet by Prey %IRI. Consumer diet is organized by size class (Large, Small). Prey items are organized by category (Pelagic Fish, Demersal Fish, Fish Other, Benthic Invert, Benthopelagic Invert, Invert, and Other).

Redfish (Genus)	
Large	
Benthic Invert	*0.78*
Ophiuroidea (Brittle star)	0.78
Benthopelagic Invert	79.02
Amphipoda sp. (Amphipod (Order))	7.42
Caridea sp. (Shrimp (generic))	1.76
Euphausiacea (Krill)	16.12
Hyperiidae (Hyperiid (Suborder))	47.25
Pandalus sp. (Boreal red shrimp)	6.48
Invertebrate	*0.11*
Crustacean (Subphylum) (Crustacean (Subphylum))	0.11
Pelagic Fish	*5.29*
Myctophum (Lantern fish (Family))	5.29
Unidentified	*10.46*
Unidentified digested material (Unidentified digested material)	10.46
Unidentified Fish	*4.35*
Unidentified Fish (Unidentified Fish)	4.35
Medium	
Benthopelagic Invert	*61.02*
Amphipoda sp. (Amphipod (Order))	10.16
Caridea sp. (Shrimp (generic))	6.30
Euphausiacea (Krill)	23.04
Hyperiidae (Hyperiid (Suborder))	18.48
Pandalus sp. (Boreal red shrimp)	3.03
Invertebrate	*10.40*
Crustacean (Subphylum) (Crustacean (Subphylum))	10.40
Pelagic Fish	*1.30*
Myctophidae sp. (Lantern fish (Genus))	1.30
Unidentified	*25.11*
Unidentified digested material (Unidentified digested material)	25.11
Unidentified Fish	*2.18*
Unidentified Fish (Unidentified Fish)	2.18

Table A.3.1.1: Consumer Diet by Prey %IRI. Consumer diet is organized by size class (Large, Small). Prey items are organized by category (Pelagic Fish, Demersal Fish, Fish Other, Benthic Invert, Benthopelagic Invert, Invert, and Other).

Silver hake	
Large	
Benthopelagic Invert	*27.86*
Amphipoda sp. (Amphipod (Order))	8.33
Euphausiacea (Krill)	8.33
Hyperiidae (Hyperiid (Suborder))	11.19
Invertebrate	*6.95*
Crustacean (Subphylum) (Crustacean (Subphylum))	6.95
Pelagic Fish	*31.96*
Ammodytes dubius (Sand lance)	6.96
Barracudina sp. (Barracudina)	16.67
Myctophum (Lantern fish (Family))	8.33
Unidentified	*21.47*
Unidentified digested material (Unidentified digested material)	21.47
Unidentified Fish	*11.76*
Unidentified Fish (Unidentified Fish)	11.76
Medium	
Benthopelagic Invert	*27.19*
Amphipoda sp. (Amphipod (Order))	2.32
Caridea sp. (Shrimp (generic))	11.23
Euphausiacea (Krill)	11.49
Hyperiidae (Hyperiid (Suborder))	2.15
Invertebrate	*50.60*
Crustacean (Subphylum) (Crustacean (Subphylum))	50.60
Pelagic Fish	*4.85*
Barracudina sp. (Barracudina)	4.85
Unidentified	*13.04*
Unidentified digested material (Unidentified digested material)	13.04
Unidentified Fish	*4.32*
Unidentified Fish (Unidentified Fish)	4.32
White hake	
Large	
Benthopelagic Invert	*20.29*
Amphipoda sp. (Amphipod (Order))	8.39
Caridea sp. (Shrimp (generic))	11.90

Table A.3.1.1: Consumer Diet by Prey %IRI. Consumer diet is organized by size class (Large, Small). Prey items are organized by category (Pelagic Fish, Demersal Fish, Fish Other, Benthic Invert, Benthopelagic Invert, Invert, and Other).

Invertebrate	*5.57*
Crustacean (Subphylum) (Crustacean (Subphylum))	5.57
Pelagic Fish	*74.14*
Sebastes sp. (Redfish (Genus))	74.14
Medium	
Benthopelagic Invert	*33.33*
Amphipoda sp. (Amphipod (Order))	33.33
Invertebrate	*54.45*
Crustacean (Subphylum) (Crustacean (Subphylum))	54.45
Unidentified	*12.22*
Unidentified digested material (Unidentified digested material)	12.22
Small	
Benthopelagic Invert	*63.18*
Amphipoda sp. (Amphipod (Order))	0.78
Euphausiacea (Krill)	53.27
Pandalus sp. (Boreal red shrimp)	9.13
Invertebrate	*22.66*
Crustacean (Subphylum) (Crustacean (Subphylum))	22.66
Pelagic Fish	*5.45*
Mallotus villosus (Capelin)	4.31
Myctophum (Lantern fish (Family))	1.14
Unidentified	*0.51*
Unidentified digested material (Unidentified digested material)	0.51
Unidentified Fish	*8.21*
Unidentified Fish (Unidentified Fish)	8.21
Witch Flounder	
Large	
Benthic Invert	*12.78*
Echinoidea sp. (Sea urchin)	8.33
Ophiuroidea (Brittle star)	2.15
Polychaete (Class) (Polychaete (Class))	2.30
Unidentified	*87.22*
Unidentified digested material (Unidentified digested material)	87.22
Medium	
Benthic Invert	*16.29*
Bivalvia sp. (Bivalve (Class))	6.12

Table A.3.1.1: Consumer Diet by Prey %IRI. Consumer diet is organized by size class (Large, Small). Prey items are organized by category (Pelagic Fish, Demersal Fish, Fish Other, Benthic Invert, Benthopelagic Invert, Invert, and Other).

Polychaete (Class) (Polychaete (Class))	10.17
Benthopelagic Invert	*12.85*
Amphipoda sp. (Amphipod (Order))	6.79
Caridea sp. (Shrimp (generic))	6.06
Unidentified	*70.86*
Unidentified digested material (Unidentified digested material)	70.86
Small	
Benthic Invert	*7.57*
Bivalvia sp. (Bivalve (Class))	7.57
Benthopelagic Invert	*16.67*
Amphipoda sp. (Amphipod (Order))	16.67
Unidentified	*75.77*
Unidentified digested material (Unidentified digested material)	75.77

Table A.3.1.2: SIMPER Results: Average interspecific diet dissimilarity between species base on prey item

Species	American plaice	Arctic cod	Atlantic Cod	Argentine	Eelpout	Greenland halibut	Redfish	Silver hake	White hake	Witch flounder
American plaice		0.870	0.869	0.784	0.890	0.916	0.872	0.827	0.850	0.867
Arctic cod			0.824	0.815	0.824	0.907	0.825	0.820	0.796	0.798
Atlantic cod				0.855	0.849	0.892	0.818	0.811	0.836	0.843
Argentine					0.893	0.944	0.849	0.815	0.776	0.856
Eelpout						0.871	0.847	0.831	0.831	0.817
Greenland halibut							0.867	0.928	0.950	0.889
Redfish								0.837	0.859	0.833
Silver hake									0.799	0.829
White hake										0.826
Witch flounder										

Table A.3.1.3: Consumer Ellipse Area. Total area of the convex hull (TA), area of the standard ellipse (SEA), and corrected standard ellipse area (SEA$_C$) organized by size class of consumer (Large, Medium, and Small) when available. CN= $\delta^{15}N$ and $\delta^{13}C$, NS= $\delta^{15}N$ and $\delta^{34}S$, CS= $\delta^{13}C$and $\delta^{34}S$.

Species	**Size Class**	**Isotope**	**TA**	**SEA**	**SEAc**
American Plaice	Small	CN	1.87	0.52	0.54
	Medium	CN	3.31	1.47	1.62
	Large	CN	0.95	0.45	0.50
	Small	NS	4.67	1.08	1.12
	Medium	NS	2.64	1.31	1.44
	Large	NS	1.34	0.66	0.73
	Small	CS	2.49	0.66	0.68
	Medium	CS	3.37	1.73	1.91
	Large	CS	2.20	1.09	1.21
Arctic Cod	Small	CN	1.19	0.70	0.78
	Medium	CN	0.43	0.18	0.20
	Large	CN	1.75	1.07	1.25
	Small	NS	1.64	0.86	0.97
	Medium	NS	0.99	0.51	0.57
	Large	NS	1.84	1.22	1.43
	Small	CS	0.60	0.32	0.36
	Medium	CS	0.80	0.41	0.46
	Large	CS	1.87	0.97	1.13
Argentine	Small	CN	0.48	0.32	0.38
	Medium	CN	0.31	0.21	0.25
	Large	CN	0.11	0.19	0.39
	Small	NS	0.91	0.62	0.75
	Medium	NS	0.47	0.32	0.38
	Large	NS	0.04	0.08	0.16
	Small	CS	0.28	0.18	0.21
	Medium	CS	0.15	0.12	0.14
	Large	CS	0.02	0.04	0.08
Atlantic cod	Small	CN	1.37	0.43	0.44
	Medium	CN	0.32	0.16	0.18
	Large	CN	0.08	0.14	0.28
	Small	NS	3.57	0.87	0.90
	Medium	NS	0.07	0.12	0.24
	Large	NS	0.61	0.33	0.37
	Small	CS	2.69	0.62	0.64
	Medium	CS	0.60	0.32	0.36
	Large	CS	0.00	0.01	0.02

Table A.3.1.3: Consumer Ellipse Area. Total area of the convex hull (TA), area of the standard ellipse (SEA), and corrected standard ellipse area (SEAC) organized by size class of consumer (Large, Medium, and Small) when available. CN= $\delta^{15}N$ and $\delta^{13}C$, NS= $\delta^{15}N$ and $\delta^{34}S$, CS= $\delta^{13}C$and $\delta^{34}S$.

Eelpout	Small	CN	0.47	0.30	0.36
	Medium	CN	0.37	0.22	0.25
	Small	NS	1.99	1.28	1.54
	Medium	NS	0.65	0.36	0.41
	Small	CS	0.92	0.74	0.89
	Medium	CS	0.24	0.14	0.16
Greenland halibut	Small	CN	0.42	0.25	0.29
	Medium	CN	0.53	0.49	0.65
	Large	CN	1.60	1.97	2.96
	Small	NS	0.60	0.42	0.49
	Medium	NS	0.58	0.53	0.70
	Large	NS	1.42	1.75	2.63
	Small	CS	0.84	0.46	0.54
	Medium	CS	0.28	0.26	0.34
	Large	CS	1.36	1.45	2.18
Redfish	Medium	CN	4.39	1.44	1.50
	Large	CN	5.80	2.83	3.14
	Medium	NS	5.54	1.81	1.88
	Large	NS	2.98	1.59	1.76
	Medium	CS	1.69	0.53	0.55
	Large	CS	1.79	1.10	1.22
Silver hake	Medium	CN	0.99	0.62	0.75
	Medium	NS	0.29	0.18	0.22
	Medium	CS	1.52	0.98	1.18
White hake	Small	CN	4.98	2.49	2.80
	Medium	CN	0.23	0.25	0.38
	Large	CN	0.76	0.47	0.55
	Small	NS	6.71	3.44	3.87
	Medium	NS	0.33	0.38	0.57
	Large	NS	0.87	0.57	0.66
	Small	CS	4.99	2.46	2.77
	Medium	CS	0.07	0.09	0.14
	Large	CS	0.49	0.28	0.32

Table A.3.1.3: Consumer Ellipse Area. Total area of the convex hull (TA), area of the standard ellipse (SEA), and corrected standard ellipse area (SEA_C) organized by size class of consumer (Large, Medium, and Small) when available. CN= $\delta^{15}N$ and $\delta^{13}C$, NS= $\delta^{15}N$ and $\delta^{34}S$, CS= $\delta^{13}C$and $\delta^{34}S$.

Witch flounder	Small	CN	0.35	0.26	0.32
	Medium	CN	3.52	2.92	3.40
	Large	CN	3.57	1.80	1.98
	Small	NS	1.39	1.30	1.62
	Medium	NS	9.37	7.22	8.43
	Large	NS	6.77	3.70	4.07
	Small	CS	0.59	0.45	0.56
	Medium	CS	7.11	4.99	5.82
	Large	CS	4.62	2.60	2.86

Table A.3.1.4: Consumer Ellipse Area. Total area of the convex hull (TA), area of the standard ellipse (SEA), and corrected standard ellipse area (SEA_C) a) δ15N and δ13C. b) δ15N and δ34S c) δ13Cand δ34S

a) $\delta^{15}N$ and $\delta^{13}C$	**Atlantic cod**	**American plaice**	**Arctic cod**	**Eelpout**	**Greenland Halibut**	**Witch flounder**	**Redfish**	**Argentine**	**Silver hake**	**White hake**
TA	2.45	6.00	4.29	0.87	2.93	6.62	8.11	0.84	1.72	9.26
SEA	0.57	1.66	1.11	0.34	1.06	2.25	2.11	0.29	0.83	2.67
SEAc	0.59	1.69	1.15	0.36	1.14	2.34	2.17	0.31	0.92	2.78
b) $\delta^{15}N$ and $\delta^{34}S$										
TA	5.17	7.44	4.16	2.48	2.43	11.75	5.84	1.16	0.70	11.85
SEA	1.20	1.50	1.42	1.10	0.87	4.34	1.91	0.41	0.37	3.01
SEAc	1.22	1.53	1.47	1.18	0.93	4.52	1.96	0.44	0.41	3.14
c) $\delta^{13}C$and $\delta^{34}S$										
TA	3.54	8.61	3.22	1.28	2.91	13.16	3.28	0.64	2.21	4.99
SEA	0.80	2.01	0.84	0.59	1.02	3.85	0.75	0.20	1.18	1.18
SEAc	0.82	2.04	0.87	0.63	1.09	4.01	0.78	0.21	1.32	1.24

Table A.3.1.5: Trophic Position (TP) of Consumers: Mean and SD TP from a benthic source and a pelagic source for each size class of consumers.

Consumer	**Size Class**	**Benthic Source**		**Pelagic Source**	
		Mean	**SD**	**Mean**	**SD**
American plaice	Large	3.39	0.1	3.31	0.1
	Medium	3.64	0.2	3.56	0.2
	Small	3.61	0.2	3.53	0.2
Arctic cod	Large	3.94	0.2	3.86	0.2
	Medium	3.89	0.1	3.81	0.1
	Small	3.48	0.2	3.40	0.2
Argentine	Large	3.46	0.1	3.39	0.1
	Medium	3.52	0.1	3.45	0.1
	Small	3.56	0.2	3.48	0.2
Atlantic Cod	Large	3.79	0.1	3.71	0.1
	Medium	3.90	0.1	3.82	0.1
	Small	3.51	0.1	3.43	0.1
Eelpout	Medium	3.63	0.1	3.55	0.1
	Small	3.59	0.1	3.51	0.1
Greenland halibut	Large	3.46	0.3	3.38	0.3
	Medium	3.31	0.2	3.23	0.2
	Small	3.31	0.1	3.23	0.1
Redfish (Genus)	Large	3.92	0.4	3.84	0.4
	Medium	3.56	0.4	3.48	0.4
Silver hake	Large	3.34	0.2	3.26	0.2
	Medium	3.21	0.1	3.13	0.1
	Small	3.26	0.0	3.18	0.0
White hake	Large	3.82	0.2	3.74	0.2
	Medium	3.52	0.1	3.44	0.1
	Small	3.22	0.3	3.14	0.3
Witch Flounder	Large	4.13	0.3	4.05	0.3
	Medium	3.96	0.4	3.88	0.4
	Small	3.99	0.2	3.91	0.2

Table A.3.1.6: SIMM Results: %IRI Diet by Species

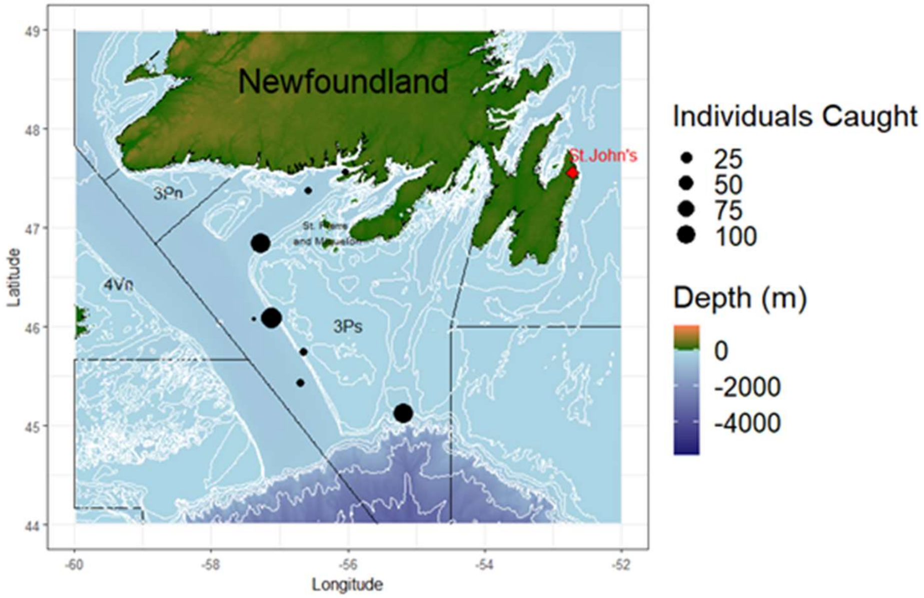
Prey Item	**%IRI**
American plaice	
Bivalve	1.6

Brittle star	0.4
Crustacean	0.1
Decapod	0.1
Hyperiid	1.7
Sand lance	96
Shrimp	0.1
Atlantic cod	
Amphipods	0.1
Benthic Fish	13.7
Benthic Invert	1
Benthopelagic Fish	0.1
Benthopelagic Invert	0.9
Crustacean	0.6
Hyperiid	21.7
Invert	0.3
Pelagic Fish	0.7
Sand lance	1
Toad Crab	59.9
Arctic cod	
Boreal red shrimp	0.2
Hyperiid	87.7
Shrimp	12.1
Argentine	
Amphipod (Order)	81.7
Shrimp	18.3
Eelpout	
Amphipods	0.5
Brittle star	6.3
Decapod	3.4
Euphausiids	22.6
Polychaete	33.6
Sculpins	16.8
Shrimp	0.5
Toad Crab	16.3
Greenland halibut	
Amphipods	0.3
Brittle star	0.3
Crustacean	1
Hyperiid	69.9
Shrimp	28.5
Redfish	
Amphipods	0.1

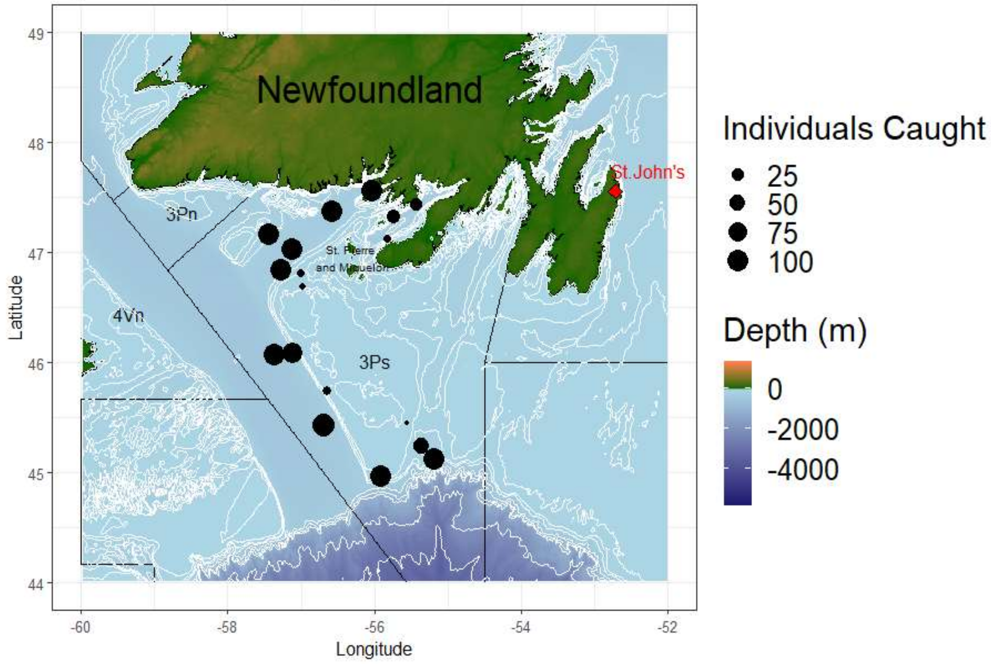
Shrimp	0.2
Crustacean	0.3
Euphausiids	54.8
Hyperiid	3.6
Pelagic Fish	41
Silver hake	
Amphipods	0.1
Crustacean	0.7
Euphausiids	87.6
Hyperiid	0.1
Pelagic Fish	11.2
Sand lance	0.1
Shrimp	0.1
White hake	
Amphipods	0.4
Atlantic cod	1.3
Boreal red shrimp	0.7
Capelin	12.2
Codfish	0.7
Crustacean	7.5
Euphausiids	67.3
Redfish	3.8
Shrimp	6
Witch flounder	
Amphipods	0.1
Bivalve	0.4
Polychaete	82.1
Sea urchin	0.2
Shrimp	17.2

A.3.2 Figures

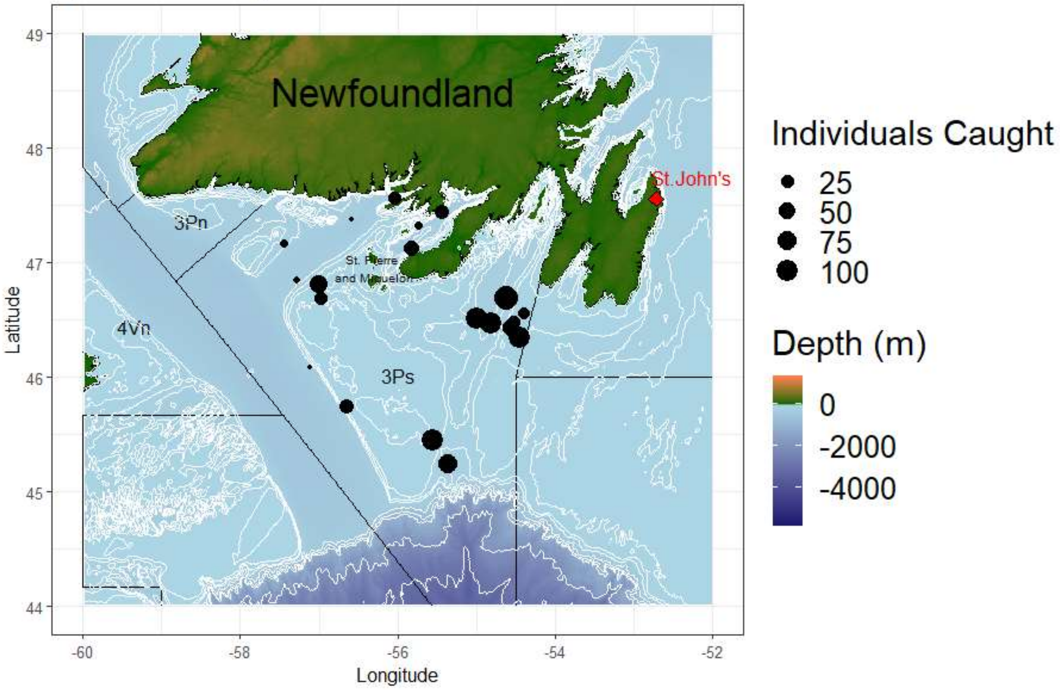
a) Silver hake



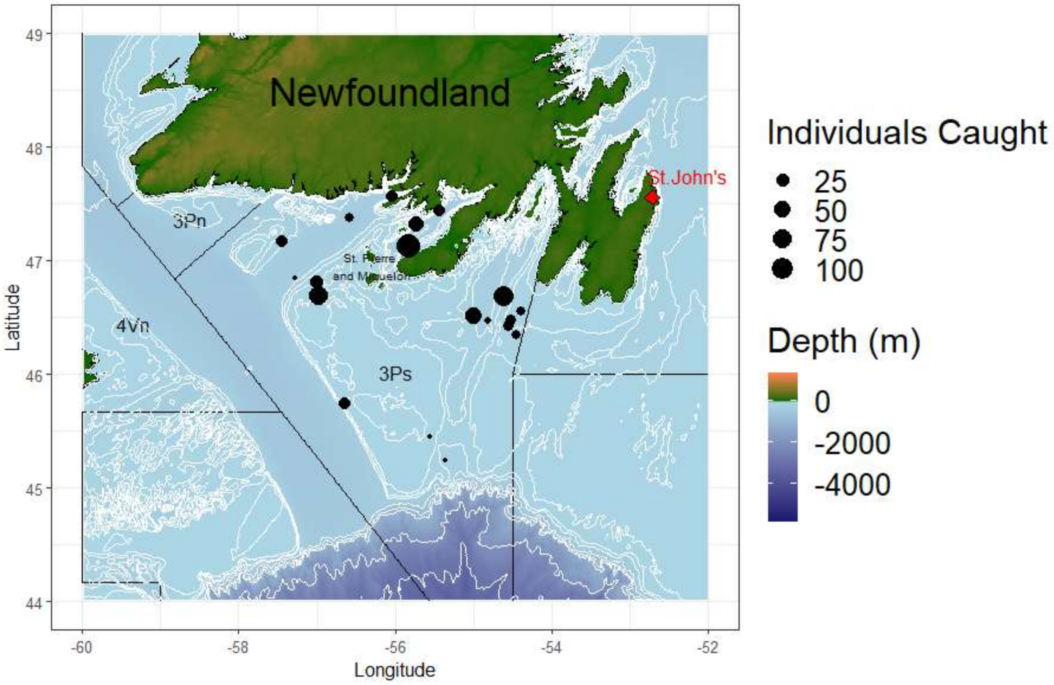
b) Redfish (Genus)

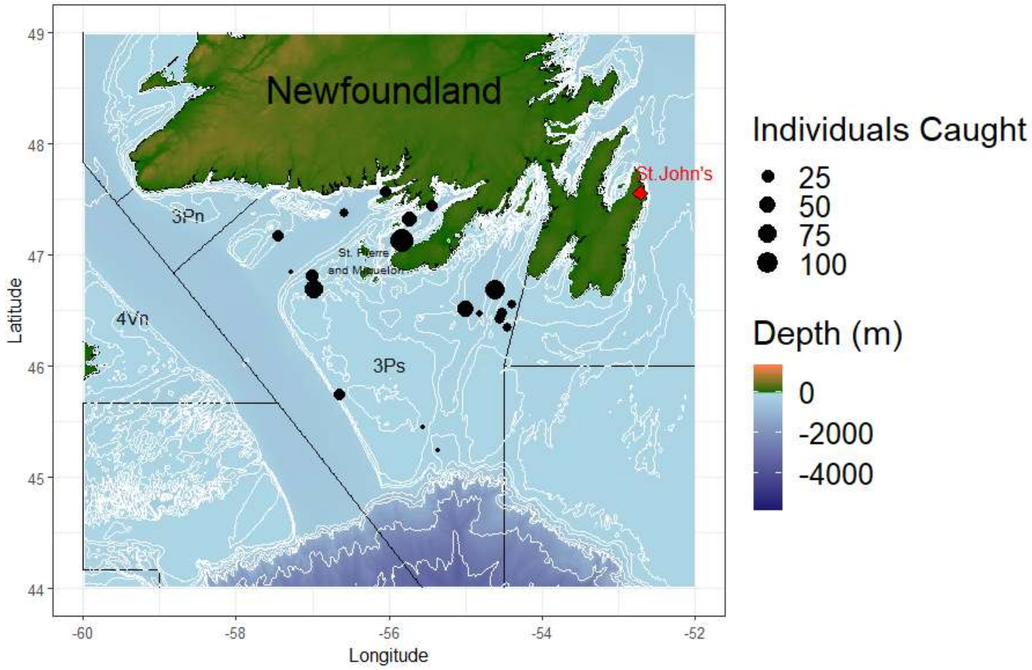


c) American plaice

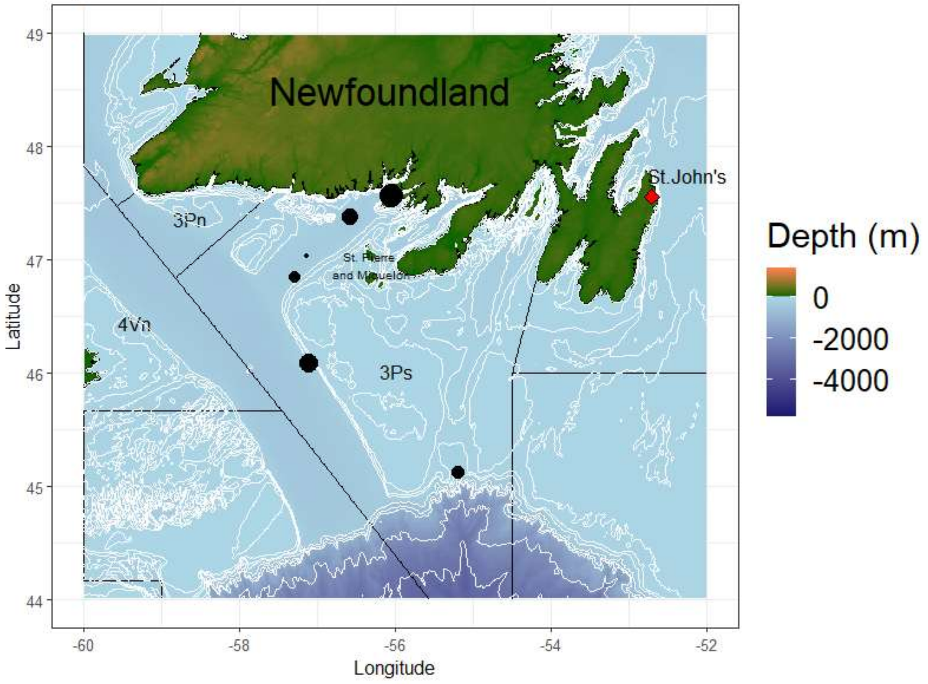


d) Atlantic Cod



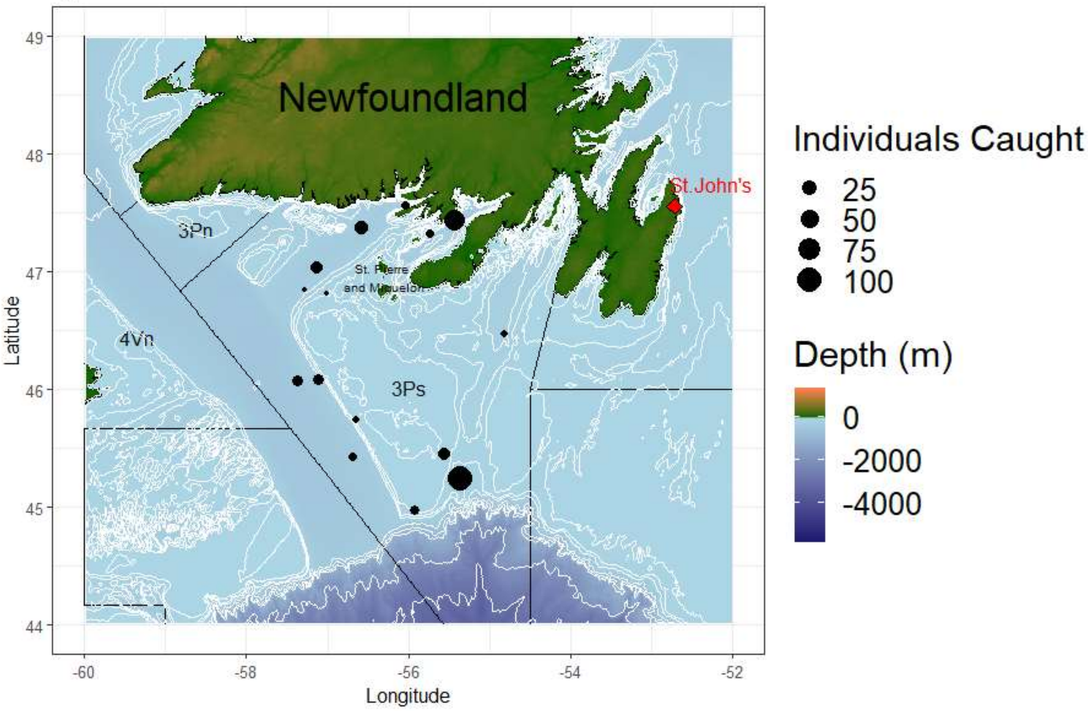


d) Atlantic Cod

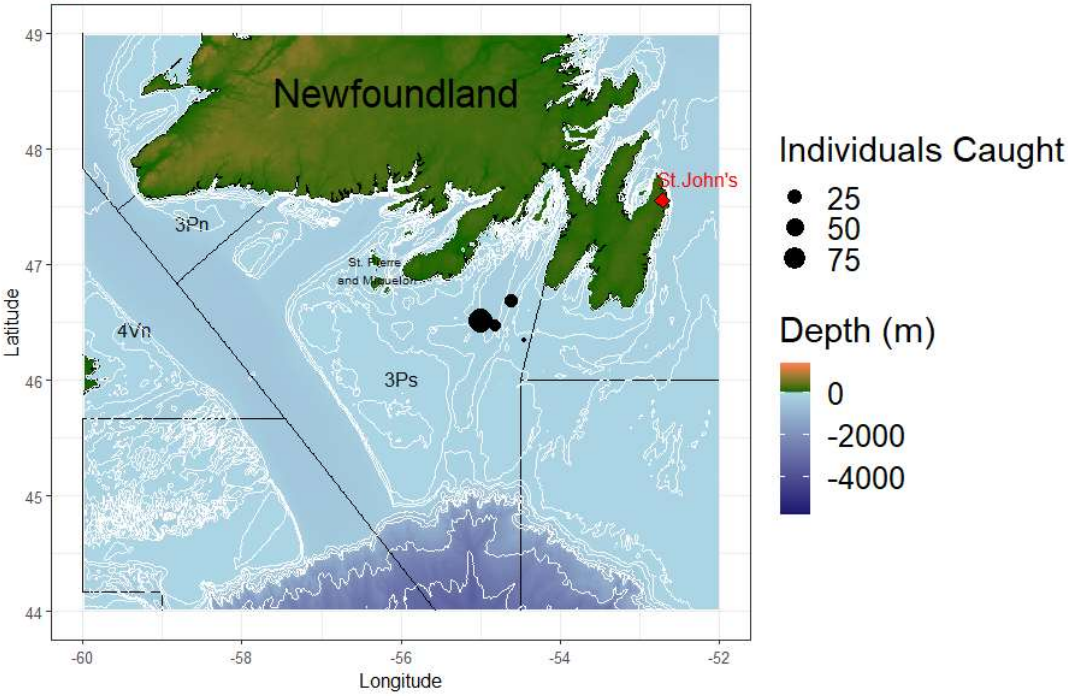


e) White hake

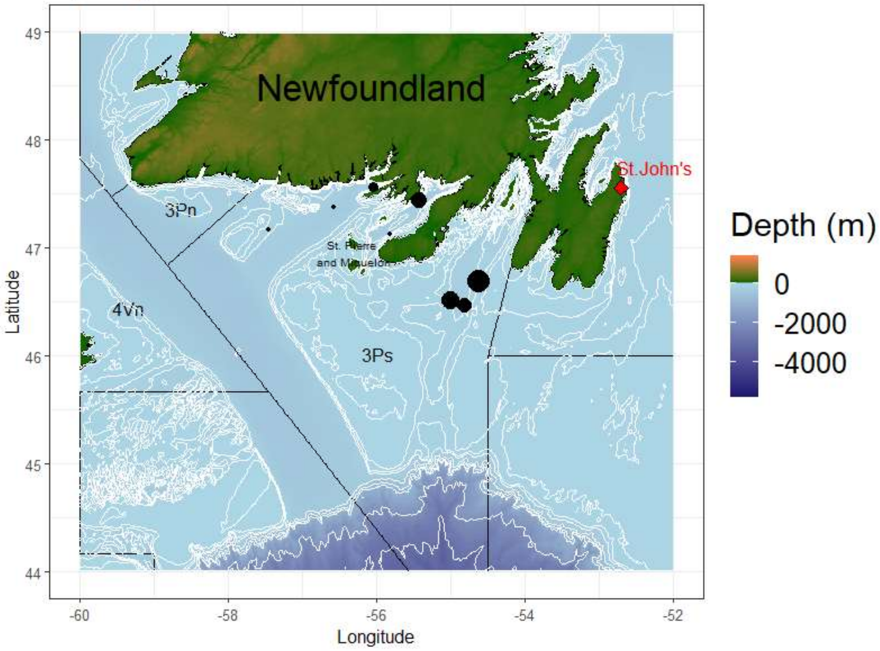
f) Witch Flounder



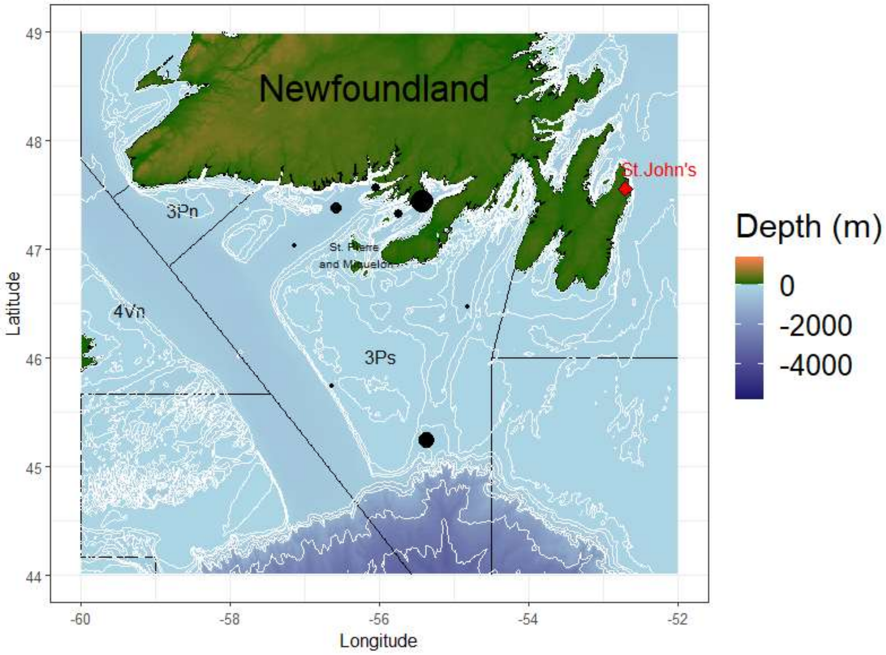
g) Arctic cod



h) Eelpout



i) Greenland halibut



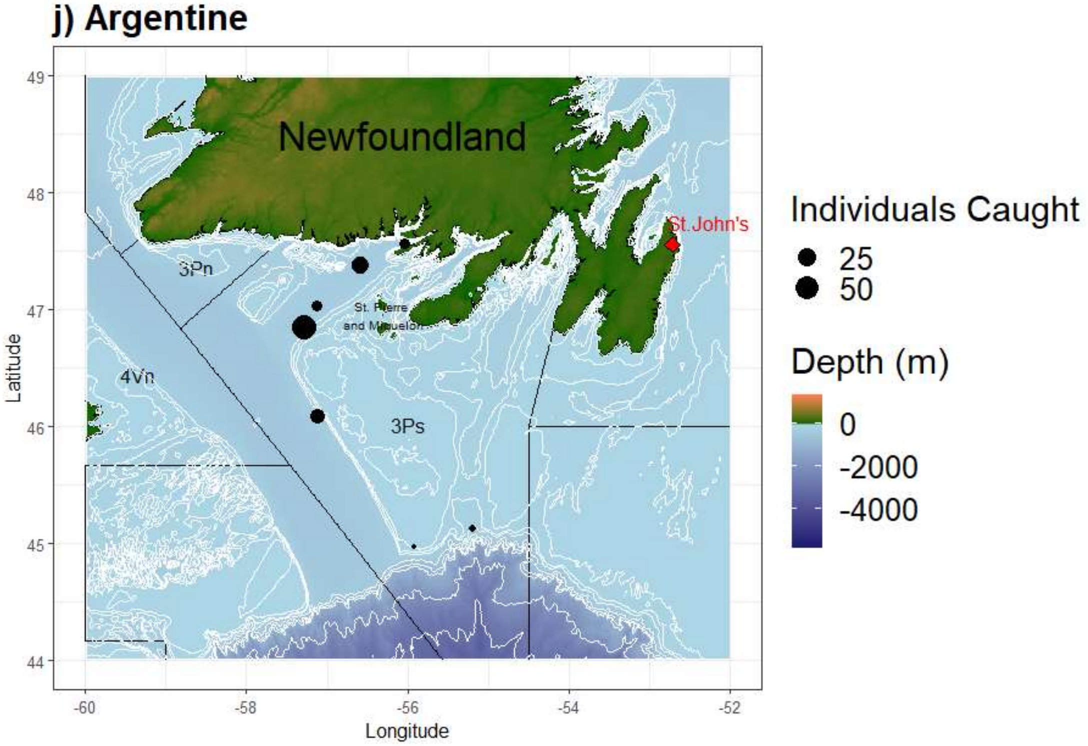


Figure A3.2.1: Southern Newfoundland Sampling Locations by species- Depth contours are shown at 100m intervals. a) Silver hake, b) Redfish, c) American Plaice, d) Atlantic cod, e) White hake, f) Witch flounder, g) Arctic cod, h)Eelpout, i)Greenland Halibut, j) Argentine.

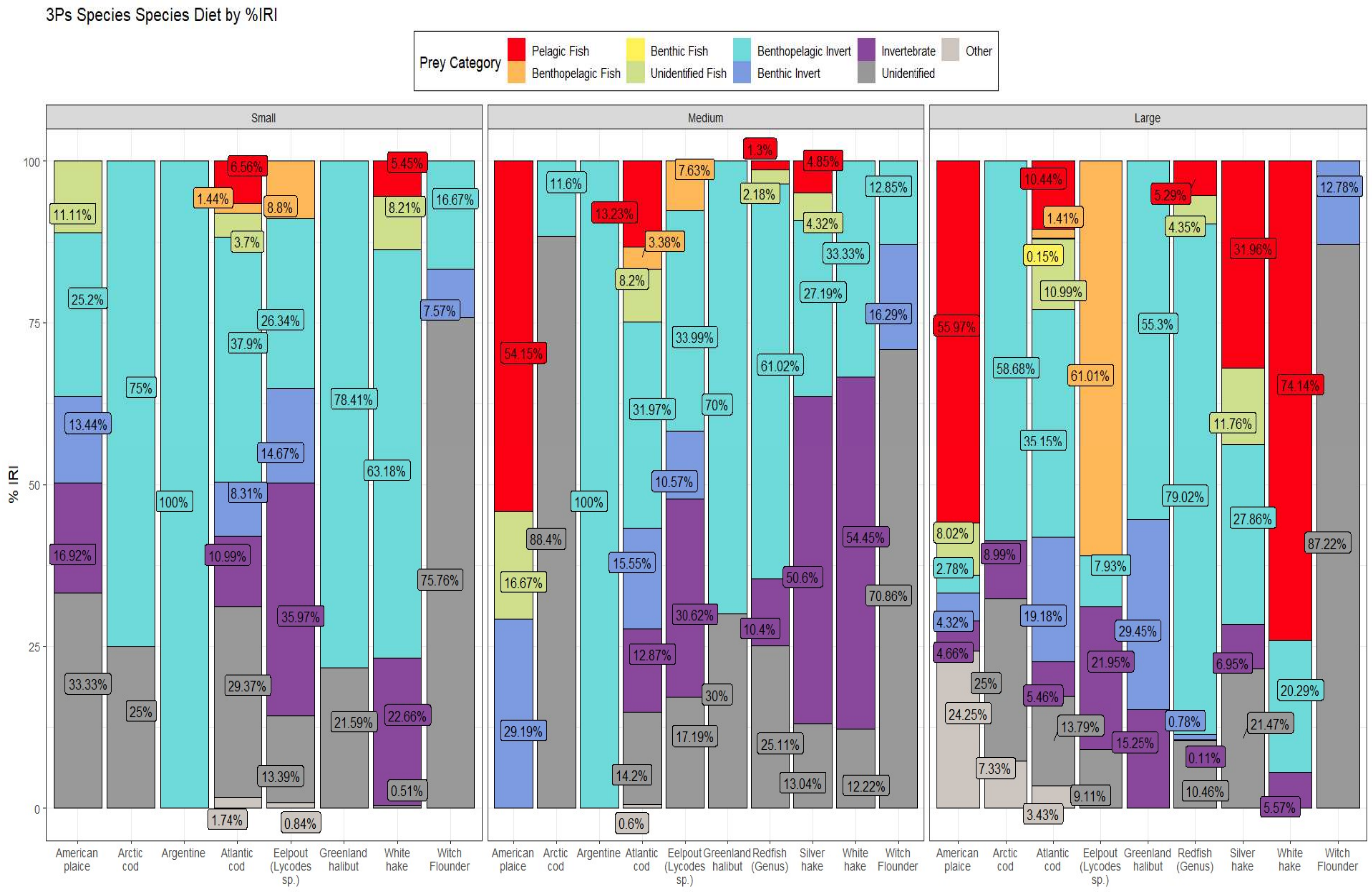
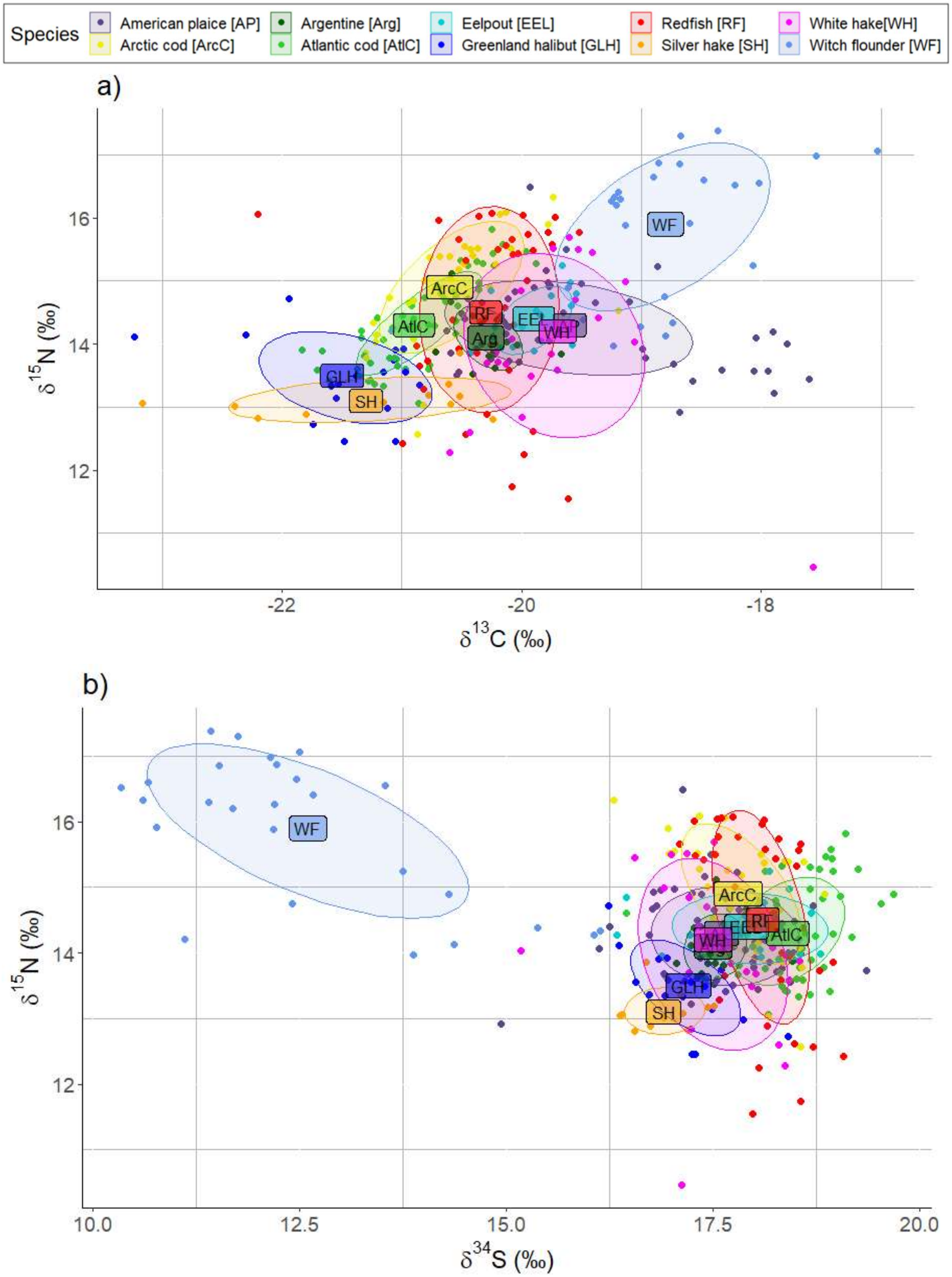


Figure A.3.2.2: Consumer Diet by %Index of Relative Importance (%IRI): 10 Consumers analyzed by Size Class (Large and Small), showing the total %IRI contribution to diet of each prey category (Pelagic Fish (🟥), Benthopelagic Fish (🟧), Benthic Fish (🟨), Fish Other (🟩), Benthopelagic Invert (🟦), Benthic Invert (🟦), Invertebrate (🟪), Unidentified (⬛) & Other (⬜)).


Species
American plaice [AP]
Arctic cod [ArcC]
Argentine [Arg]
Atlantic cod [AtlC]
Eelpout [EEL]
Greenland halibut [GLH]
Redfish [RF]
Silver hake [SH]
White hake[WH]
Witch flounder [WF]
a)
δ^{15}N (‰)
16
14
12
-22
-20
-18
δ^{13}C (‰)
WF
ArcC
RF
EEL
WH
AtlC
Arg
GLH
SH
b)
δ^{15}N (‰)
16
14
12
10.0
12.5
15.0
17.5
20.0
δ^{34}S (‰)
WF
ArcC
RF
EEL
AtlC
WH
GLH
SH

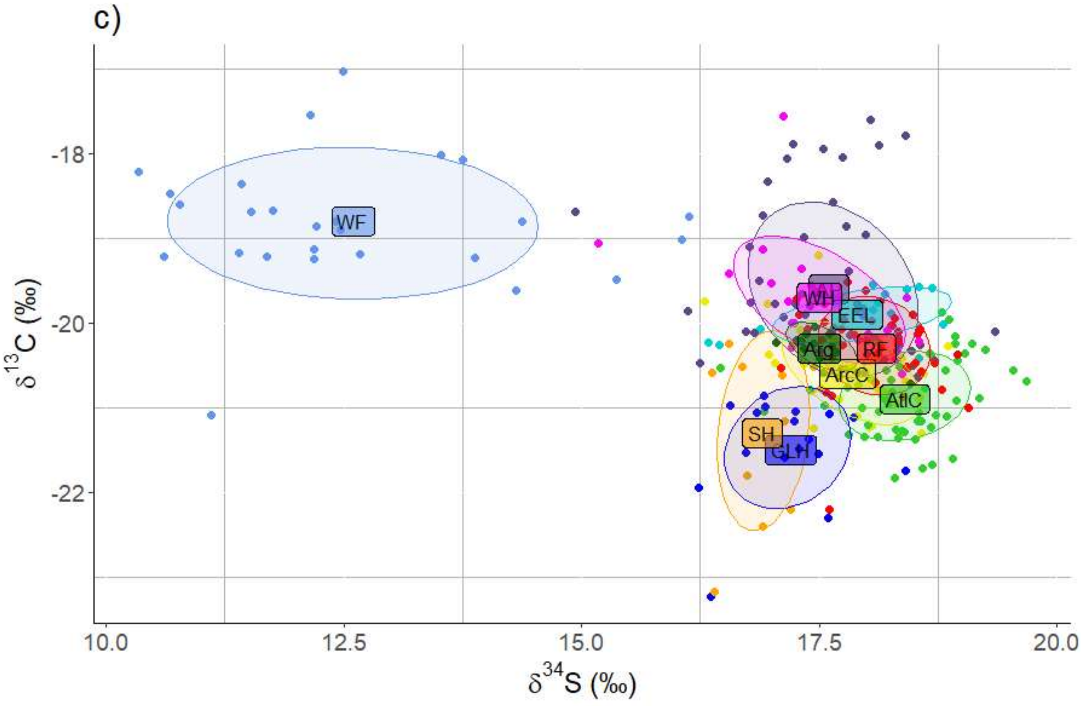


Figure A.3.2.3: Bayesian ellipses for Consumers. a) δ^{15}N and δ^{13}C. b) δ15N and δ^{34}S c) δ^{13}Cand δ^{34}S. Ellipses are organized by consumer species and outlined in the legend

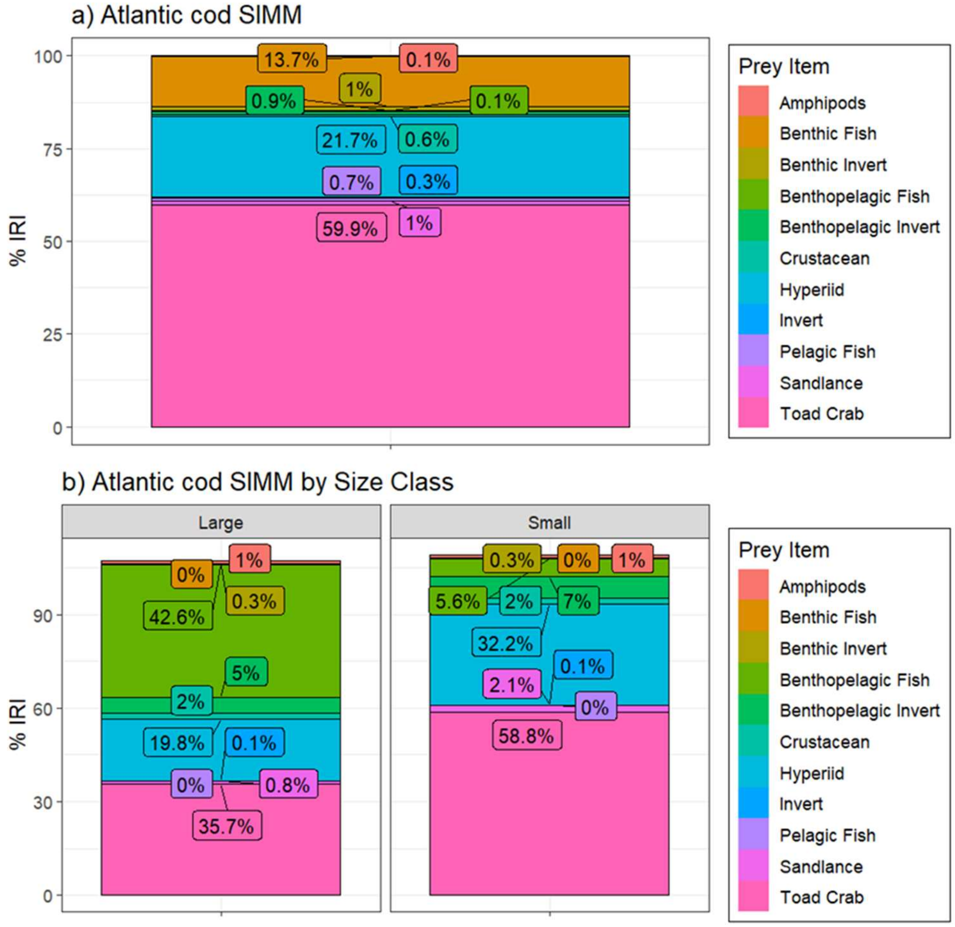


Figure A.3.2.4: Stable Isotope Mixing Model Diet Composition Results. Atlantic cod diet showing the total %IRI contribution to diet of each prey category. a) All Individuals, b) Organized by Small, and Large Length Classes.