Sex- and Age-Dependent Differences and Habitat Influences on Demersal Arctic Cod, *Boreogadus saida* (Lepechin 1774) Diet and Energy Allocation in the Canadian Beaufort Sea

by

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Abstract

Arctic Cod, *Boreogadus saida* (Lepechin 1774) occur throughout the circumpolar north at all levels of the water column depending on their life history stage, the time of day, the season, and their activity. Arctic Cod are the most abundant fish species in the Canadian Beaufort Sea (CBS) ecosystem, and are an important link in the flow of energy within the food web. This study examined differences in energy acquisition and usage in Arctic Cod among three depth zones in the CBS (from 15-800m) by examining stomach contents and physiological indicators, taking into account sex, age and body size. Nonparametric comparison analyses found no differences with depth, but support for an ontogenetic shift in diet regarding prey size, a difference in energy content of an average diet between size classes 1 (30-60mm) and 2-4 (2: 60-90mm; 3: 90-120mm; 4: >120mm), and a slight positive relationship between physiological indicators and body size.

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Dedications

To the people who kept asking me if I was “done that thing yet”…the answer is finally yes!

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“To anyone with “Arctic dreams”” – H. Hop (1994)

“Only the ocean remains as the last great unexpected portion of our globe; so it is to the sea that man must turn to meet the last great challenge of exploration this side of outer space” – H.B. Stewart (1966)

Table of Contents

List of Tables

List of Figures

1 Introduction

Energy is the currency of life, exchanged within a food web to power an ecosystem. Forage fishes such as Arctic Cod *Boreogadus saida* (Lepechin 1774) are an important part of Arctic food webs and Arctic ecosystems are constrained by extremely seasonal primary production due to their northerly latitude affecting light conditions, the lingering presence of ice, and the subsequent seasonality in primary production. Arctic forage fishes have adapted to the lower energy production by having slower metabolisms at colder temperatures than do southern fishes at warmer temperatures (Childress 1995; Clarke and Johnston 1999). In other words, Arctic species have high standard metabolic rates compared to species from low latitudes, but when measured at their habitat temperature, Arctic species have lower absolute metabolic rates than species from low latitudes (White *et al.* 2011). The surplus energy allocation strategy of Arctic forage fishes is important in ensuring their continued success in Arctic ecosystems. Therefore energy dynamics within Arctic ecosystems are important to understand as climate change leads to shifts in energy availability.

This thesis investigates the aspects of feeding, growth, and the energetics of Arctic Cod in the Canadian Beaufort Sea (CBS) in the context of a highly variable environment and the apparent central position of Arctic Cod in Arctic food webs (Bradstreet *et al.* 1986; Christiansen and Reist 2014). Fundamentally, the questions posed in this thesis address differences across habitats and/or between sexes in regards to energy acquisition (diet) and allocation to gonad development, energy storage in the liver, and body growth, while taking into account differences that may be affected by fish size. It was expected that fish gape size would correlate with body size, thereby influencing the size of prey consumed. An influence of body size on energy allocation strategy was also expected based on shifts in life history demands by sex, season, and level of maturity (Engen and Saether 1994; Heino and Kaitala 1999; Post and Parkinson 2001). The following section outlines the Beaufort Sea environment, the importance of Arctic Cod in this Arctic ecosystem, energetics at the ecosystem and individual organism level, and finally the analytical structure, expectations, and objectives of this thesis.

1.1 Beaufort Sea Oceanography

The Beaufort Sea, located west of the Canadian Arctic Archipelago, extends over 1.75 million km^2 and is bordered by Alaska, Yukon, and the Northwest Territories (Figure 1.1). The Beaufort Sea is a unique habitat, heavily influenced by the freshwater outflow and nutrient input of the Mackenzie River. It also receives waters from the Pacific, Atlantic, and Arctic (Polar) oceans mobilized in the Beaufort Sea through large-scale water circulations of the clockwise Beaufort Gyre and counter-clockwise Beaufort Undercurrent (Carmack and Macdonald 2002). The differences in temperature and salinity, and thus density of these waters results in a stratification of the Beaufort Sea: the relatively low-salinity upper layer including a mixed layer and halocline, a warmer Atlantic Layer, and a colder saline deep layer (Figure 1.2). McLaughlin *et al.* (2005) discussed the stratification and water mass formation in the Arctic Ocean ecosystems, of which the Beaufort Sea is part. The layers or water masses are so named because of their source, and despite continuous ice cover over the central Arctic Ocean the temporal and spatial properties of the water masses are expected to vary inter-annually due to local freezing and melting cycles within and beyond the marginal ice zone (McLaughlin *et al.* 1996). While salinity increases with depth in the Canadian Beaufort Sea, temperature can range as little as 1°C beyond the surface Polar Mixed Layer during the summer. Still, this temperature difference likely has a major impact on the biology of its residents, including Arctic Cod. The Polar Mixed

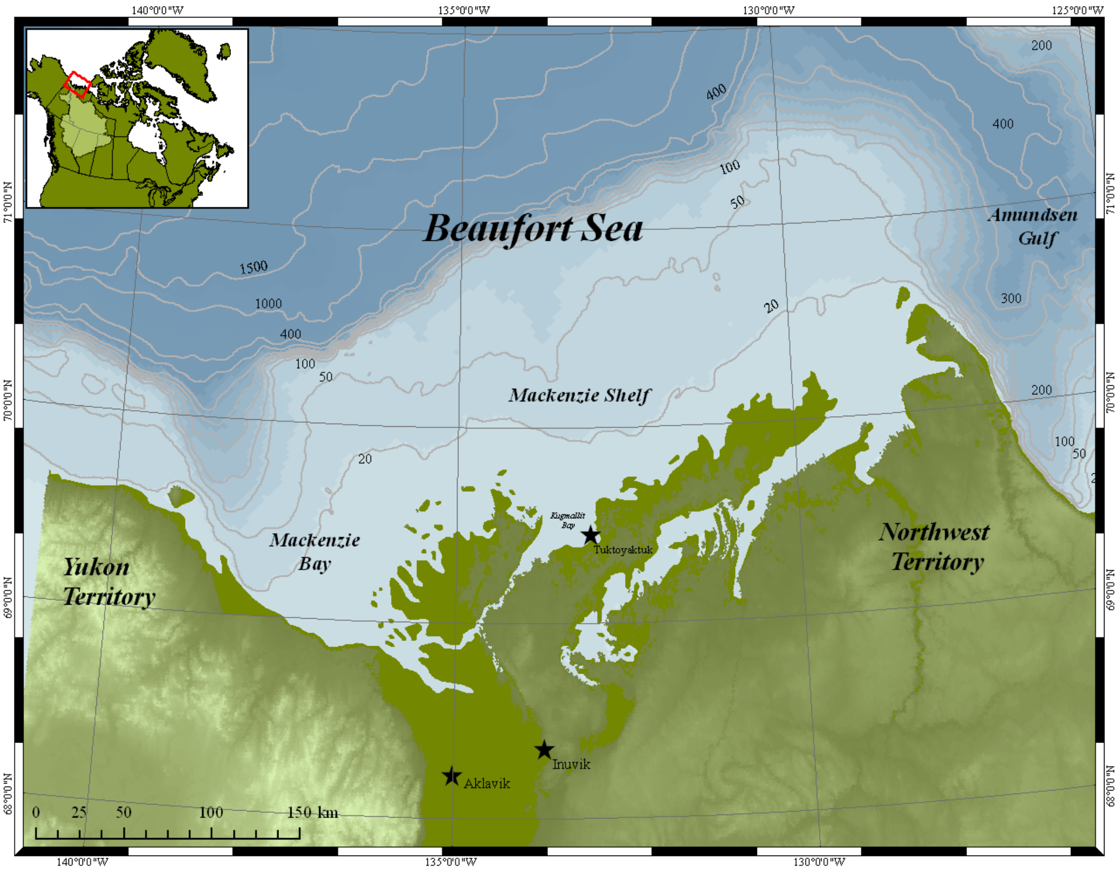

Figure 1.1 A map of the Beaufort Sea (courtesy of A. Majewski, DFO). This thesis investigated the Arctic Cod population in the Canadian Beaufort Sea.

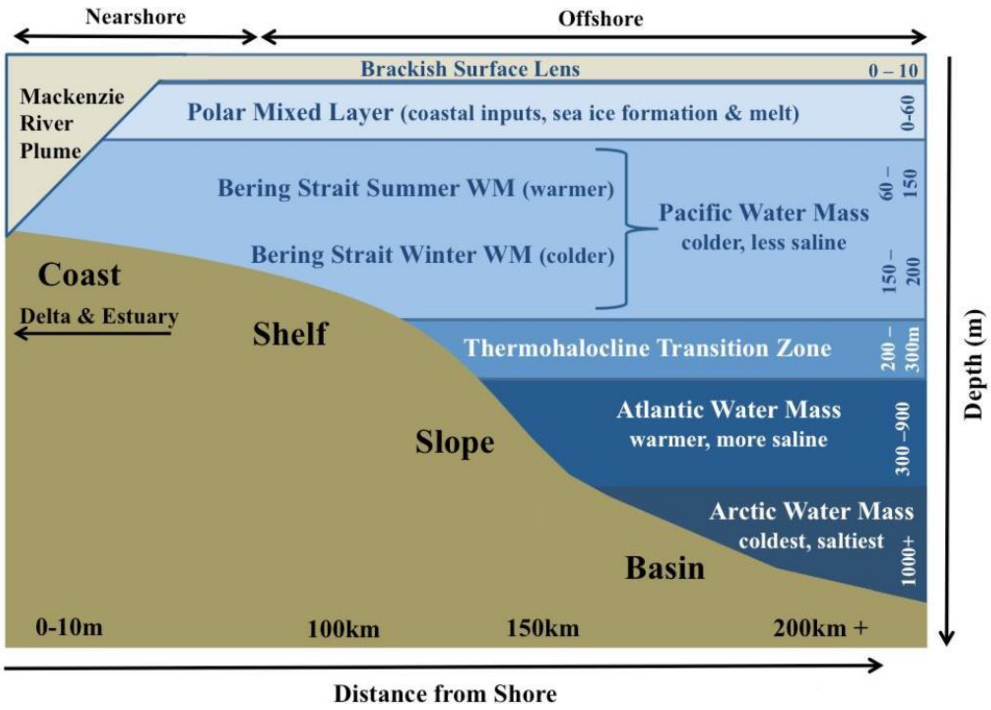

Figure 1.2 Description of water masses and their sources in the Canadian Beaufort Sea. Figure courtesy of MacPhee *et al.* (in press).

Layer, the upper 50m of the Beaufort Sea, is warm (up to 13°C in the summer) and relatively fresh (low salinity/density), influenced by precipitation as well as melting sea ice in the spring and river runoff in the summer (Crawford *et al.* 2011). According to past studies, the temperature maximum of the Canadian Beaufort Sea typically occurs at ~25m depth within the Polar Mixed Layer (Crawford *et al.* 2011). Temperature then decreases through the Pacific water mass to the warm thermohalocline at ~200m depth, is warmer in the Atlantic water mass, and is colder again in the Arctic water mass above the substrate. Through convection and freezing, mixing or homogenization of the Pacific Water Mass occurs down to the halocline and the Atlantic layer (Rudels *et al.* 1991). Below the transition between the Pacific and Atlantic water masses, the vertical structure of the Arctic Ocean remains relatively stable (Rudels *et al.* 1991). Along with the dynamic Beaufort Sea continental shelf, the continental slope and offshore regions are important habitats for many marine species, including fish, and support different marine communities based on the temperature and salinity differences among water masses.

Water currents from the Pacific and Atlantic oceans carry with them passive biota or "seed" populations that contribute to the diversity of the Beaufort Sea ecosystem among water masses (Carmack and Macdonald 2002). Many organisms have temperature and salinity preferences that can dictate their distribution. Alternatively, their prey may have preferences, and in that case temperature and salinity would indirectly influence the distribution of the organism of interest. For example, Walkusz *et al*. (2010) observed an effect of the Mackenzie River freshwater plume on zooplankton species composition. The effect could be attributed to either the effect of the plume on the physical properties of the water column or the effect of the plume on phytoplankton composition and primary production and, in turn, the zooplankton predators. Therefore, differences in temperature and salinity among water masses in the Beaufort Sea likely lead to differences in fish species composition of the community and their prey availability.

Seasonality in primary production translates to seasonality in prey quality and abundance for Arctic Cod, as the diet of many of their zooplankton prey is entirely phytoplankton, whose productivity relies on adequate nutrient levels and sunlight to fuel photosynthesis. Seasonality in the productivity of the Beaufort Sea is caused by a temporal mismatch of light energy and inorganic nutrients. Light energy in the Arctic is limited due to sea ice and/or the polar day/night annual cycle. In the Arctic, the sun sets in November and does not rise over the horizon for a long period of time until February, and this is called the Polar Night. During the Midnight Sun, the sun does not set for a long period of time from the end of April to mid-August. These phenomena occur when the Earth tilts the Arctic away or toward the sun respectively, altering the solar input to the area (Conover and Siferd 1993; Berge *et al.* 2015). In the Beaufort Sea, freeze-up begins in early to mid-October, and the ice begins to break up in late April (Cobb *et al.* 2008). The full extent of ice coverage during summer varies annually, and 2012 saw a record minimum extent of sea ice (Nghiem *et al.* 2014). This seasonal ice coverage results in seasonality of Beaufort Sea primary production due to light attenuation through the ice, despite the buildup of nutrients from the Pacific Ocean under the pack ice (Cobb *et al.* 2008). Limited solar input due to ice cover as well as incoming turbid river water contributes to seasonality of primary production in the Beaufort Sea. Nutrients are a necessary factor in primary productivity, and nutrient availability in the photic zone of the Beaufort Sea is driven by outflow from the Mackenzie River, wind mixing, as well as upwelling events along the continental slope and the presence of bathymetric features (e.g., the continental slope, Cape Bathurst, Kugmallit Canyon) (Carmack *et al.* 2004; Sallon *et al.* 2011; Walkusz *et al.* 2012). Nutrient levels are sufficient for primary production during the winter and spring, but ice coverage limits the solar input needed for photosynthesis. Ice coverage and solar input mostly control primary production throughout the year, but phosphate becomes limited in the summer when nutrients are depleted after the spring phytoplankton bloom at ice break-up. Seasonality in prey quantity and quality due to the seasonality in primary production may lead to seasonality in total energy consumption by Arctic Cod via their diet and thus seasonally affect energy pathways within individual Arctic Cod.

1.2 Arctic Cod in an Arctic Ecosystem

Biodiversity declines with increasing latitude, but there is no agreement on an explanation for this phenomenon (Payer *et al.* 2013). In the Arctic Ocean and surrounding seas, including the Beaufort Sea, marine fish diversity makes up only 2% of species and 20% of families worldwide. Species richness in the Beaufort Sea is currently estimated as containing only 66 species from 41 genera and 17 families (Christiansen and Reist 2014). Of those, nearly all are benthic. Arctic Cod are an abundant and semipelagic species (Benoit *et al.* 2008; Benoit 2012; Majewski *et al.* 2013; Geoffroy *et al.* 2015; Majewski *et al.* 2015). Young individuals will use sea ice as a habitat and eggs incubate there whereas adults migrate deeper in the water column during the summer, thus driving vertical energy fluxes in Arctic marine ecosystems (Geoffroy *et al.* 2015).

Arctic Cod occupy a pivotal role in the Beaufort Sea ecosystem structure. They are one of only a few forage fishes in the Beaufort Sea and are the most abundant fish in this ecosystem throughout the water column, classifying this a ‘wasp-waisted ecosystem’ (Lowry and Frost 1981; Welch *et al.* 1992; Rand and Logerwell 2011; Christiansen and Reist 2014). Arctic Cod occupy an intermediate position in the trophic structure in the Beaufort Sea, controlling the abundance of their predators (seals, beluga whales, seabirds, predatory fish such as turbot and Arctic skates) through bottom-up interactions and regulating the abundance of their prey (zooplankton) through top-down interactions (Fauchald *et al.* 2011). In other words, the flow of energy between the base of the food web and larger fish, marine mammals, and seabirds mostly moves through Arctic Cod as a central conduit (Hauser *et al.* 2015). Other forage fishes such as Capelin (*Mallotus villosus,* O.F. Müller 1776) and Polar Cod (*Arctogadus glacialis*, W.K.H. Peters 1872) are currently low in abundance in the Beaufort Sea, and thus appear to occupy minor roles in comparison to Arctic Cod. Warming of the Arctic due to climate change, however, may lead to a further northerly shift in distribution and/or increased abundance of subarctic forage fish species such as Capelin in the Beaufort Sea, which is expected to affect the structure of the Beaufort Sea ecosystem (Boulva 1979; Renaud *et al.* 2011; Hop and Gjøsæter 2013; McNicholl *et al.* 2015). Future competition for resources from other forage fishes could affect energy dynamics at the species and ecosystem level through a shift in prey by Arctic Cod or their predators.

Arctic Cod are the smallest gadid species, and are one of only a few that are native to the Arctic. They can live up to 7 years and may grow to 400mm length. Their life span is the shortest of all gadids, though *Arctogadus glacialis* may also be just as short-lived but age data on this species is lacking (Sufke *et al.* 1998). Arctic Cod are generally the most abundant fish captured in both the Alaskan and Canadian portions of the Beaufort Sea, comprising 92% of the total catch by number in Alaska (Rand and Logerwell 2011) and 84% in the current study area in the CBS (Majewski *et al.* 2015). Because of this, Arctic Cod are the most abundant, of highest biomass, and arguably the most ecologically important forage fish species in the high Arctic (Nahrgang *et al.* 2014).

Arctic Cod are found throughout the water column in Arctic seas up to at least 1000m depth, due to their relatively large tolerance limits for salinity, temperature, turbidity, and hydrostatic pressure (Hop and Graham 1995; Drost *et al.* 2014). Arctic Cod will often form aggregations, but are also found dispersed over large areas (Geoffroy *et al.* 2011; Majewski *et al.* 2013; Walkusz *et al.* 2013). Arctic Cod may aggregate to avoid predators, take advantage of an abundance of prey, or for spawning (Crawford and Jorgenson 1996; Benoit *et al.* 2008; Geoffroy *et al.* 2011), and they may be seasonally sympagic, i.e., aggregate under the ice, which is assumed to provide protection from diving predators (e.g., seals, seabirds; Benoit *et al.* 2010; Melnikov and Chernova 2013). Aggregating Arctic Cod can have a high proportion of empty stomachs, suggesting this behaviour compromises feeding success, in turn further suggesting the advantages of aggregation must be significant (Hop *et al.* 1997b).

Though Arctic Cod are found throughout the water column, vertical segregation by size or life history stage occurs. Arctic Cod larvae hatch and remain at the surface until they reach approximately 30-35mm length and become juveniles (Sekerak 1982; Falk-Petersen *et al.* 1986; Parker-Stetter *et al.* 2011; Benoit *et al.* 2013). Juveniles then descend, and adults remain generally associated with the bottom, though some individuals will make diel vertical migrations (DVMs) from the end of August to mid-May (Benoit *et al.* 2010; Geoffroy *et al.* 2015). The motivation for migrating to depth with age and remaining at depth as adults is likely to avoid predators (Benoit 2012). Prey energy density (e.g., lipid-rich *Calanus hyperboreus*, B. Lynn, *unpublished data*) and abundance in the CBS have also been observed to increase with depth (W. Walkusz, *unpublished data*), which may be advantageous to adults.

Because the average size of Arctic Cod increases with depth (Geoffroy *et al.* 2015; Majewski *et al.* 2015) and consequently their average gape size also increases with depth, these larger fish are concomitantly able to consume larger prey items as they move deeper. The life history of zooplankton suggests that older, more lipid-rich life stages of zooplankton (copepods and amphipods) are found deeper in the water column by the end of summer (Dalpadado *et al.* 2001; Falk-Petersen *et al.* 2009). Thus, beyond the need to avoid diving predators, the vertical migrations of older Arctic Cod may be to take advantage of prey of optimal size relative to their own, if the prey is also found that deep. Also, deeper water masses are cooler, thus metabolic costs may be lesser at depth. Although the variability in temperature is within 2°C, summed over months or years, this could have substantial consequences for Arctic Cod bioenergetics. See Section 1.3.2 for a discussion of thermal effects on metabolism.

1.3 Zooplankton Community

Copepods dominated the zooplankton samples numerically and by mass in this study of the CBS, and along with amphipods are the major prey of Arctic Cod (Walkusz *et al.* 2013). The distribution of copepods varies vertically among water masses due to their lipid content, as the individuals undergo a vertical ontogenetic migration to depth to overwinter once they accumulate enough energy stores (Scott *et al.* 2000; Pućko *et al.* 2014). Zooplankton distribution is also highly affected spatially by water currents and in their depth distribution by salinity conditions (Walkusz *et al.* 2010). While studying an ice station (2000m depth) in the Svalbard Archipelago, Berge *et al.* (2014) found multiple aggregations of zooplankton in the water column based on acoustic analysis, all ascending to the surface at night and descending up to 300m when ambient light increased, a typical DVM pattern. DVMs by zooplankton are also common in Arctic seas (Falkenhaug *et al.* 1997; Hattori and Saito 1997; Fortier *et al.* 2001; Berge *et al.* 2014), thus affecting their availability to fish predators, which may also affect the amount of energy needed by Arctic Cod to pursue prey. Aside from DVM, many copepods make vertical migrations depending on their life stage and the season (Falkenhaug *et al.* 1997; Falk-Petersen *et al.* 1999; Falk-Petersen *et al.* 2008; Pućko *et al.* 2014). A comprehensive, pan-Arctic study by Kosobokova and Hopcroft (2011) of zooplankton diversity in the Arctic found that common Arctic Cod prey, specifically *Calanus hyperboreus*, *Themisto libellula*, and *Themisto abyssorum* are found from the epipelagic (0-200m) to bathypelagic (1000-2000m) depths in the Canada Basin. Amphipods are typically found deeper than calanoid copepods in Arctic and subarctic waters (Dalpadado *et al.* 2001; Kosobokova and Hopcroft 2011). While there is little to no information on the seasonal or annual distribution of copepods in the CBS, an investigation of the zooplankton community in the Barents Sea observed *Calanus* making seasonal vertical migrations in July, shifting from the upper 100m of the water column to below 100m (Arashkevich *et al.*, 2002). Knowledge of the vertical distribution of prey in the CBS would aid in understanding the foraging behaviour of this Arctic Cod population, including the probability of selective foraging, as well as the energy needed to pursue and capture a migrating prey.

1.4 Energetics

1.4.1 Ecosystem Energetics

As noted above (Section 1.1), productivity on the Beaufort Shelf is highly seasonal. Ice coverage, seasonal light/dark cycles due to the high latitude, and nutrient use limits primary production and affects the seasonal distributions of some invertebrates including zooplankton. In turn, this affects the amount of energy available to the ecosystem directly and indirectly (Carmack *et al.*, 2004; Falkenhaug *et al.*, 1997). Still, underwater light conditions limited by snow and ice cover in the landfast and pack ice domains dictate under-ice primary productivity on the Beaufort Sea shelf (Carmack *et al.* 2004). Seasonality of nutrient levels also impacts under-ice primary production, and is largely influenced by river inputs. Open water allows for stratification by temperature and density that is counteracted by wind-driven vertical mixing and upwelling events along the shelf break, which replenish nutrient levels in the water column and promote productivity (Carmack *et al.* 2004). However, under-ice primary production is occurring year-long and its contribution to total primary production in polar regions is not negligible; however, good estimates of its actual contribution still elude researchers (Mundy *et al.* 2009). A predominant energy pathway in the CBS links energy from phytoplankton to zooplankton, to Arctic Cod, and then to larger fish, marine mammals, or seabirds. Under-ice primary producers and phytoplankton blooms initiate this energy flow in the spring. Blooms will either coincide with the spring ice break-up, occur in areas of episodic nutrient upwelling such as that near Cape

Bathurst in the southeastern Beaufort Sea, or via wind-driven upwelling events (Walkusz *et al.* 2012). Photosynthesis and primary productivity increase with temperature due to the effect of temperature on enzyme activity and chemical reaction rates (Li *et al.* 1984).

1.4.2 Fish Bioenergetics

Bioenergetics is the study of energy flow through living systems. Energy flow in living systems occur at various levels – that of the individual, collectively within populations, or at higher aggregations such as the ecosystem. Though many studies have noted the importance of Arctic Cod in Arctic food webs, only two studies have examined their importance in the flow of energy through the food webs and their individual energy usage or bioenergetics (Welch *et al.* 1992; Hop *et al.* 1997a) . The bioenergetics model for an individual fish, as in Rombough (1994) is:

$$C = R + P + E,$$

where

C = energy from prey consumption

R = basal metabolism, osmoregulation

P = growth, gonad development, lipid deposition in liver, muscle

E = activity costs, waste removal, specific dynamic action (SDA), heat

Energy consumed (C) is used to either support life (respiration, R), produce new tissue (P), or is lost from the system (E). The current study investigated differences in C and P, and assumed R and E were constant among individuals. If the physiological state of the fish is maintained, the energy obtained via consumption (C) of food determines the amount of energy available for allocation to basal requirements (R; e.g., basal metabolism, osmoregulation), but also to increase individual condition (P; e.g., growth, lipid storage) and contribute to the next generation (P, i.e., reproduction), or that which is lost (E; SDA, waste removal, activity, heat). Basal metabolism (R) is the energy expended to perform life-sustaining chemical reactions within the cells of a living organism while at rest. The cost of waste removal, part of E, involves the energy required to remove feces from the body and to excrete nitrogenous wastes including ammonia (an end product of protein catabolism in teleost fishes), and specific dynamic action (SDA) is the cost of metabolizing a meal including processing it for fuel and storage.

1.4.3 Foraging

The diet of organisms is generally dependent upon the prey quality and availability, as well as the selectivity of the forager (McNair 1982; Matley *et al.* 2013). Sensory abilities of the organism and their mobility and proximity to prey determine what is encountered. Foraging models help ecologists understand foraging behaviour in the natural environment by predicting how potential food items will be treated upon encounter. Prey and patch models are average-rate-maximizing models, meaning they maximize the average rate of energy gain while foraging, taking into consideration costs such as the energy required for handling and searching, while also considering the rate of prey encountered by type and the expected net energy gained from an individual prey item (Stephens 1986; Brown and Kotler 2004). These models address two basic problems: which prey items should a predator consume and when should the consumer leave a patch, patches being either patches of food or heterogeneities in prey distribution (McNair 1982). An organism may interpret the quality of a prey item from its size by using sensory characteristics. The cost of being a selective forager and targeting certain high energy (per individual) or easily obtainable prey is high when availability of some (desired) prey is unpredictable, thus Arctic fishes such as Arctic Cod are more likely to be generalists (Emlen 1966). As an example, copepods are energy dense and plentiful, but amphipods are larger and will provide more energy in one single meal, but are more rare. See Section 3.4.7 for energy densities of common Arctic Cod prey. A shift from small copepods to larger amphipods by older Arctic Cod could suggest they are opting for the reward of a ‘riskier’ high total energy prey (amphipods) relative to the reliability of a more abundant and readily available source of energy (copepods) in a highly seasonal Arctic environment.

1.4.4 Energy Allocation

Allocation of surplus energy to body growth, reproduction, or lipid storage typically depends on life history stage. As a juvenile fish, energy and nutrient usage is directed toward growth in order to reach a size that makes the individual less vulnerable to predation, although reproductive priorities may also be relevant. For slow-growing fish such as Arctic Cod, a strategy of somatic growth maximization is optimum, where all surplus energy is allocated to growth early in life history, especially when younger (Post and Parkinson 2001). Once fish reach the age or size of maturity, an appreciable portion of any surplus energy is typically diverted towards reproduction (Engen and Saether 1994; Heino and Kaitala 1999). However, living in a productively variable Arctic climate increases the need to store energy as energy-dense lipids during the summer when primary productivity is relatively higher. Thus, energy is split between growth and accumulating stores (e.g., lipids) to ensure over-winter survival (Post and Parkinson 2001).

1.5 The Analytical Structure

The goal of this thesis is to determine the differences in energy usage and flow within Arctic Cod in the Canadian Beaufort Sea ecosystem among three depth-defined habitats: Shelf, Upper Slope, and Lower Slope. Temperature and salinity vary among depth zones; metabolic costs are influenced by temperature as a result of the relationship between temperature and metabolic reaction rates, and osmoregulatory costs may also be influenced by salinity. To determine the effect of the environment on energy allocation by Arctic Cod, depth habitats (Shelf, Upper Slope, Lower Slope) were chosen as the controlling parameter.

The thermohalocline of the Beaufort Sea is the transition zone between the cold, lower salinity Pacific water mass and warmer, higher salinity Atlantic water mass. This area is a highly productive area of the water column, having sufficient nutrient levels and warmer temperatures within the euphotic zone away from diving predators. Warmer water temperatures should promote an increased speed of digestion, resulting in increased assimilation efficiency and thus growth rate. However, metabolic rates would also be higher with the higher temperature. The high productivity and possibly a high density of prey may still lead to Arctic Cod seeking out this habitat in order to grow faster. Hydroacoustic data in 2012 suggested aggregations of Arctic Cod had formed in the slope region (350-500m depth) extending offshore, in the thermohalocline (Geoffroy *et al.* 2015). This aggregation could be linked to a predator avoidance mechanism, both from diving predators and cannibalism by larger, benthic individuals (Geoffroy *et al.* 2015). However, there is no evidence that this type of aggregation of Arctic Cod occurs annually.

To understand differences in Arctic Cod diet with depth, prey vertical distribution must also be considered. Prey vertical distribution is dependent upon the temperature and salinity preferences of the zooplankton species, but also on the life stage, as well as their diel vertical migrations (Arashkevich *et al.* 2002; Falk-Petersen *et al.* 2009; Berge and Nahrgang 2013). Despite these vertical migrations, the zooplankton prey species composition varied among depths at the time of sampling. Thus, depth (and associated water mass) structure in the environment influences both the prey type (and thus energy density and content) and the size (and thus consumption and energy allocations) of Arctic Cod.

1.6 Objectives

The objectives of this study are thus to investigate: 1) differences in energy allocation and consumption (diet) of demersal Arctic Cod captured in August 2012 among the three depth-related habitats - Shelf, Upper Slope, and Lower Slope; and, 2) examine differences between sexes in regards to energy allocation. Diet was described by analysis of stomach contents of individuals at capture, whereas energy allocation was estimated by calculating body growth (length and mass at age), GSI (gonadosomatic index, gonad mass/somatic mass), HSI or energy storage in the liver (hepatosomatic index, liver mass/somatic mass), and Condition Factor (body mass/fork length) of individual fish.

Chapter 2 of this thesis describes the Beaufort Sea demersal Arctic Cod population in 2012 and compares it to other Arctic Cod populations around the world, and to the sample population analyzed in subsequent chapters. Chapter 3 investigates the relationship between depth habitats and Arctic Cod diet, taking into account the size of the individual cod. Chapter 4 determines how depth habitats, sex, and age relate to energy allocation in demersal Arctic Cod. Finally, Chapter 5 integrates the results, summarizes the findings, and describes possible future research to further understand Arctic Cod bioenergetics and energy flow in the Canadian Beaufort Sea.

1.7 Predictions for Depth- and Size Class-Specific Differences in Arctic Cod Diet and Energy Allocation in the Canadian Beaufort Sea

It is expected that demersal Arctic Cod diet and energy allocation will differ with depth. This is based on the differences in energetic requirements associated with living in each depth habitat, and differences in prey availability that are expected to affect diets among the depth habitats.

Ontogenetic differences in diet have been documented in Arctic Cod, related to their body size (Walkusz *et al.* 2013). A size class-related difference in diet is expected due to differences in vertical distribution of Arctic Cod with body size, but also due to the correlation between fish gape size and body length, which should dictate the maximum size of prey the fish can consume. Offspring of Arctic Cod hatch at the surface and descend to depth as they get larger and older, and larger prey is found deeper seasonally in the Canadian Beaufort Sea. A size class-related difference in diet may lead to a difference in energy available for allocation (Hop *et al.* 1997a), and because allocation strategy is expected to change with the stage of life history (i.e., age of the individual) (Post and Parkinson 2001; Alonso-Fernández and Saborido-Rey 2012), energy allocation likely also changes with size class.

1.8 Predictions for Sexual Differences in Energy Allocation by Arctic Cod in the Canadian Beaufort Sea

In many species of fish, the amount of energy invested into the next generation differs between the sexes. Sexes may differ in their mating and spawning behaviour, as well as their parental investment due to the inherent risks and costs associated with reproducing (Smith and Wootton 1995; Hayward and Gillooly 2011). This is expected to lead to differences in energetic cost of reproduction between the sexes. A lack of knowledge regarding behaviour of Arctic Cod in their natural environment makes it difficult to estimate activity costs and differences that may exist between sexes. Activity costs associated with mate attraction (e.g., mating calls in cods; Skjæraasen *et al.* 2012; Cott *et al.* 2014) and spawning (Rowe and Hutchings 2006) constitute a significant portion of the energy needed for reproduction. Hop *et al.* (1995) estimated that males and females drew 300kJ of energy from liver and muscle combined during the gonad development period, with the majority (>80%) from the liver. The total energy loss relative to their body size was 30-50% higher than for Atlantic Cod (*Gadus morhua* Linnaeus, 1758), Pacific Cod (*Gadus macrocephalus* Tilesius, 1810), and Walleye Pollock (*Theragra chalcogramma* Pallas, 1814). For females, total energy invested into egg mass was positively correlated with body mass and gonad size. Existing research on Arctic Cod reproductive biology has determined that they spawn under the ice in winter, releasing their gametes externally, and that the females' eggs are the largest of all Gadidae species, relative to their body size (Hop *et al.* 1995). During spawning in gadids, some species form mating balls with one female in the center of the aggregation around many males competing to fertilize the females' eggs (McPhail and Paragamian 2008). Whether this occurs in Arctic Cod is unknown, but the nature of broadcast spawning and the often-observed skewed sex ratio toward males suggests that sperm competition is a significant issue for Arctic Cod. Developing large gonads that can produce lots of sperm may be a way to compete in these mating balls, at a high cost to the individual. Hop *et al.* (1995) estimated that spawning costs for Arctic Cod differed overall between sexes (an average of 125kJ for ripe females and 67kJ for the one ripe male in the study). The ripe male in the Hop *et al.* (1995) study was smaller and weighed less (233mm and 77.4g) than the average ripe female (245 ± 2mm and 141.2 ± 5.8g, n = 51). Male Arctic Cod develop their gonads earlier in their life history than do females and males of other gadid species, thus may be more vulnerable to predation because they are larger and heavier, and therefore more conspicuous and move slower. However, males expend less energy than females to produce their gametes, and are expected to expend most of their reproductive energy to attract mates and achieve a successful reproductive event, as is the case in other cod species (Hop *et al.* 1995). In fish, the cost of producing a female gamete or egg is higher than that for producing a single sperm, but total sperm production is higher than total egg mass in fish (Hayward and Gillooly 2011). Still, the cost of gamete production is expected to be higher overall in females than males because an egg must contain a yolk sac to supply the growing larva with energy. Based on these established differences in the timing and energetic cost of producing gametes between sexes, it was expected that energy allocation to reproduction would differ by sex, being higher in females. Further, as growth has been shown to differ between sexes in other Arctic Cod populations (Jensen *et al.* 1991; Gjøsæter and Ajiad 1994), it was expected, *a priori*, that a difference in energy allocation to reproduction would translate to significant sexual differences in energy allocation to growth and energy storage, with males having more surplus energy available for allocation to growth and energy storage (Chapter 4).

1.9 References

Alonso-Fernández A, Saborido-Rey F (2012) Relationship between energy allocation and reproductive strategy in Trisopterus luscus. J Exp Mar Bio Ecol 416-417:8–16. doi: 10.1016/j.jembe.2012.02.001

Arashkevich E, Wassmann P, Pasternak A, Wexels C (2002) Seasonal and spatial changes in biomass, structure, and development progress of the zooplankton community in the Barents Sea. 38:125–145.

Benoit D (2012) Oceanographie, distribution et cycle annuel de la morue Arctique (Boreogadus saida) en mer de Beaufort: Une approche hydroacoustique. Universite Laval, Quebec

Benoit D, Simard Y, Fortier L (2008) Hydroacoustic detection of large winter aggregations of Arctic cod (Boreogadus saida) at depth in ice-covered Franklin Bay (Beaufort Sea). J Geophys Res 113:C06S90. doi: 10.1029/2007JC004276

Benoit D, Simard Y, Fortier L (2013) Pre-winter distribution and habitat characteristics of polar cod (Boreogadus saida) in southeastern Beaufort Sea. Polar Biol 37:149–163. doi: 10.1007/s00300-013-1419-0

Benoit D, Simard Y, Gagné J, Geoffroy M, Fortier L (2010) From polar night to midnight sun: photoperiod, seal predation, and the diel vertical migrations of polar cod (Boreogadus saida) under landfast ice in the Arctic Ocean. Polar Biol 33:1505–1520. doi: 10.1007/s00300-010-0840-x

Berge J, Cottier F, Varpe Ø, Renaud PE, Kwasniewski S, Griffiths C, Søreide JE, Johnsen G, Aubert A, Bjærke O, Hovinen J, Jung-Madsen S, Tveit M, Majaneva S (2014) Arctic complexity: A case study on diel vertical migration of zooplankton. J Plankton Res 36:1279–1297. doi: 10.1093/plankt/fbu059

Berge J, Nahrgang J (2013) The Atlantic spiny lumpsucker Eumicrotremus spinosus: life history traits and the seemingly unlikely interaction with the pelagic amphipod Themisto libellula. Polish Polar Res 34:279–287. doi: 10.2478/popore

Berge J, Renaud PE, Darnis G, Cottier F, Last K, Gabrielsen TM, Johnsen G, Seuthe L, Weslawski JM, Leu E, Moline M, Nahrgang J, Søreide JE, Varpe O, Lønne OJ, Daase M, Falk-Petersen S (2015) In the dark: A review of ecosystem processes during the Arctic polar night. Prog Oceanogr 139:258–271. doi: 10.1016/j.pocean.2015.08.005

Boulva J (1979) Comparison of the Arctic cod (Boreogadus saida), the polar cod (Arctogadus glacialis) and the toothed cod (Arctogadus borisovi). CAFSAC Res Doc 50:1–12.

Bradstreet M, Finley K, Sekerak A, Griffiths WB, Evans CR, Fabijan MF, Stallard HE (1986) Aspects of the biology of Arctic cod (Boreogadus saida) and its importance in the Arctic marine food chains. In: Canadian Technical Report of Fisheries and Aquatic Sciences. p 202

Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. Ecol Lett 7:999–1014. doi: 10.1111/j.1461-0248.2004.00661.x

Carmack EC, Macdonald RW (2002) Oceanography of the Canadian Shelf of the Beaufort Sea: A setting for marine life. Arctic 55:29–45. doi: 10.1126/science.100.2596.291

Carmack EC, Macdonald RW, Jasper S (2004) Phytoplankton productivity on the Canadian Shelf of the Beaufort Sea. Mar Ecol Prog Ser 277:37–50.

Childress JJ (1995) Are there physiological and biochemical adaptations of metabolism in deep-sea animals? Trends Ecol Evol 10:30–36.

Christiansen JS, Reist JD (2014) Fishes. In: Meltofte H, Josefson AB, Payer D (eds) Arctic Biodiversity Assessment. pp 192–245

Clarke A, Johnston N (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. J Anim Ecol 893–905.

Cobb D, Fast H, Papst D, Rosenberg R, Rutherford R, Sareault JE (2008) Beaufort Sea large ocean management area: ecosystem overview and assessment report. Can Tech Rep Fish Aquat Sci 2780:ii-ix + 188 pp.

Conover RJ, Siferd TD (1993) Dark-season survival strategies of coastal zone zooplankton in the Canadian Arctic. Arctic 46:303–311.

Cott PA, Hawkins AD, Zeddies D, Martin B, Johnston TA, Reist JD, Gunn JM, Higgs DM (2014) Song of the burbot: Under-ice acoustic signaling by a freshwater gadoid fish. J Great Lakes Res 40:435–440. doi: 10.1016/j.jglr.2014.02.017

Crawford RE, Jorgenson JK (1996) Quantitative studies of Arctic Cod (Boreogadus saida) schools: Important energy stores in the Arctic food web. Arctic 49:181–193.

Crawford RE, Vagle S, Carmack EC (2011) Water mass and bathymetric characteristics of polar cod habitat along the continental shelf and slope of the Beaufort and Chukchi seas. Polar Biol 35:179–190. doi: 10.1007/s00300-011-1051-9

Dalpadado P, Borkner N, Bogstad B, Mehl S (2001) Distribution of Themisto (Amphipoda) spp. in the Barents Sea and predator-prey interactions. ICES J Mar Sci 58:876–895. doi: 10.1006/jmsc.2001.1078

Drost HE, Carmack EC, Farrell AP (2014) Upper thermal limits of cardiac function for Arctic cod Boreogadus saida, a key food web fish species in the Arctic Ocean. J Fish Biol 84:1781–92. doi: 10.1111/jfb.12397

Emlen JM (1966) The role of time and energy in food preference. Am Soc Nat 100:611–617.

Engen S, Saether B (1994) Optimal allocation of resources to growth and reproduction. Theor

Popul Biol 46:232–248. doi: 10.1006/tpbi.1994.1026

Falk-Petersen I, Frivoll V, Gulliksen B, Haug T (1986) Occurrence and size/age relations of polar cod, Boreogadus saida (Lepechin), in Spitsbergen coastal waters.

Falk-Petersen S, Leu E, Berge J, Kwasnieswki S, Nygård H, Rostad A, Keskinen E, Thormar J, von Quillfeldt C, Wold A, Gulliksen B (2008) Vertical migration in high Arctic waters during autumn 2004. Deep Sea Res Part II Top Stud Oceanogr 55:2275–2284. doi: 10.1016/j.dsr2.2008.05.010

Falk-Petersen S, Mayzaud P, Kattner G, Sargent JR (2009) Lipids and life strategy of Arctic Calanus. Mar Biol Res 5:18–39. doi: 10.1080/17451000802512267

Falk-Petersen S, Pedersen G, Kwasniewski S, Nøst E (1999) Spatial distribution and life-cycle timing of zooplankton in the marginal ice zone of the Barents Sea during the summer melt season in 1995. J Plankton Res 21:1249–1264.

Falkenhaug T, Tande K, Semenova T (1997) Diel, seasonal and ontogenetic variations in the vertical distributions of four marine copepods. Mar Ecol Prog Ser 149:105–119.

Fauchald P, Skov H, Skern-Mauritzen M, Johns D, Tveraa T (2011) Wasp-waist interactions in the North Sea ecosystem. PLoS One. doi: 10.1371/journal.pone.0022729

Fortier M, Fortier L, Hattori H, Saito H, Legendre L (2001) Visual predators and the diel vertical migration of copepods under Arctic sea ice during the midnight sun. J Plankton Res 23:1263–1278. doi: 10.1093/plankt/23.11.1263

Geoffroy M, Majewski A, LeBlanc M, Gauthier S, Walkusz W, Reist JD, Fortier L (2015) Vertical segregation of age-0 and age-1 + polar cod (Boreogadus saida) over the annual cycle in the Canadian Beaufort Sea. Polar Biol. doi: 10.1007/s00300-015-1811-z

Geoffroy M, Robert D, Darnis G, Fortier L (2011) The aggregation of polar cod (Boreogadus saida) in the deep Atlantic layer of ice-covered Amundsen Gulf (Beaufort Sea) in winter. Polar Biol 34:1959–1971. doi: 10.1007/s00300-011-1019-9

Gjøsæter H, Ajiad A (1994) Growth of polar cod, Boreogadus saida (Lepechin), in the Barents Sea. ICES J Mar Sci: 1–8.

Hattori H, Saito H (1997) Diel changes in vertical distribution and feeding activity of copepods in ice-covered Resolute Passage, Canadian Arctic, in spring 1992. J Mar Syst 11:205–219. doi: 10.1016/S0924-7963(96)00039-5

Hauser DDW, Laidre KL, Parker-Stetter SL, Horne JK, Suydam RS, Richard PR (2015) Regional diving behavior of Pacific Arctic beluga whales Delphinapterus leucas and possible associations with prey. Mar Ecol Prog Ser 541:245–264. doi: 10.3354/meps11530

Hayward A, Gillooly JF (2011) The cost of sex: Quantifying energetic investment in gamete production by males and females. PLoS One. doi: 10.1371/journal.pone.0016557

Heino M, Kaitala V (1999) Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. J Evol Biol 12:423–429. doi: 10.1046/j.1420-9101.1999.00044.x

Hop H, Gjøsæter H (2013) Polar cod (Boreogadus saida) and capelin (Mallotus villosus) as key species in marine food webs of the Arctic and the Barents Sea. Mar Biol Res 9:878–894. doi: 10.1080/17451000.2013.775458

Hop H, Graham M (1995) Respiration of juvenile Arctic cod (Boreogadus saida): effects of acclimation, temperature, and food intake. Polar Biol 15:359–367.

Hop H, Graham M, Wordeau VL (1995) Spawning energetics of Arctic cod (Boreogadus saida) in relation to seasonal development of the ovary and plasma sex steroid levels. Can J Fish Aquat Sci 52:541–550.

Hop H, Tonn WM, Welch HE (1997a) Bioenergetics of Arctic cod (Boreogadus saida) at low temperatures. Can J Fish Aquat Sci 54:1772–1784. doi: 10.1139/f97-086

Hop H, Welch HE, Crawford RE (1997b) Population structure and feeding ecology of Arctic cod schools in the Canadian Arctic. In: American Fisheries Society Symposium. pp 68–79

Jensen T, Ugland KI, Anstensrud M (1991) Aspects of growth in Arctic cod, Boreogadus saida (Lepechin 1773). Polar Res 10:547–552. doi: 10.1111/j.1751-8369.1991.tb00672.x

Kosobokova KN, Hopcroft RR (2011) Patterns of zooplankton diversity through the depths of the Arctic's central basins. 29–50. doi: 10.1007/s12526-010-0057-9

Li W, Smith J, Platt T (1984) Temperature response of photosynthetic capacity and carboxylase activity in Arctic marine phytoplankton. Ecology 17:237–243. doi: 10.3354/meps017237

Lowry L, Frost K (1981) Distribution, growth, and foods of Arctic cod (Boreogadus saida) in the Bering, Chukchi, and Beaufort seas. Can Field-Naturalist 95:186–191.

MacPhee, SA, Kamula CM, Majewski AR, Alfonso NA, Coad BW, Reist JD. (in prep) Distribution, diversity, and basic habitat associations of marine fishes of the Canadian Beaufort Sea/Amundsen Gulf Ecozone. Canadian Manuscript Report of Fisheries and Aquatic Sciences.

Majewski AR, Lynn BR, Lowdon MK, Williams WJ, Reist JD (2013) Community composition of demersal marine fishes on the Canadian Beaufort Shelf and at Herschel Island, Yukon Territory. J Mar Syst. doi: 10.1016/j.jmarsys.2013.05.012

Majewski AR, Walkusz W, Lynn BR, Atchison S, Eert J, Reist JD (2015) Distribution and diet of demersal Arctic Cod, Boreogadus saida, in relation to habitat characteristics in the Canadian Beaufort Sea. Polar Biol. doi: 10.1007/s00300-015-1857-y

Matley JK, Fisk AT, Dick TA (2013) The foraging ecology of Arctic cod (Boreogadus saida) during open water (July–August) in Allen Bay, Arctic Canada. Mar Biol 160:2993–3004. doi: 10.1007/s00227-013-2289-2

McLaughlin F, Shimada K, Carmack E, Itoh M, Nishino S (2005) The hydrography of the southern Canada Basin, 2002. Polar Biol 182–189. doi: 10.1007/s00300-004-0701-6

McLaughlin FA, Carmack EC, Macdonald RW, Bishop JKB (1996) Physical and geochemical properties across the Atlantic/Pacific water mass front in the southern Canadian Basin. J Geophys Res 101:1183–1197.

McNair JN (1982) Optimal giving-up times and the marginal value theorem. 119:511–529.

McNicholl DG, Walkusz W, Davoren GK, Majewski AR (2015) Dietary characteristics of co-occurring polar cod (Boreogadus saida) and capelin (Mallotus villosus) in the Canadian Arctic, Darnley Bay. Polar Biol 1–10. doi: 10.1007/s00300-015-1834-5

McPhail JD, Paragamian VL (2008) Burbot biology and life history. In: Paragamian VL, Willis DW (eds) BURBOT: Biology, Ecology, and Management. Fisheries Management Section of the American Fisheries Society, p 270

Melnikov IA, Chernova N V. (2013) Characteristics of under-ice swarming of polar cod Boreogadus saida (Gadidae) in the Central Arctic Ocean. J Ichthyol 53:7–15. doi: 10.1134/S0032945213010086

Mundy CJ, Gosselin M, Ehn J, Gratton Y, Rossnagel A, Barber DG, Martin J, Tremblay JÉ, Palmer M, Arrigo KR, Darnis G, Fortier L, Else B, Papakyriakou T (2009) Contribution of under-ice primary production to an ice-edge upwelling phytoplankton bloom in the Canadian Beaufort Sea. Geophys Res Lett 36:L17601. doi: 10.1029/2009GL038837

Nahrgang J, Varpe O, Korshunova E, Murzina S, Hallanger IG, Vieweg I, Berge J (2014) Gender specific reproductive strategies of an Arctic key species (Boreogadus saida) and implications of climate change. PLoS One 9:11. doi: 10.1371/journal.pone.0098452

Nghiem S, Hall D, Rigor I, Li P, Neumann G (2014) Effects of Mackenzie River discharge and bathymetry on sea ice in the Beaufort Sea. Geophys Res Lett 873–879. doi: 10.1002/2013GL058954.Received

Parker-Stetter SL, Horne JK, Weingartner TJ (2011) Distribution of polar cod and age-0 fish in the U.S. Beaufort Sea. Polar Biol 34:1543–1557. doi: 10.1007/s00300-011-1014-1

Payer DC, Josefson AB, Fjeldså J (2013) Species diversity in the Arctic. In: Meltofte H, Josefson AB, Payer D (eds) Arctic Biodiversity Assessment. pp 66–77

Post J, Parkinson E (2001) Energy allocation strategy in young fish: allometry and survival. Ecology 82:1040–1051.

Pućko M, Burt A, Walkusz W, Wang F, Macdonald RW, Rysgaard S, Barber DG, Tremblay JÉ, Stern GA (2014) Transformation of mercury at the bottom of the Arctic food web: An overlooked puzzle in the mercury exposure narrative. Environ Sci Technol 48:7280–7288. doi: 10.1021/es404851b

Rand KM, Logerwell EA (2011) The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. Polar Biol 34:475–488. doi: 10.1007/s00300-010-0900-2

Renaud PE, Berge J, Varpe Ø, Lønne OJ, Nahrgang J, Ottesen C, Hallanger I (2011) Is the poleward expansion by Atlantic cod and haddock threatening native polar cod, Boreogadus saida? Polar Biol 35:401–412. doi: 10.1007/s00300-011-1085-z

Rombough P (1994) Energy partitioning during fish development: additive or compensatory allocation of energy to support growth? Funct Ecol 8:178–186.

Rowe S, Hutchings JA (2006) Sound production by Atlantic Cod during spawning. Trans Am

Fish Soc 135:529–538. doi: 10.1577/T04-061.1

Rudels B, Larsson A, Sehlstedt P (1991) Stratification and water mass formation in the Arctic Ocean: some implications for the nutrient distribution. Polar Res 19–31. doi: 10.1111/j.1751-8369.1991.tb00631.x

Sallon A, Michel C, Gosselin M (2011) Summertime primary production and carbon export in the southeastern Beaufort Sea during the low ice year of 2008. Polar Biol 34:1989–2005. doi: 10.1007/s00300-011-1055-5

Scott CL, Kwasniewski S, Falk-Petersen S, Sargent JR (2000) Lipids and life strategies of Calanus finmarchicus, Calanus glacialis and Calanus hyperboreus in late autumn, Kongsfjorden, Svalbard. Polar Biol 23:510–516.

Sekerak A (1982) Young-of-the-year cod (Boreogadus) in Lancaster Sound and western Baffin Bay. Arctic 35:75–87.

Skjæraasen JE, Meager JJ, Heino M (2012) Secondary sexual characteristics in codfishes (Gadidae) in relation to sound production, habitat use and social behaviour. Mar Biol Res 8:201–209. doi: 10.1080/17451000.2011.637562

Smith C, Wootton RJ (1995) The costs of parental care in teleost fishes. Rev Fish Biol Fish 5:7–22. doi: 10.1007/BF01103363

Stephens DW, Krebs JR (1986) Foraging theory. Princeton, NJ: Princeton University Press.

Sufke L, Piepenburg D, von Dorrien CF (1998) Body size, sex ratio and diet composition of Arctogadus glacialis (Peters, 1874) (Pisces: Gadidae) in the Northeast Water Polynya (Greenland). Polar Biol 20:357–363.

Walkusz W, Majewski A, Reist JD (2013) Distribution and diet of the bottom dwelling Arctic cod in the Canadian Beaufort Sea. J Mar Syst 127:65–75. doi:

10.1016/j.jmarsys.2012.04.004

Walkusz W, Paulić JE, Kwaśniewski S, Williams WJ, Wong S, Papst MH (2010) Distribution, diversity and biomass of summer zooplankton from the coastal Canadian Beaufort Sea. Polar Biol 33:321–335. doi: 10.1007/s00300-009-0708-0

Walkusz W, Williams WJ, Harwood LA, Moore SE, Stewart BE, Kwasniewski S (2012) Composition, biomass and energetic content of biota in the vicinity of feeding bowhead whales (Balaena mysticetus) in the Cape Bathurst upwelling region (south eastern Beaufort Sea). Deep Sea Res Part I Oceanogr Res Pap 69:25–35. doi: 10.1016/j.dsr.2012.05.016

Welch HE, Bergmann MA, Siferd TD, Martin KA, Curtis MF, Crawford RE, Conover RJ, Hop H (1992) Energy flow through the marine ecosystem of the Lancaster Sound Region, Arctic Canada. Arctic 45:343–357.

White CR, Alton LA, Frappell PB (2011) Metabolic cold adaptation in fishes occurs at the level of whole animal, mitochondria and enzyme. Proc R Soc London B Biol Sci 279:1740–1747. doi: 10.1098/rspb.2011.2060

2 Demersal Arctic Cod, *Boreogadus saida* (Lepechin 1774) in the Canadian Beaufort Sea Compared to Other Populations

2.1 Introduction

Arctic Cod, *Boreogadus saida,* is a small, circumpolar gadid that is important in the Arctic marine food web. Arctic Cod are found throughout the water column, but this study concentrated on demersally captured individuals for ease of comparison among depth zones. Variability in temperature and salinity among circumpolar environments in which Arctic Cod live are expected to lead to spatial differences in their basal energy requirements and therefore to the amount of energy available for allocation to somatic growth, and thus to differences in size at age (Engen and Saether 1994). Basal energy requirements in animals are dependent on the size of the organism, but can be affected by environmental temperature (Clarke and Johnston 1999). Salinity may affect the energetic cost of osmoregulation in fish, though this cost is low in marine fishes (Boeuf and Payan 2001). Whereas Arctic Cod are tolerant to differences in salinity and temperature typical of Arctic ecosystems, their vertical distribution may be indirectly influenced by water mass stratification, and temperature and salinity variances among water masses (see Section 1.3.2 for more information on the effect of salinity and temperature on fish bioenergetics).

Arctic Cod have been observed to closely associate with their zooplankton prey (Geoffroy *et al*. 2011) while also distributing themselves deep enough to avoid diving predators (e.g., seals and seabirds; Benoit *et al*. 2010). The vertical distribution of zooplankton changes seasonally depending on their developmental stage and the availability of their prey (Hirche 1997; Dalpadado *et al*. 2001; Dalpadado 2002; Pućko *et al*. 2014). This likely contributes to the seasonal and regional variation in vertical distribution of Arctic Cod among and within the water masses. Interspecific competition for zooplankton prey appears to be currently minimal for Arctic Cod in the Canadian (BREA 2012) and Alaskan Beaufort seas (Rand and Logerwell 2011), but is prevalent in the Barents Sea (Rose 2005; Orlova *et al.* 2010). The lack of competition for Arctic Cod in the Beaufort Sea evidenced by a low abundance of other forage fishes (Crawford 2003; Majewski *et al.* 2009b) was thought to be due to the effect of the Polar Night, the darkness reducing the chance of a prey encounter for fish that rely on visual detection, due to a reduction in food availability and light. Recent research suggests it may be the adaptation by Arctic Cod to reproduce during the Polar Night rather than an inability of sub-Arctic forage fishes to capture prey that prevents colonization of these areas to a large degree by sub-Arctic forage fishes (Berge *et al.* 2015). However, the geographic range of Capelin has been spreading further north into the geographic range of Arctic Cod, attributable to climate change (Hop and Gjøsæter 2013; McNicholl *et al.* 2015). The dietary niche of Capelin overlaps significantly with Arctic Cod, so they have the potential to compete for prey when they co-occur (McNicholl *et al.* 2015). Differences in environmental conditions, prey species composition and abundance, and competition from other forage fishes may lead to differences in the bioenergetics and diet of Arctic Cod among different Arctic ecosystems around the world.

To place the population of Arctic Cod in the Canadian Beaufort Sea (CBS) studied herein (as captured in August 2012) in the wider context and also to provide background information relevant to the additional analytical chapters of this thesis, the objective of this chapter was to compare the 2012 CBS Arctic Cod sample to past surveys of the same area, to other populations of Arctic Cod around the world, to a pelagic sample from the same area captured in the same year, and to a sub-sample of the 2012 CBS Arctic Cod used in the rest of this thesis. This establishes the 2012 sample used herein in the context of existing knowledge of Arctic Cod, and specifically the CBS population. Population characteristics are also compared between the entire 2012 sample and the sub-sample used in the analyses of diet (Chapter 3) and energy allocation (Chapter 4) to determine if the sub-sample is representative of the broader sample of the CBS Arctic Cod population in 2012. If this is the case, the interpretation of the results will have wider applicability to our understanding of Arctic Cod in the global context (see discussions in Chapters 3, 4, and 5).

2.2 Methods

2.2.1 Sample Collection

In August 2012, Atlantic Western IIA otter trawl nets, with a 22.86m head rope, 21.23m foot rope, and a cod-end with a mesh size of 1.27cm (0.5in), were towed from the F/V *Frosti*, a 39.9m-long stern trawler, at 26 benthic stations along four transects (Figure 2.1) in the CBS as part of the BREA-MFP to sample the bottom-dwelling fish community. The trawl net was paired with Thyborøn Type II, 2.72 m (107 in) bottom-tending doors. Net deployments were standardized to 20 minutes bottom-time at a target speed-over-ground (SOG) of 1.49 ms^{-1} (2.9 kts). If the bottom was too rough, trawling time was shortened to avoid damaging the net. Average door spread, speed, and the duration of each net deployment was recorded and used to calculate area swept. Transects ran perpendicular to shore across the continental shelf and slope to deeper-water habitats, in an attempt to establish baselines and to understand linkages between coastal and offshore habitats (Figure 2.1). Hydroacoustic analysis identified densities of biota that were then targeted with pelagic trawl nets, where a Cosmos-Swam 260m trawl net with a 1.27cm cod-end liner was towed in the pelagic zone at 50-1000m depth for 10-20 minutes at 3-

5kts along the Beaufort Shelf slope in conjunction with additional hydroacoustic analyses. Hydroacoustic analyses were conducted along both the on-to-offshore transects as well as alongshore following the 300m depth isobath. After each catch was collected, fish fork length was measured to the nearest mm and then identified by species or the lowest taxonomic level

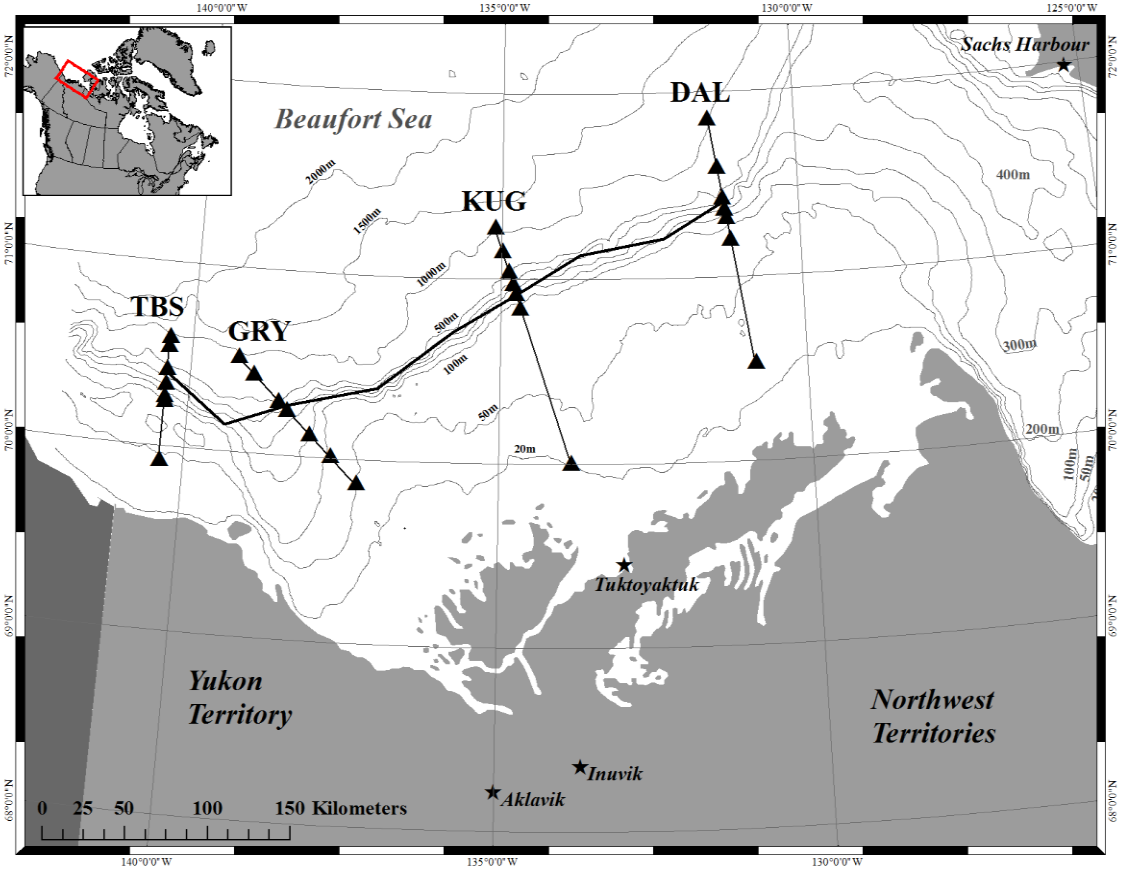

Figure 2.1 Map of the sampling area for the Beaufort Sea Regional Environmental Assessment Marine Fishes Project (BREA-MFP) in 2012. Stations are indicated by black triangles along sampling transects, oriented perpendicular to shore. The line connecting the sampling transects along the continental slope is where hydroacoustic sampling of high densities of Arctic Cod occurred. Map courtesy of Andrew Majewski, DFO.

possible (Mecklenburg *et al*. 2002). The fish were initially stored on the ship at -50°C, then transferred to a holding area at -30°C and shipped to the Freshwater Institute, Winnipeg, Manitoba, Canada. Follow-on processing in the laboratory included length measurements, mass determinations, otolith extraction, and analysis of gonads to determine sex. All pelagic trawls captured 665 Arctic Cod. Of all benthic catches from these transects, 3317 Arctic Cod were captured and a sub-sample of 237 fish were selected for detailed examination of the energetic questions in this thesis (see below).

2.2.2 Data Collection

All sample handling was performed in ways to best preserve the integrity of the tissues by reducing the extent of thawing. In the lab (at 4°C) at the Freshwater Institute, standard biological measurements were taken including length (standard, fork, and total ± 0.01mm) and mass (± 0.001g) of whole fish. Gonads and livers were dissected, removed, and mass determined (± 0.001g). Visual examination of gonads was used to determine the sex of the individual (Appendix A, Table 6.1; Majewski *et al*. 2009). Sex was determined for 1448 of the 3317 demersal Arctic Cod captured. Otoliths were also removed and dried for age estimation. Age was estimated for 286 of the 3317 demersal Arctic Cod captured, including all individuals in the sub-sample (see Sec 2.2.1 for selection strategy) as well as those remaining in the overall sample that were large in body length. There is insofar no interest in aging any other individuals captured during the 2012 sampling season.

2.2.3 Age Estimation

Once dried, otoliths were read whole after being cleared by soaking in deionized water for two hours to increase visibility of annuli as the water molecules bind to the proteinaceous annuli (Gauldie *et al*. 1998). The otoliths were read against a black background with reflected light at 1.25x magnification with the sulcus, convex surface facing down. Higher magnifications were used if necessary to observe annuli more clearly. In cases where clearing did not allow for full visibility of annuli, the otolith was polished on a soft stone. After initial training, all otoliths were aged by the author. To ensure reliability of the age estimations, 15% of the sample was checked and blindly re-aged by R. Wastle, fish-ageing technician at the Freshwater Institute, Winnipeg, Manitoba, Canada. If consensus on the age estimate was not reached between both readers (3.4% of those checked), the otolith(s) in question were embedded and sectioned. Using this method, the otolith was placed with its sulcus up in Cold Cure Epoxy Resin (System Three Resins, Inc.) on a square of Parafilm. The nucleus was then marked with a fine-tip marker, and a thin section of it was made by a double-blade Buehler Isomet low speed saw with two Buehler Diamond Wafering Blades. It was important that the nucleus be included in the section in order to capture all annuli. The thin section was then examined under a microscope with either reflected or transmitted light and re-aged without knowledge of previous age estimates. This age was then compared with the age determined via the whole-otolith method. If there was still disagreement on the age-estimate for the specimen, then that individual fish was not included in further age analyses. Age was estimated for only 286 of the 3317 Arctic Cod captured by benthic trawls on transect and 237 of those were included in a sub-sample analyzed in subsequent chapters. An age of 1+ (age-1+) indicates that the individual was estimated to be between 1 and 2 years old.

2.2.4 Rationale for Subsampling

Fish size influences the diet of Arctic Cod (Walkusz *et al*. 2011; Rand *et al*. 2013) and thus the proportion of energy allocated to fish growth (Heino and Kaitala 1999). Ten (10) individuals were selected from each sampling station in order to represent the entire size range demersally captured therein (n = 237 fish for 26 stations) for further analysis in the following work on Arctic Cod diet (Chapter 3) and growth (Chapter 4). Sample sizes were low at deep stations, thus fewer than 10 individuals were included in the analyses from those. That is, in so far as possible individual station samples were selected in a stratified manner to cover the entire size range present within that sample. Arctic Cod of intermediate sizes were common and therefore are under-represented in the sub-sample in terms of their actual abundance in the overall 2012 sample compared to the small and large individuals, which were over-represented. Overall, individual fish were chosen for this study in order to represent a random sub-sample stratified by fish length both for individual stations and for the overall sample of n = 237 examined herein. Other than fish length, all other biological information (e.g., sex, mass) was unknown during the selection of individuals for the sub-sample. Population-level characteristics and morphometrics are compared between the larger sample and the sub-sample to determine whether the sub-sample is representative of the Beaufort Sea Arctic Cod population sampled in 2012.

2.2.5 Analytical Structure of the Study

The Beaufort Sea was delineated into three depth zones (Shelf, Upper Slope, and Lower Slope), as outlined in Chapter 1, based on established differences in temperature and salinity. The temperature and salinity data from the 2012 sampling are summarized below (Table 2.1). Prey composition and presumably availability to Arctic Cod similarly varied among these depth zones and the associated Arctic Ocean water masses. In order to standardize the sampling for statistical comparisons, only Arctic Cod captured by demersal nets were included in the analyses.

2.2.6 Statistical Analyses

To determine whether habitat could explain detected differences in the Canadian Beaufort Sea Arctic Cod population, environmental data was compared among depth zones. As the data did not meet the parametric assumptions of homogeneity of variance, median values for temperature and salinity data, analyzed over the bottom 2m of the water at each station or the height of the trawl net, were compared among depth zones using a Kruskal-Wallis test. Median temperature and salinity were also compared among transects.

For the biological data, a Chi-square test was used to determine whether the observed sex ratio of demersally captured Arctic Cod was significantly different from 1:1. A z-test was then used to determine if the proportion of males was significantly different between the sample and sub-sample of CBS Arctic Cod. A Bartlett's test was used to test for homogeneity of variance in: 1) length at age between the demersal sample and sub-sample of CBS Arctic Cod, and 2) fork length among depth zones. The groups in both tests did not meet the parametric assumptions due to heterogeneity of variances and unequal sample sizes, thus Kruskal-Wallis tests were used to determine if median length at age was significantly different between the sample and sub-sample, and if median fork length was significantly different among depth zones. The data for Arctic Cod captured by mid-water trawls also did not meet the parametric assumptions, so Kruskal-Wallis tests were used to compare median fork length between the demersal and pelagic sample of CBS Arctic Cod.

2.3 Results and Discussion

2.3.1 Physical Properties of Sampling Location

Temperature of the sampling location in the Canadian Beaufort Sea varied from -1.44 to 0.75°C. Median temperature increased significantly with depth (Table 2.1; Kruskal-Wallis with

Holm correction; Shelf-Upper Slope: p-adj < 0.0001; Shelf-Lower Slope: p-adj = 0.002; Upper Slope-Lower Slope: p-adj < 0.0001). This is comparable to conditions in the referenced studies from the Svalbard archipelago, the Alaskan Beaufort Sea, and the Chukchi Sea, except for Kongsfjorden which is a fjord and is slightly warmer with no shelf area (Table 2.3; Frost and Lowry; Craig *et al.* 1982; Nahrgang *et al.* 2014). Median salinity on the Shelf also increased significantly with depth (Table 2.1; Kruskal-Wallis with Holm correction; Shelf-Upper Slope: p-adj < 0.0001; Shelf-Lower Slope: p-adj < 0.0001; Upper Slope-Lower Slope: p-adj < 0.0001). The range of salinity levels are comparable to those of the referenced studies from the other regions (Table 2.3).

Table 2.1 Description of three depth zones in the Canadian Beaufort Sea by temperature and salinity conditions (PSU: practical salinity unit (dimensionless), used to describe the concentration of dissolved salts in water in terms of a conductivity ratio). Differing letter superscripts indicate a difference in temperature and salinity among depth zones. Median temperature increased with depth (Kruskal-Wallis with Holm correction; Shelf-Upper Slope, p-adj < 0.0001; Shelf-Lower Slope, p-adj $= 0.002$; Upper Slope-Lower Slope: p-adj < 0.0001) and the Lower Slope (p-adj $= 0.002$). Median salinity increased with depth, and was significantly different among all depth zones (Shelf-Upper Slope: p-adj < 0.0001; Shelf-Lower Slope: p-adj < 0.0001; Upper Slope-Lower Slope: p-adj < 0.0001).

Depth Zone	Depth	Water Masses Within	n	Median Temperature (°C ± SE)	Median Salinity (PSU ± SE)
1) Shelf	15-220	Polar Mixed Layer (PML), Pacific Water Mass (PWM)	71	$-0.85^{a} \pm 0.08$	$32.32^{a} \pm 0.10$
2) Upper Slope	>220-510	Thermohalocline, Atlantic Water Mass (AWM)	161	$0.51^{b} \pm 0.01$	$34.81^{b} \pm 0.03$
3) Lower Slope	>510-800	Atlantic Water Mass (AWM), Arctic Water Mass (ArWM)	86	$0.07^{c} \pm 0.01$	$34.89^{c} \pm 0.00$

2.3.2 Vertical Distribution of Arctic Cod

Though Arctic Cod are found throughout the water column, a vertical and spatial segregation by size or life history stage is present in all populations, with juveniles hatching and remaining at the surface and proximal to shore until they reach approximately 30-35mm length (Sekerak 1982; Falk-Petersen *et al*. 1986; Parker-Stetter *et al*. 2011; Benoit *et al*. 2013). The current study population showed a slightly increasing body size with depth across benthic samples as sampling depth increases along transects (Figure 2.2). A Kruskal-Wallis test with a Holm correction determined there was a significant difference in median fork length of CBS Arctic Cod in the sample as well as the subsample between the Shelf and Upper Slope (sample and subsample: $p < 0.0001$, 2 d.f.) as well as the Shelf and Lower Slope zones (sample and subsample: $p < 0.0001$, 2 d.f.), but not between the Upper and Lower Slope zones (sample: $p = 0.18$; sub-sample: $p = 0.15$). Moving offshore and migrating deep in the water column with age in Arctic Cod is assumed to be a predator-avoidance mechanism, but prey energy density (*Calanus hyperboreus*; B. Lynn, unpublished data) in the CBS increased from the surface waters to deeper in the water column, and prey abundance in the Beaufort Sea has also been observed to increase with distance from shore (W. Walkusz, *pers. comm.*). Thus, age-related emigration offshore to depth in Arctic Cod may also be a response to prey composition, quality, and size. In addition to a migration to depth due to life history stage, smaller (age-1+) Arctic Cod may also make diel vertical migrations (DVM) higher in the water column toward more productive waters at dusk as a way to avoid competition for the low abundance of food at depth (Chapter 3) and their vulnerability to cannibalism (Benoit *et al.*, 2010). Whereas the depth of the general aggregation of Arctic Cod was synchronized with the seasonally increasing photoperiod, migrating offshore from 220m to 550m bottom depths in winter (Geoffroy *et al.* 2011), DVM of smaller (< 25g) Arctic Cod has been observed via hydroacoustics in Franklin Bay (Benoit 2012). This corresponds to fish of age 0-3 in the 2012 CBS sample. The length-frequency distribution of mid-water ($n = 665$) and benthic trawl ($n = 2989$) catches by depth zone in the current study suggests that smaller individuals are making the DVM (Figure 2.3). The more frequent shallow dives (≤ 130m) of predatory seals are often to shallower depths than the cod aggregations, but

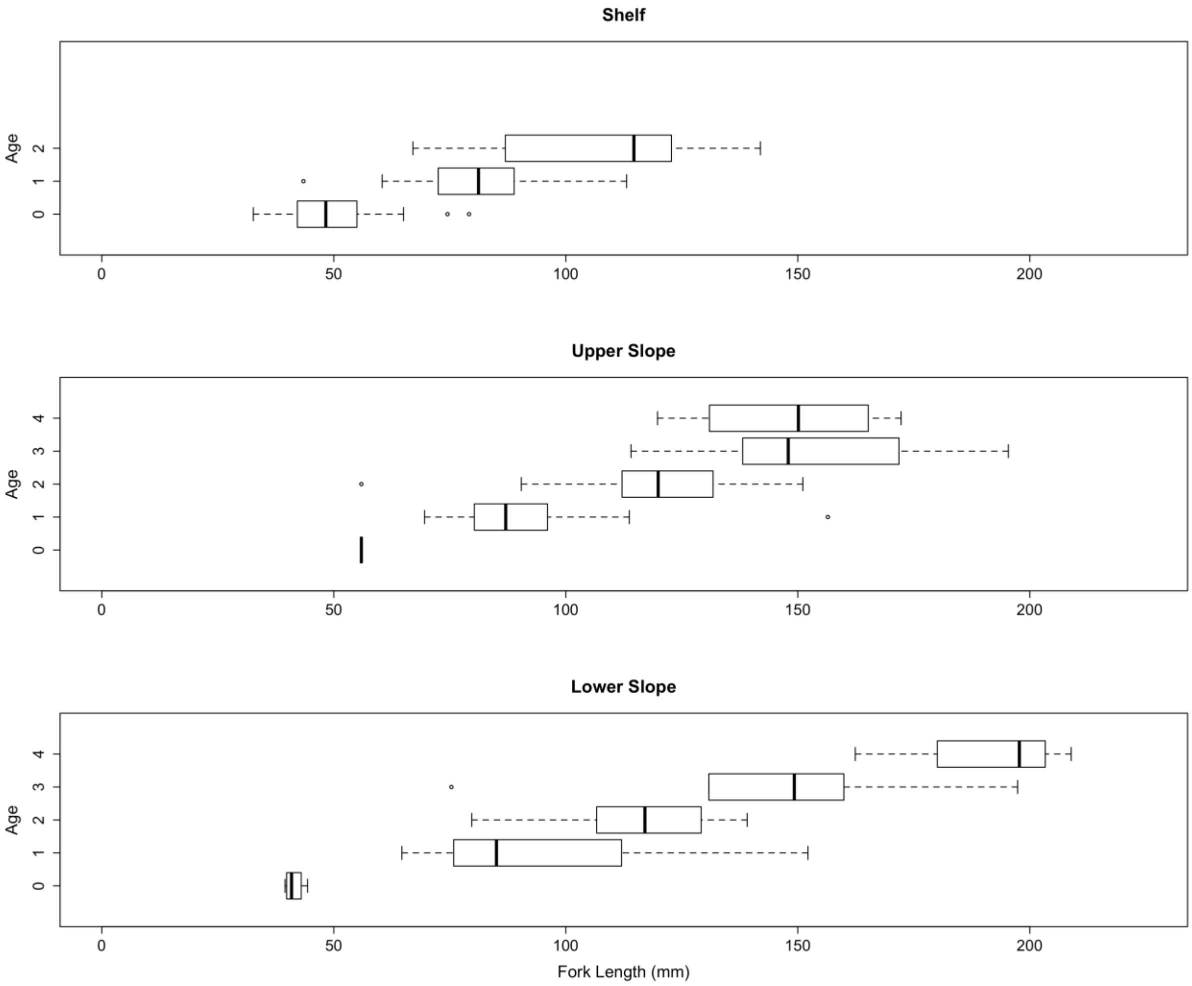

Figure 2.2 Fork length-at-age box and whisker plots of the sub-sample of Beaufort Sea Arctic Cod by depth zone (Shelf, n = 104; Upper Slope, n = 77; Lower Slope, n = 36). Thick vertical black lines indicate the mean fork length-at-age (Table 2.2), dashed lines error bars, and dots are outliers. An outlier was defined as any value outside 1.5 times the interquartile range above the upper quartile and below the lower quartiles. There was no significant difference in median fork length-at-age among depth zones in the sub-sample (see Appendix F, Table 6.10).

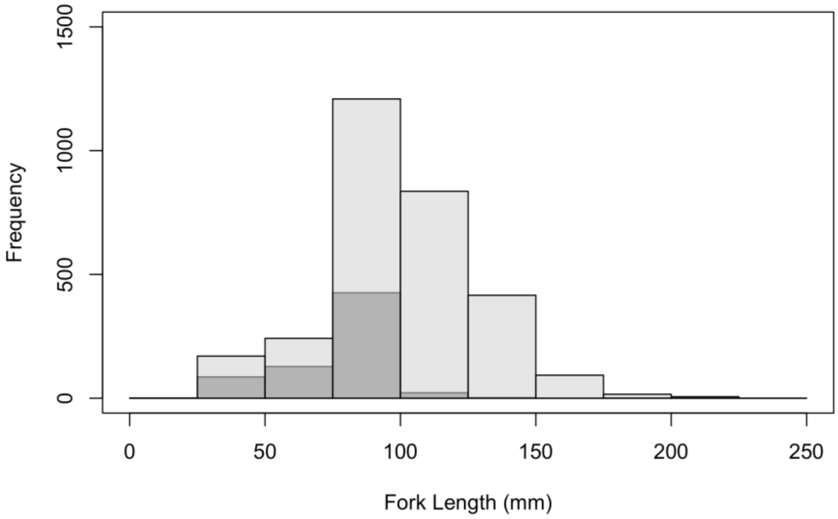

Figure 2.3 Fork length-frequency histogram of the Beaufort Sea Arctic Cod captured by benthic trawl (light grey) and the pelagic or mid-water trawl (dark grey). Individuals captured in the pelagic zone were smaller than those in demersal catches (Kruskal-Wallis, p = 0.0002, d.f. = 1)..

there is also some evidence that their dives are deeper during daylight when the fish are distributed deeper (i.e., ≥ 130m) (Benoit 2012).

2.3.3 Population-Level Characteristics: Sex Ratio

Of the 3317 demersal Arctic Cod captured during the BREA-MFP in the CBS in 2012, sex was determined for 1456. Of those, sex could not be determined for 268 individuals. When only those definitively identified to sex were considered, there was a slightly skewed sex ratio toward males in the sample, with 57% males and 43% females. A skewed sex ratio toward males was also present in the sub-sample where sex was defined for 177 of 237 individuals, but it was 68% males and 32% females. Both of these sex ratios are significantly different from 1:1 (Chi-square test, $p < 0.001$). When the sample was split into depth zones (Shelf, Upper Slope, and

Lower Slope), the sex ratios were still skewed toward males (Shelf: 70% male, 30% female; Upper Slope: 56% male, 44% female; Lower Slope: 60% male, 40% female) and all were significantly different from 1:1 (Chi-sqaure test, $p < 0.001$). However, when the subsample was split into age classes and depth zones, there was a skew in the sex ratios toward females with increasing age on the Upper Slope (Appendix E, Table 6.7; Chi-square test, $p = 0.003$). A survey of the Arctic Cod population in the CBS as part of the Northern Coastal Marine Studies (NCMS) program in 2008-09 (A. Majewski, *unpublished data*) only sampled the Beaufort Shelf and the area around Herschel Island. This survey also discovered a skewed sex ratio toward males; of the 149 Arctic Cod captured and sexed, 60% were male and 40% were female (29 individuals were of unknown sex).

European Arctic Cod populations exhibited a sex ratio skewed in the opposite direction. In the Norwegian populations of Arctic Cod in the coastal waters of the Svalbard Archipelago captured between 2010 and 2013 in January and September, there were more females than males and the relative proportion of females increased with age (Nahrgang *et al*. 2014). Such a skew toward females in the sex ratio was also observed in the Alaskan Beaufort Sea (ABS) coastal waters (Craig *et al*. 1982; Rand and Logerwell 2011) and the northeastern Chukchi Sea (Gillispie *et al.* 1997). Nahrgang *et al.* (2014) used this skewed sex ratio to support their argument that male Arctic Cod are semelparous, dying after one spawning event (also Korshunova 2012). This reproductive strategy proposed by Nahrgang *et al.* (2014) has not been investigated nor confirmed in any other Arctic Cod populations. The studies noted above were based on data from shallower regions than the CBS, but the sex ratio of the CBS Shelf zone was still skewed toward males in the sample (see above). Indeed, the sex ratio data in the current study suggests the proposed male semelparous reproductive strategy is not present in the Beaufort Sea Arctic Cod population. It is possible that the slightly larger proportion of males to females observed in the samples mentioned above is regulated by intrasexual competition; males competing for reproductive females establish territories and causing females to spread apart. However, the study sample was collected in August, when Arctic Cod are only beginning to develop gonads. Arctic Cod do not begin spawning until at least December.

2.3.4 Population-Level Characteristics: Size at Age

By examining 95% confidence intervals for mean length at age, Arctic Cod in the Beaufort Sea have a smaller size at age than the Norwegian population (Table 2.2). Note that the surveys in Norway of the Spitsbergen coast and the area north of Svalbard was focused solely upon coastal waters with warmer temperatures (Table 2.3; Jensen *et al*., 1991; Lonne & Gulliksen, 1989). There was more overlap among sizes at age in the current study than a previous study of the CBS Arctic Cod population combined with the Chukchi Sea (Lowry and Frost 1981). There was less variability in size at age observed in the 2008-09 survey of the Beaufort Shelf than in the current study of the Beaufort Sea in 2012 (Bartlett test, $p < 0.01$), but different trawl types (benthic beam trawl vs. modified Western IIA benthic trawl and Cosmos-Swam 260m midwater trawl, respectively), age-estimators, and ageing techniques were used that could bias the catch and age estimates (Majewski *et al.* 2009; Majewski, unpublished data).

Table 2.2 Length at age (± SE) of Arctic Cod in various locations. An asterick (*) indicates only standard deviation (SD) was reported. 95% confidence intervals are given in square brackets ([ ]).

	Length (mm ± SE)							
Location	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Reference
Canadian Beaufort Sea	49 ± 2.1 [44.9, 53.1] (n=29)	86 ± 1.7 [82.7, 89.3] (n=107)	118 ± 2.8 [112.5, 123.5] (n=58)	155 ± 4.4 [146.4, 163.6] (n=31)	173 ± 6.4 [160.5, 185.5] (n=16)	200 ± 9.7 [181.0, 219.0] (n=4)	209 (n=1)	This study, sub-sample of 2012 Beaufort Sea
Canadian Beaufort Sea	44 ± 1.3 [41.5, 46.5] (n=74)	90 ± 0.7 [88.6, 91.4] (n=184)	115 ± 1.9 [111.3, 118.7] (n=20)	129 ± 1.2 [126.6, 131.4] (n=4)	140 (n=1)	157 (n=1)	192 (n=1)	A. Majewski, DFO Canada (2008-09)

Table 2.2 continued…

	Length (mm ± SE)							
Location	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Reference
North of Svalbard		102 ± 12.6* (N=101)	125 ± 21.6* (N=101)					Lonne & Gulliksen 1989
West Barents Sea		82 ± 9.3* (N=101)	109 ± 9.1* (N=101)					Lonne & Gulliksen 1989
Unknown		up to 87						Sameoto 1984
Baffin Island				up to 190			up to 240	Sameoto 1984
Chukchi and Beaufort Seas		75	120	145	175			Lowry & Frost 1981
Bering Sea		100	135	155	175	190	210	Lowry & Frost 1981

2.4 The Canadian Beaufort Sea Population Compared to Other Populations

The population-level characteristics of Arctic Cod are distinctly different between the CBS and other Arctic regions. The differences are likely not attributable to the temperature and salinity conditions, as these are comparable among the regions analyzed (Table 2.3). However, other physical properties, e.g., turbidity could be different from other sampling regions due to the influence of the Mackenize River. Regions other than the CBS also have more interspecific competition, which could affect energy consumption and the energy available for growth, as well as successful reproduction via competition for mates. Future comparative studies should also analyze differences in prey availability among these circumpolar regions, as that could affect energy consumption as well. Meanwhile, genetic analysis would determine if distinct isolated populations exist in the circumpolar area and if they could have different reproductive strategies, and thus explain differences in the observed sex ratio among Arctic regions.

Table 2.3 Salinity and temperature ranges for other Arctic Cod habitats around the world. Note that many of the studies included in the current study's comparative analysis of Arctic Cod populations did not contain environmental data. In these cases, other sources were used and the environmental data may be from different times. All efforts were made to describe the environment in these areas at the same time of year that the Arctic Cod studies were performed.

Region	**Salinity (PSU)**	**Temperature (°C)**	**Description**
Alaskan Beaufort Sea	1-32 (Craig *et al.* 1982)	0 to 14 (Craig *et al.* 1982)	Atlantic, Pacific, Arctic, and river input; coastal
Spitsbergen coast	34.4 (Beszczynska-Moller *et al.* 1997)	-1.5 to +3.2 (Falk-Petersen *et al.* 1986)	Atlantic, Arctic, glacial, and river influence
Kongsfjorden, Svalbard	33.52-34.23	0-5 in upper 50m (Hop *et al.* 2002)	Atlantic, Arctic, glacial, and river input; coastal
West Barents Sea	34.45-34.5	-2 to -1	Three water masses: surface mixed layer; cold and relatively fresh Arctic layer; deep, warm, and saline Atlantic layer

Baffin Island	32.6-34.4	< 3.5 (Sameoto 1984)	Atlantic & Arctic input; Shelf, slope, basin
Chukchi Sea	31.9-33	-1.8 to +2.3	Pacific & Arctic input; shallow, max depth of 200m (Crawford 2003)
Bering Sea	31-35	-2 to 8	Subarctic; Pacific & Arctic input; extraordinarily productive; shallow

2.5 Sample vs. Sub-sample

As the other analytical chapters of this thesis investigate depth-related differences in diet and energy allocation, comparisons were made between the overall 2012 Arctic Cod sample and the sub-sample within the same three depth groups (Shelf, Upper Slope, and Lower Slope) to determine if the sub-sample is representative of the larger sample. The length-frequency of the individuals by depth zone in the sub-sample was compared to the overall sample (Figure 2.4). Efforts were made to ensure the sub-sample represented the total distribution (range) of sizes in the sample. Within each depth zone, there was no significant difference in median fork length between the sample and sub-sample ($p > 0.05$). For both the sample and sub-sample, there was a significant difference in median fork length among depth zones (Figure 2.4). There was a significant difference in the median fork length of Arctic Cod between the Shelf and Upper Slope (Kruskal-Wallis, $p < 0.01$) as well as the Shelf and Lower Slope zones (Kruskal-Wallis, $p < 0.01$), but no significant difference in median fork length of Arctic Cod between the Upper Slope and Lower Slope zones (Kruskal-Wallis, sample: $p = 0.18$; sub-sample: $p = 0.15$). Length-at-age was not compared between the overall sample and sub-sample, as very few individuals that were not included in the subsequent analytical chapters were aged (Figure 2.4). The maximum age in the sub-sample was 4+, while the maximum age in the overall sample was 6+. According to a z-test, the proportion of males was different between the sample and sub-sample ($p < 0.01$), but there was still a skewed ratio toward males in both the sample and sub-sample (Chi-square test, $p < 0.001$; sample: 57% male, 43% female; sub-sample: 68% male, 32% female).

Apart from the significant difference in the proportion of males and the expected higher variance in the sub-sample, the sub-sample of Arctic Cod is representative of the sample of CBS Arctic Cod in 2012 and covers the range of lengths of Arctic Cod present. Because diet and growth are dependent on the size of the fish (Post and Parkinson 2001; Walkusz *et al*. 2013), it was most important that the length distribution at each sampling station was similar within the current study. Therefore, it was concluded that the sub-sample used herein is representative of the much larger population of Arctic Cod in the CBS in terms of body size, but not sex. There were insufficient data to determine if the age distribution in the sub-sample was representative of the total population of CBS Arctic Cod in 2012. The results of additional studies of the sub-sample on the relationship between habitat and age class on diet (Chapter 3) and energy allocation (Chapter 4) can thus be related to the ecology and physiology of a Beaufort Sea Arctic Cod of a given size or age class in 2012.

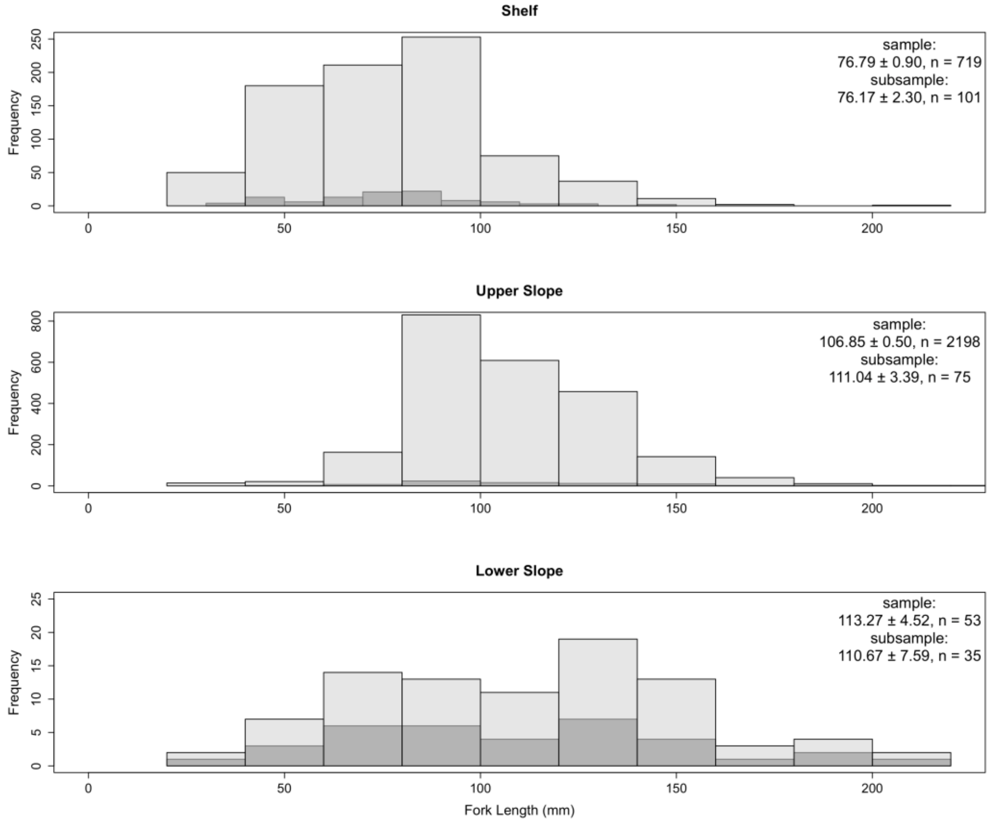

Figure 2.4 Fork length-frequency histogram of the Beaufort Sea Arctic Cod sample (grey, N = 2970) and sub-sample (dark grey, n = 211) by depth zone. Within each depth zone, there was no significant difference in the median fork length of Arctic Cod between the overall sample and sub-sample (Kruskal-Wallis; Shelf, p = 0.80; Upper Slope, p = 0.35; Lower Slope, p = 0.55). Comparison tests were also performed among depth zones for the overall sample and sub-sample separately. For both the sample and sub-sample, there was a significant difference in the median fork length of Arctic Cod between the Shelf and Upper Slope ($p < 0.0001$) as well as the Shelf and Lower Slope zones ($p < 0.0001$), but no significant difference in median fork length of

Arctic Cod between the Upper Slope and Lower Slope zones (sample: p = 0.18; sub-sample: p = 0.15). The numbers in the top corner of each panel indicate mean ± SE for the sample and subsample.

2.6 References

Benoit D (2012) Oceanographie, distribution et cycle annuel de la morue Arctique (Boreogadus saida) en mer de Beaufort: Une approche hydroacoustique. Universite Laval, Quebec

Benoit D, Simard Y, Fortier L (2013) Pre-winter distribution and habitat characteristics of polar cod (Boreogadus saida) in southeastern Beaufort Sea. Polar Biol 37:149–163. doi: 10.1007/s00300-013-1419-0

Benoit D, Simard Y, Gagné J, Geoffroy M, Fortier L (2010) From polar night to midnight sun: photoperiod, seal predation, and the diel vertical migrations of polar cod (Boreogadus saida) under landfast ice in the Arctic Ocean. Polar Biol 33:1505–1520. doi: 10.1007/s00300-010-0840-x

Berge J, Renaud PE, Darnis G, Cottier F, Last K, Gabrielsen TM, Johnsen G, Seuthe L, Weslawski JM, Leu E, Moline M, Nahrgang J, Søreide JE,Varpe Ø, Lønne OJ, Daase M, Falk-Petersen S (2015) In the dark: A review of ecosystem processes during the Arctic polar night. Prog Oceanogr 139:258–271. doi: 10.1016/j.pocean.2015.08.005

Beszczynska-Moller A, Marcin Weslawski J, Walczowski W, Zajaczkowski M (1997) Estimation of glacial meltwater discharge into Svalbard coastal waters. Oceanologia 39:289–299.

Boeuf G, Payan P (2001) How should salinity influence fish growth? Comp Biochem Physiol C Toxicol Pharmacol 130:411–23.

Clarke A, Johnston N (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. J Anim Ecol 893–905.

Craig PC, Griffiths WB, Haldorson L, McElderry H (1982) Ecological studies of Arctic Cod (Boreogadus saida) in Beaufort Sea Coastal Waters, Alaska. Can J Fish Aquat Sci 39:395–406.

Crawford RE (2003) Forage fish habitat distribution near the Alaskan coastal shelf areas of the Beaufort and Chukchi seas . 1–101.

Dalpadado P (2002) Inter-specific variations in distribution, abundance and possible life-cycle patterns of Themisto spp. (Amphipoda) in the Barents Sea. Polar Biol 25:656–666. doi: 10.1007/s00300-002-0390-y

Dalpadado P, Borkner N, Bogstad B, Mehl S (2001) Distribution of Themisto (Amphipoda) spp. in the Barents Sea and predator-prey interactions. ICES J Mar Sci 58:876–895. doi: 10.1006/jmsc.2001.1078

Engen S, Saether B (1994) Optimal allocation of resources to growth and reproduction. Theor Popul Biol 46:232–248. doi: 10.1006/tpbi.1994.1026

Falk-Petersen I, Frivoll V, Gulliksen B, Haug T (1986) Occurrence and size/age relations of polar cod, Boreogadus saida (Lepechin), in Spitsbergen coastal waters.

Frost KJ, Lowry LE Demersal fishes and invertebrates trawled in the Northeastern Chukchi and Western Beaufort Seas, 1976-77.

Gauldie RW, Thacker CE, West IF, Wang L (1998) Movement of water in fish otoliths. 120:551–556.

Geoffroy M, Robert D, Darnis G, Fortier L (2011) The aggregation of polar cod (Boreogadus saida) in the deep Atlantic layer of ice-covered Amundsen Gulf (Beaufort Sea) in winter. Polar Biol 34:1959–1971. doi: 10.1007/s00300-011-1019-9

Gillispie J, Smith R, Barbour E, Barber W (1997) Distribution, abundance, and growth of Arctic cod in the northeastern Chukchi Sea. In: Fish ecology in Arctic North America: proceedings of the Fish Ecology in Arctic North America Symposium, held at Fairbanks, Alaska, USA, 19-21 May 1992. pp 81–89

Heino M, Kaitala V (1999) Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. J Evol Biol 12:423–429. doi: 10.1046/j.1420-9101.1999.00044.x

Hirche HJ (1997) Life cycle of the copepod Calanus hyperboreus in the Greenland Sea. Mar Biol 128:607–618. doi: 10.1007/s002270050127

Hop H, Gjøsæter H (2013) Polar cod (Boreogadus saida) and capelin (Mallotus villosus) as key species in marine food webs of the Arctic and the Barents Sea. Mar Biol Res 9:878–894. doi: 10.1080/17451000.2013.775458

Hop H, Pearson T, Hegseth EN, Kovacs KM, Wiencke C, Eiane K, Gulliksen B, Wlodarska-Kowalczuk M, Lydersen C, Weslawski JM, Cochrane S, Gabrielsen GW, Leakey RJG, Lønne OJ, Zajaczkowski M, Falk-Petersen S, Kendall M, Wängberg S-Å, Bischof K, Voronkov AY, Kovaltchouk NA, Wiktor J, Poltermann M, Prisco G, Papucci C, Gerland S (2002) The marine ecosystem of Kongsfjorden, Svalbard. Polar Res 21:167–208.

Jensen T, Ugland KI, Anstensrud M (1991) Aspects of growth in Arctic cod, Boreogadus saida (Lepechin 1773). Polar Res 10:547–552. doi: 10.1111/j.1751-8369.1991.tb00672.x

Korshunova E (2012) Reproduction and winter biology of polar cod Boreogadus saida from Svalbard waters. Thesis. University of Tromso

Lonne OJ, Gulliksen B (1989) Size, age and diet of Polar Cod, Boreogadus saida (Lepechin 1773), in ice covered waters. Polar Biol 9:187–191.

Lowry L, Frost K (1981) Distribution, growth, and foods of Arctic cod (Boreogadus saida) in the Bering, Chukchi, and Beaufort seas. Can Field-Naturalist 95:186–191.

Majewski A, Reist J, Park B, Lowdon M (2009a) Fish catch data from offshore sites in the Mackenzie River estuary and Beaufort Sea during the open water season, August 2006, aboard the CCGS Nahidik. Winnipeg

Majewski AR, Reist JD, Park BJ, Sareault JE, Lowdon MK (2009b) Fish catch data from offshore sites in the Mackenzie River estuary and Beaufort Sea during the open water season, July and August, 2005, aboard the CCGS Nahidik. Winnipeg

McNicholl DG, Walkusz W, Davoren GK, Majewski AR (2015) Dietary characteristics of co-occurring polar cod (Boreogadus saida) and capelin (Mallotus villosus) in the Canadian Arctic, Darnley Bay. Polar Biol 1–10. doi: 10.1007/s00300-015-1834-5

Mecklenburg CW, Mecklenburg TA, Thorsteinson LK (2002) Fishes of Alaska. American Fisheries Society

Nahrgang J, Varpe O, Korshunova E, Murzina S, Hallanger IG, Vieweg I, Berge J (2014) Gender specific reproductive strategies of an Arctic key species (Boreogadus saida) and implications of climate change. PLoS One 9:11. doi: 10.1371/journal.pone.0098452

Orlova EL, Rudneva GB, Renaud PE, Eiane K, Savinov V, Yurko AS (2010) Climate impacts on feeding and condition of capelin Mallotus villosus in the Barents Sea: evidence and mechanisms from a 30 year data set. Aquat Biol 10:105–118. doi: 10.3354/ab00265

Parker-Stetter SL, Horne JK, Weingartner TJ (2011) Distribution of polar cod and age-0 fish in the U.S. Beaufort Sea. Polar Biol 34:1543–1557. doi: 10.1007/s00300-011-1014-1

Post J, Parkinson E (2001) Energy allocation strategy in young fish: allometry and survival. Ecology 82:1040–1051.

Pućko M, Burt A, Walkusz W, Wang F, Macdonald RW, Rysgaard S, Barber DG, Tremblay JÉ, Stern GA (2014) Transformation of mercury at the bottom of the Arctic food web: An overlooked puzzle in the mercury exposure narrative. Environ Sci Technol 48:7280–7288. doi: 10.1021/es404851b

Rand KM, Logerwell EA (2011) The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. Polar Biol 34:475–488. doi: 10.1007/s00300-010-0900-2

Rand KM, Whitehouse A, Logerwell EA, Ahgeak E, Hibpshman R, Parker-Stetter S (2013) The diets of polar cod (Boreogadus saida) from August 2008 in the US Beaufort Sea. Polar Biol. doi: 10.1007/s00300-013-1303-y

Rose GA (2005) Capelin (Mallotus villosus) distribution and climate: a sea "'canary'" for marine ecosystem change. ICES J Mar Sci 62:1524–1530. doi: 10.1016/j.icesjms.2005.05.008

Sameoto D (1984) Review of current information on Arctic cod (Boreogadus saida, Lepechin) and bibliography. Bedford Institute of Oceanography Report, Dartmouth: 71 pp.

Sekerak A (1982) Young-of-the-year cod (Boreogadus) in Lancaster Sound and western Baffin Bay. Arctic 35:75–87.

Walkusz W, Majewski A, Reist JD (2013) Distribution and diet of the bottom dwelling Arctic cod in the Canadian Beaufort Sea. J Mar Syst 127:65–75. doi: 10.1016/j.jmarsys.2012.04.004

Walkusz W, Paulić JE, Williams WJ, Kwasniewski S, Papst MH (2011) Distribution and diet of larval and juvenile Arctic cod (Boreogadus saida) in the shallow Canadian Beaufort Sea. J Mar Syst 84:78–84. doi: 10.1016/j.jmarsys.2010.09.001

3 Size-Dependent Differences and the Influence of Depth on the Diet of Arctic Cod, *Boreogadus saida* (Lepechin 1774) in the Canadian Beaufort Sea

3.1 Introduction

Within the Beaufort Sea, Arctic Cod, *Boreogadus saida* (Lepechin 1774) are an important component of the ecosystem due to their high abundance, biomass (Jarvela and Thorsteinson 1999; Majewski *et al*. 2009; Lowdon *et al*. 2011; Logerwell *et al*. 2011), and energy density (Harter *et al*. 2013). A wasp-waisted ecosystem is an ecosystem where an intermediate trophic level controls the abundance of predators through bottom-up interactions and the abundance of prey through top-down interactions (Fauchald *et al.* 2011). Arctic Cod are a major energetic link from primary and secondary consumers (e.g., zooplankton) to higher trophic levels (larger fishes, marine mammals, and seabirds) in Arctic ecosystems (Bradstreet *et al.* 1986). This important linkage, combined with their high abundance relative to other fish species and their broad vertical distribution, means that Arctic Cod occupy the central position of the wasp-waisted Canadian Beaufort Sea ecosystem.

Bioenergetics is the study of energy flow through living systems. In fish, a general bioenergetics model, as in Rombough (1994) is:

$$C = R + P + E$$

where available energy or energy consumed (C, consumption) is used to either support life (R, basal metabolism, osmoregulation), produce new tissue (P, body growth, reproduction, and lipid storage), or is lost from the system (E, activity, waste removal, specific dynamic action), the system being defined as the individual fish in this case. The current study analyzed the differences in consumption (C) or diet by number and type of species with depth by Arctic Cod, while also considering the effect of body size in order to understand energy dynamics within an individual of this important species in the Canadian Beaufort Sea (CBS) ecosystem.

If the physiological state of the fish is maintained, the amount of energy available for allocation to each parameter in the bioenergetics model beyond basal energy requirements is limited by the amount of energy consumed by the fish through the diet. Daily consumption rates of Arctic Cod have been documented as quite low, limited by their gastric evacuation rate (Hop and Tonn 1998), thus knowledge of what they are eating and prey quality is important to understanding energetic linkages in the Arctic in general and the Beaufort Sea in particular.

The foraging behaviour of Arctic Cod is mostly unknown, but they likely rely on multiple sensory systems to detect their prey. Arctic Cod are visual predators, although their ability to see at depth will obviously be affected due to light attenuation beyond the euphotic zone (10-60m, 34m average in the eastern Beaufort Sea, Juul-Pedersen *et al*. 2010). In the current study area, Arctic Cod have been found up to approximately 1000m depth, which is almost completely devoid of light. Atlantic Cod, another gadid, hunts visually but they also rely on their chemosensory abilities to find prey (Løkkeborg 1998). This method has not been confirmed in Arctic Cod. Fish may use their lateral line system (chemoreception, electroreception, or mechanoreception) to physically sense their surrounding environment but whether this is involved in predation by Arctic Cod is unknown but likely, given the widespread use by other fishes. Geoffroy *et al.* (2011) observed mass vertical migrations of Arctic Cod during the polar night in Amundsen Gulf, presumably following their zooplankton prey, suggesting that Arctic

Cod are actively feeding during the polar night. Indeed, gut content analyses of Arctic Cod by Berge *et al*. (2015a) showed that they were actively feeding during the polar night in Kongsfjorden, Svalbard, further supporting the hypothesis that Arctic Cod are relying on other senses than strictly vision for predation. Some suggest that bioluminescent *Metridia longa*, common in the Beaufort Sea but not in great numbers, may offer some light to foraging Arctic Cod in deep water (Benoit *et al.* 2010).

There is evidence of an increasing reliance by Arctic Cod on larger copepods and amphipods with increasing body size (size-dependent prey selection, Walkusz *et al*. 2013), however, it is not known whether Arctic Cod are selective foragers, seeking out larger amphipod prey as the Arctic Cod get larger, or if the Arctic Cod are simply consuming prey they encounter relatively indiscriminately. The explanation for the shift to larger prey with increase in body size is usually assumed to be a combination of the prey distribution, the increase in size of Arctic Cod spatially from shore and with depth, as well as the mechanical constraints on consumption imposed by the size of the predator's gape (Scharf *et al*. 2000; Knickle and Rose 2014). The larval stage of Arctic Cod lasts 3-4 months, and when the larvae reach 27-35mm in length, they transition into juveniles (Walkusz *et al*. 2011). Larvae and juvenile Arctic Cod inhabit surface waters and consume primarily copepod nauplii and rotifers but are considered generalists (Walkusz *et al.* 2011). Calanoid copepods (*Calanus* spp.) and amphipods (*Themisto* spp.), and to a lesser degree mysids, are the major prey of all other life stages of Arctic Cod (Bradstreet and Cross 1982; Sameoto 1984; Walkusz *et al.* 2013). Larger prey of older Arctic Cod life stages are more abundant in deeper areas (Pućko *et al*. 2014). Therefore, adult Arctic Cod found deeper have greater access to larger prey, though these larger prey are still rare in the environment. So if larger Arctic Cod with larger gapes dwelling deep are consuming larger prey species, this would suggest that Arctic Cod are selectively choosing their prey when foraging. Prey species distribution also varies with depth. *Calanus* spp. are typically found throughout the water column, but carnivorous *Themisto* spp. are found deeper, though still closely associated with *Calanus* spp.. Thus, if Arctic Cod living in deeper depth zones are encountering and consuming more *Themisto* spp., this would suggest that Arctic Cod are indiscriminately consuming prey they encounter as they forage. Cannibalism and piscivory have been observed in Arctic Cod, but are relatively rare (Rand *et al*. 2013), and may be in response to intra- and interspecific competition for food.

The vertical distributions of the major Arctic Cod prey, *Calanus* spp. and *Themisto* spp., is unknown for the Beaufort Sea, but their behaviour has been observed in other Arctic ecosystems. Diel vertical migrations have been observed in both species, and it is assumed that aquatic organisms make diel vertical migrations to take advantage of the high abundance of food in the surface waters at dusk and overnight. *Themisto libellula* is an epipelagic amphipod with a lifespan of two years and has been observed to make distinct diel vertical migrations (DVM) in the southern Arctic Ocean (Fortier *et al*. 2001; Falk-Petersen *et al*. 2008; Prokopowicz 2011). *Themisto abyssorum* in the northern Barents Sea, also with an expected life span of two years, had a deeper distribution than did *T. libellula* in the summer and early autumn (Dalpadado *et al.* 2001). This species has been observed making DVM in the Svalbard Archipelago in September, when a day-night cycle was present in late summer (Berge *et al*. 2014). Arctic *Calanus* species have been observed making DVM to the productive surface waters, and seasonal vertical migrations to depths of 200-2000m (Falk-Petersen *et al*. 2008). *Calanus* species make a seasonal migration to overwinter at depth in the warm, deep Atlantic layer when they have accumulated enough lipids. Despite the knowledge of zooplankton vertical migrations, it is still unclear how deep they will migrate during the day in deep water environments such as in the Upper Slope and Lower Slope zones of the current study area, but likely will move just beyond the extent of the euphotic zone so they are out of the sight of visual predators (Pućko *et al*. 2014). The euphotic zone depth ranged from 10 to 60m (average of 37m) in the eastern Beaufort Sea in 2003-04 (Juul-Pedersen *et al*. 2010), and migrating each day out of the euphotic zone before daylight hours is likely a strategy by zooplankton to avoid visual predators, which include Arctic Cod (Fortier *et al*. 2001). However, Arctic Cod are likely relying on other senses to sense their prey. The current study occurred during the Midnight Sun, when zooplankton DVMs are less pronounced but still occur. Daase *et al.* (2015) observed a short (20-80m depth) DVM by young stages of *C. glacialis* and other copepodites common in Arctic Cod diet in ice-covered waters northeast of Svalbard during the Midnight Sun. Diet studies must take into account the length of time that the vertical distributions of predator and prey overlap in order to fully understand prey availability and determine if the predator is selectively choosing their prey. However, the current study did not measure DVM of the zooplankton prey and thus will concentrate on describing the diet and depth differences in the diet of Arctic Cod in the Canadian Beaufort Sea.

To estimate the amount of energy consumed by and the average diet of Arctic Cod (age 0-4, fork length 32.5-210mm) in the Beaufort Sea, diet composition was investigated through stomach contents analysis, and the energetic content of major prey species determined by calorimetric analysis to determine whether a difference in diet composition could result in a difference in energy intake. Diet composition and energy content was compared among three depth zones (Shelf, Upper Slope, and Lower Slope) with size class as a covariate to determine if energy consumption differed. Energy consumption may differ among depth zones given the known ontogenetic variation in diet and the shift in vertical distribution of Arctic Cod deeper with increase in size, but also the vertical distribution of prey relative to water masses and the differences in temperature and therefore energetic demands among them. The hypotheses tested below examine whether larger Arctic Cod found deeper will consume more energy through their diet either by consuming more low-energy per individual prey items, e.g., *Calanus* spp., or consuming larger prey that contain more energy per individual prey item, e.g., *T. libellula* despite its low abundance in the environment, will be preferentially consumed over *Calanus* spp.

3.2 Methods

3.2.1 Sample Collection

Arctic Cod were collected from 26 stations in the Canadian Beaufort Sea in August 2012 (Figure 2.1 provides a map of the sampling area). Stations were organized into transects, 6-7 stations per transect, which ran perpendicular from shore to allow investigation of depth effects. For this study, ten Arctic Cod representing the range of lengths captured were chosen from each station when possible (n = 237). Only those caught by demersal nets were included. Following collection, fish fork length was measured to the nearest mm. The fish were then individually bagged and frozen on the ship initially at -50°C, then transferred to approximately -30°C for long-term storage. Field lengths were recorded and compared to lab lengths to determine if shrinkage with freezing was a significant issue. An average shrinkage of 5.6mm or 5.4% was observed. However, some recorded measurements were unexpectedly larger in the lab than on the ship. Due to the high possibility of sampler fatigue and the error introduced when measuring to the millimeter aboard a rocking ship, only lab length measurements were used herein.

3.2.2 Analytical Structure

The region of the Canadian Beaufort Sea sampled can be separated into three depth zones (Shelf: 15-220m; Upper Slope: >220-510m; Lower Slope: >510-800m), to examine the effect of habitat (temperature, salinity, and prey availability) on the energy consumption or diet of Arctic Cod. See Table 2.1 for a description and justification of the analytical structure for this study.

3.2.3 Data Collection

In the lab (set at 4°C to maintain the integrity of fatty acids), measurements of length (total, fork, and standard ± 0.01mm) and mass (total body wet mass and non-visceral carcass mass ± 0.001g) were collected. Gape width was also measured, as the distance across the width of the mouth. Gonads and livers were dissected from each fish and their mass recorded (± 0.001g). All effort was made to reduce thawing so as to retain the integrity of the tissues. Sex and maturity level were visually determined based on gonad development (Appendix A, Table 6.1; Majewski *et al.* 2009). Stomachs and intestines were removed and placed in formalin for diet analysis, and otoliths were extracted and dried for age determination.

3.2.4 Morphometrics and Size Classes

Following length determination, Arctic Cod were grouped into four size classes based on 30mm increments and knowledge of diet shifts in Arctic Cod with increase in gape size and body size (Walkusz *et al.* 2013; Majewski *et al.* 2015). Individuals of greater length should exhibit larger gapes and be able to consume larger prey (Scharf *et al*. 2000; Knickle and Rose 2014). This was examined for the sample of Arctic Cod used herein. To prevent pseudo-replication that would arise by analyzing each individual separately, and while still maintaining the variability associated with size class, the sampling unit for diet analysis at each station was designated as the size class.

3.2.5 Stomach Contents Analysis

The stomachs of Arctic Cod that had been preserved in formalin after dissection (n = 229 of the 237 in the Beaufort Sea Arctic Cod sub-sample) were cut open and their contents examined. The sample included 120 males, 54 females, and 55 fish of indeterminate sex. The contents were rinsed with deionized water and identified to the lowest taxonomic level possible under a stereomicroscope. Individual prey items were measured on the longest axis (mm) to estimate their dry mass through literature-based dry mass-length relationships (Appendix C, Table 6.3). The dry mass data was used to estimate the number of prey actually consumed by the individual fish (Kanaeva 1962; Berestovskii *et al*. 1989; Hay *et al.* 1991; Mumm 1991; Richter 1994; Hanssen 1997; Poltermann 1997). Where fragments of prey were encountered, effort was taken to identify them to the proper taxon and each fragment was considered as one whole prey item. Empty stomachs were noted.

Diet composition was summarized by percent prey count (%N), percent prey weight (%WT), and percent frequency of occurrence (%FO). These variates were calculated as follows for each size class at a station:

%N = (abundance of a prey type/number of individual prey consumed)*100

%WT = (dry mass of each prey type/total calculated prey dry mass of diet)*100

%FO = (number of stomachs with the prey type/total number of stomachs analyzed)*100

Once diet was determined for each size class at a station, values were averaged within a depth zone and compared across all depth zones. In order to maintain a balanced statistical design, diet was not compared statistically by sampling transect within a depth zone as there was no difference in areal prey density among transects (see Section 3.4.2). Due to digestion and other practical concerns it was not always possible to identify all prey to species level (<0.001% of all prey items found). There was no overlap in prey category assigned, i.e., prey items were placed strictly in the lowest taxonomic level possible.

3.2.6 Arctic Cod and Prey Distribution

Data on prey species biomass density (mg/m^2) and population density (individuals/m^2) were made available by W. Walkusz and referenced in this study. Zooplankton samples for biomass and population density estimation were stored in 4% formalin. It was assumed that the integrated prey biomass and abundance over the water column would represent the total potential food supply available to demersal fish including Arctic Cod, because: 1) the zooplankton that are major prey items for Arctic Cod, *Calanus* copepods and *Themisto* amphipods, exhibit seasonal migrations to depth as well as diel vertical migrations (Falkenhaug *et al.* 1997; Falk-Petersen *et al.* 2008; Rabindranath *et al.* 2011; Daase *et al.* 2015); 2) replacement of individuals that migrate away would occur; and 3) all decaying organic matter descends to bottom. Note that prey were captured by a vertical tow of a MultiNet (153 microns mesh), stratified but pooled together as samples were not gathered from the immediate proximity to the bottom at stations deeper than 200m, thus the biomass (wet) and population density estimates were based on the entire water column.

3.2.7 Calorimetric Analysis

Energy densities of common prey species (*Calanus* spp., *Themisto* spp., and *Paraeuchaeta* spp.) were determined via bomb calorimetry of ~0.14g of sample. Zooplankton samples included only females and those of life stage CV, as they were the largest individuals. To prepare zooplankton samples for combustion, crushing or grinding created a homogeneous mixture of similar particle size. To reduce lipid loss due to smearing in conventional grinders, all samples were prepared by lightly crushing a freeze-dried sample by hand within its individual bag. Standard procedures and those recommended by B. Stewart (Sila Consultants, *pers. comm.*) for use of the Parr 1241 Adiabatic Oxygen Bomb Calorimeter and the 1108 Oxygen bomb units (Operating Instructions Manual No. 203M and No. 205M, respectively, Parr Instrument Company) were followed. After standardization of the calorimeter, each of the two oxygen bombs was then calibrated with calorific grade benzoic acid (6318 cal/g). Also, benzoic acid was added to all samples when combusting to ensure a complete burn. All samples were analyzed in duplicate (± 5% error allowed, unless otherwise stated).

3.2.8 Statistical Analyses

Statistical significance was accepted when $\alpha < 0.05$. A Bartlett's test for homogeneity of variance was used to determine if there was a significant difference in all variables. To determine the relationship between gape size and size of the fish, a regression of fork length on gape width was performed. As the data did not meet the parametric assumptions of homogeneity of variance and normality, nonparametric Kruskal-Wallis analyses determined whether there is a significant difference in the maximum size of prey consumed, gape size among size classes, an effect of depth zone and transect on estimates of areal prey density integrated over the water column, and to test for differences in the prey type %FO, %N, and %WT in the Arctic Cod diet among depth zones by size class. A Dunn's test was used for nonparametric post-hoc analyses of pair-wise differences in the maximum size of prey consumed, gape size, and diet. All post-hoc analyses included a Holm adjustment of p-values to account for multiple comparisons (Holm 1979). A Holm adjustment involves ranking the p-values of the hypothesis tests in order from smallest to largest and sequentially analyzing whether the p-values are $< \alpha/n$. If the p-value is $< \alpha/n$, the hypothesis is statistically significant and the next largest p-value is analyzed. If the p-value is >

α/n, then none of the hypotheses are statistically significant. This adjustment is less conservative, and does not inflate the probability of a Type II error, as is the case with a Bonferroni adjustment.

3.3 Results

3.3.1 Morphometric Constraints on Diet

A regression of gape size on fork length (Figure 3.1) confirmed the direct relationship of these parameters, and a Kruskal-Wallis test determined there was a significant difference in gape width among size classes (Figure 3.2; Holm adjustment, p-adj $< 2.2 \times 10^{-16}$, 3 d.f.). There was a weak positive relationship between gape width and maximum size prey consumed (Figure 3.3; R2 = 0.16, $p = 1.57 \times 10^{-9}$, d.f. = 202). Variation in the maximum size of prey consumed by individual Arctic Cod increased with gape width (Bartlett's test, $p < 2.2 \times 10^{-16}$, 3 d.f.; Figure 3.4 & 3.4). The median of the maximum size of prey consumed by fish of size class 1 was significantly smaller than the median for size classes 2-4 (Kruskal-Wallis test with Holm adjustment, p-adj < 0.0001 for all three comparisons). The size of prey consumed by the Arctic Cod in this study ranged from the small *Copepoda* nauplii, *Harpacticoida* spp., *Microcalanus* spp., *Oithona similis*, *Acartia longiremis*, *Pseudocalanus* spp., *Limacina helicina*, *Ostracoda*, and *Triconia borealis*, to the large *Erythrops erythropthalma*, *T. libellula*, and *Mysis* spp. By size class within the depth zones, the range of sizes of prey consumed increased. However, the number of small species in the diet decreased with increasing size class (Appendix D, Table 6.5).

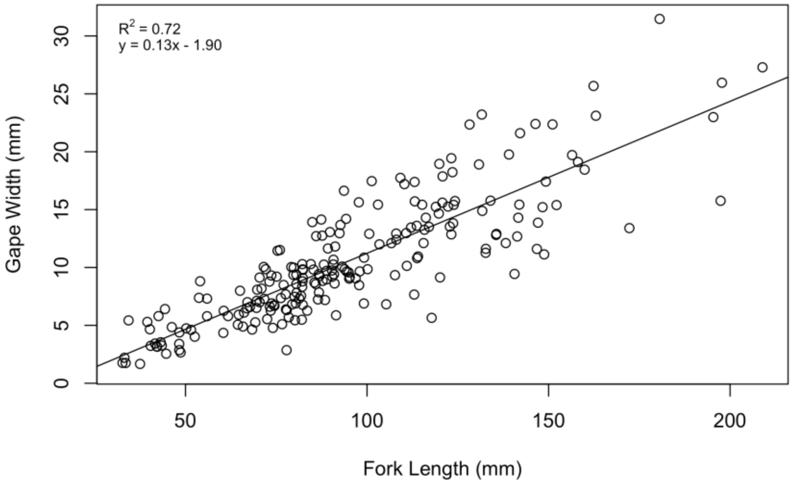

Figure 3.1 A plot of fork length and gape width of each Arctic Cod. There was a strong positive linear relationship between the fork length and gape width of Arctic Cod ($R^2 = 0.72$, $p < 2.2 \times 10^{-16}$).

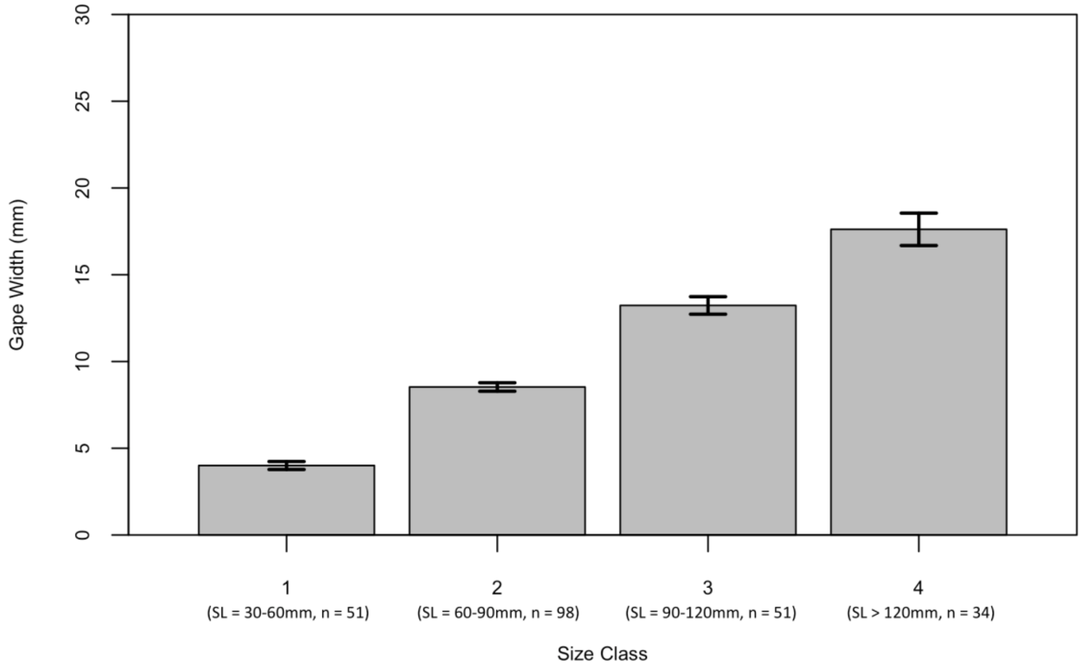

Figure 3.2 Mean (± SE) gape width of Arctic Cod by size class. There was a significant difference in the gape width of Arctic Cod among all pair-wise comparisons of size classes (SL = standared length; Kruskal-Wallis, Holm adjustment, p-adj < 2.2×10^{-16}, 3 d.f.).

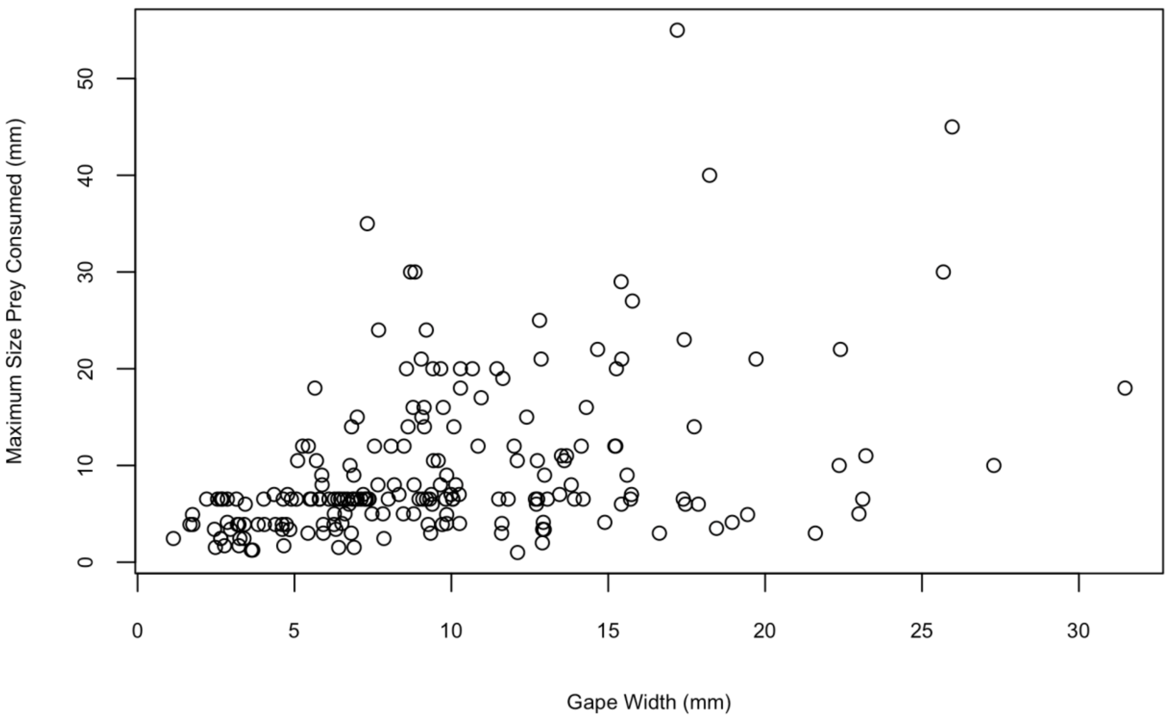

Figure 3.3 A plot of Arctic Cod gape width by the maximum size of prey consumed by individual Arctic Cod of whose stomachs contained prey (n = 203). There was a weak positive relationship between gape size and the maximum size of prey consumed ($R^2 = 0.16$, $p = 1.57 \times 10^{-9}$. Empty stomachs were not included (n = 25).

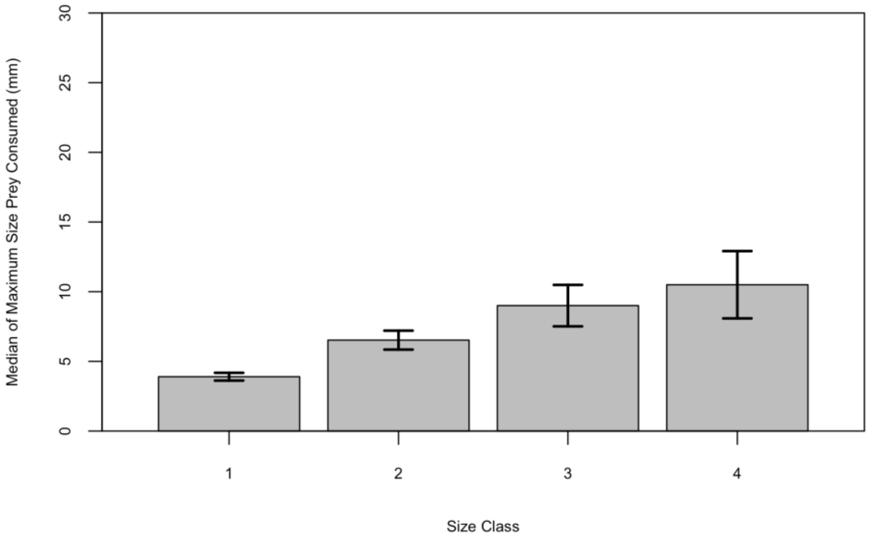

Figure 3.4 Median (± SE) of the maximum size of prey consumed by Arctic Cod by size class. There was a significant difference in the maximum size of prey consumed between fish of size class 1 and all larger size classes (Holm adjustment, p-adj < 0.0001 for all three comparisons), likely due to the significant difference in gape width among size classes (Figure 3.3). Empty stomachs were not included in the analysis (n = 25).

3.3.2 Prey Density

Besides physical constraints, prey distribution likely influenced species composition in the diet. There was a significant difference in the areal prey density (mg/m^2) of all prey species among depth zones (p = 0.004, 2 d.f.) (W. Walkusz, unpublished data). Median density of Arctic Cod prey species biomass was significantly lower in the Shelf zone than in the Upper Slope and Lower Slope zones (Figure 3.5a; Holm correction, p-adj = 0.01 and 0.005, respectively). There were no significant differences in total prey biomass density (Shelf: p = 0.26, 3 d.f.; Upper Slope: p = 0.15, 3 d.f.; Lower Slope: p = 0.24, 3 d.f.) and species-specific biomass density

(*Calanus* (Shelf: p = 0.68; Upper Slope: p = 0.42; Lower Slope: p = 0.54; 3 d.f.) and *Themisto* (Shelf: p = 0.39; Upper Slope: p = 0.76; Lower Slope: p = 0.28; 3 d.f.)) among transects within each depth zone. There was a significant difference in the biomass density of *Calanus* (Figure 3.5b; p = 0.001, 2 d.f.) and *Themisto* (Figure 3.5c; p = 0.0004, 2 d.f.) among the depth zones, pooled across transects (W. Walkusz, unpublished data). Biomass density of *Calanus* was significantly lower in the Shelf zone than the Upper Slope (Holm correction, p-adj = 0.003) and the Lower Slope zones (Holm correction, p-adj = 0.002). The biomass density of *Themisto* was also significantly lower in the Shelf zone than the Upper Slope (Holm correction, p-adj = 0.001) and the Lower Slope zones (Holm correction, p-adj = 0.001).

There was no significant difference in *Calanus* (Kruskal-Wallis; Shelf: p = 0.35; Upper Slope: p = 0.24; Lower Slope: p = 0.13; 2 d.f.) and *Themisto* (Kruskal-Wallis; Shelf: p = 0.64; Upper Slope: p = 0.16; Lower Slope: p = 0.26; 2 d.f.) population density across transects within depth zones. There was no significant difference in the population density of *Calanus* among depth zones pooled across transects (Figure 3.6a; Kruskal-Wallis; p = 0.86; 2 d.f.). Population density of *Themisto* spp. was significantly lower on the Shelf than both the Upper (Figure 3.6b; Kruskal-Wallis with Holm correction, p-adj = 0.0005) and Lower Slope (p-adj = 0.0002), pooled across transects.

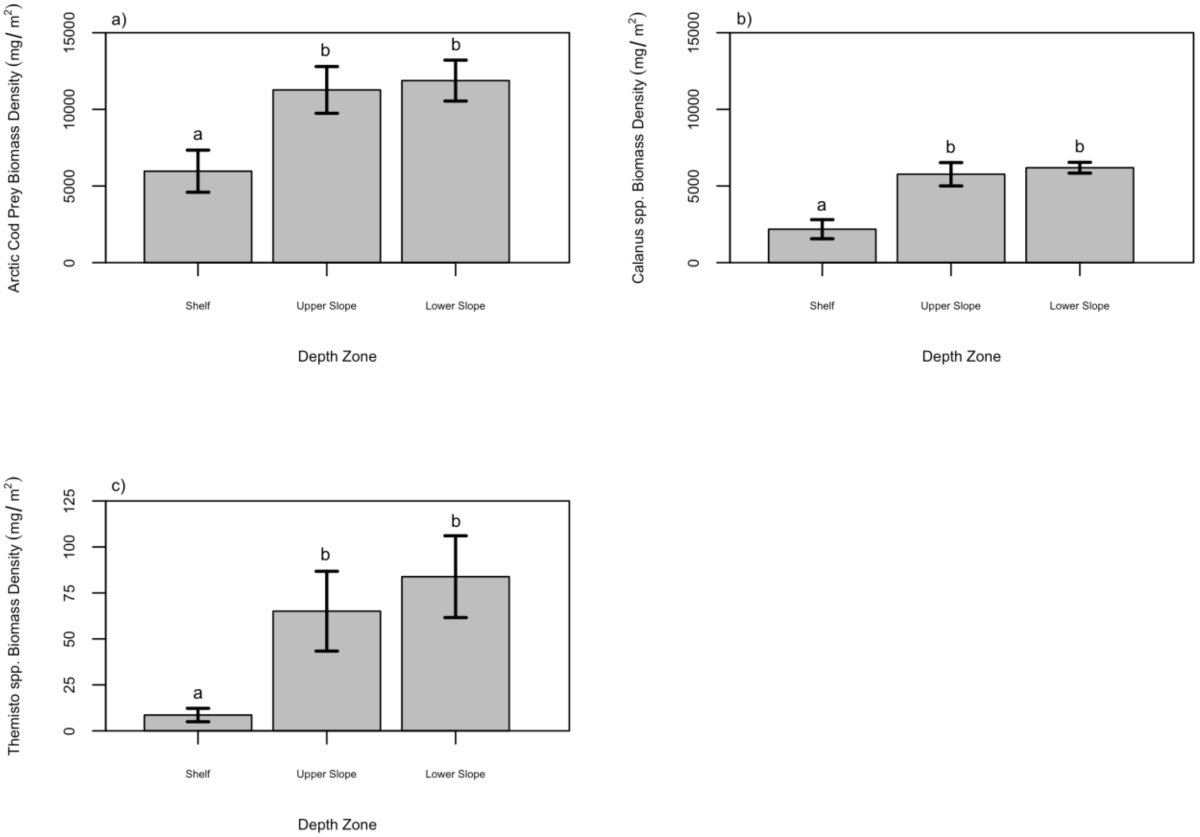

Figure 3.5 Mean areal Arctic Cod prey biomass density (mg wet mass/m^2) by depth zone in the Canadian Beaufort Sea for a) all taxa, and by the main prey species: b) *Calanus* spp. and c) *Themisto* spp.. Note the difference in scale for c). There is significantly less areal prey biomass density overall (a), as well as *Calanus* (b) and *Themisto* (c) specifically, on the Shelf than both the Upper Slope and Lower Slope zones. Differing letters above the bars within the panels indicate statistically significant differences among depth zones.

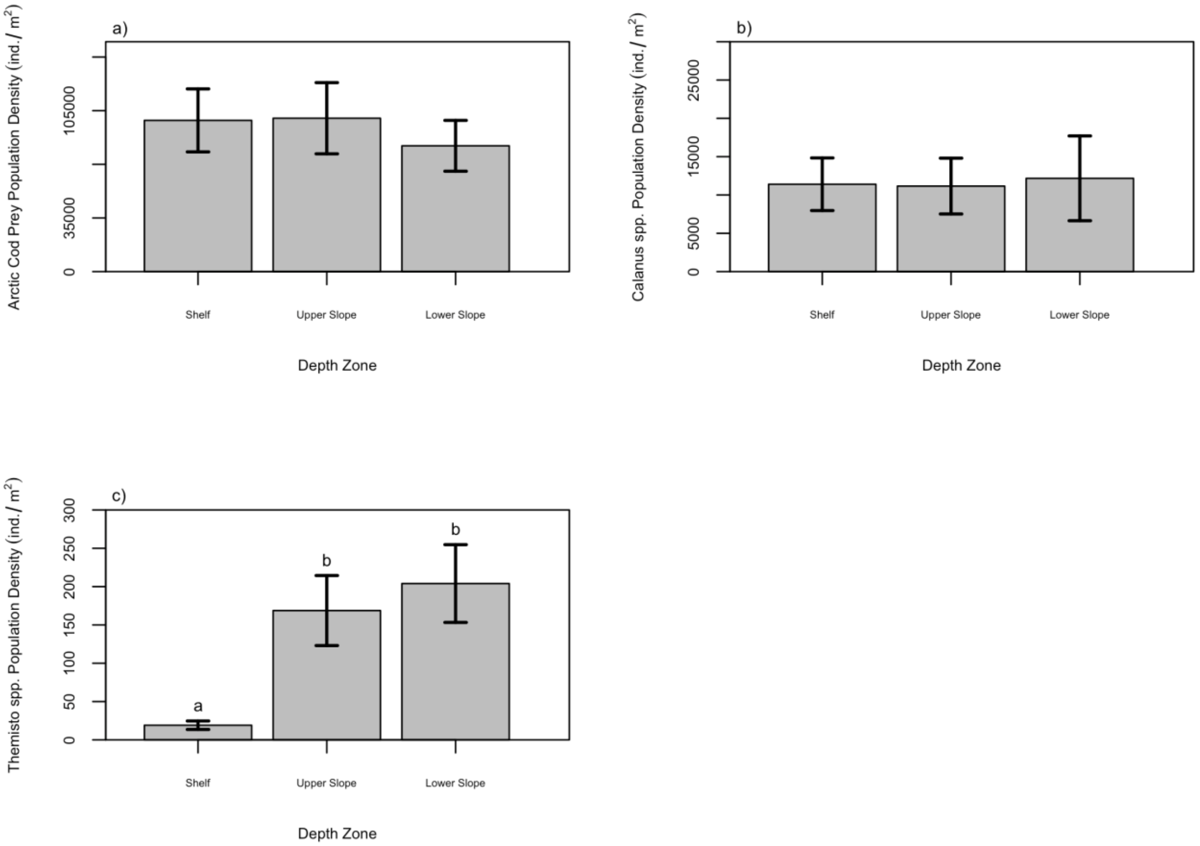

Figure 3.6 Mean areal population density of a) all taxa, and the major Arctic Cod prey species b) *Calanus* spp. and c) *Themisto* spp. across depth zones. Note the difference in scale between the species, as *Calanus* are much more abundant in the area. There is significantly less areal population density of *Themisto* spp. on the Shelf compared to the Upper (Kruskal-Wallis with Holm correction, p-adj = 0.0005) and Lower Slope (p-adj = 0.0002) zones. Letters above the bars within the panels indicate statistically significant differences among depth zones or transects.

3.3.3 Arctic Cod Diet: Species Composition

When the sample was separated into size classes by depth zone (Tables 3.1 and 3.2), the diets of Arctic Cod in size classes 1 and 2 had the highest number of species in the Shelf zone (16 and 17 spp., respectively), and the diets of Arctic Cod in size classes 3 and 4 had the highest number of species on the Upper Slope (16 and 12 spp., respectively). A significant p-value from a Kruskal-Wallis comparison test, however, indicated there was a difference in the number of species in the diet among depth zones for size classes 2 ($p = 0.05$, 2 d.f.) and 3 ($p = 0.03$, 2 d.f.), but post-hoc tests with a Holm correction determined the differences were not significant. Thus, there was no significant difference in the number of species in the diet among depth zones within each of the size classes (Kruskal-Wallis; size class 1: $p = 0.11$, 2 d.f.; size class 4: $p = 0.94$, 2 d.f.).

In general, the diet of Arctic Cod was dominated by small, energy rich calanoid copepods. There is evidence of an ontogenetic shift in the diet, as large *Themisto* were only a major prey item in the diet for cod of size classes 2-4 (Table 3.2-3.4). For clarity, only species that contributed $> 5\%$ FO to any of the groups' diets were included in this table. See Appendix D for a complete itemization of Arctic Cod diet by species.

Table 3.1 Total and mean (Mean (Median) ± SE) species diversity of the diet of Arctic Cod in the Canadian Beaufort Sea in August 2012 by size class and depth zone. A significant p-value indicated there was a difference in median species diversity among depth zones for size classes 2 and 3 ($p < 0.05$), but post-hoc tests with a Holm correction by depth zone within these two size classes determined these differences were not significant.

Depth Zone	**Size Class**	**Total Diet Species Diversity**	**Mean (Median) Diet Species Diversity**
Shelf	1	16	5.8 (6.0) ± 0.6
Upper Slope	1	3	3.0 (3.0)
Lower Slope	1	9	4.3 (2.5) ± 2.7
Shelf	2	17	6.9 (7.5) ± 0.4
Upper Slope	2	12	5.3 (6.0) ± 0.7
Lower Slope	2	12	4.8 (5.0) ± 0.8
Shelf	3	12	4.0 (3.0) ± 1.0
Upper Slope	3	16	7.0 (7.0) ± 0.6
Lower	3	6	3.3 (4.0) ± 1.2

Slope			
Shelf	4	8	4.0 (4.0) ± 4.0
Upper Slope	4	12	3.7 (3.0) ± 1.1
Lower Slope	4	10	2.8 (2.0) ± 0.7

3.3.4 Arctic Cod Diet: Comparisons Among Size Classes

There were significant differences among size classes in the median %FO (Table 3.2), %N (Table 3.3), and %WT (Table 3.4) of some major prey species in the diet of Arctic Cod on the Shelf. There was a significant difference in median %FO of *T. libellula* (1 and 2, p-adj = 0.008) and of *C. glacialis* (1 and 3, p-adj = 0.01; 1 and 4, p-adj = 0.009). There was also a significant difference in median %N of *T. abyssorum* (1 and 3, p-adj = 0.02) and *C. glacialis* (1 and 3, p-adj = 0.009; 1 and 4, p-adj = 0.01). Finally, there was a significant difference in median %WT of *T. libellula* (1 and 2, p-adj = 0.02), *T. abyssorum* (1 and 3, p-adj = 0.02), and *C. glacialis* (1 and 3, p-adj = 0.001; 1 and 4, p-adj = 0.006). There was no significant difference in the diet species composition between size class 1 and 2, or among larger size classes (size classes 2-4). With increase in size class, there was a shift away from *C. glacialis* in the diet and toward *T. libellula*..

Table 3.2 Dominant prey species in the diet of Arctic Cod in the Beaufort Sea by frequency of occurrence (%FO ± SE) for each size class within each depth zone. Only species that contributed >5% frequency of occurrence to any of the groups' diets were included in this table. A superscript indicates a significant difference in %FO of that prey species among depth zones for that size class.

Size Class		**1**			**2**		
		Depth Zone			**Depth Zone**		
Class	**Species**	**Shelf**	**Upper Slope**	**Lower Slope**	**Shelf**	**Upper Slope**	**Lower Slope**
Copepoda	*Calanus hyperboreus*	45 ± 12	0	0	85 ± 4	39 ± 16	64 ± 17
	Calanus glacialis	96 ± 3	100 ± 0	100 ± 0	64 ± 8^{a}	35 ± 15^{a,b}	17 ± 17^{b}
	Metridia longa	13 ± 5	0	17 ± 17	29 ± 8	20 ± 9	17 ± 17
	Jaschnovia tolli	6 ± 6	0	0	13 ± 5	0	11 ± 7
	Paraeuchaeta glacialis	12 ± 5	0	0	16 ± 5	7 ± 5	14 ± 9
	Acartia longiremis	0	0	11 ± 11	0	0	0
	Heterorhabdus norvegicus	3 ± 3	0	0	0	0	0
	Pseudocalanus	75 ± 27	100 ± 0	72 ± 15	25 ± 8	17 ± 7	28 ± 16
	Microcalanus	24 ± 6	0	11 ± 11	4 ± 4	3 ± 3	0

	Copepoda nauplii	15 ± 7	100 ± 0	11 ± 11	0	0	0
	Harpacticoida	5 ± 5	0	11 ± 11	0	0	0
	Triconia	5 ± 5	0	11 ± 11	0	0	0
	Triconia borealis	0	0	11 ± 11	2 ± 2	0	0
	Oithona	0	0	11 ± 11	0	0	0
	Oithona similis	18 ± 10	0	0	0	3 ± 3	0
Malacostraca	*Themisto libellula*	4 ± 3	0	0	35 ± 8	38 ± 12	28 ± 18
	Themisto abyssorum	0	0	0	33 ± 11	68 ± 10	58 ± 20
	Apherusa glacialis	0	0	0	0	0	17 ± 17
	Amphipod undetermined	0	0	0	0	0	8 ± 8
	Thysanoessa raschii	0	0	0	8 ± 3	0	0
	Thysanoessa inermis	0	0	0	0	0	0
	Mysis undetermined	0	0	0	0	0	0
	Mysis oculata	0	0	0	0	0	6 ± 6
	Sabinea septemcarinata	0	0	0	2 ± 2	0	0
Ostracoda	*Ostracoda*	0	0	0	0	17 ± 13	50 ± 19

	Boroecia maxima	0	0	0	3 ± 2	17 ± 10	31 ± 16
Bivalvia	*Bivalvia*	0	0	11 ± 11	0	0	0
Gastropoda	*Limacina helicina*	0	0	11 ± 11	0	0	0

Table 3.2 continued…

	Size Class	**3**			**4**		
		Depth Zone			**Depth Zone**		
Class	**Species**	**Shelf**	**Upper Slope**	**Lower Slope**	**Shelf**	**Upper Slope**	**Lower Slope**
Copepoda	*Calanus hyperboreus*	56 ± 16	35 ± 11	50 ± 29	50 ± 50	24 ± 12	7 ± 7
	Calanus glacialis	42 ± 18	46 ± 9	11 ± 11	0	29 ± 16	0
	Metridia longa	26 ± 14	21 ± 9	0	0	15 ± 7	0
	Jaschnovia tolli	4 ± 4	11 ± 8	0	50 ± 50	0	0
	Paraeuchaeta glacialis	26 ± 14	10 ± 5	0	50 ± 50	0	0
	Acartia longiremis	0	0	0	0	0	0
	Heterorhabdus norvegicus	0	13 ± 9	0	0	0	0
	Pseudocalanus	0	6 ± 4	0	0	13 ± 9	20 ± 20
	Microcalanus	0	0	0	50 ± 50	13 ± 16	7 ± 7
	Copepoda nauplii	0	0	0	0	0	0
	Harpacticoida	0	0	0	0	0	0

	Triconia	0	0	0	0	0	0
	Triconia borealis	0	0	0	0	0	0
	Oithona	0	0	0	0	0	0
	Oithona simils	0	0	0	0	0	0
Malacostraca	*Themisto libellula*	29 ± 15	65 ± 12	50 ± 29	50 ± 50	21 ± 16	40 ± 19
	Themisto abyssorum	49 ± 18	52 ± 8	50 ± 29	50 ± 50	29 ± 16	13 ± 8
	Apherusa glacialis	0	4 ± 4	0	50 ± 50	0	20 ± 20
	Amphipod undetermined	14 ± 14	4 ± 4	0	0	0	0
	Thysanoessa raschii	5 ± 5	0	0	50 ± 50	0	0
	Thysanoessa inermis	0	0	0	50 ± 50	0	0
	Mysis undetermined	0	0	0	0	0	7 ± 7
	Mysis oculata	0	4 ± 4	0	0	0	7 ± 7
	Sabinea septemcarinata	5 ± 5	0	0	0	0	0
Ostracoda	*Ostracoda*	4 ± 4	4 ± 4	67 ± 33	0	18 ± 9	20 ± 20
	Boroecia maxima	0	33 ± 13	0	0	14 ± 9	20 ± 20
Bivalvia	*Bivalvia*	0	0	0	0	0	0

Gastropoda	*Limacina helicina*	0	0	0	0	0	0

Table 3.3 Dominant prey species in the diet of Arctic Cod in the Beaufort Sea by number (%N ± SE) for each size class within each depth zone. Only species that contributed > 5% by number to any of the groups' diets were included in this table.

Size Class		1			2		
		Depth Zone			Depth Zone		
Class	**Species**	**Shelf**	**Upper Slope**	**Lower Slope**	**Shelf**	**Upper Slope**	**Lower Slope**
Copepoda	*Calanus hyperboreus*	8 ± 4	0		35 ± 8	27 ± 12	18 ± 6
	Calanus glacialis	50 ± 8	0	24 ± 24	30 ± 9^a	11 ± 6^b	4 ± 4
	Metridia longa	2 ± 1	0	1 ± 1	6 ± 3	5 ± 2	3 ± 3
	Pseudocalanus	27 ± 5.17	81 ± 6	53 ± 22	14 ± 7	5 ± 3	6 ± 3
	Copepoda nauplii	5 ± 4	19 ± 6	13 ± 13	0	0	0
Malacostraca	*Stilomysis grandis*	0	0	0	0	0	0
	Themisto libellula	0 ± 0	0	0	4 ± 1	6 ± 3	11 ± 7
	Themisto abyssorum	0	0	0	8 ± 5^a	36 ±	31 ± 12^b

						$11^{a,b}$	
Ostracoda	*Ostracoda*	0	0	0	0	2 ± 2	17 ± 8
	Boroecia maxima	0	0	0	0 ± 0	6 ± 3	3 ± 1
Bivalvia	*Bivalvia*	0	0	11 ± 11	0	0	0
Oligochaeta	*Oligochaete*	0	0	0	0	0	0

Table 3.3 continued…

	Size Class	**3**			**4**		
		Depth Zone			**Depth Zone**		
Class	**Species**	**Shelf**	**Upper Slope**	**Lower Slope**	**Shelf**	**Upper Slope**	**Lower Slope**
Copepoda	*Calanus hyperboreus*	32 ± 13	14 ± 7	27 ± 25	0 ± 0	7 ± 5	1 ± 1
	Calanus glacialis	13 ± 10	7 ± 3	1 ± 1	0	1 ± 1	0
	Metridia longa	6 ± 4	1 ± 1	0	0	7 ± 5	0
	Pseudocalanus	0	0 ± 0	0	0	7 ± 7	3 ± 3
	Copepoda nauplii	0	0	0	0	0	0
Malacostraca	*Stilomysis grandis*	0	0	0	0	8 ± 8	0
	Themisto libellula	11 ± 7	16 ± 4	2 ± 1	4 ± 4	7 ± 7	31 ± 13
	Themisto abyssorum	30 ± 12	47 ± 9	34 ± 27	44 ± 44	31 ± 15	13 ± 11
Ostracoda	*Ostracoda*	0 ± 0	1 ± 1	35 ± 33	0	18 ± 16	10 ± 10
	Boroecia maxima	0	7 ± 3	0	0	4 ± 3	17 ± 17

Bivalvia	*Bivalvia*	0	0	0	0	0	0
Oligochaeta	*Oligochaete*	0	0	0	0	6 ± 6	0

Table 3.4 Dominant prey species in the diet of Arctic Cod in the Beaufort Sea by mass (%WT ± SE) for each size class within each depth zone. Only species that contributed > 5% by mass to any of the groups' diets were included in this table.

Size Class		**1**			**2**		
		Depth Zone			**Depth Zone**		
Class	**Species**	**Shelf**	**Upper Slope**	**Lower Slope**	**Shelf**	**Upper Slope**	**Lower Slope**
Copepoda	*Calanus hyperboreus*	29 ± 10	0	0	75 ± 23	31 ± 13	27 ± 9
	Calanus glacialis	62 ± 55.838	72 ± 9	87 ± 9	20 ± 9^{a}	7 ± 4^{a,b}	6 ± 6^{b}
	Metridia longa	1 ± 0	0	1 ± 1	2 ± 2	0 ± 0	1 ± 1
	Paraeuchaeta glacialis	1 ± 0	0	0	10 ± 7	0 ± 0	3 ± 2
	Pseudocalanus	4 ± 2	28 ± 8	6 ± 3	1 ± 0	0 ± 0	0 ± 0
Malacostraca	*Stilomysis grandis*	0	0	0	0	0	0
	Themisto libellula	1 ± 1	0	0	14 ± 4	30 ± 12	32 ± 20

	Themisto abyssorum	0	0	0	2 ± 1[a]	25 ± 13[b]	14 ± 9[a,b]
	Apherusa glacialis	0	0	0	0	0	4 ± 4
	Thysanoessa raschii	0	0	0	2 ± 1	0	0
Ostracoda	*Ostracoda*	0	0	0	0 ± 0	5 ± 3	11 ± 8

Table 3.4 continued…

	Size Class	3			4		
		Depth Zone			Depth Zone		
Class	**Species**	**Shelf**	**Upper Slope**	**Lower Slope**	**Shelf**	**Upper Slope**	**Lower Slope**
Copepoda	*Calanus hyperboreus*	40 ± 15	15 ± 7	36 ± 26	0 ± 0	12 ± 8	0 ± 0
	Calanus glacialis	8 ± 6	3 ± 1	1 ± 1	0	2 ± 1	0
	Metridia longa	2 ± 2	0 ± 0	0	0	8 ± 8	0
	Paraeuchaeta glacialis	8 ± 7	3 ± 2	0	1 ± 1	0	0
	Pseudocalanus	0	0 ± 0	0	0	1 ± 1	0 ± 0
Malacostraca	*Stilomysis grandis*	0	0	0	0	13 ± 13	0
	Themisto libellula	25 ± 13	55 ± 8	15 ± 10	0 ± 0	19 ± 15	55 ± 23
	Themisto abyssorum	16 ± 12	16 ± 6	12 ± 1	16 ± 16	20 ± 12	1 ± 0
	Apherusa glacialis	0	1 ± 1	0	0 ± 0	0	20 ± 20
	Thysanoessa raschii	0 ± 0	0	0	6 ± 6	0	0

Ostracoda	*Ostracoda*	0 ± 0	1 ± 1	33 ± 33	0	22 ± 16	20 ± 20

3.3.5 Arctic Cod Diet: Comparisons Among Depth Zones

The diet of Arctic Cod by %FO, %N, and %WT of common prey species was not significantly different among depth zones for size classes 1, 3, and 4, but there were significant differences in the diet of size class 2 Arctic Cod. For size class 1 Arctic Cod, there were significant differences for uncorrected p-values of median %FO, %N, and %WT of *Calanus hyperboreus* and the %N of *Calanus glacialis* in the stomachs among depth zones (p = 0.03 for all, 3 d.f.), and for size class 3 Arctic Cod there were also significant differences for uncorrected p-values of median %FO of *Themisto libellula* in the stomachs among depth zones (p = 0.04, 3 d.f.). However, post-hoc pair-wise comparisons found no significant differences in their diet (%FO, %N, or %WT) among depth zones. There was no significant difference in the diet of size class 4 Arctic Cod among depth zones. For size class 2 Arctic Cod there were significant differences among depth zones in the median %FO of *C. glacialis* (Shelf-Lower Slope, Kruskal-Wallis with Holm adjustment, p-adj = 0.004), %N of *T. abyssorum* (Shelf-Lower Slope, p-adj = 0.02) and *C. glacialis* (Shelf-Upper Slope, p-adj = 0.002), and %WT of *Themisto abyssorum* (Shelf-Upper Slope, p-adj = 0.007) and *C. glacialis* (Shelf-Lower Slope, p-adj = 0.002). See Figures 6.1-6.3 in Appendix D for bar graphs of %FO, %N, and %WT of common prey species of Arctic Cod among depth zones within size classes. *C. glacialis* became less common in the diet of this size class of Arctic Cod with depth, whereas *T. abyssorum* became more frequent in the diet and accounted for more of the diet mass between the Shelf and Upper Slope zones, and was more abundant in the diet of Arctic Cod in the Lower Slope zone than the Shelf.

3.3.6 Prey Density in Diet Related to Density in Environment

The areal density by mass and number of *Themisto* spp. in the CBS was low relative to all prey available to Arctic Cod, ranging from 0-1.4% by mass and 0-0.5% by abundance compared to 10-70% by mass and 0-30% by abundance for *Calanus* spp. Figure 3.5a compares the mass percentage of *Themisto* spp. available in the environment by station to the mass percentage of *Themisto* spp. in the diet of Arctic Cod by size class by station, and Figure 3.5b makes the same comparisons for *Calanus* spp. Figure 3.5c compares the percent abundance of *Themisto* spp. available in the environment by station to the percent abundance of *Themisto* spp. in the diet of Arctic Cod by size class by station, and Figure 3.5d indicates the same comparisons for *Calanus* spp. Despite the low density by mass and abundance of *Themisto* in the environment relative to *Calanus, Themisto* still constitutes a large percentage of the diet. Note that all stomachs included in the analysis contained prey, but may not have contained either *Themisto* or *Calanus*.

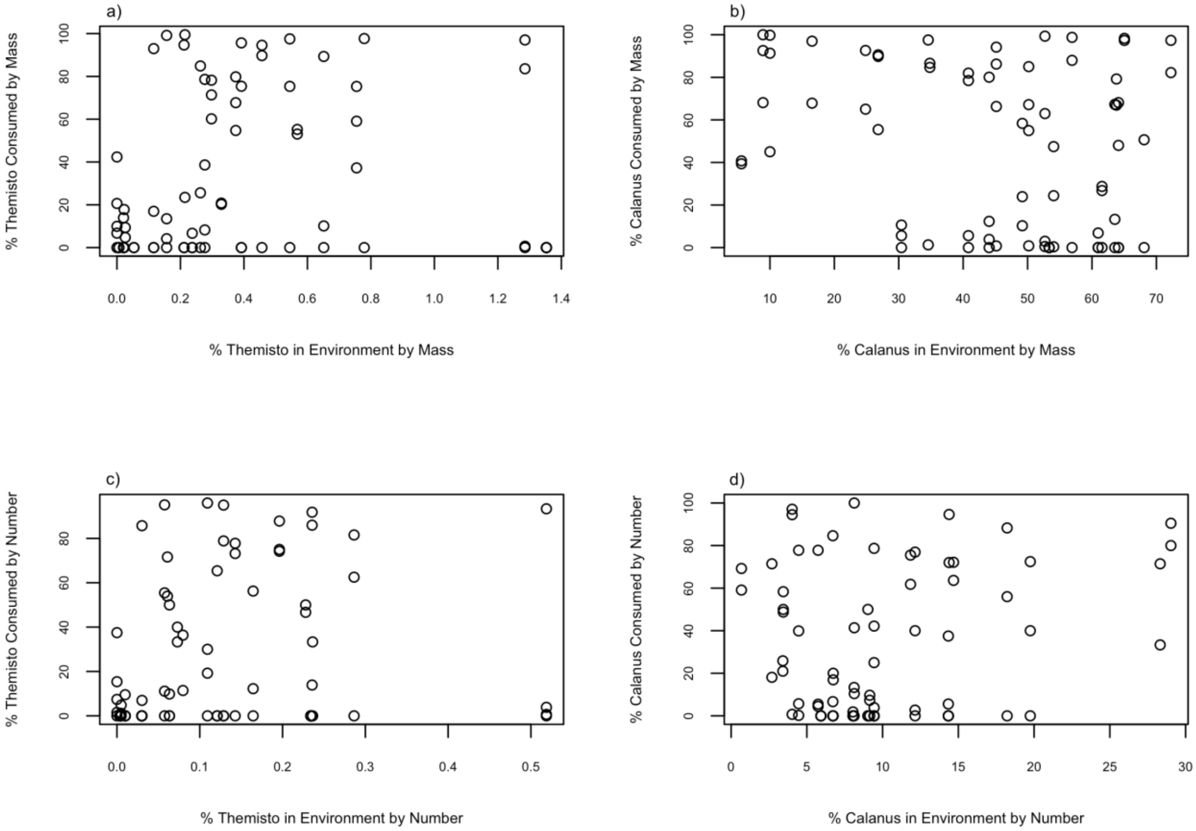

Figure 3.7 The mass percentage (a, b) and percent abundance (c, d) of the main Arctic Cod prey species in the environment, (a, c) *Themisto* and (b, d) *Calanus*, compared to their mass percentage and percent abundance in stomach contents. Note that all stomachs included were not empty, but may not have contained either of these common prey species.

3.3.7 Energy Density of Common Prey

Energy densities of some common prey are provided for the CBS in Table 3.5. For reference, energy density values from similar areas to the CBS were also included for common Arctic Cod prey items when samples for calorimetry were not collected during the current study.

The energy densities obtained in the current study were similar to those for the same species in other Arctic locations, thus these data are likely representative (Table 3.5). *Metridia longa* had the highest energy density of all prey included in this study (7151 cal/g dry mass, April in the Northeast (NE) Atlantic Ocean, Norrbin and Båmstedt 1984). Of the most common prey types observed in the stomachs, *C. hyperboreus* had the highest energy density in the Canadian Beaufort Sea (6394.5 cal/g dry mass, n = 16) and *T. abyssorum* the lowest (4461.9 cal/g mass, n = 1). However, further studies with larger sample sizes are needed to confirm the values provided herein. Due to the small sample size from 2012, the energy density of *C. glacialis* and *T. abyssorum* used in calculations of the energy content of an average diet was an average of the energy densities of samples from 2012 and 2014 (*C. glacialis*: 6414.5 cal/g dry mass; *T. abyssorum*: 4729.6 cal/g dry mass).

Note that there is a bias in the results for the energy content of an average diet by size class by depth zone due to a lack of information on the energy density of some prey items. The energy content of prey items with no information was not included in the analyses, and therefore the total energy content of the diet is underestimated herein. The energy content of the average diet by size class by depth zone was based on the prey energy density values provided in Table 3.5 and the average dry mass of those species in the diet for each size class within each depth zone. The total energy content of an average diet was highest for those of size class 4 on the Shelf (1021.7 cal), and the lowest for those of size class 1 on the Upper Slope (2.9 cal). However, Arctic Cod of size class 4 on the Shelf and size class 1 on the Upper Slope were very rare; only n = 2 were used in the analysis. By size class, the highest energy content of an average diet for size classes 2 and 3 Arctic Cod by depth zone was on the Shelf (195.3 and 283.9 cal) and lowest in the Lower Slope zone (98.2 and 150.9 cal). Within each depth zone, the diet energy

Table 3.5 Energy density (calories per gram, cal/g dry mass) of common prey of Arctic Cod (mean ± SD, n = number of bombs, CBS = Canadian Beaufort Sea, SB = Spitsbergen & Barents Sea). The energy density of *C. glacialis* and *T. abyssorum* was an average of the energy densities of samples from 2012 and 2014 to increase sample sizes to statistical relevance.

Species	Stage	Energy Density (cal/g DW)	Location	Source
Calanus hyperboreus		6394.5 ± 371.4 (n=16)	CBS	BREA 2012, this study
		7350.7 ± 99.6 (n=2)	Amundsen Gulf, Midwater	BREA 2014, this study
		5417.1 ± 787.8 (n=3)	Amundsen Gulf, Surface	BREA 2014, this study
	CII	6139.8	Spitsbergen & Barents Sea	Weslawski *et al.*, 1999
	CIII	5972.6	Spitsbergen & Barents Sea	Weslawski *et al.*, 1999
	CIV	4156.9	Spitsbergen & Barents Sea	Weslawski *et al.*, 1999
	CV	3822.4	Spitsbergen & Barents Sea	Weslawski *et al.*, 1999
	CVI	3989.7	Spitsbergen & Barents Sea	Weslawski *et al.*, 1999
Calanus glacialis		5397.1 (n=1)	CBS	BREA 2012, this study
		6541.7 ± 484.4 (n=8)	Amundsen Gulf	BREA 2014, this study
	CI-II	6139.8	Spitsbergen & Barents Sea	Weslawski *et al.*, 1999
	CIII-IV	5638.1	Spitsbergen & Barents Sea	Weslawski *et al.*, 1999
	CV	4156.9	Spitsbergen & Barents Sea	Weslawski *et al.*, 1999
	CVI	3822.4	Spitsbergen & Barents Sea	Weslawski *et al.*, 1999

Paraeuchaeta glacialis		5715.3 ± 348.3 (n=4)	CBS	This study
	Female	6617.6 ± 1529.0 (n=13)	White Sea	Kosobokova, 1980
	CV female	3273 ± 862.4 (n=10)	White Sea	Kosobokova, 1980
	CV male	2014 ± 974.7 (n=8)	White Sea	Kosobokova, 1980
	CIV	989.1 ± 360.7 (n=5)	White Sea	Kosobokova, 1980
Themisto abyssorum		4461.9 (n=1)	CBS	BREA 2012, this study
		4997.25 (n=1)	Amundsen Gulf	BREA 2014, this study
		4395.8	Spitsbergen & Barents Sea	Weslawski *et al.*, 1999
Themisto libellula		5177.1 ± 387.3 (n=5)	CBS	This study
		4220-5620 (n=22)	Frobisher Bay	Percy and Fife, 1981
		4061.4	Spitsbergen & Barents Sea	Weslawski *et al.*, 1999
		3258.6 ± 121.8 (n=4)	Hornsund, Spitsbergen	Wolowicz and Szaniawska, 1986
Thysanoessa raschii		5861.0	Bristol Bay	Nishiyama, 1977 as in Davis, 1993
Thysanoessa inermis		6799.0 (n=1)	CBS	BREA 2012, this study
Pseudocalanus minutus		5070.9 ± 181.7	N Atlantic	NOAA Fishery Bulletin
Pseudocalanus elongates	Female	4800.0 (n=6)	White Sea	Kosobokova, 1980
Metridia longa		6489.0	NE Atlantic	Norrbin *et al.*, 1984, December as in Davis, 1993
		7151.0	NE Atlantic	Norrbin *et al.*, 1984, April as in Davis, 1993
Copepod nauplii, Ostracoda, Oithona similis, Boroecia		4682.5	Spitsbergen & Barents Sea	Weslawski *et al*. 1999

maxima				
Jaschnovia tolli (same as Pseudocalanus)	Female	5070.9	N Atlantic	NOAA Fishery Bulletin
Gammarellus homari		4051.8 ± 100.3	Hornsund, Spitsbergen	Wolowicz and Szaniawska, 1986

content increased with size class. An exception is size class 4 Arctic Cod on the Upper Slope, where the energy content of an average diet in this depth zone was only 42.4 cal. Kruskal-Wallis tests determined there was a significant difference in the median diet energy content of size class 1 Arctic Cod by depth zone (Kruskal-Wallis, p-adj = 0.01, 2 d.f.; Table 3.6). The energy content of a diet of Arctic Cod captured on the Shelf averaged across all size classes was 186.5 cal, on the Upper Slope was 114.0 cal, and on the Lower Slope was 165.2 cal. Overall, the energy content of diet was higher on the Shelf than in the other depth zones (Table 3.6), but there was no significant difference in average diet energy content among depth zones (Kruskal-Wallis, p = 0.28, 2 d.f.; Table 3.7).

Table 3.6 Mean (Mean (Median) ± SE) energy content (cal) of an average diet by size class by depth zone based on the energy density of common prey species (Table 3.5). Due to low sample size, the energy density of *C. glacialis* used in the calculations was based on the mean energy density of samples from 2012 and 2014 in the Beaufort Sea. There was a significant difference in the median diet energy content of size class 1 Arctic Cod between the Shelf and Lower Slope zones (p-adj = 0.01). Significant differences among habitats are indicated by lettered superscripts.

Zone	**Size Class**	**N**	**Mean (Median) Energy Content (± SE) of Average Diet (cal)**
Shelf	1	40	49.1 (54.0) ± 9.9^{a}
Upper Slope	1	2	1.6 (1.6) ± 1.0^{a,b}
Lower Slope	1	8	4.4 (1.5) ± 3.4^{b}
Shelf	2	55	176.6 (183.7) ± 25.9
Upper Slope	2	23	111.9 (54.6) ± 40.3
Lower Slope	2	10	87.2 (100.1) ± 26.9
Shelf	3	13	180.5 (52.8) ± 107.0
Upper Slope	3	29	206.7 (180.2) ± 68.0
Lower Slope	3	4	169.9 (47.0) ± 146.5
Shelf	4	2	1021.7 (1021.7) ± 1021.7
Upper Slope	4	15	42.4 (3.6) ± 26.4
Lower Slope	4	9	384.4 (215.3) ± 267.7

Table 3.7 Mean energy content (cal) of an average diet for a CBS Arctic Cod from each of the depth zones and size classes. A Kruskal-Wallis test found no significant difference in median energy content of an average diet among depth zones ($p = 0.43$), but there was a significant difference among size classes (Kruskal-Wallis with Holm correction; 1-2, p-adj = 0.005; 1-3, p-adj = 0.02).

Depth Zone	**Mean (Median) Energy Content (± SE) of Average Diet (cal)**
Shelf	186.5 (77.8) ± 65.6
Upper Slope	114.0 (48.8) ± 29.1
Lower Slope	165.2 (30.8) ± 80.1
Size Class	
1	33.0 (18.7) ± 8.4
2	136.1 (123.4) ± 19.2
3	190.4 (72.9) ± 53.4
4	304.5 (11.6) ± 167.3

3.4 Discussion

Arctic Cod are primarily visual predators, thus their ability to see prey is likely limited at depth in the Beaufort Sea, where the euphotic zone only extends down from an average of 10-60m depth (Juul-Pedersen *et al*. 2010). In deep, dark waters beyond the euphotic zone Arctic Cod sense prey using their other senses. The lateral line system in fish detects movement and may be able to give clues on the size of that prey based on the size of the silhouette produced from the contrast between the zooplankton and the surrounding environment (Lazzaro 1987).

With a seasonal difference in prey distribution due to seasonal vertical migrations outlined above (Falk-Petersen *et al*. 2008; Rabindranath *et al*. 2011), the diet of Arctic Cod likely varies similarly. Therefore, the diet of Arctic Cod as presented in this study, determined via analysis of stomach contents, represents what was in the stomach at the time of capture only and does not represent the entire diet of this species or even the individual. However, data exist for investigation of the fatty acid composition of the fish in this study, which should give insight into the overall diet of Arctic Cod in the CBS integrated over a longer time scale of weeks to months (B. Lynn, unpublished data). Regardless, analysis of stomach contents data in the current study provides valuable baseline information on the diet of Arctic Cod during the open water season, the primary feeding window in the CBS. Feeding by Arctic Cod during the polar night was not investigated in the current study, though recent research in Svalbard discovered that Arctic Cod were indeed foraging in the dark (Berge *et al.* 2015a; Berge *et al.* 2015b).

The literature has shown that Arctic Cod diet changes with increase in age (Walkusz *et al*. 2013). The current study classified Arctic Cod into four groups or size classes (1-4+) based on 30mm bins (size class 1: 30-60mm; size class 2: 60-90mm; size class 3: 90-120mm; size class 4: 120mm+), but further differences are likely between individuals of 120 and 210mm. However, because of a very low number of larger individuals captured at each of the stations, these individuals were combined into size class 4+ and the analysis of further ontogenetic variation in diet beyond size class 4+ was precluded due to low sample sizes and statistical power. Future studies should investigate the variation in diet present among larger individuals.

Diet species composition (Tables 3.4-3.6) was presented as only that which represents > 5% of the diet by percent frequency of occurrence, number, and mass. While it was important to show the species diversity in the diet, only those species that constitute a significant proportion of the diet would give insight into the diet preferences of, or make a significant contribution to, energy intake by Arctic Cod insofar as can be determined in this study. Therefore all other species were removed. See Appendix D for a complete list of the diet of CBS Arctic Cod, including rare species.

Analysis of species composition of Arctic Cod diet indicated notable differences in the proportion of larger prey species such as *T. libellula* among Arctic Cod size classes, specifically between size class 1 and size classes 2 - 4. This further supports the ontogenetic shift in the diet suggested for this species (Walkusz *et al*. 2013).

The current study was designed to analyze differences in the diet of Arctic Cod captured in the demersal zone. However, vertical migrations by smaller adult Arctic Cod have been observed in other Arctic environments (Benoit *et al*. 2010). A hydroacoustic analysis conducted in parallel with the mid-water trawling on the Beaufort Shelf slope has suggested that Arctic Cod were not making diel vertical migrations over significant depth intervals during the time of sampling (Geoffroy *et al*. 2015). Two distinct concentrations of Arctic Cod were observed in the water column: young-of-the-year at the surface and adults age-1+ and greater 200m above the bottom and down to 300-500m depth, extending offshore in the water column over deeper areas. While DVM was observed within both aggregations, the migrations were limited and they appeared to stay within the Pacific-Atlantic layer, even at night (M. Geoffroy, *pers. comm.*). Some fish were also distributed individually at depth. Of those Arctic Cod migrating upward in the water column, it was likely only the younger (age 1+) cod that did so to avoid competition and possibly cannibalism by older individuals at depth (Benoit *et al*. 2010). Due to a lack of definitive information on the vertical migrations of Arctic Cod captured on the bottom and analyzed in the current study, it was assumed that they were living and foraging entirely in the demersal zone. This may confound the results, as vertical migration could vary among age classes and lead to differences in prey availability. Future studies should consider this vertical migration.

Despite the fact that Arctic Cod are known to exhibit a sexual difference in body size, analyses of diet in this study could not be made based on sex while still analyzing diet by size class without sacrificing statistical power. Investigating differences in diet by sex by size class would result in severely unbalanced statistical designs (Table 3.2). Future studies should consider differences in diet between sexes while controlling for size class as well as habitat.

In the current study, comparisons of Arctic Cod diet were made based on depth zone and size class. Differences among sampling transects were not considered, as prey species composition did not vary considerably and environmental conditions including nutrient and light availability due to upwelling events and river outflow are assumed to be consistent by depth zone across transects (W. Walkusz, unpublished data).

While the biomass density of common Arctic Cod prey species and population density of *Themisto* spp. increased with depth, there was no effect of depth on the number of species in the diet. Alternatively, the population density of *Calanus* spp. decreased with depth zone, which would be expected given the high productivity on the continental shelf. Generally, the diet contained a higher number of species on the Shelf than in the other depth zones. In other words, the number of prey species in the diet of Arctic Cod is related to the distribution of both Arctic Cod and their prey. The number of species in the diet was generally lower in the deep Lower

Slope zone, coinciding with an increase in areal density of major prey species. The total number of Arctic Cod prey species in the environment was unknown. Pelagic zooplankton species (e.g., copepods and amphipods) were relatively common in the diet, whereas sympagic (ice-associated, e.g., *Apherusa glacialis*) and benthic prey (e.g., *Ostracoda*) were more rare. The Arctic Cod included in the present study were captured just above the bottom (benthic zone), thus the predominance of pelagic prey in the diet suggests that Arctic Cod are vertically migrating to a certain degree to forage. The generally lower presence of sympagic prey in the diet was because sampling occurred during the open water season (August 2012), or the availability of zooplankton prey as they migrate down during their DVM or passive drifting. However, future studies should involve zooplankton sampling at targeted depths in order to understand prey availability for Arctic Cod that associate with the bottom for some length of time.

A comparison of the percentage of *Themisto* in the diet by mass and abundance with the percentage of *Themisto* available in the environment by mass and abundance relative to all possible Arctic Cod prey suggests that while this species is rare compared to other known prey species, it constitutes a major proportion of the diet of older Arctic Cod (size class 2-4). The areal density of *Calanus* increased moving off the shelf, and it was the most common prey species in the environment in terms of biomass and abundance, but constituted proportionally less of the diet of all size classes with increasing depth zone. Whereas the energy density of *Calanus* is higher than *Themisto* on a dry-mass basis, the total energy of an individual *Themisto* would be higher due to their larger body size. For reference, an average *T. libellula* is 10.5mg and 54.4 cal, while an average (adult female) *C. hyperboreus* is 3.2mg and 20.5 cal. Comparisons among Arctic Cod size classes showed that larger prey, e.g., *T. libellula*, are absent from the diet of small Arctic Cod (size class 1), and only become a major component of diet once the fish becomes larger. Also, the increase in variance in the size of prey taken with increasing gape width suggests that the gape size likely limits the ability of smaller Arctic Cod to consume the large prey. Thus, these two factors reinforce each other, i.e., gape-size limitations and the limited availability of larger prey species in the environment, act together to result in consumption of prey that are larger and contain more energy. This size-dependent prey consumption has been observed in many other studies of Arctic Cod diet (Pirtle and Mueter 2011; Rand *et al*. 2013; Walkusz *et al.* 2013). Given the likely sparse and seasonal prey distribution, Arctic Cod would be expected to maximize the average rate of energy gain while foraging. Although data collected on prey density integrated over the water column showed that prey biomass increased with depth (W. Walkusz, unpublished data), this was based on integrated vertical MultiNet tows and it is not known exactly how much prey is immediately available to a demersal Arctic Cod. Future sampling for prey availability in this region should be done at targeted depths to understand the species composition of prey across depths, so as to determine if it reflects what is found in their stomachs or if Arctic Cod are selectively foraging.

The only significant differences in diet species composition among depth zones were observed within size class 2 Arctic Cod. The decrease in the percentage of *C. glacialis* in the diet (%FO) with depth for this size class could be explained by the increase in density of larger prey with depth or a decrease in density of *C. glacialis* with depth. Indeed, a survey of the vertical distribution of *Calanus* spp. around the Svalbard archipelago found that the density of *C. glacialis* decreased with depth (Daase *et al*. 2008). The increase in *T. abyssorum* in the diet of size class 2 Arctic Cod with depth may also be associated with prey distribution. However, as mentioned species-specific information on the vertical distribution of prey was not available for the current study area. Intraspecific competition with larger individuals may also factor in to diet.

As larger individuals are able to consume larger *T. libellula* that are higher in energy, competition for smaller *T. abyssorum* could be reduced for smaller individuals, such as those of size class 2.

There was a significant difference in the energy content of an average diet between size class 1 and larger size classes, and differences in the energy available for allocation likely increase with body size as energy requirements change. Across life stages, different energy allocation strategies are expected. Small, young-of-the-year (YOY) Arctic Cod are expected to allocate most of their energy to growth, as it affords them the ability to migrate out of the surface waters where they hatched to deeper waters and to grow to a size that makes them less likely to be eaten, thus decreasing their vulnerability to diving predators. Meanwhile, adult Arctic Cod must allocate their surplus energy to body growth, presumably increasing their intra-specific competitive ability, to reproduction to contribute to future generations (i.e., gamete production), to energy storage for survival, or to locomotion for vertical migrations in search of food, if necessary. Some energy requirements are also relative to body size. Activity and foraging become more energetically efficient relative to body size as the fish gets bigger, as mass-specific costs of transport go down in most animals up to a critical mass (Bale *et al*. 2014). Also, resting metabolic rates are correlated with body mass (Clarke and Johnston 1999), so total metabolic costs would be lower in young compared to older Arctic Cod, but mass-specific metabolic costs would be lower in older Arctic Cod. Therefore, less total energy is needed to sustain life in a young Arctic Cod, which could explain why the energy content of their average diet is low. See Chapter 4 for a further discussion of the energy needs and allocation strategies of adult Arctic Cod, and spatial as well as sexual differences in energy allocation.

The decline in energy content of an average diet for size class 1 Arctic Cod with depth was likely a result of prey species distribution. Small energy-rich prey that are common in the diet of small Arctic Cod, such as *Pseudocalanus* spp., are abundant on the Shelf (Walkusz *et al*. 2010; Walkusz *et al.* 2011). The high %WT of *Pseudocalanus* in the stomachs of size class 1 Arctic Cod on the Upper Slope (Tables 3.2-3.4) was likely due to the high density of *Pseudocalanus* on the Upper Slope (W. Walkusz, unpublished data). However, zooplankton life stage and thus body size increases with depth, and smaller Arctic Cod that migrate deeper would be unable to consume these larger prey. Small Arctic Cod are also vulnerable to predation on the Shelf, and are therefore likely to consume as large an amount of energy as possible in that habitat so they can migrate away from surface waters and diving predators (Post and Parkinson 2001). At depth, however, they are still potentially vulnerable to deep-dwelling predators such as Greenland Halibut (*Reinhardtius hippoglosoides*, T.N. Gill 1861) (Rodriguez-Marin *et al.* 1995) and Arctic Skates (*Amblyraja hyperborea*, Collett 1879), though very little is known about the diets of these predators in the CBS. Small cod also are vulnerable to cannibalism from larger individuals of their own species. Still, growing larger comes with a better ability to avoid predation due to an increase in swimming speed (Sambilay 1990) and access to more, larger types of prey with a higher energy content.

The average diet of Arctic Cod of size class 4 had the highest energy content in the Shelf zone. This could be attributed to the ability of these large fish to out-compete the more abundant smaller Arctic Cod on the Shelf for food, and their ability to consume larger prey unavailable to those individuals with a smaller gape despite the lower density of food available on the Shelf, or the fact that their gut storage is larger. There was a lower frequency of large individuals on the Shelf compared to the other depth zones, possibly due to the low density of larger prey items and the higher density on the Upper Slope. Also, the negative size-specific relationship between body mass and the cost of swimming indicates that the larger fish would be able to forage more efficiently over a greater distance than would younger fish (Sambilay 1990; Helfman *et al*. 2009). However, if the cost of swimming is standardized by unit weight of the animal, swimmers beyond a critical mass of 1kg are equally efficient (Bale *et al*. 2014). Arctic Cod do not reach this critical mass. Future studies should investigate the variation in foraging behaviour of Arctic Cod with body size to determine differences in foraging costs and the extent of intraspecific competition for prey in Arctic Cod.

There are seasonal and depth differences in zooplankton lipid compositions in the Arctic. The seasonal pulse in primary productivity that is initiated by the spring melt eventually leads to seasonal changes in the diet of omnivorous *Themisto* amphipods and phytoplanktivorous zooplankton, which translates to seasonal differences in their lipid composition and concentration (Lee 1974; Prokopowicz 2011). This could result in seasonal variation in the caloric content of zooplankton prey and thus the energy content of an Arctic Cod diet. Meanwhile, depth differences in zooplankton lipid composition are related to their life cycle, with developmentally later and more energy-rich stages being found deeper. The current study did not have access to zooplankton separated by developmental stage nor depth, thus the caloric contents of prey used in the analyses included all developmental stages and did not take into account variability in energy density that could exist relative to developmental stage.

In conclusion, although diet composition, species proportions in the diet, and total energy content consumed varied significantly among groups of Arctic Cod both biologically (size class) and spatially (depth), and while this study provided further evidence of the importance of *Calanus* copepods and *Themisto* amphipods in the diet of Arctic Cod, the ability of Arctic Cod to selectively forage is still uncertain. Information on the availability of food at targeted depths and observation of foraging behaviour are needed to understand the specific ways in which Arctic Cod obtain energy from their environment and the differences that may exist with depth. This study reinforced the idea of an ontogenetic change in Arctic Cod diet and observed a depth-related effect species composition of the diet, suggesting that gape size as well as the vertical distribution of prey affects the diet of Arctic Cod in the CBS.

3.5 References

Bale R, Hao M, Bhalla APS, Patankar NA (2014) Energy efficiency and allometry of movement of swimming and flying animals. Proc Natl Acad Sci U S A 111:7517–21. doi: 10.1073/pnas.1310544111

Benoit D, Simard Y, Gagné J, Geoffroy M, Fortier L (2010) From polar night to midnight sun: photoperiod, seal predation, and the diel vertical migrations of polar cod (Boreogadus saida) under landfast ice in the Arctic Ocean. Polar Biol 33:1505–1520. doi: 10.1007/s00300-010-0840-x

Berestovskii E, Anisimova N, Denisenko C, Luppova EN, Savinov VM, Timofeev CF (1989) Relationships between size and body mass of some invertebrates and fish of the North-East Atlantic. In: Academy of Sciences of the USSR. Murman Marine Biological Institute, Apatity,

Berge J, Cottier F, Varpe Ø, Renaud PE, Falk-Petersen S, Kwasniewski S, Griffiths C, Søreide JE, Johnsen G, Aubert A, Bjærke O, Hovinen J, Jung-Madsen S, Tveit M, Majaneva S (2014) Arctic complexity: A case study on diel vertical migration of zooplankton. J Plankton Res 36:1279–1297. doi: 10.1093/plankt/fbu059

Berge J, Daase M, Renaud PE, Gonchar A, Krapp R, Callesen TA, Berge J, Daase M, Renaud PE, Ambrose WG, Darnis G, Last KS, Leu E, Ke M (2015a) Unexpected levels of biological activity during the polar night offer new perspectives on a warming Arctic. Curr Biol 25:2555–2561. doi: 10.1016/j.cub.2015.08.024

Berge J, Renaud PE, Darnis G, Cottier F, Last K, Gabrielsen TM, Johnsen G, Seuthe L, Weslawski JM, Leu E, Moline M, Nahrgang J, Søreide JE, Varpe Ø, Lønne OJ, Daase M, Falk-Petersen S (2015b) In the dark: A review of ecosystem processes during the Arctic polar night. Prog Oceanogr 139:258–271. doi: 10.1016/j.pocean.2015.08.005

Bradstreet MSW, Finley KJ, Sekerak AD, Griffiths WB, Evans CR, Fabijan MF, Stallard HE (1986) Aspects of the biology of Arctic cod (Boreogadus saida) and its importance in the Arctic marine food chains. In: Canadian Technical Report of Fisheries and Aquatic Sciences. p 202

Bradstreet MSW, Cross WE (1982) Trophic relationships at High Arctic ice edges. Arctic 35:1–12.

Clarke A, Johnston N (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. J Anim Ecol 893–905.

Daase M, Eiane K, Aksnes DL, Vogedes D (2008) Vertical distribution of Calanus spp. and Metridia longa at four Arctic locations. Mar Biol Res 4:193–207. doi: 10.1080/17451000801907948

Daase M, Hop H, Falk-Petersen S (2015) Small-scale diel vertical migration of zooplankton in the High Arctic. Polar Biol 39:1–11. doi: 10.1007/s00300-015-1840-7

Dalpadado P, Borkner N, Bogstad B, Mehl S (2001) Distribution of Themisto (Amphipoda) spp. in the Barents Sea and predator-prey interactions. ICES J Mar Sci 58:876–895. doi: 10.1006/jmsc.2001.1078

Falk-Petersen S, Leu E, Berge J, Kwasniewski S, Nygård H, Røstad A, Keskinen E, Thormar J, von Quillfeldt C, Wold A, Gulliksen B (2008) Vertical migration in high Arctic waters during autumn 2004. Deep Sea Res Part II Top Stud Oceanogr 55:2275–2284. doi: 10.1016/j.dsr2.2008.05.010

Falkenhaug T, Tande K, Semenova T (1997) Diel, seasonal and ontogenetic variations in the vertical distributions of four marine copepods. Mar Ecol Prog Ser 149:105–119.

Fauchald P, Skov H, Skern-Mauritzen M, Johns D, Tveraa T (2011) Wasp-waist interactions in the North Sea ecosystem. PLoS One. doi: 10.1371/journal.pone.0022729

Fortier M, Fortier L, Hattori H, Saito H, Legendre L (2001) Visual predators and the diel vertical migration of copepods under Arctic sea ice during the midnight sun. J Plankton Res 23:1263–1278. doi: 10.1093/plankt/23.11.1263

Geoffroy M, Majewski A, LeBlanc M, Gauthier S, Walkusz W, Reist JD, Fortier L (2015) Vertical segregation of age-0 and age-1 + polar cod (Boreogadus saida) over the annual cycle in the Canadian Beaufort Sea. Polar Biol. doi: 10.1007/s00300-015-1811-z

Geoffroy M, Robert D, Darnis G, Fortier L (2011) The aggregation of polar cod (Boreogadus saida) in the deep Atlantic layer of ice-covered Amundsen Gulf (Beaufort Sea) in winter. Polar Biol 34:1959–1971. doi: 10.1007/s00300-011-1019-9

Hanssen H (1997) Mesozooplankton of the Laptev Sea and the adjacent eastern Nansen Basin-distribution and community structure in late summer. Berichte zur Polarforsch 229:1–131.

Harter B, Elliott K, Divoky G, Davoren G (2013) Arctic Cod (Boreogadus saida) as prey: Fish length-energetics relationships in the Beaufort Sea and Hudson Bay. Arctic 66:191–196.

Hay SJ, Kiorboe T, Matthews A (1991) Zooplankton biomass and production in the North Sea during the Autumn Circulation Experiment, October 1987-March 1988. Cont Shelf Res 11:1453–1476.

Helfman G, Collette BB, Facey DE, Bowen BW (2009) The diversity of fishes: Biology, evolution, and ecology. John Wiley & Sons

Holm S (1979) A simple sequentially rejective multiple test procedure. Scand J Stat 6:65–70. doi: 10.2307/4615733

Hop H, Tonn WM (1998) Gastric evacuation rates and daily rations of Arctic cod (Boreogadus saida) at low temperatures. Polar Biol 19:293–301. doi: 10.1007/s003000050249

Jarvela LE, Thorsteinson LK (1999) The epipelagic fish community of Beaufort Sea coastal waters, Alaska. Arctic 52:80–94.

Juul-Pedersen T, Michel C, Gosselin M (2010) Sinking export of particulate organic material from the euphotic zone in the eastern Beaufort Sea. Mar Ecol Prog Ser 410:55–70. doi: 10.3354/meps08608

Kanaeva I (1962) Nekotorye osobennosti raspredeleniya planktona v Atlanticheskom okeane (Some Features of Plankton Distribution in the Atlantic Ocean). Okeanologiya 2:253–288.

Knickle DC, Rose GA (2014) Dietary niche partitioning in sympatric gadid species in coastal Newfoundland: evidence from stomachs and C-N isotopes. Environ Biol Fishes 97:343–355. doi: 10.1007/s10641-013-0156-0

Lazzaro X (1987) A review of planktivorous fishes: Their evolution, feeding behaviours, selectivities, and impacts. Hydrobiologia 146:97–167.

Lee RF (1974) Lipid composition of the copepod Calanus hyperboreas from the Arctic Ocean. Changes with depth and season. Mar Biol 26:313–318. doi: 10.1007/BF00391515

Logerwell E, Rand K, Weingartner TJ (2011) Oceanographic characteristics of the habitat of benthic fish and invertebrates in the Beaufort Sea. Polar Biol 34:1783–1796. doi: 10.1007/s00300-011-1028-8

Løkkeborg S (1998) Feeding behaviour of cod, Gadus morhua: activity rhythm and chemically mediated food search. Anim Behav 56:371–378. doi: 10.1006/anbe.1998.0772

Lowdon MK, Majewski AR, Reist JD (2011) Fish catch data from Herschel Island, Yukon Territory, and other offshore sites in the Canadian Beaufort Sea, July and August 2008, aboard the CCGS Nahidik. Winnipeg

Majewski A, Reist J, Park B, Lowdon M (2009) Fish catch data from offshore sites in the Mackenzie River estuary and Beaufort Sea during the open water season, August 2006, aboard the CCGS Nahidik. Winnipeg

Majewski AR, Walkusz W, Lynn BR, Atchison S, Eert J, Reist JD (2015) Distribution and diet of demersal Arctic Cod, Boreogadus saida, in relation to habitat characteristics in the Canadian Beaufort Sea. Polar Biol. doi: 10.1007/s00300-015-1857-y

Mumm N (1991) Zur sommerlichen Verteilung des Mesozooplanktons im Nansen-Becken, Nordpolarmeer = On the summerly distribution of mesozooplankton in the Nansen Basin, Arctic Ocean. Alfred-Wegener-Inst. für Polar- und Meeresforschung, Bremerhaven

Norrbin F, Båmstedt U (1984) Energy contents in benthic and planktonic invertebrates of Kosterfjorden, Sweden. A comparison of energetic strategies in marine organism groups. Ophelia 23:47–64. doi: 10.1080/00785236.1984.10426604

Pirtle JL, Mueter FJ (2011) Beaufort Sea fish and their trophic linkages: Literature search and synthesis.

Poltermann M (1997) Biology and ecology of cryopelagic amphipods from Arctic sea ice.

Post J, Parkinson E (2001) Energy allocation strategy in young fish: allometry and survival. Ecology 82:1040–1051.

Prokopowicz A-J (2011) Ecophysiologie de L ’ Amphipode Themisto libellula sur le plateau du Mackenzie et dans la polynie du Cap Bathurst (mer de Beaufort, Ocean Arctique). Universite Laval

Pućko M, Burt A, Walkusz W, Wang F, Macdonald RW, Rysgaard S, Barber DG, Tremblay JÉ, Stern GA (2014) Transformation of mercury at the bottom of the Arctic food web: An overlooked puzzle in the mercury exposure narrative. Environ Sci Technol 48:7280–7288.

doi: 10.1021/es404851b

Rabindranath A, Daase M, Falk-Petersen S, Wold A, Wallace MI, Berge J, Brierley AS (2011) Seasonal and diel vertical migration of zooplankton in the High Arctic during the autumn midnight sun of 2008. Mar Biodivers 41:365–382. doi: 10.1007/s12526-010-0067-7

Rand KM, Whitehouse A, Logerwell EA, Ahgeak E, Hibpshman R, Parker-Stetter S (2013) The diets of polar cod (Boreogadus saida) from August 2008 in the US Beaufort Sea. Polar Biol. doi: 10.1007/s00300-013-1303-y

Richter C (1994) Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. Berichte zur Polarforsch 96.

Rodriguez-Marin E, Punzon A, Paz J (1995) Feeding patterns of Greenland halibut (Reinhardtius hippoglossoides) in Flemish Pass (northwest Atlantic). NAFO Sci Counc Stud 23:43–54.

Rombough P (1994) Energy partitioning during fish development: additive or compensatory allocation of energy to support growth? Funct Ecol 8:178–186.

Sambilay VC (1990) Interrelationships between swimming speed, caudal fin aspect ratio and body length of fishes. Fishbyte 16–20.

Sameoto D (1984) Review of current information on Arctic cod (Boreogadus saida, Lepechin) and bibliography. Bedford Institute of Oceanography Report, Dartmouth: 71 pp.

Scharf FS, Juanes F, Rountree RA (2000) Predator size - prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar Ecol Prog Ser 208:229–248.

Walkusz W, Majewski A, Reist JD (2013) Distribution and diet of the bottom dwelling Arctic cod in the Canadian Beaufort Sea. J Mar Syst 127:65–75. doi: 10.1016/j.jmarsys.2012.04.004

Walkusz W, Paulić JE, Kwaśniewski S, Williams WJ, Wong S, Papst MH (2010) Distribution, diversity and biomass of summer zooplankton from the coastal Canadian Beaufort Sea. Polar Biol 33:321–335. doi: 10.1007/s00300-009-0708-0

Walkusz W, Paulić JE, Williams WJ, Kwasniewski S, Papst MH (2011) Distribution and diet of larval and juvenile Arctic cod (Boreogadus saida) in the shallow Canadian Beaufort Sea. J Mar Syst 84:78–84. doi: 10.1016/j.jmarsys.2010.09.001

4 Sex-Dependent Differences and the Influence of Habitat on Energy Allocation by Arctic Cod, *Boreogadus saida* (Lepechin 1774) in the Canadian Beaufort Sea

4.1 Introduction

Allocation of surplus energy in fish usually follows an allocation strategy dependent upon life history stage (Post and Parkinson 2001). As larvae, the optimal allocation strategy for Arctic Cod is to maximize body growth, rather than storage, in order to reach a size where they are competitive and have accumulated enough energy stores (i.e., lipids) for it to be energetically efficient to migrate deeper, where they are less vulnerable to predators (Gjøsæter and Ajiad 1994; Post and Parkinson 2001). As fish get larger, growth becomes less important compared to reproduction. Previous growth studies have found spatial (Craig *et al*. 1982; Gjøsæter and Ajiad 1994; Johannessen 2007), temporal (Jensen *et al*. 1991), and sexual (Christiansen 1995) differences in Arctic Cod growth, but none have investigated the effect of depth and age. Depth may affect basal energy requirements due to salinity and temperature differences among water masses, and age or life history may dictate the energy allocation strategy of fish. In the present study, growth as length and mass at age was compared between sexes and among depth-related habitats in the Canadian Beaufort Sea (CBS).

The CBS is a stratified body of water, containing waters from the Arctic, Pacific, and Atlantic oceans (Figure 1.1). Each of the water masses had up to ~ 1.4°C difference in median temperature and up to ~ 2.5 PSU difference in median salinity (Table 2.1). This may affect metabolic reaction rates and the production of nitrogenous wastes, salinity affecting the gradient against ions are exchanged across the gill membrane. This effect is explained in more detail below. Prey distribution is also affected by temperature and salinity, and availability of some important prey species (*Themisto* spp.) differed among water masses or depth-related habitats (Chapter 3). This study aimed to determine whether depth-related habitats influences energy allocation due to the possible effect of differing environmental conditions, i.e., salinity and temperature, or a difference in basic energetic requirements.

Temperature and salinity vary among water masses in the CBS, so depth-related habitats may have an effect on Arctic Cod bioenergetics and specifically their basal energy requirements. For a 50g Arctic Cod, Hop *et al*. (1997) estimated 24% of daily energy intake was needed for basal metabolism at an ambient temperature of -1.5 to 0.5°C and ~30‰ salinity.

See Chapter 3 for an overview of a bioenergetics model. Differences in diet among three depth zones (Shelf: 15-220m, Upper Slope: >220-510m, Lower Slope: >510-800m) were investigated in Chapter 3 because a difference in salinity and temperature with depth zone (Figure 1.1, Table 2.1) in the CBS may affect basal energy requirements (R). Basal metabolism is proportional to body size, and there is also a positive relationship between temperature and metabolism (Clarke and Johnston 1999). This pattern is described by the Arrhenius relationship between temperature and reaction rate, where there is a positive relationship between temperature and metabolic reaction rate (Clarke and Johnston 1999). Meanwhile, costs of ion regulation associated with living in a marine environment likely vary with salinity, though slightly; a higher ambient salinity would mean fish have a more hypotonic relationship with their surroundings. Marine fish including Arctic Cod drink seawater to replace the water they lose through osmosis, which increases their internal osmotic concentration. The ingested ions must be actively excreted. In Arctic Cod and other marine fishes, most ions are actively excreted across the gills. However, osmoregulation constitutes a low proportion of the total fish energy budget (~10%, Boeuf and Payan 2001). Waste removal costs associated with excretion and faecal egestion are considered negligible in relation to other energetic costs for Arctic Cod (Hop *et al*. 1997), but there is still some energetic value to the products of both. Though there was only a ~1°C difference among most among water masses, this could impact an Arctic species when temperatures in an Arctic aquatic environment do not vary significantly below the surface as they do in more southerly stratified aquatic environments. Therefore, it was expected that basal metabolic costs would be higher for Arctic Cod in warmer depth zones. This study assumed that the cost of basal metabolism, excretion, and egestion were the same among individuals for the purpose of the analyses, due to a lack of data on the energetic cost of these processes.

The surplus energy that remains once basal energy requirements are met is then available for allocation based on life history. When a fish reaches the size of maturity, the energy allocation strategy shifts and maximizing fitness requires a balance between producing offspring and surviving to be able to produce offspring during the next breeding season. The optimal allocation strategy for Arctic Cod then may be to devote energy to growth early in the year and then to reproduction later in the year (Heino and Kaitala 1999; Post and Parkinson 2001). Evidence for sex-dependent differences in reproductive costs for Arctic Cod may also exist. Arctic Cod females produce the largest eggs of gadid species, and female spawning output is between 9000 and 21000 eggs (Hop *et al*. 1995). Gamete biomass production has been recorded at approximately two to four orders of magnitude higher in female fishes (Hayward and Gillooly 2011), but some have argued that sperm in general are more expensive than believed (Olsson *et al.* 1996), and some studies of Arctic Cod have observed a significant loss of mass from the liver and muscle in males during gonad development, suggesting that male Arctic Cod invest a lot of energy into reproduction (Hop *et al.* 1995; Korshunova 2012). Although the reproductive behaviour of Arctic Cod has not been studied, males of other gadid species, and presumably also Arctic Cod, engage in complex reproductive behaviours to attract a mate. These include courtship behaviours with potential mates (spawning sound production, a lateral display, paired swimming, mounting, and circling) and aggressive behaviours with competing males (approaching, chasing, prodding, nipping or biting) (Rowe and Hutchings 2006; Skjæraasen *et al*. 2010; Skjæraasen *et al*. 2012). Arctic Cod males develop their gonads earlier in their life history than females and have to maintain their large gonads for a longer period of time. This increases their chances of mortality, as they are larger or heavier, and thus more conspicuous to predators and may also be less motile due to their size or need to conserve energy (Nahrgang *et al*. 2014). This may lead to a significant sex-dependent difference in energy requirements for reproduction.

A sex-dependent difference in reproductive strategy in Arctic Cod was suggested by Nahrgang *et al*. (2014), where males are suspected to be semelparous and females iteroparous due to a tradeoff between reproducing early to reduce the risk of predation for a higher energy investment into reproduction at a smaller size, leading to higher post-spawning mortality. They based this hypothesis on a difference in life expectancy exhibited by a skewed sex ratio toward females in adults, and also because males have a higher energy investment into gonad production (gonadosomatic index, GSI) at a young age. However, the reproductive strategy of the study population in the Canadian Beaufort Sea is not known, and the evidence used by Nahrgang *et al.* (2014) to support their hypothesis, including a skewed sex ratio toward females, was not evident in the current Canadian Beaufort Sea sample (Chapter 2). Therefore, further investigation is needed to determine if the reproductive strategy of Canadian Beaufort Sea Arctic Cod also differs between sexes.

Apart from the cost of sustaining life and reproducing, living in a seasonal Arctic environment with low productivity demands that a fish accumulate energy when available in the event of a food shortage in the winter or a delay in the spring phytoplankton bloom. In Arctic Cod, energy is mostly stored as lipids in the liver (males: 83.82% ± 1.54, females: 79.70% ± 1.95) and small amounts in the muscle tissue (male carcass, i.e., muscle and bone: 14.25% ± 0.83, female carcass: 12.87% ± 0.83) (Hop *et al*., 1997), whereas carbohydrates and amino acids resulting from protein catabolism that are not needed to be reconfigured back into a protein are stored as glycogen in the body. Lipid storage is approximated by two ratios: Fulton's condition factor, the ratio of body weight to length of a fish, and the hepatosomatic index (HSI), the ratio of liver mass to somatic mass (Korshunova 2012; Nahrgang *et al*. 2014). Stored energy as lipids in the liver or muscle tissue can be mobilized in the event of starvation to fuel metabolic reactions and may be used when additional energy is needed, such as in the production of gonads (Korshunova 2012). The current study aimed to determine whether energetic demands based on habitat or sex influenced the amount of surplus energy stored by Arctic Cod.

Foraging follows a sequence of search-encounter-decide behaviours, but includes all activities required to obtain resources, i.e., the search, pursuit, and handling (killing, eating) of prey (Calow 2009). The energy needed to digest, absorb, and metabolize the nutrients in prey, making them available for the consumer, is called the specific dynamic action or SDA (a component of E). Unfortunately, this study did not have the means to compare SDA among prey items, so SDA was assumed to be constant across individuals for the purposes of these analyses. Optimal foraging theory, developed by MacArthur and Pianka (1966) as well as Emlen (1966), indicates that natural selection would favour foraging behaviour that maximizes the net energy gained per unit of time spent foraging (Calow 2009).

The energy allocation strategy by Arctic Cod in the CBS was investigated herein. Differences in Fulton's condition factor as well as investment into growth (body length and mass), reproduction (gonads, GSI) and energy storage (liver, HSI) were considered among three depth zones, four sampling transects arranged perpendicular to shore, and between sexes. Differences in allocation between sexes were expected, given the possible differences in reproductive strategy as found in the Norwegian populations (Nahrgang *et al*. 2014). The expectation was that males invest more energy into reproduction, as gadid males engage in complex behaviours to attract mates, and male Arctic Cod develop their gonads sooner in the year than females. The amount of energy allocated to reproduction in individual Arctic Cod in the current study was approximated by the energy invested into developing gonads, or the gonadosomatic index (GSI), which is the ratio of gonad mass to somatic mass. Differences in allocation among depth-related habitats would be expected given differences in temperature and salinity and prey concentrations among water masses and their effects on metabolism, osmoregulation, and energy consumption, respectively. However, energy consumption did not differ with depth when separated by size class (Chapter 3), so the amount of energy available for allocation to growth, reproduction, and energy storage may change with depth as a consequence. Age differences are also likely relevant due to a shift in energy allocation strategy with size and life history stage (Rombough 1994; Post and Parkinson 2001).

4.2 Methods

4.2.1 Sample Collection

Arctic Cod were collected from 26 stations in the Canadian Beaufort Sea in August 2012. See Chapter 2, Figure 2.1 for a map of the sampling area. Stations were organized into transects, 6-7 stations per transect, which ran perpendicular from shore to allow investigation of depth effects. For this study, ten (10) Arctic Cod captured with demersal nets representing the range of lengths captured were chosen from each station when possible (n = 237). The sample included 121 males, 56 females, and 60 individuals of indeterminate sex (Table 4.1). Following initial measurements of fork length, the fish were individually bagged and frozen on the ship at -50°C, then transferred to approximately -30°C for long-term storage. Field lengths were recorded and compared, but lab length measurements were used herein.

4.2.2 Analytical Structure

The Canadian Beaufort Sea was separated into three depth zones in order to determine the effect of habitat (temperature and salinity) on energy allocation. See Chapter 2 and Table 2.1 for a description and justification of the analysis structure for this study.

4.2.3 Data Collection

In the lab (4°C), measurements of length (total, fork, and standard ± 0.01mm) and mass (total body wet mass and non-visceral caracass mass ± 0.001g) were collected. Gonads and livers were dissected from each fish and individual masses recorded (± 0.001g). All effort was made to reduce thawing so as to retain the integrity of the tissues. Sex and maturity levels were visually determined based on gonad development (Appendix A, Table 6.1; Majewski *et al*. 2009). Individuals of unknown sex were not included in the dataset. Stomachs and intestines were removed and placed in formalin for diet analysis (Chapter 3), and otoliths were extracted and dried for age estimation.

4.2.4 Age Estimation and Age Classes

Ages were estimated by examination of otoliths. See Chapter 2 for more information on the age estimation technique used. Age classes were defined based on the estimated age of the fish. Age class 1 included those that were aged 1 to 2, age class 2 included those that were aged 2-3, etc.

4.2.5 Physiological Indices

Five physiological indicators were calculated to approximate the biological state of the Arctic Cod. Note that carcass mass was calculated by (wet mass – gonad wet mass – liver wet mass – mass of digestive tract):

1) Condition factor is a proxy for nutritional status of the individual, and was calculated by (Busacker *et al*. 1990):

   $$\text{Condition Factor} = 100 \text{ x total body mass (g)/(fork length (cm))}^3$$

2) Gonadosomatic Index (GSI) is a proxy for gonad development and was calculated by (see below for the calculation of carcass mass) (Hop *et al*. 1995):

   $$\text{GSI} = (\text{gonad mass/carcass mass})*100$$

3) Hepatosomatic Index (HSI) represents the investment into energy storage as lipids in the liver, and was calculated by (Busacker *et al*. 1990):

   $$\text{HSI} = (\text{liver mass/carcass mass})*100$$

4) Lipid Proportion indicated the proportion of lipid in the carcass of the fish. To determine the mass proportion of total lipids in the carcass, the carcass tissue was freeze-dried and

lipids were extracted from one half of the carcass using a modified Folch method (Iverson *et al*. 2001). Lipid Proportion was calculated by:

Lipid Proportion = mass total lipids in carcass/carcass dry mass

5) The lipid-free dry mass proportion of the carcass may include protein, carbohydrates, crystallized ions from the skeleton, and negligibly RNA and DNA, metabolites, and free ions. This dry mass, less the lipid, should decline if the skeletal muscle to skeletal mass ratio declines (e.g. they are in poor condition) because the skeletal elements should be relatively insensitive to caloric deficiency while body protein should reflect successful feeding (Jobling 1980; Black and Love 1986; Wang *et al*. 2006). Lipid-Free Dry Mass Proportion was calculated by:

Lipid-Free Dry Mass Proportion = (dry mass of carcass-mass total lipids)/wet mass of carcass

4.2.6 Data Analysis

Open-source statistical analyses software R studio, version 3.0.1, was used for the statistical analyses. The experimental unit in the analyses was each individual Arctic Cod. Chi-square and Fisher's exact tests were used within depth zones to determine if sex ratio differed with age class. Sample sizes did not allow for comparisons at the level of age class by sex by transect within depth zones without sacrificing statistical power, so analyses were made by sex by transect within depth zones and by age class by transect within depth zones. Comparisons also controlled for maturity. Only those fish of age class 1 to 3+ were included in the analyses, as those individuals of age class 0 were expected to have a different physiology and energy allocation strategy, and there were not enough older individuals (age 4+) to allow statistical comparisons without compromising statistical power in the analyses.

Energy allocation was estimated by static measurements of body length and weight, as well as the size of gonads and liver, at the time of sampling. This study did not have the means to compare costs of reproductive behaviour or activity between sexes, and estimated energy allocation to reproduction only by GSI. This may not fully capture the variability in energy allocation among individuals of the same age class. Metabolic costs, energy lost as heat, and activity costs were not investigated in the current study and therefore were assumed to be constant across individuals within a size class.

Assumptions of normality and homogeneity of variances were examined using QQ-plots and Levene's tests, respectively. Fork length met the assumption of homogeneity, but mass, GSI, HSI, lipid proportion, condition factor, and lipid-free dry mass failed the normality test. Therefore, transformations were applied to these variables (mass values were converted to log base 10; GSI and HSI values were converted to square root). However, no transformation was suitable for lipid proportion and lipid-free dry mass proportion nor condition factor, thus non-parametric rank-based tests (Kruskal-Wallis) were used to analyze differences in these parameters among groups. By sex within each age class, GSI, HSI, lipid proportion, condition factor, and lipid-free dry mass also did not meet the assumption of homogeneity and normality, and transformations were not suitable. Non-parametric rank-based tests were used to analyze differences in these parameters between groups. Statistical significance was accepted when $\alpha < 0.05$. When significant differences were determined, post-hoc pair-wise comparisons among groups were performed using a Dunn's test with a Holm correction (Holm 1979) for nonparametric analyses and a Tukey honest significant difference test (HSD) for parametric analyses. T-tests were used when comparing two groups, such as between sexes.

Regressions with linear or quadratic trends and interaction effects were used to determine the effect of depth zone and transect on GSI, HSI, lipid proportion of the carcass, and lipid-free dry mass proportion of the carcass. To determine differences in growth among groups, mean length and mass at age was compared among groups using nonparameteric Kruskal-Wallis tests, as the data did not meet the assumptions of homogeneity of variance (examination of plots of raw and transformed data, Bartlett’s tests) and normality (QQ-plots and histograms of raw and transformed data).

4.3 Results

4.3.1 Sex Ratio by Age Class by Depth Zone

See Appendix E, Table 6.7 for the sex ratio of Arctic Cod by age class by depth zone. Chi-square and Fisher’s exact tests determined that sex ratio differed by age class (Chi-square: p = 0.003, d.f. = 2; Fisher’s: p = 0.003) on the Upper Slope zone, with a shift in skew toward females in age classes 2 and 3. There was no difference in sex ratio with age class on the Shelf (Chi-square: p = 0.11, d.f. = 1; Fisher’s: p = 0.11) and Lower Slope (Chi-square: p = 0.81, d.f. = 2; Fisher’s: p = 0.89). The sex ratio on the Shelf and Lower Slope was toward males through all age classes (Table 4.1).

Table 4.1 Abundance of Arctic Cod by sex in each of the sampling transects, depth zones, and the entire sample population. Sample sizes in subsequent analyses may not agree, as all data was not necessarily available for all individuals.

Transect	**Male**	**Female**
DAL	33	20
KUG	29	15
GRY	34	7
TBS	25	14
Depth Zone		
Shelf	60	15
Upper Slope	42	31
Lower Slope	19	10
Sex		
Male	121	
Female	56	

4.3.2 Growth

See Appendix F, Table 6.10 and Appendix G, Figures 6.7-6.12 for plots of median length- and mass-at-age by sex, transect, and depth zone. When sex was included as a covariate, Kruskal-Wallis tests found a significant difference in the median length and mass of age 2 male Arctic Cod between the Shelf and Upper Slope zones (p-adj = 0.0115 and 0.0086, respectively). Within each age class (1-3), there was no significant difference in the length or mass at age between male and female Arctic Cod (Figure 4.1 and Table 4.2; Kruskal-Wallis with 1 d.f.; length and mass: age class 1: $p = 0.24$ and $p = 0.27$; age class 2: $p = 0.15$ and $p = 0.27$; age class 3: $p = 0.78$ and $p = 0.89$), among transects (Figure 4.2 and Table 4.2; Kruskal-Wallis with 3 d.f.; length and mass: age class 1: $p = 0.52$ and $p = 0.33$; age class 2: $p = 0.70$ and $p = 0.85$; age class 3: $p = 0.71$ and $p = 0.58$), nor among depth zones (Figure 4.3 and Table 4.2; Kruskal-Wallis with 2 d.f.; length and mass; age class 1: $p = 0.10$ and $p = 0.33$; age class 2: $p = 0.54$ and $p = 0.18$; age class 3: $p = 0.88$ and $p = 0.66$). Fish of unknown sex were not included as there were insufficient length data.

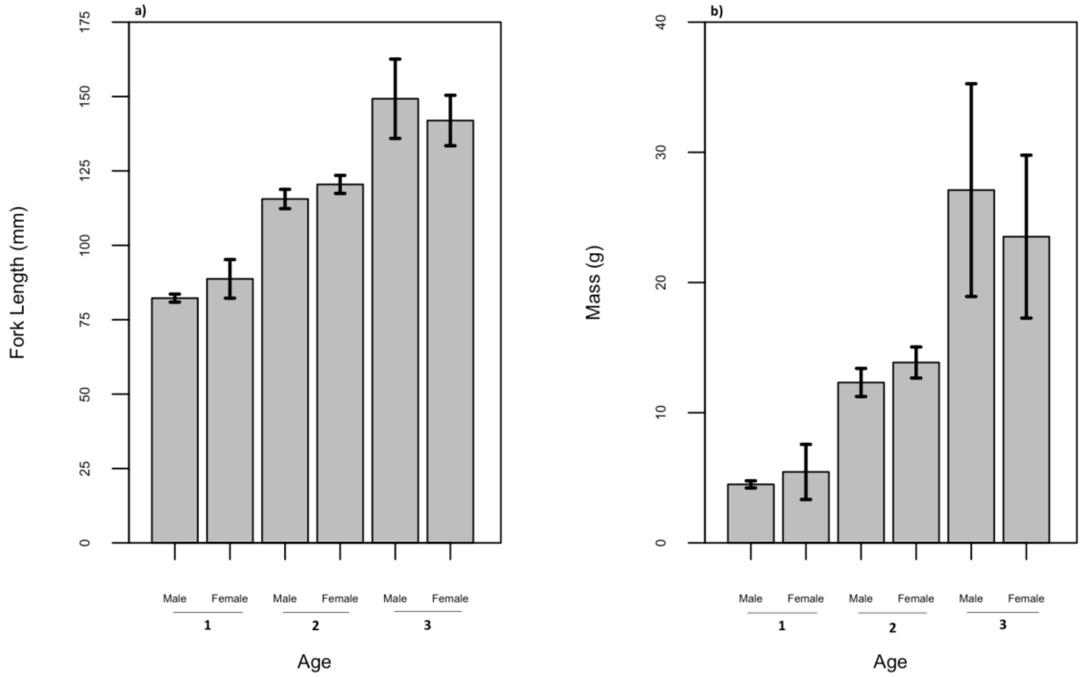

Figure 4.1 Arctic Cod growth as fork length (mm) and mass (g) at age by sex (median ± SE). Those of unknown sex were not included as there were insufficient length data. There was no significant difference in the median length or mass at age between male and female Arctic Cod (Kruskal-Wallis with 1 d.f.; length and mass: age class 1: p = 0.24 and p = 0.27; age class 2: p = 0.15 and p = 0.27; age class 3: p = 0.78 and p = 0.89; Table 4.2).

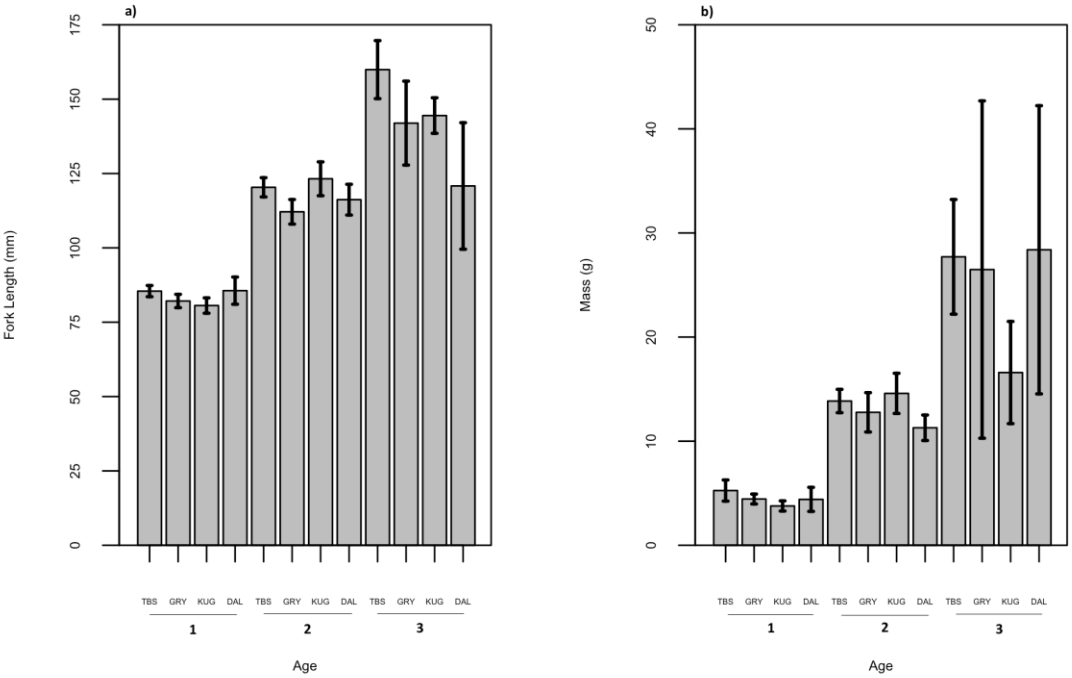

Figure 4.2 Arctic Cod growth as fork length (mm) and mass (g) at age by sampling transect (median ± SE). According to Kruskal-Wallis tests, there were no significant differences in median length or mass at age among transects in the Canadian Beaufort Sea (Kruskal-Wallis with 3 d.f.; length and mass: age class 1: p = 0.52 and p = 0.33; age class 2: p = 0.70 and p = 0.85; age class 3: p = 0.71 and p = 0.58; Table 4.2).

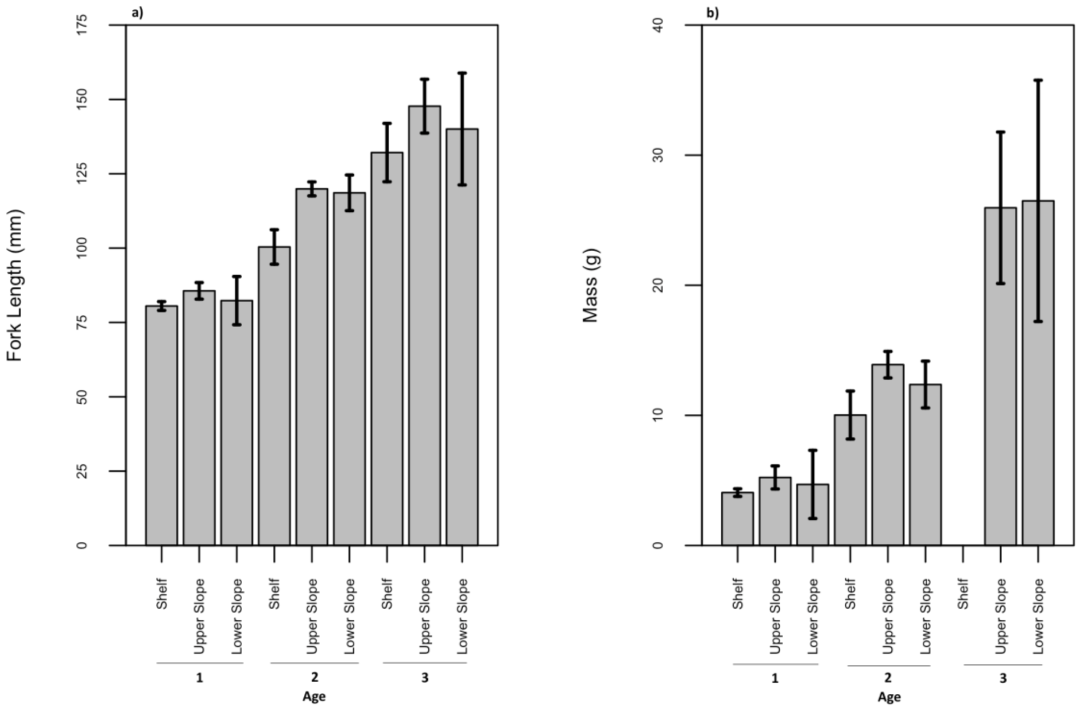

Figure 4.3 Arctic Cod growth as fork length (mm) and mass (g) at age by depth zone (median ± SE). According to Kruskal-Wallis tests, there were no significant differences in Arctic Cod length or mass at age by depth zone in the Canadian Beaufort Sea (Kruskal-Wallis with 2 d.f.; length and mass; age class 1: p = 0.10 and p = 0.33; age class 2: p = 0.54 and p = 0.18; age class 3: p = 0.88 and p = 0.66; Table 4.2).

4.3.3 Energy Allocation

Energy allocation to gonad development (GSI) and energy storage in the liver as lipids (HSI), Fulton's condition factor, the proportion of lipid in the carcass of Arctic Cod by dry mass (lipid proportion), and the proportion of lipid-free dry mass were compared by age class and sex within transects and depth zones (Table 4.2), as well as across depth zones, transects, and between sexes overall (Table 4.3).

Table 4.2 Mean (± SE) values by depth zone among age classes for physiological indicators as a proxy for energy allocation. Differing letter superscripts indicate a significant difference among age classes within a depth zone. Median GSI was significantly higher on the Upper Slope.

Zone	**Age Class**	**GSI**	**HSI**	**Condition Factor**	**Lipid-Free Dry Mass Proportion**	**Lipid Proportion**
Shelf	1	0.019 ± 0.002	0.045 ± 0.002	0.787 ± 0.011	0.408 ± 0.013	0.287 ± 0.018
	2	0.023 ± 0.003	0.049 ± 0.007	0.799 ± 0.028	0.431 ± 0.014	0.228 ± 0.022
Upper Slope	1	0.017 ± 0.002^{a}	0.039 ± 0.003^{a}	0.759 ± 0.015	0.405 ± 0.022	0.243 ± 0.019^{a}
	2	0.033 ± 0.003^{b}	0.047 ± 0.003^{b}	0.782 ± 0.014	0.426 ± 0.034	0.210 ± 0.028^{b}
	3	0.027 ± 0.002^{b}	0.063 ± 0.007^{b}	0.753 ± 0.029	0.437 ± 0.011	0.169 ± 0.014^{b}
Lower Slope	1	0.017 ± 0.003	0.043 ± 0.008	0.776 ± 0.017	0.448 ± 0.010	0.197 ± 0.019
	2	0.027 ± 0.007	0.059 ± 0.009	0.769 ± 0.029	0.430 ± 0.012	0.219 ± 0.017
	3	0.027 ± 0.006	0.067 ± 0.013	0.766 ± 0.030	0.461 ± 0.007	0.168 ± 0.014

Table 4.3 Mean (± SE) values by age class, depth zone, transect, and sex for physiological indicators as a proxy for energy allocation. Superscripts indicate a significant difference in the physiological parameter among age classes, depth zones, transects, or sexes is present.

Age Class	**GSI**[1]	**HSI**[2]	**Condition Factor**[3]	**Lipid Proportion**[4]	**Lipid-Free Dry Mass Proportion**
1	0.018 ± 0.001^{a}	0.043 ± 0.002^{a}	0.78 ± 0.008	0.27 ± 0.014^{a}	0.42 ± 0.009
2	0.030 ± 0.002^{b}	$0.050 \pm 0.003^{a,b}$	0.78 ± 0.012	0.22 ± 0.016^{b}	0.43 ± 0.016
3	0.027 ± 0.002^{b}	0.064 ± 0.006^{b}	0.76 ± 0.021	0.17 ± 0.010^{b}	0.45 ± 0.007
Depth Zone	**GSI**[1]	**HSI**[2]	**Condition Factor**[3]	**Lipid Proportion**[4]	**Lipid-Free Dry Mass Proportion**
Shelf	0.019 ± 0.001	0.042 ± 0.002	0.78 ± 0.011	$0.20\ (0.19) \pm 0.01^{a}$	0.39 ± 0.011
Upper Slope	0.025 ± 0.002	0.046 ±0.002	0.76 ± 0.010	$0.29\ (0.25) \pm 0.02^{b}$	0.43 ± 0.016
Lower Slope	0.024 ± 0.003	0.054 ± 0.005	0.77 ± 0.014	$0.22\ (0.19) \pm 0.01^{a}$	0.41 ± 0.015
Transect	**GSI**[1]	**HSI**[2]	**Condition**	**Lipid**	**Lipid-Free Dry**

			Factor[3]	**Proportion[4]**	**Mass Proportion**
TBS	0.022 ± 0.003	0.039 ± 0.003	0.80 ± 0.015^{a}	0.29 (0.21) ± 0.03	0.37 ± 0.017
GRY	0.027 ± 0.003	0.042 ± 0.003	0.76 ± 0.013^{a,b}	0.23 (0.20) ± 0.02	0.42 ± 0.011
KUG	0.019 ± 0.001	0.044 ± 0.003	0.76 ± 0.013^{a,b}	0.26 (0.22) ± 0.02	0.40 ± 0.015
DAL	0.022 ± 0.001	0.054 ± 0.003	0.76 ± 0.011^{b}	0.22 (0.20) ± 0.01	0.42 ± 0.015

Sex	**GSI[1]**	**HSI[2]**	**Condition Factor[3]**	**Lipid Proportion[4]**	**Lipid-Free Dry Mass Proportion**
Male	0.023 ± 0.001	0.045 ± 0.002	0.78 ± 0.008	0.25 (0.22) ± 0.01	0.42 ± 0.008
Female	0.023 ± 0.001	0.052 ± 0.004	0.77 ± 0.011	0.22 (0.19) ± 0.02	0.43 ± 0.014

[1] Median GSI was significantly lower for age class 1 Arctic Cod compared to both age class 2 and 3 (p-adj < 0.001). There was no significant difference in GSI (Kruskal-Wallis, p = 0.17) across transects.

[2] Median HSI was significantly lower for age class 1 Arctic Cod than age class 3 (p-adj < 0.001). There was no significant difference in HSI (Kruskal-Wallis, p = 0.06) across transects.

[3] There was a significant difference in mean condition factor between Arctic Cod captured on the TBS and DAL transects (ANOVA, p = 0.01).

[5] Lipid proportion of the carcass was significantly higher for age class 1 Arctic Cod than both age class 2 (p-adj = 0.004) and age class 3 (p-adj < 0.001) Arctic Cod. There was a significant difference in median lipid proportion of the carcass of Arctic Cod among depth zones (Kruskal-Wallis with Holm correction; Shelf-Upper Slope, p-adj = 0.005; Upper Slope-Lower Slope, p-adj = 0.001).

4.3.3.1 Gonadosomatic Index (GSI)

Kruskal-Wallis tests determined median GSI was significantly lower for age class 1 than both age class 2 (Holm correction, p-adj < 0.001) and 3 (p-adj = 0.001) on the Upper Slope (Table 4.2). There was no significant difference in GSI between sexes within age classes (depth zone and transect pooled) (T-test; age 1, p = 0.11; age 2, p = 0.09; age 3, p = 0.99). Further pooling by maturity and sex, median GSI was significantly higher for age class 2 than age class 3 in mature males on the Upper Slope (Kruskal-Wallis with Holm correction, p-adj = 0.01), and was significantly higher in mature males than females on the Shelf (t-test, p = 0.04). Within mature individuals, there was a significant difference in HSI between the Shelf and Lower Slope (Kruskal-Wallis with Holm correction, p-adj = 0.004). Analyses of variance determined that sex (p = 0.53), transect (p = 0.10) and depth zone (p = 0.07) did not have an effect on GSI.

4.3.3.2 Hepatosomatic Index (HSI)

Kruskal-Wallis tests determined HSI was significantly lower for age class 1 Arctic Cod and both age class 2 (Holm correction, p-adj = 0.02) and 3 (p-adj = 0.001) Arctic Cod on the Upper Slope (Table 4.2). There was no significant difference in HSI between sexes within age classes (depth zone and transect pooled) (T-test; age 1, p = 0.32; age 2, p = 0.67; age 3, p = 0.33). There was no effect of sex (ANOVA, p = 0.17, 1 d.f.) or depth zone (ANOVA, p = 0.63, 2 d.f.) on HSI, but there was a significant effect of transect on HSI (ANOVA, p = 0.03, 3 d.f.;

Table 4.4), with a significant difference between those captured on the TBS and DAL transects (Tukey honest significant difference test, p-adj = 0.04).

4.3.3.3 Fulton's Condition Factor

Kruskal-Wallis tests determined there was a significant difference in Fulton's condition factor between the Upper Slope and Lower Slope depth zones in males on the DAL transect (Holm correction, p-adj = 0.003), but no significant difference in the Fulton's condition factor of males (p = 0.89) or females (p = 0.25) among depth zones, nor among transects by depth zone (Shelf: p = 0.09; Upper Slope, p = 0.07; Lower Slope, p = 0.57), or depth zone (p = 0.34) or sex overall (p = 0.13). There was no significant difference in condition factor between sexes within age classes (depth zone and transect pooled) (T-test; age 1, p = 0.58; age 2, p = 0.24; age 3, p = 0.61). However, Fulton's condition factor was significantly higher on the TBS transect than the DAL transect overall (p = 0.01; Table 4.4). Note that none of the other physiological indices corresponded with the differences in condition factor observed.

4.3.3.4 Lipid Proportion

Median lipid proportion of the carcass was significantly higher for age class 1 Arctic Cod than both age class 2 and 3 Arctic Cod (Holm correction, p-adj = 0.02) on the Upper Slope. Following determination of non-significant interaction effects, Kruskal-Wallis tests determined that median lipid proportion of the carcass was higher on the Upper Slope than the Shelf (p-adj = 0.005) and the Lower Slope (p-adj = 0.01). There was no significant difference in lipid proportion between sexes within age classes (depth zone and transect pooled) (T-test; age 1, p = 0.15; age 2, p = 0.73; age 3, p = 0.32). There was also no significant difference in median lipid proportion among transects (Kruskal-Wallis, p = 0.21, d.f. = 3) or between sexes (t-test, p = 0.08).

4.3.3.5 Lipid-Free Dry Mass Proportion

There was no significant difference in lipid-free dry mass proportion between sexes within age classes (depth zone and transect pooled) (T-test; age 1, $p = 0.28$; age 2, $p = 0.52$; age 3, $p = 0.99$). Following further Kruskal-Wallis analyses of interaction effects that were not significant ($p > 0.05$), analyses of differences in lipid-free dry mass proportion of the carcass across depth zones, transects, and sexes overall determined there was no significant difference in median lipid-free dry mass proportion of the carcass among the depth zones ($p = 0.10$), transects ($p = 0.09$), nor sexes ($p = 0.60$) in Arctic Cod (Table 4.4).

4.4 Discussion

In order to understand energy use by an important forage fish in the CBS ecosystem, the current study examined static measurements of energy allocation by age 1-3 Arctic Cod sampled during the month of August 2012. This study investigated whether depth-related habitat had any effect on energy allocation to growth, gonad production, and energy storage, while also considering east-west differences and the influence of sex. The results indicate that there were no direct relationships with sampling transect, depth, or sex on growth of the individuals, but there was a trend in surplus energy allocation across sampling transects and with depth.

It was expected that the energy allocation strategy of Arctic Cod would change with increase in body size, with size as a proxy for life history stage. In the current study, GSI, HSI, condition factor, and lipid-free dry mass proportion of the carcass increased with age class, though weakly. This corresponds with the established theoretical decrease in body growth rate as an organism grows larger, the fish shifting their resources toward reproduction and surviving to reproduce in the future. The increase in surplus energy allocation to reproductive output agrees with theories about energy allocation strategy, which suggest that shifts should occur seasonally and with changing life history demands (Rombough 1994; Post and Parkinson 2001). In mature males on the Upper Slope, energy allocated to gonad development increases in age class 2, but decreases in age class 3 individuals. This observation may be due to a temporal bias, as it would be expected for energy allocation to reproductive input to increase with age. A decrease in the proportion of lipid in the carcass with increase in age suggests that as the fish gets older, these lipids may be metabolized and their energy re-allocated according to their life history demands, e.g., to gonad development or energy storage in the liver or muscle. It also supports the shift in energy allocation strategy with increase in body size or age away from storing energy as lipids to muscle accumulation, and suggests muscle is the primary lipid storage organ in these small fish (Post and Parkinson 2001).

Energy allocation is often influenced by life history stage (Post and Parkinson 2001), but what about sex? Sexual differences in energy allocation have been observed in other Arctic Cod populations (Christiansen 1995; Korshunova 2012; Nahrgang *et al*. 2014), but this study only found a significant difference in GSI between mature males and females on the Shelf. Females are consistently larger than males in the CBS population, with a higher growth model intercept (see Appendix G, Figure 6.7-6.8). These differences or lack of does not definitively exclude nor indicate a sexual difference in the reproductive investment. For instance, a lack of difference in investment into gonadal development (GSI) in the current study on the Upper and Lower Slope may be due to a temporal bias and does not exclude possible sexual differences in reproductive investment in CBS Arctic Cod. Arctic Cod spawn in winter and become sexually mature at age 2+ to 3+ (females at age 3+) or likely once they reach a size threshold, but begin to develop their gonads in August (Craig *et al*. 1982). The samples for the current study were collected near the beginning of gonadal development, and even though males begin developing their gonads more rapidly and at a smaller size than females, they may not have developed enough in August 2012 for a significant difference to be detected (Hop *et al.* 1995). Furthermore, gonad development is only part of total reproductive investment. There may be a differential cost of gametes between sexes. Relative to their body size, female Arctic Cod develop the largest eggs of any gadid but small in number, and males produce an abundance of energetically cheap sperm (Hop *et al*. 1995). Although knowledge of Arctic Cod reproductive behaviour is lacking, males of other gadid species (e.g., Atlantic Cod *Gadus morhua*, and haddock *Melanogrammus aeglefinus*) invest a disproportionate amount of energy into mate attraction than females including vibration of a drumming muscle that produces a sound to attract mates, and act to synchronize gamete release with females. However, the total cost of such behaviour relative to normal Arctic Cod activity costs is unknown.

Despite studies into Arctic Cod reproduction, it is still unknown if Arctic Cod are semelparous or iteroparous. A Norwegian study suggested a difference in reproductive strategy based on sex, and some studies suspect males are iteroparous due to their exhaustive effort to successfully reproduce and outcompete other males which leaves them too weak to survive after one season (Sakurai *et al*. 1998; Nahrgang *et al*. 2014). This notion is supported by a skewed sex ratio toward females in the adult Arctic Cod population. However, the current study found an oppositely skewed sex ratio overall (see Chapter 2) and only on the Upper Slope did the sex ratio skew toward females with age (Appendix E, Table 6.7), so the hypotheses generated regarding semelparity in males in the Norwegian Arctic Cod population cannot be applied to the CBS Arctic Cod population. Nevertheless, in order to fully understand the bioenergetics and population dynamics of Arctic Cod, more information and observations are needed on their reproductive behaviour.

The only differences in energy allocation among transects were detected in HSI, where HSI was significantly higher in individuals captured on the DAL than the TBS transect. A temporal sampling bias may explain this variation, with sampling occurring from the easternmost transect (DAL) to the westernmost (TBS) transect over the month of August 2012. Upwelling events at Cape Bathurst east of the sampling area throughout the year, as well as fresh water and nutrient inputs from the Mackenzie River amplified during the spring melt, create seasonal spatial variability in productivity that may provide a spontaneous increase in prey not captured in this study. These pulses in productivity may be reflected in the body composition of Arctic Cod across east-to-west transects. Also, evidence exists for a lack of nutrients in an area of the CBS north of Tuktoyaktuk in proximity to the KUG sampling transect. Since 1992, beluga whales have been conspicuously absent from the area (Harwood *et al*. 1996; Harwood and Smith 2012), suggesting that this is an area of low productivity. This anomaly may be due to reduced currents, resulting in no nutrient upwelling from offshore and no nutrient input from the Mackenzie River (B. Kissinger, *pers. comm.*). However, a difference in energy allocation attributable to the variability of nutrients in the environment should also be reflected in a difference in size at age, which was not observed, which would suggest a type I statistical error had occurred. This study did not analyze nutrient levels, but temperature and salinity data collected during sampling did not differ among transects and thus differences in temperature and salinity could not explain the differences in energy allocation (Carmack and Macdonald 2002; Juul-Pedersen *et al*. 2010). Future studies should investigate spatial variation in productivity within this area.

Though a statistically significant difference in Fulton's condition factor of males from the DAL transect at age 2 between the Upper Slope and Lower Slope zones was detected, this difference is likely not biologically significant given that there were no analogous differences detected in other groups of males. There was a significant difference in HSI among depth zones in mature individuals. In contrast, this study found there was a significantly higher proportion of lipid in the carcass of Arctic Cod on the Upper Slope than both the Shelf and the Lower Slope zones. Hydroacoustic analysis of this Arctic Cod population observed an aggregation in the area of the Upper Slope extending off the continental shelf, along with an abundance of what was assumed to be large amphipods (Geoffroy *et al.* 2015; Majewski *et al.* 2015). Therefore, lipid deposits may be higher in Arctic Cod on the Upper Slope because of a high density of food in this habitat. The increase in energy consumption may not be reflected in other tissues such as gonads or liver because of differences in assimilation rates between tissue types (Armstrong and Bond 2013). However, the energy content of an average diet on the Upper Slope was the lowest of all depth zones, combining all size classes (Table 3.6). Also, the higher temperature in the Upper Slope zone, which includes the thermohalocline and below it (Table 2.1), would be expected to increase metabolic rates, decreasing net assimilation efficiency, which may also explain why the increase in energy consumption on the Upper Slope did not affect growth or energy allocation to other tissues (gonads, liver). However, there was a significant difference in HSI of mature individuals between the Shelf and Lower Slope. The significant increase in HSI with depth may be due to the higher density of food with depth increasing the amount of surplus energy. The higher proportion of lipid in the liver in the Lower Slope may increase buoyancy capabilities in these mature individuals.

Even though this study concentrated on Arctic Cod captured just above the seafloor, Arctic Cod are found throughout the water column and there has been evidence of daily and even seasonal vertical migrations in Arctic ecosystems (Benoit *et al*. 2010; Geoffroy *et al.* 2015). No Arctic Cod have been individually tracked in the CBS, but hydroacoustics generally suggest that cod are not moving over a great distance in this ecosystem (M. Geoffroy, *pers. comm.*). Thus variability in temperature and salinity among water masses may have an effect on energy allocation among Arctic Cod captured in different depth zones. However, depth differences are hard to determine decisively because Arctic Cod are migrating, vertically and horizontally, into shallower areas and higher in the water column. Migrating among water masses via diel vertical migrations (DVM) would mean that the effects that variability in temperature and salinity could have on energy allocation would not be noticeable.

In conclusion, the energy Arctic Cod allocated to body growth appeared to depend more on the life history stage of the individual and whether it had reached maturity, rather than its surroundings or even its sex. The surplus energy allocated to gonad development and energy storage in the liver varied from east to west, which could only be related to variation in productivity as temperature and salinity did not vary in the same direction. A depth difference in the proportion of lipid in the carcass could also be related to higher productivity in the Upper Slope zone, but a higher temperature may prevent further increases in energy allocation. Studies of energy allocation in mature Capelin *Mallotus villosus* (Müller 1776), another forage fish species, observed an influence of sex on GSI (Huse 1998) and latitude on size and growth (Hedelholm *et al*. 2011), but these studies are from subarctic ecosystems. The current study determined there was no sex difference in energy allocation, but there may be a temporal bias. More information at targeted depths is needed to determine if east-west differences in GSI and HSI as well as depth differences in the proportion of lipid in the muscle could be attributed to differences in prey density, as in the Hedelholm *et al*. (2011) study of Capelin across a latitudinal gradient. Information on energy dynamics within Arctic Cod is important in understanding the effects of habitat and sex on energy allocation in the CBS, or lack thereof. More information is needed on Arctic Cod behaviour in order to completely understand the cost of living as an Arctic Cod. Furthermore, due to constraints on the samples used in the current study, an analysis of spatial and sexual effects of energy allocation in older Arctic Cod (age 3+) is also necessary for a complete understanding of Arctic Cod bioenergetics.

4.5 References

Armstrong JB, Bond MH (2013) Phenotype flexibility in wild fish: Dolly Varden regulate assimilative capacity to capitalize on annual pulsed subsidies. J Anim Ecol 82:966–975. doi: 10.1111/1365-2656.12066

Benoit D, Simard Y, Gagné J, Geoffroy M, Fortier L (2010) From polar night to midnight sun: photoperiod, seal predation, and the diel vertical migrations of polar cod (Boreogadus saida) under landfast ice in the Arctic Ocean. Polar Biol 33:1505–1520. doi: 10.1007/s00300-010-0840-x

Black D, Love RM (1986) The sequential mobilisation and restoration of energy reserves in tissues of Atlantic cod during starvation and refeeding. 156:469–479.

Boeuf G, Payan P (2001) How should salinity influence fish growth? Comp Biochem Physiol C Toxicol Pharmacol 130:411–23.

Busacker GP, Adelman IR, Goolish EM (1990) Growth. In: Schreck CB, Moyle PB (eds) Methods for Fish Biology. American Fisheries Society, Bethesda, Maryland, USA, pp 363–387

Calow PP (2009) Optimal foraging theory. In: Encyclopedia of Ecology and Environmental Management. Blackwell Publishing Ltd, Hoboken,

Carmack EC, Macdonald RW (2002) Oceanography of the Canadian Shelf of the Beaufort Sea: A setting for marine life. Arctic 55:29–45. doi: 10.1126/science.100.2596.291

Christiansen JS (1995) Food consumption and growth rate variations in male and female polar cod (Boreogadus saida). ICES 10.

Clarke A, Johnston N (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. J Anim Ecol 893–905.

Craig PC, Griffiths WB, Haldorson L, McElderry H (1982) Ecological studies of Arctic Cod (Boreogadus saida) in Beaufort Sea Coastal Waters, Alaska. Can J Fish Aquat Sci 39:395–406.

Emlen JM (1966) The role of time and energy in food preference. Am Soc Nat 100:611–617.

Geoffroy M, Majewski A, LeBlanc M, Gauthier S, Walkusz W, Reist JD, Fortier L (2015) Vertical segregation of age-0 and age-1 + polar cod (Boreogadus saida) over the annual cycle in the Canadian Beaufort Sea. Polar Biol. doi: 10.1007/s00300-015-1811-z

Gjøsæter H, Ajiad A (1994) Growth of polar cod, Boreogadus saida (Lepechin), in the Barents Sea. ICES J Mar Sci 1–8.

Harwood LA, Innes S, Norton P, Kingsley MCS (1996) Distribution and abundance of beluga whales in the Mackenzie estuary, southeast Beaufort Sea, and west Amundsen Gulf during late July 1992. 2262–2273.

Harwood LA, Smith TG (2012) Whales of the Inuvialuit Settlement Region in Canada’s Western Arctic: An overview and outlook. 55:77–93.

Hayward A, Gillooly JF (2011) The cost of sex: Quantifying energetic investment in gamete production by males and females. PLoS One. doi: 10.1371/journal.pone.0016557

Hedelholm R, Grønkjær P, Rysgaard S (2011) Energy content and fecundity of capelin (Mallotus villosus) along a 1,500-km latitudinal gradient. Mar Biol 158:1319–1330. doi: 10.1007/s00227-011-1651-5

Heino M, Kaitala V (1999) Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. J Evol Biol 12:423–429. doi: 10.1046/j.1420-9101.1999.00044.x

Holm S (1979) A simple sequentially rejective multiple test procedure. Scand J Stat 6:65–70.

doi: 10.2307/4615733

Hop H, Graham M, Wordeau VL (1995) Spawning energetics of Arctic cod (Boreogadus saida) in relation to seasonal development of the ovary and plasma sex steroid levels. Can J Fish Aquat Sci 52:541–550.

Hop H, Tonn WM, Welch HE (1997) Bioenergetics of Arctic cod (Boreogadus saida) at low temperatures. Can J Fish Aquat Sci 54:1772–1784. doi: 10.1139/f97-086

Huse G (1998) Sex-specific life history strategies in capelin (Mallotus villosus)? Can J Fish Aquat Sci 55:631–638.

Iverson SJ, Lang SL, Cooper MH (2001) Comparison of the Bligh and Dyer and Folch methods for total lipid determination in a broad range of marine tissue. Lipids 36:1283–7.

Jensen T, Ugland KI, Anstensrud M (1991) Aspects of growth in Arctic cod, Boreogadus saida (Lepechin 1773). Polar Res 10:547–552. doi: 10.1111/j.1751-8369.1991.tb00672.x

Jobling M (1980) Effects of starvation on proximate chemical composition and energy utilization of plaice , Pleuronectes platessa L. 325–334.

Johannessen LS (2007) Feeding and growth of Polar cod in fjords of Svalbard. Universitetet I Oslo

Juul-Pedersen T, Michel C, Gosselin M (2010) Sinking export of particulate organic material from the euphotic zone in the eastern Beaufort Sea. Mar Ecol Prog Ser 410:55–70. doi: 10.3354/meps08608

Korshunova E (2012) Reproduction and winter biology of polar cod Boreogadus saida from Svalbard waters. Thesis. University of Tromso

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Nat 100:603–609.

Majewski A, Reist J, Park B, Lowdon M (2009) Fish catch data from offshore sites in the Mackenzie River estuary and Beaufort Sea during the open water season, August 2006, aboard the CCGS Nahidik. Winnipeg

Majewski AR, Walkusz W, Lynn BR, Atchison S, Eert J, Reist JD (2015) Distribution and diet of demersal Arctic Cod, Boreogadus saida, in relation to habitat characteristics in the Canadian Beaufort Sea. Polar Biol. doi: 10.1007/s00300-015-1857-y

Nahrgang J, Varpe O, Korshunova E, Murzina S, Hallanger IG, Vieweg I, Berge J (2014) Gender specific reproductive strategies of an Arctic key species (Boreogadus saida) and implications of climate change. PLoS One 9:11. doi: 10.1371/journal.pone.0098452

Olsson M, Madsen T, Shine R (1996) Is sperm really so cheap? Costs of reproduction in male adders, Vipera berus. Proc R Soc London B 455–459.

Post J, Parkinson E (2001) Energy allocation strategy in young fish: allometry and survival. Ecology 82:1040–1051.

Rombough P (1994) Energy partitioning during fish development: additive or compensatory allocation of energy to support growth? Funct Ecol 8:178–186.

Rowe S, Hutchings JA (2006) Sound production by Atlantic Cod during spawning. Trans Am Fish Soc 135:529–538. doi: 10.1577/T04-061.1

Sakurai Y, Ishii K, Nakatani T, Yamaguchi H, Anma G, Jin M (1998) 15. Reproductive Characeristics and Effects of Temperature and Salinity on the Development and Survival of Eggs and Larvae of Arctic cod (Boreogadus saida). Mem Fac Fish Hokkaido Univ 45:77–89.

Skjæraasen JE, Meager JJ, Heino M (2012) Secondary sexual characteristics in codfishes (Gadidae) in relation to sound production, habitat use and social behaviour. Mar Biol Res

8:201–209. doi: 10.1080/17451000.2011.637562

Skjæraasen JE, Meager JJ, Hutchings JA (2010) A cost of reproduction in male Atlantic cod (Gadus morhua). Can J Zool 88:595–600. doi: 10.1139/Z10-033

Wang T, Hung CCY, Randall DJ (2006) The comparative physiology of food deprivation: from feast to famine. Annu Rev Physiol 68:223–251. doi: 10.1146/annurev.physiol.68.040104.105739

Zimmerman MS, Krueger CC, Eshenroder RL (2006) Phenotypic Diversity of Lake Trout in Great Slave Lake: Differences in Morphology, Buoyancy, and Habitat Depth. Trans Am Fish Soc 135:1056–1067. doi: 10.1577/T05-237.1

5 Summary

The goal of this study was to determine whether a certain depth habitat in the Canadian Beaufort Sea was optimum for the prosperity of demersal Arctic Cod. To determine this, the current study considered the effect of the environment on basal energetics requirements associated with differences in temperature and salinity among depth zones and their influence on basal metabolism, as well as the effect of prey distribution on energy acquisition. The effect of life history requirements on energy allocation was also taken into account by comparing the species composition of the diet and energy content of the diet, as well as values for physiological indicators (condition factor, GSI, HSI, proportion of lipid in the carcass, lipid-free dry mass proportion of the carcass) and growth (length- and mass-at-age) among age and size classes of Arctic Cod, respectively. It was expected that demersal Arctic Cod diet and energy allocation would differ among depth-related habitats. This was based on the differences in energetic requirements associated with living in each depth habitat, and differences in prey availability that affect diet among the depth habitats. A sex-dependent difference in the energetic costs of reproduction was also expected based on differences in mating and spawning behaviour, as well as the risks associated with reproduction and parental investment.

This study showed that although diet (Chapter 3) and population dynamics (Chapter 2) may differ slightly including a possible difference in reproductive strategy from cod in northern European countries, the Canadian Beaufort Sea Arctic Cod population is typical of all Arctic Cod populations studied to date and highlights the fact that very little is known generally about Arctic Cod behaviour and the ways in which they spend time in their environment. In order to better inform policy makers of just how fragile the Arctic ecosystems are, and especially the

Canadian Arctic, increased research is required to understand the role of this important forage fish in Arctic ecosystems.

Habitat or depth differences in energy consumption (Chapter 3) and allocation (Chapter 4) were detected in this study of the Canadian Beaufort Sea Arctic Cod population, but further work is needed to determine more accurately what could be driving this variability. For example, this study used prey density values integrated over the water column. Sampling of zooplankton prey at targeted depths would provide more accuracy in regards to the habitat description and whether prey species composition and biomass differs among habitats. Information about nutrient availability beyond coastal regions would also give a clearer picture of variation in productivity among habitats and some insight into the influence of currents on environmental conditions. The current study found that there was no effect of depth on diet species diversity, but generally diet diversity was related to the distribution of both Arctic Cod and their prey. Prey that were common in the environment in terms of biomass were predominant in the diet, e.g., *Calanus* spp.. But more than habitat or the environment, the current study found that age and whether the individual had reached maturity seemed to affect energy consumption and allocation through size-selective foraging and life history demands on energy allocation, respectively. Chapter 3 found that prey consumption was likely related to the fish's gape size limiting the size of prey the fish could take, intraspecific competition between small and larger individuals, or the larger gut storage in larger fish. Larger prey was absent from the diet of small (size class 1) Arctic Cod, becoming a major diet item as the fish grew. Sex had no influence on energy consumption (Chapter 3) or allocation (Chapter 4) in the current study, but a temporal bias may have impacted the observed values for diet composition and physiological indicators. The results from these diet and energy allocation analyses should help in further understanding Arctic Cod bioenergetics and the present energy dynamics of the Beaufort Sea ecosystem.

6 Appendices

Appendix A: Maturity Quality Code, as in Majewski *et al.* (2009)

Table 6.1 Maturity quality code for male and female Arctic Cod, as in (Majewski *et al.* 2009b).

Maturity State		Female		Male
Immature	1	- ovaries granular in texture	6	- testes long and thin
		- hard and triangular in shape		- tubular and scalloped shape
		- up to full length of body cavity		- up to full body length
		- membrane full		- putty-like firmness
		- eggs distinguishable		
Mature	2	- current year spawner	7	- current year spawner
		- ovary fills body cavity		- testes large and lobate
		- eggs near full size but not loose		- white to purplish colour
		- not expelled by pressure		- centers may be fluid
				- milt not expelled by pressure
Ripe	3	- ovaries greatly extended and fill body cavity	8	- testes full size
				- white and lobate
		- eggs full size and transparent		- milt expelled by slight pressure

Spent	4	- expelled by slight pressure	9	- spawning complete
		- spawning complete		- testes flaccid with some milt
		- ovaries ruptured and flaccid		- blood vessels obvious
		- developing oocytes visible		- testes violet-pink in color
Resting	5	- some retained eggs in body cavity	10	- testes tubular, less lobate
		- ovary 40-50% of body cavity		- healed from spawning
		- membrane thin, loose, and semi-transparent		- no fluid in center
				- usually full length
		- healed from spawning		- mottled and purplish in color
		- developing oocytes apparent with few atretic eggs		
		- some eggs may be retained in body cavity		

Appendix B: Mean and Median Temperature and Salinity by Habitat

Table 6.2 Mean (± SE) and median (± SD) of environmental variables (average bottom temperature, °C, and average bottom salinity, PSU) for each of the transects by depth zone. Kruskal-Wallis tests determined there was no significant difference in median temperature or salinity across transects within each depth zone ($p > 0.05$).

		Temperature		Salinity	
Depth Zone	Transect	Mean	Median	Mean	Median
Shelf	TBS	-0.97 ± 0.02	-0.95 ± 0.09	32.45 ± 0.25	31.79 ± 1.02
	GRY	-0.97 ± 0.08	-0.83 ± 0.35	32.14 ± 0.16	31.72 ± 0.66
	KUG	-0.87 ± 0.18	-1.35 ± 0.74	32.02 ± 0.20	32.22 ± 0.87
	DAL	-0.59 ± 0.23	-1.25 ± 0.98	32.67 ± 0.14	32.35 ± 0.60
Upper Slope	TBS	0.43 ± 0.02	0.44 ± 0.09	34.83 ± 0.01	34.83 ± 0.03
	GRY	0.47 ± 0.00	0.47 ± 0.00	34.84 ± 0.00	34.84 ± 0.00
	KUG	0.53 ± 0.00	0.53 ± 0.00	34.80 ± 0.00	34.80 ± 0.00
	DAL	0.45 ± 0.02	0.50 ± 0.10	34.82 ± 0.02	34.87 ± 0.09
Lower Slope	TBS	0.09 ± 0.04	0.08 ± 0.15	34.87 ± 0.00	34.87 ± 0.01
	GRY	0.04 ± 0.02	0.00 ± 0.10	34.90 ± 0.00	34.91 ± 0.02
	KUG	0.07 ± 0.02	0.12 ± 0.10	34.88 ± 0.00	34.87 ± 0.01
	DAL	0.12 ± 0.04	0.13 ± 0.15	34.87 ± 0.00	34.87 ± 0.01

Table 6.3 Mean (± SE) and median (± SD) of environmental variables (average bottom temperature, °C, average bottom salinity, PSU) for each of the transects and depth zones. Kruskal-Wallis tests determined there was no significant difference in median average bottom temperature and salinity among transects, but there were significant differences in these parameters among depth zone. Lettered superscripts indicate a significant difference in temperature or salinity among transects or depth zones.

	Temperature		Salinity	
Transect	Mean	Median	Mean	Median
TBS	-0.25 ± 0.10	-0.06 ± 0.63^{a}	33.86 ± 0.21	34.81 ± 1.36^{a}
GRY	-0.14 ± 0.06	0.00 ± 0.54^{a}	34.19 ± 0.15	34.86 ± 1.25^{a}
KUG	0.30 ± 0.04	0.53 ± 0.53^{a}	34.47 ± 0.08	34.80 ± 0.96^{a}
DAL	0.05 ± 0.09	0.27 ± 0.71^{a}	34.15 ± 0.14	34.86 ± 1.07^{a}
Depth Zone				
Shelf	-0.85 ± 0.08	-1.02 ± 0.65^{a}	32.32 ± 0.10	32.21 ± 0.82^{a}
Upper Slope	0.51 ± 0.00	0.53 ± 0.06^{b}	34.81 ± 0.00	34.80 ± 0.04^{b}
Lower Slope	0.07 ± 0.01	0.01 ± 0.11^{a,b}	34.89 ± 0.00	34.89 ± 0.02^{b}

Appendix C: Length-Mass Relationship for Arctic Cod Prey

Table 6.4 Length-mass relationships for known Arctic Cod prey.

Species	**Length-Mass Equation**	**Reference**
Calanus hyperboreus AF	0.003*6.525mm^3.718	Ashjian *et al.* 2003, as cited in Hopcroft *et al.* 2005
Calanus hyperboreus CV	0.003*4.925mm^3.718	Ashjian *et al.* 2003, as cited in Hopcroft *et al.* 2005
Calanus hyperboreus CIV	0.003*3.375mm^3.718	Ashjian *et al.* 2003, as cited in Hopcroft *et al.* 2005
Calanus hyperboreus CIII	0.003*2mm^3.718	Ashjian *et al.* 2003, as cited in Hopcroft *et al.* 2005
Calanus hyperboreus CII	0.003*1.4mm^3.718	Ashjian *et al.* 2003, as cited in Hopcroft *et al.* 2005
Calanus hyperboreus CI	0.003*1mm^3.718	Ashjian *et al.* 2003, as cited in Hopcroft *et al.* 2005
Calanus glacialis AF	0.01*3.9mm^3.414	Ashjian *et al.* 2003, as

		cited in Hopcroft *et al.* 2005
Calanus glacialis AM	0.01*3.9mm^3.414	Ashjian *et al.* 2003, as cited in Hopcroft *et al.* 2005
Calanus glacialis CV	0.01*3.4mm^3.414	Ashjian *et al.* 2003, as cited in Hopcroft *et al.* 2005
Calanus glacialis CIV	0.01*2.45mm^3.414	Ashjian *et al.* 2003, as cited in Hopcroft *et al.* 2005
Calanus glacialis CIII	0.01*1.7mm^3.414	Ashjian *et al.* 2003, as cited in Hopcroft *et al.* 2005
Calanus glacialis CII	0.01*1.25mm^3.414	Ashjian *et al.* 2003, as cited in Hopcroft *et al.* 2005
Calanus glacialis CI	0.01*0.825mm^3.414	Ashjian *et al.* 2003, as cited in Hopcroft *et al.* 2005
Metridia longa AF	0.281	Hansen 1997
Metridia longa CV	0.112	Hansen 1997
Metridia longa CIII	0.005	Hansen 1997

Metridia longa CII	0.002	Hansen 1997
Paraeuchaeta glacialis AF	4.672	Hansen 1997
Paraeuchaeta glacialis AM	4.672	Hansen 1997
Paraeuchaeta glacialis CV	1.681	Hansen 1997
Paraeuchaeta glacialis CIV	0.900	Hansen 1997
Paraeuchaeta glacialis CIII	0.121	Hansen 1997
Pseudocalanus AF	0.015	Hansen 1997
Pseudocalanus AM	0.013	Hansen 1997
Pseudocalanus CV	0.009	Hansen 1997
Pseudocalanus CIV	0.005	Hansen 1997
Pseudocalanus CIII	0.004	Kanaeva
Pseudocalanus CII	0.002	Kanaeva
Pseudocalanus CI	0.001	Kanaeva
Jaschnovia tolli AF	0.015	same as Pseudocalanus
Jaschnovia tolli CV	0.009	same as Pseudocalanus
Jaschnovia tolli CIV	0.005	same as

		Pseudocalanus
Jaschnovia tolli CIII	0.004	same as Pseudocalanus
Jaschnovia brevis CIV	0.005	same as Pseudocalanus
Aetideopsis armata	0.529	Richter 1994
Heterorhabdus norvegicus AF	0.139	Kanaeva
Pseudochirella spectabilis AF	4.672	same as Paraeuchaeta glacialis AF
Aetideopsis minor AF	0.529	Richter 1994
Microcalanus	0.007	Hansen 1997
Triconia borealis	0.002	Richter 1994
Acartia longiremis	0.005	Kanaeva
Oithona simils	0.003	Richter 1994
Harpacticoida	0.001	Hay *et al.* 1991
Copepoda nauplii	0.001	Hansen 1997
Themisto libellula (< 12mm)	10^(0.1691+0.0667*length in mm)	
Themisto libellula (> 12mm)	10^(0.1469+0.0588*length in mm)	
Themisto abyssorum	0.009*length in mm^2.407	
Gammaracanthus	0.001085*POWER(length in	Poltermann 1997

loricatus	mm,3.064)	
Apherusa glacialis	0.17*1000*0.02291*POWER(length in mm/10,2.36)	Berestovskii *et al.* 1989
Gammarus wilkitzkii	0.001085*POWER(length in mm,3.064)	Poltermann 1997
Gammarellus homari	0.001085*POWER(length in mm,3.064)	Poltermann 1997
Amphipod undetermined	0.001085*POWER(length in mm,3.064)	Poltermann 1997
Ostracoda	0.222	Mumm 1991
Bopyridae (isopod)	0.030	Richter 1994
Thysanoessa rashii	0.0157*POWER(length in mm,1.8477)/0.9	Mumm 1991
Thysanoessa inermis	0.17*1000*0.01236*POWER(length in mm/10,3.063)	Berestovskii *et al.* 1989
Mysis oculata	1.525	Berestovskii *et al.* 1989
Pseudomma truncatum	1.525	Berestovskii *et al.* 1989
Erythrops erythropthalma	1.525	Berestovskii *et al.* 1989
Mysis undetermined	1.525	Berestovskii *et al.* 1989

Hymenodora glacialis	1.525	Berestovskii *et al.* 1989
Sabinea septemcarinata	0.17*1000*0.00563*POWER(length in mm/10,3.538)	Berestovskii *et al.* 1989
Decapoda larva	0.17*1000*0.00563*POWER(length in mm/10,3.538)	Berestovskii *et al.* 1989
Oligochaeta	0.025	
Cumacea	0.030	
Bivalvia	0.001	
Limacina helicina	0.043	Mumm 1991
Eukrohnia hamata	0.133	Mumm 1991
Sagitta elegans	0.109	Mumm 1991
Oikopleura spp.	0.743	Mumm 1991
Boreogadus saida	11.87	own data
Cottidae	18.70	own data

Appendix D: Canadian Beaufort Sea Arctic Cod Diet by %FO, %N, and %WT

Table 6.5 %FO for each prey species in the diet of Arctic Cod by size class by depth zone.

Size Class	**1**			**2**			**3**			**4**		
Species	**Shelf**	**Upper Slope**	**Lower Slope**	**Shelf**	**Upper Slope**	**Lower Slope**	**Shelf**	**Upper Slope**	**Lower Slope**	**Shelf**	**Upper Slope**	**Lower Slope**
% Empty Stomachs	4.76	33.33	22.22	1.67	8.00	8.33	0	3.33	20.00	50.00	21.05	30.77
Calanus hyperboreus	44.54	0	0	85.48	38.54	63.89	55.95	35.36	50.00	50.00	23.61	6.67
Calanus glacialis	96.21	100.00	100.00	64.31	35.42	16.67	41.67	46.22	11.11	0	29.17	0
Pseudocalanus	75.00	100.00	72.22	25.08	16.67	27.78	0	5.95	0	0	12.50	20.00
Copepoda nauplii	15.15	100.00	11.11	0	0	0	0	0	0	0	0	0
Microcalanus	23.94	0	11.11	4.17	3.13	0	0	0	0	50.00	12.50	6.67
Themisto libellula	4.09	0	0	35.50	37.50	27.78	28.57	64.88	50.00	50.00	20.83	40.00
Themisto abyssorum	0	0	0	32.92	67.71	58.33	48.81	52.02	50.00	50.00	29.17	13.33
Amphipod und.	0	0	0	0	0	8.33	14.29	4.17	0	0	0	0
Paraeuchaeta glacialis	11.67	0	0	16.13	7.29	13.89	26.19	10.12	0	50.00	0	0
Ostracoda	0	0	0	0	16.67	50.00	3.57	4.17	66.67	0	18.06	20.00
Harpacticoida	4.55	0	11.11	0	0	0	0	0	0	0	0	0
Triconia	4.55	0	11.11	0	0	0	0	0	0	0	0	0
Triconia borealis	0	0	11.11	2.08	0	0	0	0	0	0	0	0
Oithona	0	0	11.11	0	0	0	0	0	0	0	0	0
Oithona simils	18.48	0	0	0	3.13	0	0	0	0	0	0	0
Oikopleura	4.55	0	0	0	0	0	0	0	0	0	0	0
Mysis und.	0	0	0	0	0	0	0	0	0	0	0	6.67
Mysis oculata	0	0	0	0	0	5.56	0	4.17	0	0	0	6.67
Gammaracanthus lacustris	0	0	0	0	0	0	0	0	0	0	0	6.67
Heterorhabdus norvegicus	3.03	0	0	0	0	0	0	12.50	0	0	0	0
Boroecia maxima	0	0	0	3.06	16.67	30.56	0	32.74	0	0	13.89	20.00
Jaschnovia tolli	6.06	0	0	12.78	0	11.11	3.57	11.31	0	50.00	0	0

Jaschnovia brevis	4.55	0	0	0	0	0	0	0	0	0	0	0
Erythrops erythropthalma	0	0	0	0	0	0	0	0	16.67	0	0	0
Metridia longa	13.33	0	16.67	29.44	19.79	16.67	26.19	20.65	0	0	15.28	0
Apherusa glacialis	0	0	0	0	0	16.67	0.00	4.17	0	50.00	0	20.00
Oligochaete	0	0	0	0	0	0	0	0	0	0	5.56	0
Hymenodora glacialis	0	0	0	0	0	0	0	0	0	0	5.56	0
Cumacea	0	0	0	2.86	0	0	14.29	0	0	0	0	0
Bivalvia	0	0	11.11	0	0	0	0	0	0	0	0	0
Acartia longiremis	0	0	11.11	0	0	0	0	0	0	0	0	0
Limacina helicina	0	0	11.11	0	0	0	0	0	0	0	0	0
Gammarellus homari	0	0	0	0	0	0	0	0	0	0	5.56	0
Aetideopsis minor	0	0	0	0	0	0	0	0	0	0	0	6.67
Gammarus wilkitzkii	0	0	0	0	0	0	0	1.79	0	0	0	0
Thysanoessa raschii	0	0	0	7.5	0	0	4.76	0	0	50.00	0	0
Thysanoessa inermis	0	0	0	0	0	0	0	0	0	50.00	0	0
Sabinea septemcarinata	0	0	0	2.08	0	0	4.76	0	0	0	0	0
Pseudomma truncatum	0	0	0	0	0	0	0	0	0	0	5.56	0
Eukrohnia hamata	0	0	11.11	1.67	0	0	0	0	0	0	0	0
Bopyridae	0	0	0	1.39	0	0	0	0	0	0	0	0
Decapoda larva	3.03	0	0	0	0	0	0	0	0	0	0	0
Sagitta elegans	0	0	0	2.08	0	0	0	0	0	0	0	0
Pseudochirella spectabilis	0	0	0	0	0	0	0	2.50	0	0	0	0
Boreogadus saida	0	0	0	0	3.125	0	0	0	0	0	0	0
Cottidae spp.	0	0	0	0	0	0	0	4.17	0	0	0	0
Aetideopsis armata	0	0	0	0	0	0	0	4.17	0	0	0	0
Stilomysis grandis	0	0	0	0	0	0	0	0	0	0	5.56	0
# Stomachs	42	3	9	60	25	12	13	30	5	2	19	13

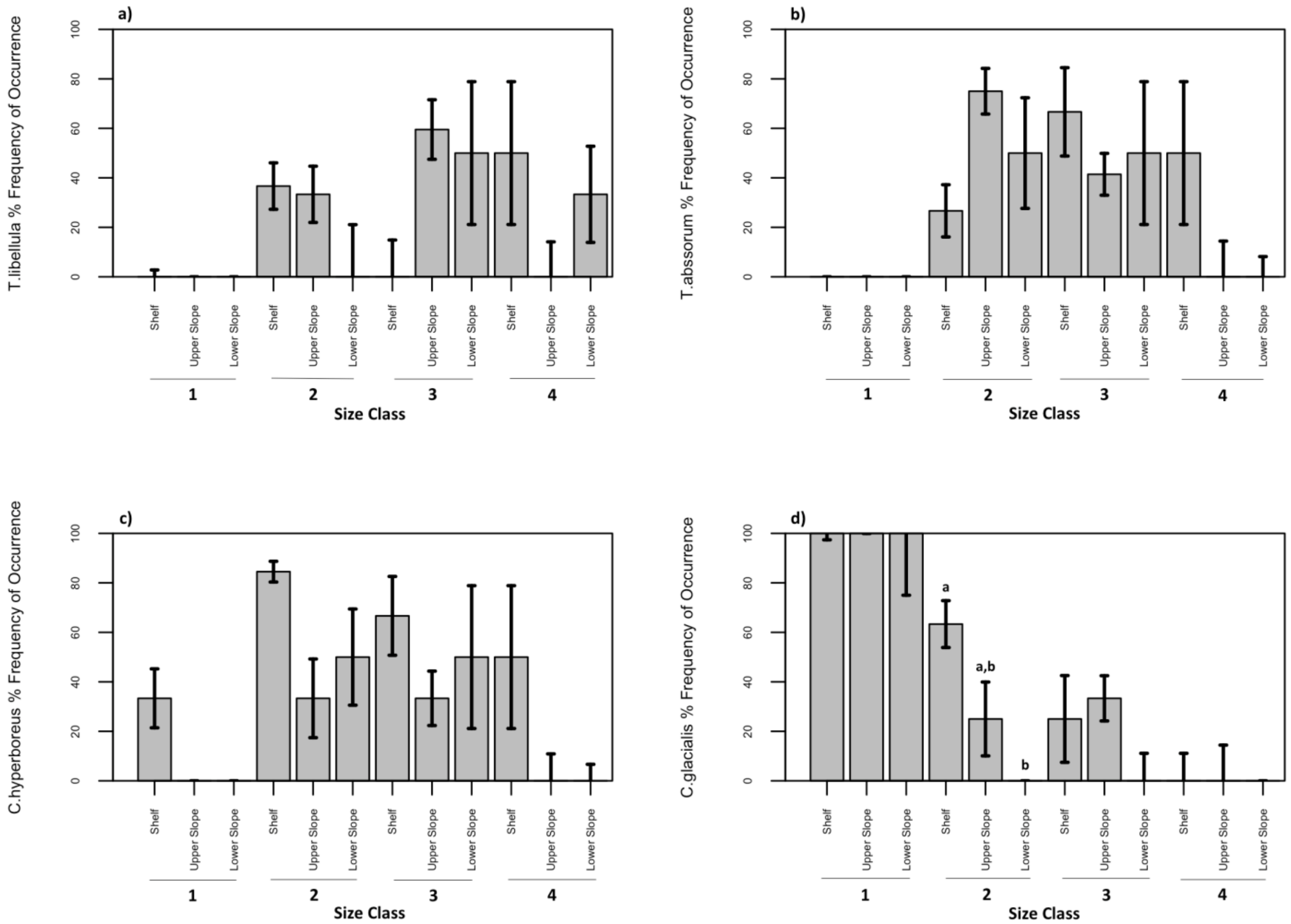

Figure 6.1 Median % frequency of occurrence (%FO ± SE) in the diet of Arctic Cod by size class and depth zone. Letters indicate significant differences within a size class among depth zones. In those of size class 2, there was a significant difference in the median %FO of *C.glacialis* (d) between the diets of Shelf and Offshelf zones (Kruskal-Wallis, p-adj = 0.004). There was no significant difference in the median species %FO in the diet of size classes 1, 3, and 4 Arctic Cod among depth zones. A lack of error bars indicates that none of that species was consumed. Where error bars are present but no column, there was a low frequency of occurrence. Where error bars are present with bars indicating 100% FO, median %FO was 100 but this species was not found in all stomachs at all stations.

Table 6.6 %N for each prey species in the diet of Arctic Cod by size class by depth zone.

Size Class	**1**						**2**					
Species	**Shelf**	**SE**	**Upper Slope**	**SE**	**Lower Slope**	**SE**	**Shelf**	**SE**	**Upper Slope**	**SE**	**Lower Slope**	**SE**
# Empty Stomachs	2		1		2		1		2		1	
Calanus hyperboreus	8.28	3.57	0	0	0	0	34.97	8.11	26.66	11.74	18.47	5.85
Calanus glacialis	49.61	7.57	0	0	23.81	23.81	29.86	9.09	11.07	5.81	3.89	3.89
Pseudocalanus	27.36	5.17	80.68	5.68	52.80	21.65	13.75	7.43	5.38	3.18	6.40	3.29
Copepoda nauplii	4.88	4.29	19.32	5.68	13.24	13.24	0	0	0	0	0	0
Microcalanus	4.11	2.66	0	0	0.98	0.98	0.14	0.14	0.30	0.30	0	0
Themisto libellula	0.24	0.16	0	0	0	0	3.97	1.44	6.34	2.98	10.68	6.77
Themisto abyssorum	0	0	0	0	0	0	7.61	4.77	35.50	11.12	31.32	11.93
Amphipod und.	0	0	0	0	0	0	0	0	0	0	0.56	0.56
Paraeuchaeta glacialis	0.43	0.20	0	0	0	0	4.10	3.06	0.47	0.35	1.20	0.76
Ostracoda	0	0	0	0	0	0	0	0	2.19	1.60	17.39	8.23
Harpacticoida	0.10	0.10	0	0	0.49	0.49	0	0	0	0	0	0
Triconia	0.72	0.72	0	0	1.47	1.47	0	0	0	0	0	0
Triconia borealis	0	0	0	0	0.49	0.49	0.07	0.07	0	0	0	0
Oithona	0	0	0	0	2.94	2.94	0	0	0	0	0	0
Oithona simils	1.88	0.93	0	0	0	0	0	0	0.26	0.26	0	0
Oikopleura	0.10	0.10	0	0	0	0	0	0	0	0	0	0
Mysis und.	0	0	0	0	0	0	0	0	0	0	0	0
Mysis oculata	0	0	0	0	0	0	0	0	0	0	1.11	1.11
Gammaracanthus lacustris	0	0	0	0	0	0	0	0	0	0	0	0
Heterorhabdus norvegicus	0.11	0.11	0	0	0	0	0	0	0	0	0	0
Boroecia maxima	0	0	0	0	0	0	0.08	0.06	5.56	2.82	3.33	1.49
Jaschnovia tolli	0.25	0.25	0	0	0	0	0.98	0.51	2.56	1.73	1.75	1.17

Jaschnovia brevis	0.05	0.05	0	0	0	0	0.14	0.14	0	0	0	0
Erythrops erythropthalma	0	0	0	0	0	0	0	0	0	0	0	0
Metridia longa	1.75	0.87	0	0	1.33	1.33	6.16	2.61	3.58	1.67	3.33	3.33
Apherusa glacialis	0	0	0	0	0	0	0	0	0	0	0.56	0.56
Oligochaete	0	0	0	0	0	0	0	0	0	0	0	0
Hymenodora glacialis	0	0	0	0	0	0	0	0	0	0	0	0
Cumacea	0	0	0	0	0	0	0.15	0.15	0	0	0	0
Bivalvia	0	0	0	0	0.98	0.98	0	0	0	0	0	0
Acartia longiremis	0	0	0	0	0.49	0.49	0	0	0	0	0	0
Limacina helicina	0	0	0	0	0.49	0.49	0	0	0	0	0	0
Gammarellus homari	0	0	0	0	0	0	0	0	0	0	0	0
Aetideopsis minor	0	0	0	0	0	0	0	0	0	0	0	0
Gammarus wilkitzkii	0	0	0	0	0	0	0	0	0	0	0	0
Thysanoessa raschii	0	0	0	0	0	0	0.72	0.40	0	0	0	0
Thysanoessa inermis	0	0	0	0	0	0	0	0	0	0	0	0
Sabinea septemcarinata	0	0	0	0	0	0	0	0	0	0	0	0
Pseudomma truncatum	0	0	0	0	0	0	0	0	0	0	0	0
Eukrohnia hamata	0	0	0	0	0.49	0.49	0.07	0.07	0	0	0	0
Bopyridae	0	0	0	0	0	0	0.04	0.04	0	0	0	0
Decapoda larva	0.11	0.11	0	0	0	0	0	0	0	0	0	0
Sagitta elegans	0	0	0	0	0	0	0.17	0.17	0	0	0	0
Pseudochirella spectabilis	0	0	0	0	0	0	0	0	0	0	0	0
Boreogadus saida	0	0	0	0	0	0	0	0	0.13	0.13	0	0
Cottidae spp.	0	0	0	0	0	0	0	0	0	0	0	0
Aetideopsis armata	0	0	0	0	0	0	0	0	0	0	0	0
Stilomysis grandis	0	0	0	0	0	0	0	0	0	0	0	0

Total N Prey Items	1576	26	100	1547	258	112
# Stomachs	42	3	9	60	25	12

Table 6.6 continued…

Size Class	**3**						**4**					
Species	**Shelf**	**SE**	**Upper Slope**	**SE**	**Lower Slope**	**SE**	**Shelf**	**SE**	**Upper Slope**	**SE**	**Lower Slope**	**SE**
# Empty Stomachs	0		1		1		0		5		4	
Calanus hyperboreus	31.78	12.74	12.58	6.84	27.31	24.85	0.10	0.10	7.28	5.32	0.54	0.54
Calanus glacialis	12.82	9.92	7.04	2.84	0.83	0.83	0	0	1.11	1.11	0	0
Pseudocalanus	0	0	0.33	0.24	0	0	0	0	7.04	6.60	3.33	3.33
Copepoda nauplii	0	0	0	0	0	0	0	0	0	0	0	0
Microcalanus	0	0	0	0	0	0	0	0	0	0	0	0
Themisto libellula	10.52	6.91	16.47	3.72	2.12	1.13	3.77	3.77	6.92	6.62	30.90	13.42
Themisto abyssorum	29.85	12.14	46.97	9.39	34.29	26.97	43.79	43.79	30.61	15.25	13.29	11.32
Amphipod und.	2.04	2.04	0.89	0.89	0	0	0	0	0	0	0	0
Paraeuchaeta glacialis	2.51	1.99	1.33	0.88	0	0	0.31	0.31	0	0	0	0
Ostracoda	0.16	0.16	0.96	0.96	34.62	32.71	0	0	17.77	16.47	10.00	10.00
Harpacticoida	0	0	0	0	0	0	0	0	0	0	0	0
Triconia	0	0	0	0	0	0	0	0	0	0	0	0
Triconia borealis	0	0	0	0	0	0	0	0	0	0	0	0
Oithona	0	0	0	0	0	0	0	0	0	0	0	0
Oithona similis	0	0	0	0	0	0	0	0	0	0	0	0
Oikopleura	0	0	0	0	0	0	0	0	0	0	0	0
Mysis und.	0	0	0	0	0	0	0	0	0	0	1.67	1.67
Mysis oculata	0	0	0.89	0.89	0	0	0	0	0	0	1.67	1.67
Gammaracanthus lacustris	0	0	0	0	0	0	0	0	0	0	1.67	1.67
Heterorhabdus norvegicus	0	0	0.72	0.50	0	0	0	0	0	0	0	0
Boroecia maxima	0	0	6.60	2.62	0	0	0	0	4.31	3.28	16.67	16.67
Jaschnovia tolli	2.41	2.41	1.34	0.94	0	0	0.10	0.10	0	0	0	0
Jaschnovia brevis	0	0	0	0	0	0	0	0	0	0	0	0

Erythrops erythropthalma	0	0	0	0	0.83	0.83	0	0	0	0	0	0
Metridia longa	5.69	3.79	1.16	0.51	0	0	0	0	6.66	5.42	0	0
Apherusa glacialis	0	0	2.08	2.08	0	0	0.31	0.31	0	0	20.00	20.00
Oligochaete	0	0	0	0	0	0	0	0	5.56	5.56	0	0
Hymenodora glacialis	0	0	0	0	0	0	0	0	0.98	0.98	0	0
Cumacea	1.79	1.79	0	0	0	0	0	0	0	0	0	0
Bivalvia	0	0	0	0	0	0	0	0	0	0	0	0
Acartia longiremis	0	0	0	0	0	0	0	0	0	0	0	0
Limacina helicina	0	0	0	0	0	0	0	0	0	0	0	0
Gammarellus homari	0	0	0	0	0	0	0	0	2.94	2.94	0	0
Aetideopsis minor	0	0	0	0	0	0	0	0	0	0	0.27	0.27
Gammarus wilkitzkii	0	0	0.09	0.09	0	0	0	0	0	0	0	0
Thysanoessa raschii	0.37	0.37	0	0	0	0	1.43	1.43	0	0	0	0
Thysanoessa inermis	0	0	0	0	0	0	0.20	0.20	0	0	0	0
Sabinea septemcarinata	0.07	0.07	0	0	0	0	0	0	0	0	0	0
Pseudomma truncatum	0	0	0	0	0	0	0	0	0.98	0.98	0	0
Eukrohnia hamata	0	0	0	0	0	0	0	0	0	0	0	0
Bopyridae	0	0	0	0	0	0	0	0	0	0	0	0
Decapoda larva	0	0	0	0	0	0	0	0	0	0	0	0
Sagitta elegans	0	0	0	0	0	0	0	0	0	0	0	0
Pseudochirella spectabilis	0	0	0.16	0.16	0	0	0	0	0	0	0	0
Boreogadus saida	0	0	0	0	0	0	0	0	0	0	0	0
Cottidae spp.	0	0	0.29	0.29	0	0	0	0	0	0	0	0
Aetideopsis armata	0	0	0.10	0.10	0	0	0	0	0	0	0	0
Stilomysis grandis	0	0	0	0	0	0	0	0	7.84	7.84	0	0
Total N Prey Items	309		538		67		491		180		95	

# Stomachs	13	30	5	2	19	13

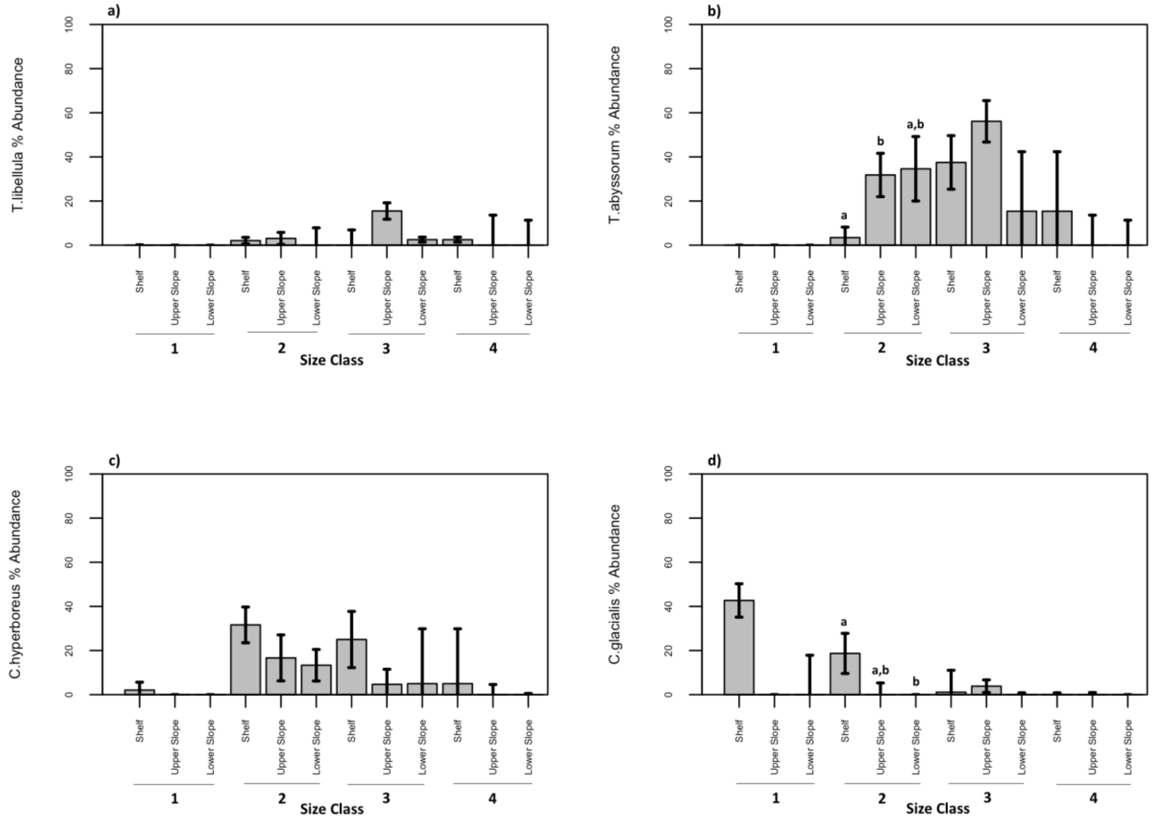

Figure 6.2 Median % Number or Abundance (N ± SE) in the diet of Arctic Cod by size class and depth zone. Letters indicate significant differences within a size class among depth zones. In those of size class 2, there was a significant difference in the median %N of *T. abyssorum* (b) between the diets of Shelf and Upper Slope zones (Kruskal-Wallis, p-adj = 0.02) and of *C. glacialis* between the Shelf and Lower Slope zones (Kruskal-Wallis, p-adj = 0.002). There was no significant difference in the median species %N in the diet of size classes 1, 3, and 4 Arctic Cod among depth zones. A lack of error bars indicates that none of that species was consumed. Where error bars are present but no column, the species was consumed but in low abundance.

Table 6.7 %WT for each prey species in the diet of Arctic Cod by size class by depth zone.

Size Class	**1**						**2**					
Species	**Shelf**	**SE**	**Upper Slope**	**SE**	**Lower Slope**	**SE**	**Shelf**	**SE**	**Upper Slope**	**SE**	**Lower Slope**	**SE**
# Empty Stomachs	2		1		2		1		2		2	
Calanus hyperboreus	29.157	9.755	0	0	0	0	75.334	22.852	30.711	13.030	26.871	8.992
Calanus glacialis	61.585	55.838	71.507	8.544	86.606	9.298	19.630	8.669	7.368	4.142	5.625	5.625
Pseudocalanus	3.975	1.745	27.804	8.204	5.538	2.629	0.529	0.369	0.170	0.149	0.109	0.084
Copepoda nauplii	0.117	0.108	0.689	0.340	0	0	0	0	0.00	0.000	0	0
Microcalanus	0.084	0.030	0	0	0.481	0.481	0.002	0.002	0.00	0.002	0	0
Themisto libellula	1.467	1.000	0	0	0	0	14.334	3.787	29.922	12.376	31.533	19.959
Themisto abyssorum	0	0	0	0	0	0	1.874	1.497	25.496	13.107	14.253	8.858
Amphipod und.	0	0	0	0	0	0	0	0	0	0	0.210	0.210
Paraeuchaeta glacialis	0.810	0.435	0	0	0	0	9.643	7.280	0.491	0.491	3.122	2.304
Ostracoda	0	0	0	0	0	0	0.015	0.010	4.647	3.252	10.613	8.243
Harpacticoida	0.003	0.003	0	0	0	0	0	0	0	0	0	0
Triconia	0	0	0	0	0	0	0	0	0	0	0	0
Triconia borealis	0.036	0.036	0	0	0.275	0.275	0.000	0.000	0	0	0	0
Oithona	0	0	0	0	0	0	0	0	0	0	0	0
Oithona simils	0.111	0.066	0	0	0	0	0	0	0.000	0.000	0	0
Oikopleura	1.919	1.919	0	0	0	0	0	0	0	0	0	0
Mysis und.	0	0	0	0	0	0	0	0	0	0	0	0
Mysis oculata	0	0	0	0	0	0	0	0	0	0	2.97	2.974
Gammaracanthus lacustris	0	0	0	0	0	0	0	0	0	0	0	0
Heterorhabdus norvegicus	0.029	0.029	0	0	0	0	0	0	0	0	0	0
Boroecia maxima	0	0	0	0	0	0	0	0	0	0	0	0
Jaschnovia tolli	0.017	0.017	0	0	0	0	0.011	0.007	0.074	0.068	0.032	0.029
Jaschnovia brevis	0.007	0.007	0	0	0	0	0	0	0	0	0	0

Erythrops erythropthalma	0	0	0	0	0	0	0	0	0	0	0	0
Metridia longa	0.627	0.396	0	0	0.817	0.817	2.320	1.727	0.376	0.155	1.023	1.023
Apherusa glacialis	0	0	0	0	0	0	0	0	0	0	3.634	3.634
Oligochaete	0	0	0	0	0	0	0	0	0	0	0	0
Hymenodora glacialis	0	0	0	0	0	0	0	0	0	0	0	0
Cumacea	0	0	0	0	0	0	0.004	0.003	0	0	0	0
Bivalvia	0	0	0	0	0.069	0.069	0	0	0	0	0	0
Acartia longiremis	0	0	0	0	0.169	0.169	0	0	0	0	0	0
Limacina helicina	0	0	0	0	1.477	1.477	0	0	0	0	0	0
Gammarellus homari	0	0	0	0	0	0	0	0	0	0	0	0
Aetideopsis minor	0	0	0	0	0	0	0	0	0	0	0	0
Gammarus wilkitzkii	0	0	0	0	0	0	0	0	0	0	0	0
Thysanoessa raschii	0	0	0	0	0	0	2.334	1.241	0	0	0	0
Thysanoessa inermis	0	0	0	0	0	0	0	0	0	0	0	0
Sabinea septemcarinata	0	0	0	0	0	0	0.054	0.054	0	0	0	0
Pseudomma truncatum	0	0	0	0	0	0	0	0	0	0	0	0
Eukrohnia hamata	0	0	0	0	4.569	4.569	0.010	0.010	0	0	0	0
Bopyridae	0	0	0	0	0	0	0.004	0.004	0	0	0	0
Decapoda larva	0.055	0.055	0	0	0	0	0	0	0	0	0	0
Sagitta elegans	0	0	0	0	0	0	0.075	0.075	0	0	0	0
Pseudochirella spectabilis	0	0	0	0	0	0	0	0	0	0	0	0
Boreogadus saida	0	0	0	0	0	0	0	0	0.744	0.744	0	0
Cottidae spp.	0	0	0	0	0	0	0	0	0	0	0	0
Aetideopsis armata	0	0	0	0	0	0	0	0	0	0	0	0
Stilomysis grandis	0	0	0	0	0	0	0	0	0	0	0	0
Total Mass Prey (mg)	343.073		0.957		6.118		1756.372		478.644		190.714	

# Stomachs	42	3	9	60	25	12

Table 6.7 continued…

Size Class	**3**						**4**					
Species	**Shelf**	**SE**	**Upper Slope**	**SE**	**Lower Slope**	**SE**	**Shelf**	**SE**	**Upper Slope**	**SE**	**Lower Slope**	**SE**
# Empty Stomachs	0		5		4		0		5		4	
Calanus hyperboreus	39.751	15.299	14.871	6.941	36.421	25.771	0.407	0.407	12.380	7.905	0.154	0.154
Calanus glacialis	8.080	6.272	3.270	1.333	1.249	1.249	0	0	1.583	0.933	0	0
Pseudocalanus	0	0	0.111	0.108	0	0	0	0	0.690	0.677	0.267	0.267
Copepoda nauplii	0	0	0	0	0	0	0	0	0	0	0	0
Microcalanus	0	0	0	0	0	0	0	0	0	0	0	0
Themisto libellula	24.504	13.457	54.888	8.229	14.776	9.898	0.231	0.231	18.587	14.508	54.996	22.751
Themisto abyssorum	16.366	12.275	15.915	5.849	12.292	10.955	16.181	16.181	20.163	11.553	0.689	0.429
Amphipod und.	0.418	0.418	0	0	0	0	0	0	0	0	0	0
Paraeuchaeta glacialis	8.494	7.296	3.195	1.737	0	0	1.021	1.021	0	0	0	0
Ostracoda	0.017	0.017	1.372	0.503	33.433	33.284	0	0	21.832	16.380	19.839	19.707
Harpacticoida	0	0	0	0	0	0	0	0	0	0	0	0
Triconia	0	0	0	0	0	0	0	0	0	0	0	0
Triconia borealis	0	0	0	0	0	0	0	0	0	0	0	0
Oithona	0	0	0	0	0	0	0	0	0	0	0	0
Oithona simils	0	0	0	0	0	0	0	0	0	0	0	0
Oikopleura	0	0	0	0	0	0	0	0	0	0	0	0
Mysis und.	0	0	0	0	0	0	0	0	0	0	0.156	0.156
Mysis oculata	0	0	1.540	1.540	0	0	0	0	0	0	0.156	0.156
Gammaracanthus lacustris	0	0	0	0	0	0	0	0	0	0	3.730	3.730
Heterorhabdus norvegicus	0	0	0.098	0.070	0	0	0	0	0	0	0	0
Boroecia maxima	0	0	0	0	0	0	0	0	0	0	0	0
Jaschnovia tolli	0.018	0.018	0.006	0.004	0	0	0.001	0.001	0	0	0	0
Jaschnovia brevis	0	0	0	0	0	0	0	0	0	0	0	0

Erythrops erythropthalma	0	0	0	0	1.828	1.828	0	0	0	0	0	0
Metridia longa	1.735	1.503	0.201	0.130	0	0	0	0	8.166	8.020	0	0
Apherusa glacialis	0	0	1.174	1.174	0	0	0.367	0.367	0	0	20	20
Oligochaete	0	0	0	0	0	0	0	0	0.716	0.716	0	0
Hymenodora glacialis	0	0	0	0	0	0	0	0	0.305	0.305	0	0
Cumacea	0.036	0.036	0	0	0	0	0	0	0	0	0	0
Bivalvia	0	0	0	0	0	0	0	0	0	0	0	0
Acartia longiremis	0	0	0	0	0	0	0	0	0	0	0	0
Limacina helicina	0	0	0	0	0	0	0	0	0	0	0	0
Gammarellus homari	0	0	0	0	0	0	0	0	2.335	2.335	0	0
Aetideopsis minor	0	0	0	0	0	0	0	0	0	0	0.013	0.013
Gammarus wilkitzkii	0	0	0.014	0.014	0	0	0	0	0	0	0	0
Thysanoessa raschii	0.472	0.472	0	0	0	0	5.865	5.865	0	0	0	0
Thysanoessa inermis	0	0	0	0	0	0	3.034	3.034	0	0	0	0
Sabinea septemcarinata	0.109	0.109	0	0	0	0	0	0	0	0	0	0
Pseudomma truncatum	0	0	0	0	0	0	0	0	0.305	0.305	0	0
Eukrohnia hamata	0	0	0	0	0	0	0	0	0	0	0	0
Bopyridae	0	0	0	0	0	0	0	0	0	0	0	0
Decapoda larva	0	0	0	0	0	0	0	0	0	0	0	0
Sagitta elegans	0	0	0	0	0	0	0	0	0	0	0	0
Pseudochirella spectabilis	0	0	0.108	0.108	0	0	0	0	0	0	0	0
Boreogadus saida	0	0	0	0	0	0	0	0	0	0	0	0
Cottidae spp.	0	0	3.206	3.206	0	0	0	0	0	0	0	0
Aetideopsis armata	0	0	0.030	0.030	0	0	0	0	0	0	0	0
Stilomysis grandis	0	0	0	0	0	0	0	0	12.938	12.938	0	0
Total Mass Prey (mg)	641.0396923		1369.381698		102.3581881		393.4232348		191.6535361		1072.745841	

# Stomachs	13	30	5	2	19	13

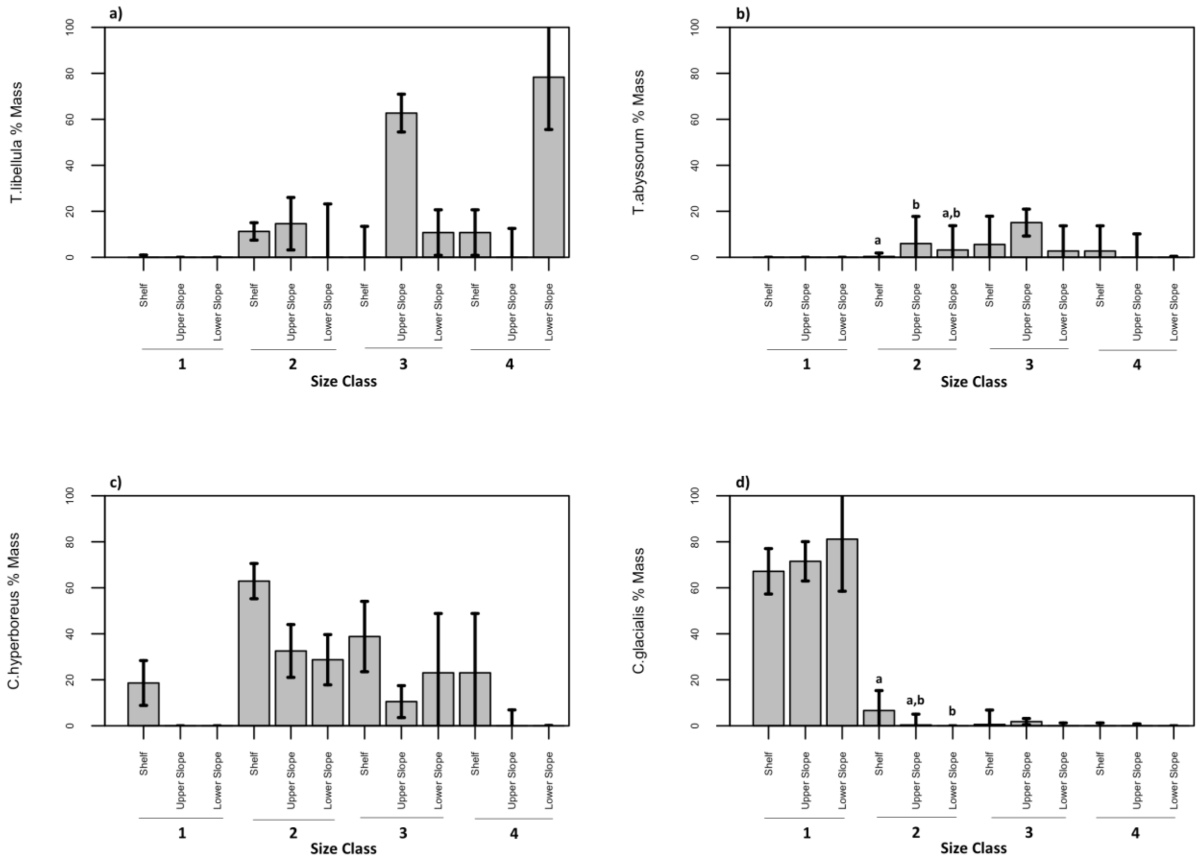

Figure 6.3 Median % mass (WT ± SE) in the diet of Arctic Cod by size class and depth zone. Letters indicate significant differences within a size class among depth zones. In those of size class 2, there was a significant difference in the median %WT of *T. abyssorum* (b) between the diets of Shelf and Upper Slope zones (Kruskal-Wallis, p-adj = 0.007) and of *C. glacialis* between the Shelf and Lower zones (Kruskal-Wallis, p-adj = 0.002). There was no significant difference in the median species %WT in the diet of size classes 1, 3, and 4 Arctic Cod among depth zones. A lack of error bars indicates that none of that species was consumed. Where error bars are present but no column, consumption by biomass of that species was low.

Appendix E: Sex Ratio by Age Class by Depth Zone

Table 6.8 Sex ratio of Arctic Cod by age class by depth zone in the Canadian Beaufort Sea subsample in August 2012.

Depth Zone	**Age Class**	**Sex**	
		Male	**Female**
Shelf	1	51 (83.6%)	10 (16.4%)
	2	7 (58.3%)	5 (41.7%)
Upper Slope	1	25 (80.6%)	6 (19.4%)
	2	13 (44.8%)	16 (55.2%)
	3	4 (33.3%)	8 (66.7%)
Lower Slope	1	8 (72.7%)	3 (27.3%)
	2	6 (60.0%)	4 (40.0%)
	3	5 (62.5%)	3 (37.5%)

Table 6.9 Number of mature and immature Arctic Cod by age class in the Canadian Beaufort Sea subsample.

Age Class	**Immature**	**Mature**	**Total**
1	73	30	103
2	12	39	51
3	2	18	20

Appendix F: Length-at-Age Distribution of the Sub-Sample of Canadian Beaufort Sea Arctic Cod

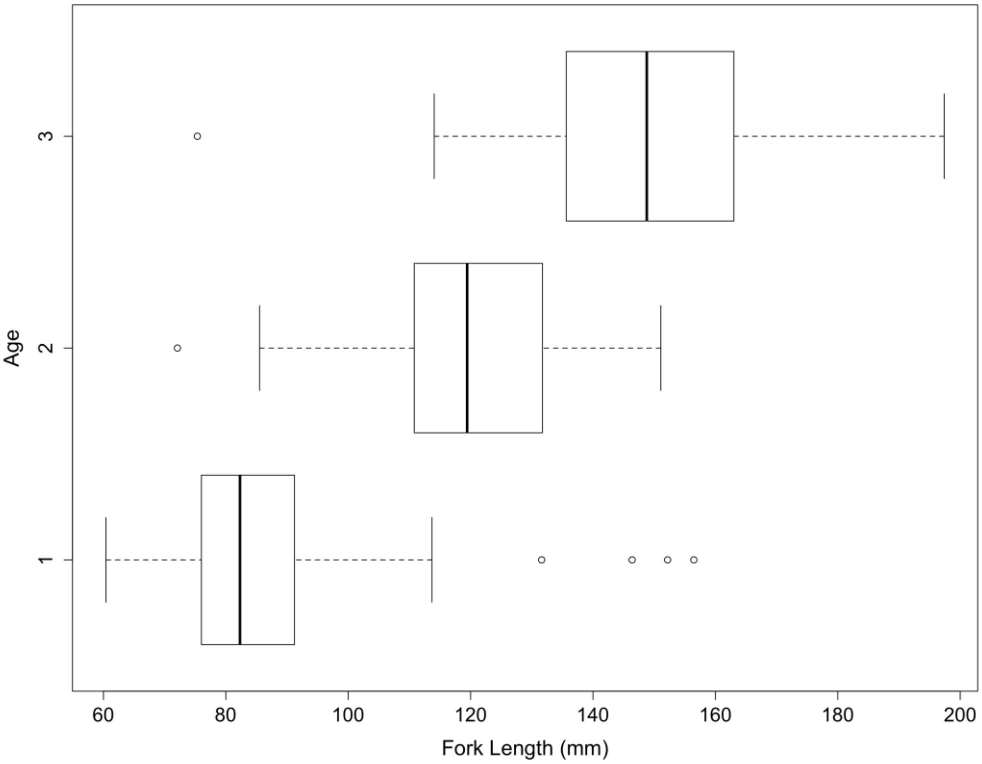

Figure 6.4 Length-at-age of the study population of Arctic Cod from the Canadian Beaufort Sea (age 1-3, n = 171). Each solid black line represents the average length at age.

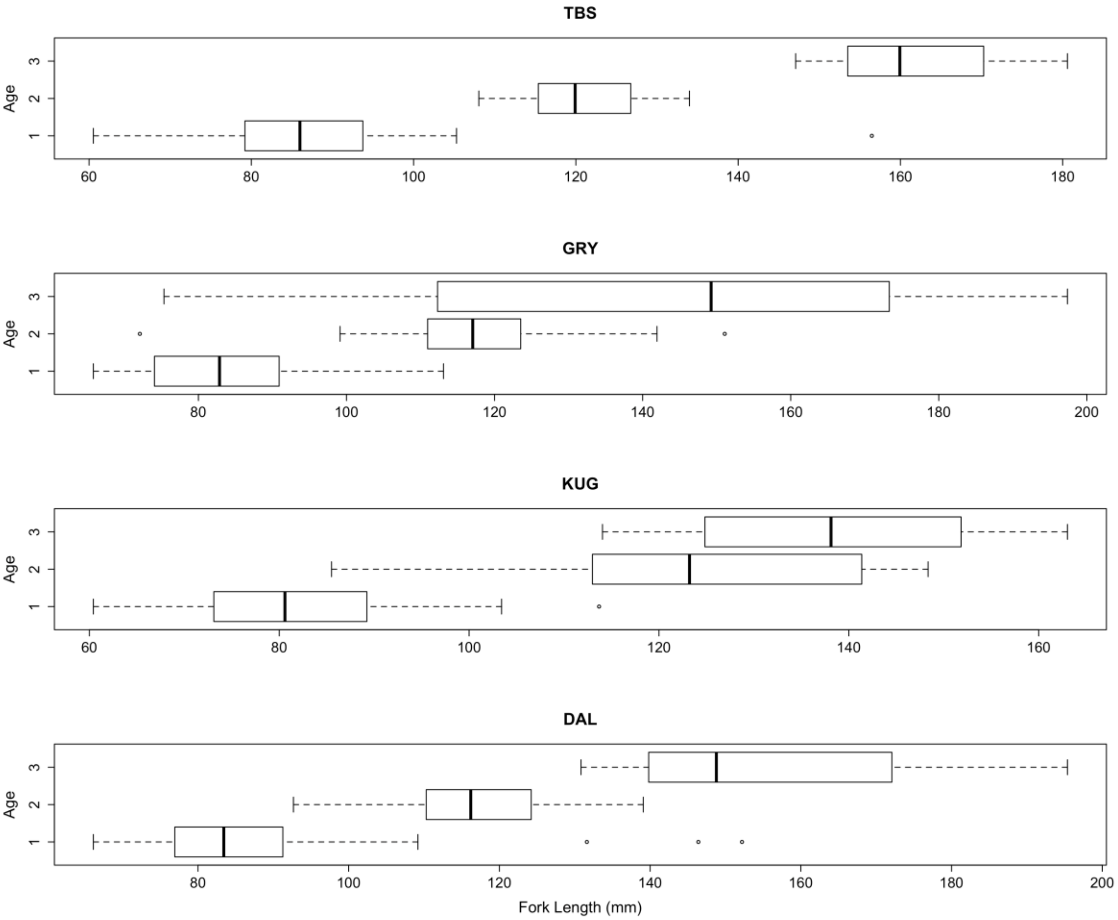

Figure 6.5 Length-at-age of Arctic Cod by transect (TBS, n = 40; GRY, n = 41; KUG, n = 42; DAL, n = 54) in the Canadian Beaufort Sea (age 1-3). Each solid black line represents the average length at age within each transect.

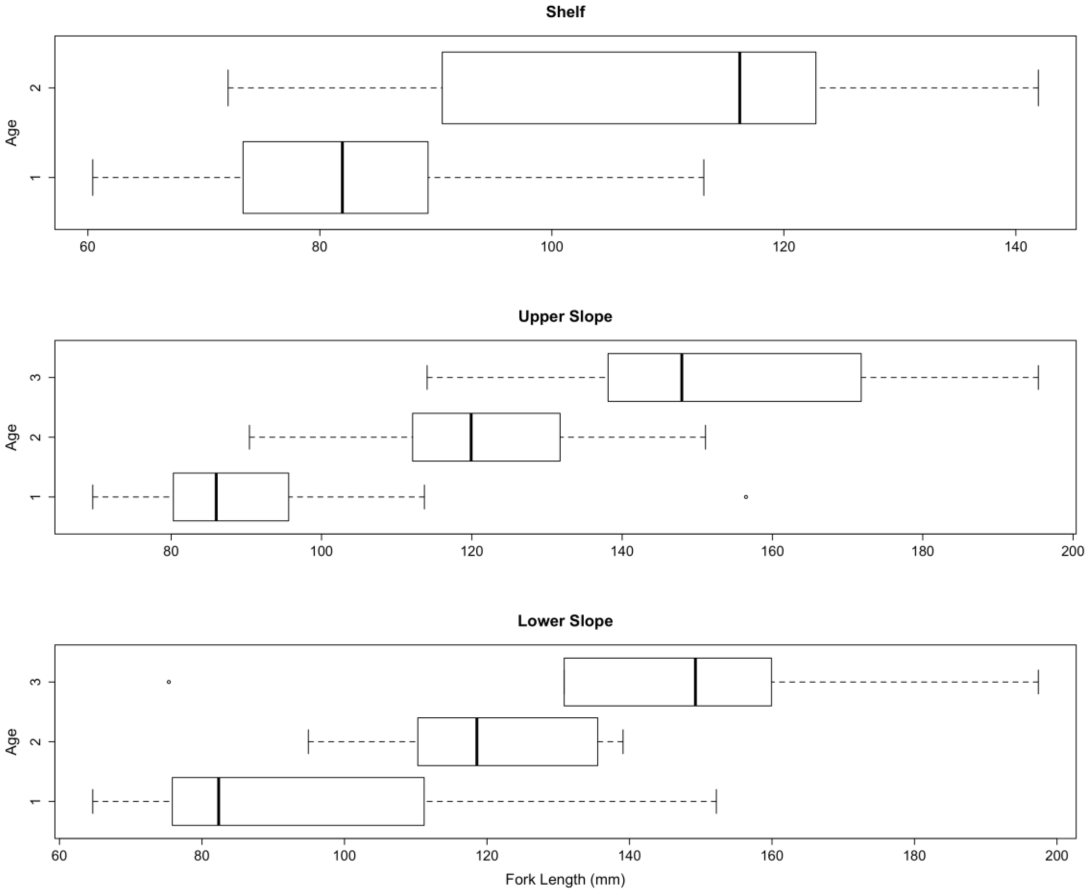

Figure 6.6 Length-at-age of Arctic Cod by depth zone (Shelf, n = 118; Upper Slope, n = 79; Lower Slope, n = 40) in the Canadian Beaufort Sea (age 1-3). Each black line represents the average length-at-age within each depth zone.

Table 6.10 Mean length and mass (Mean (Median) ± SE) at age of Arctic Cod by transect and depth zone by sex. A Kruskal-Wallis test found that there was a significant difference in the length and mass of age 2 male Arctic Cod from the Shelf and Upper Slope zones (p-adj = 0.0115 and 0.0086, respectively).

		Length at age			**Mass at age**		
Sex	**Transect**	**Age 1**	**Age 2**	**Age 3**	**Age 1**	**Age 2**	**Age 3**
Male	TBS	84.73 (82.33) ± 2.41	115.57	170.26 (170.26) ± 10.33	5.20 (5.11) ± 0.48	9.41	34.72 (34.72) ± 7.01
	GRY	81.08 (82.17) ± 2.77	108.99 (121.53) ± 7.67	124.35 (149.25) ± 35.49	4.83 (4.44) ± 0.54	14.60 (13.97) ± 2.49	29.54 (26.49) ± 16.21
	KUG	83.05 (81.32) ± 2.84	105.50 (101.70) ± 7.33		4.70 (3.94) ± 0.52	10.32 (8.78) ± 2.21	12.74
	DAL	86.41 (83.43) ± 3.20	115.21 (116.20) ± 3.94	110.79	5.24 (4.41) ± 0.68	12.72 (11.61) ± 1.32	

Female	TBS	87.95 (91.82) ± 11.35	122.70 (120.36) ± 4.11	147.09	10.61 (6.78) ± 4.53	14.04 (13.88) ± 1.07	23.52
	GRY	90.9	107.48 (110.96) ± 7.26	141.94	7.18	12.54 (10.11) ± 3.15	
	KUG	76.15 (73.39) ± 6.20	134.39 (141.36) ± 4.43	146.91 (140.62) ± 8.43	3.76 (3.10) ± 1.14	17.61 (19.58) ± 2.50	22.52 (18.43) ± 6.02
	DAL	104.88 (85.76) ± 11.72	119.76 (116.95) ± 6.93	142.27 (148.79) ± 19.24	9.91 (4.53) ± 3.70	12.58 (11.10) ± 2.27	35.45 (28.39) ± 13.84
Sex	**Depth Zone**	**Age 1**	**Age 2**	**Age 3**	**Age 1**	**Age 2**	**Age 3**
Male	Shelf	81.26 (81.19) ± 1.70	95.81 (92.67)[a] ± 7.07	122.31	4.67 (4.25) ± 0.31	8.24 (7.44)[a] ± 1.48	

	Upper Slope	87.62 (85.99) ± 2.14	118.68 (123.22)^{b} ± 3.77	147.49 (147.32) ± 33.27	5.42 (5.23) ± 0.44	14.69 (14.00)^{b} ± 1.49	27.24 (27.24) ± 14.50
	Lower Slope	85.98 (81.47) ± 6.87	120.96 (116.31)^{a,b} ± 5.03	128.18 (154.59) ± 25.55	5.74 (3.99) ± 1.64	13.24 (12.39)$^{a.b}$ ± 2.04	29.08 (27.10) ± 11.47
Female	Shelf	85.28 (88.73) ± 3.92	128.56 (132.44) ± 5.73	141.94	5.40 (5.78) ± 0.76	14.98 (13.86) ± 3.47	
	Upper Slope	95.03 (86.00) ± 12.44	121.30 (116.49) ± 3.96	147.24 (147.94) ± 8.90	9.39 (4.53) ± 4.79	14.29 (13.39) ± 1.43	30.27 (25.95) ± 6.99
	Lower Slope	121.09 (146.40) ± 28.26	122.20 (127.83) ± 9.93	130.83	18.25 (25.58) ± 8.24	14.93 (16.12) ± 3.18	15.79

Table 6.11 Mean and median length and mass (Mean (Median) ± SE) at age of Arctic Cod by sex, transect, and depth zone. Kruskal-Wallis tests determined there was no significant difference in median length or mass at age among between sexes, among transects, or among depth zones.

	Length at age			**Mass at age**		
Sex	**Age 1**	**Age 2**	**Age 3**	**Age 1**	**Age 2**	**Age 3**
Male	83.84 (82.26) ± 1.39	110.63 (116.63) ± 3.38	135.62 (154.59) ± 18.31	4.99 (4.49) ± 0.28	12.61 (12.32) ± 1.08	28.47 (27.10) ± 8.17
Female	93.96 (89.79) ± 6.36	122.45 (120.46) ± 3.22	144.83 (147.09) ± 8.28	8.69 (5.45) ± 2.12	14.53 (13.86) ± 1.19	28.20 (23.52) ± 6.26
Transect						
TBS	84.94 (85.99) ± 3.15	121.81 (119.91) ± 3.58	162.54 (159.93) ± 9.76	6.08 (5.26) ± 1.02	13.38 (13.86) ± 1.12	30.99 (27.71) ± 5.51
GRY	81.60 (83.53) ± 2.58	108.52 (117.05) ± 5.31	127.99 (149.25) ± 35.49	4.78 (4.44) ± 2.83	13.81 (12.77) ± 1.89	29.54 (26.49) ± 16.21
KUG	81.94 (80.60) ± 2.58	118.83 (123.22) ± 6.10	146.91 (138.13) ± 10.05	4.23 (3.78) ± 0.49	14.48 (14.59) ± 1.93	20.08 (16.59) ± 4.91

DAL	92.34 (83.43) ± 4.08	111.63 (113.79) ± 4.39	134.40 (148.79) ± 19.24	6.53 (4.41) ± 1.16	11.65 (11.29) ± 1.22	35.45 (28.39) ± 13.84
Depth Zone						
Shelf	81.78 (81.84) ± 1.54	100.77 (114.68) ± 7.31	132.13 (132.13) ± 9.82	4.61 (4.07) ± 0.29	10.41 (10.03) ± 1.84	
Upper Slope	88.86 (87.05) ± 2.81	120.14 (119.91) ± 2.71	147.32 (147.94) ± 9.14	5.80 (5.23) ± 0.89	14.47 (13.90) ± 1.02	29.51 (25.95) ± 5.82
Lower Slope	94.57 (85.06) ± 8.71	117.33 (117.05) ± 5.59	128.84 (149.25) ± 20.01	8.93 (4.69) ± 2.62	12.95 (12.37) ± 1.80	26.42 (26.49) ± 9.27

Table 6.12 Mean (± SE) fork length at age by depth zone for the overall 2012 sample of Beaufort Sea Arctic Cod.

Age	Shelf	Upper Slope	Lower Slope
0	49.9 ± 2.4 (n=24)	55.94 (n=1)	41.4 ± 1.1 (n=4)
1	81.8 ± 1.6 (n=62)	89.6 ± 2.8 (n=32)	95.8 ± 8.7 (n=12)
2	107.1 ± 7.3 (n=12)	118.7 ± 4.3 (n=29)	116.0 ± 5.6 (n=11)
3		153.1 ± 9.1 (n=8)	142.5 ± 20.0 (n=5)
4		148.1 ± 11.3 (n=4)	189.7 ± 14.0 (n=3)

Appendix G: Length- and Mass-at-Age Plots of Canadian Beaufort Sea Arctic Cod

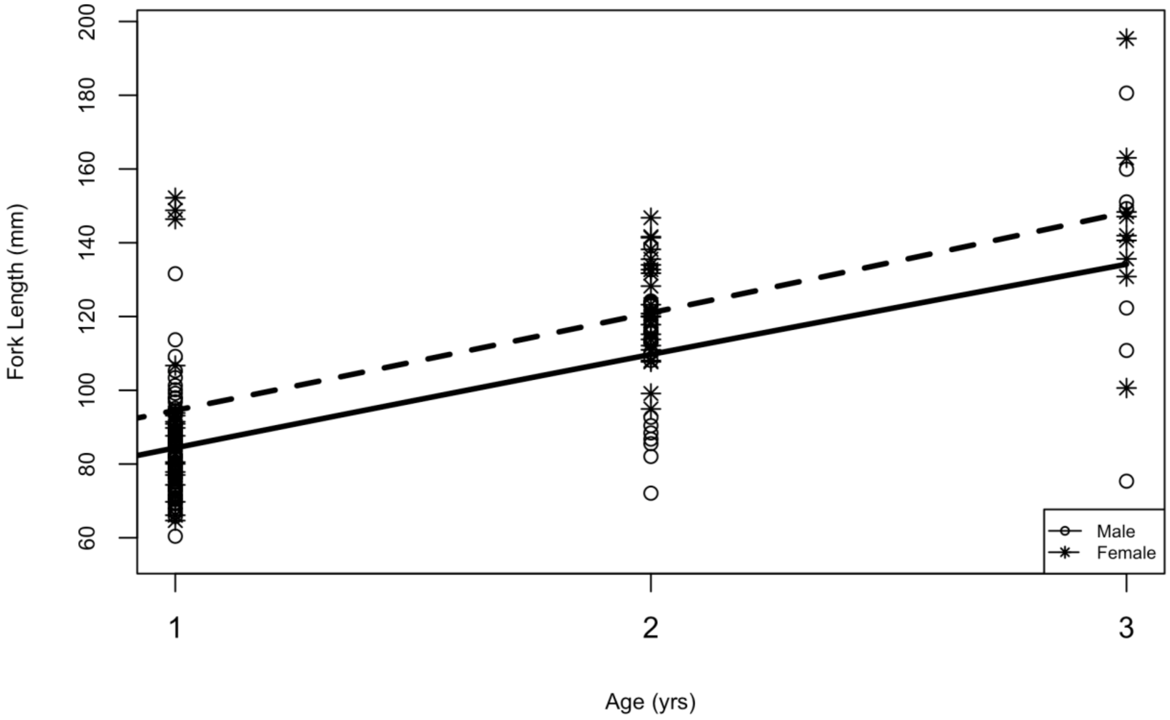

Figure 6.7 Arctic Cod growth as fork length (mm) by sex, fit to nonlinear, von Bertalannfy growth models. Those of unknown sex were not included as there was insufficient data to model their growth. There was no significant difference in the length at age of male and female Arctic Cod (Figure 4.1a; Appendix F, Table 6.11), but the female intercept is higher than the male. This indicates that females are consistently larger than males in the Canadian Beaufort Sea.

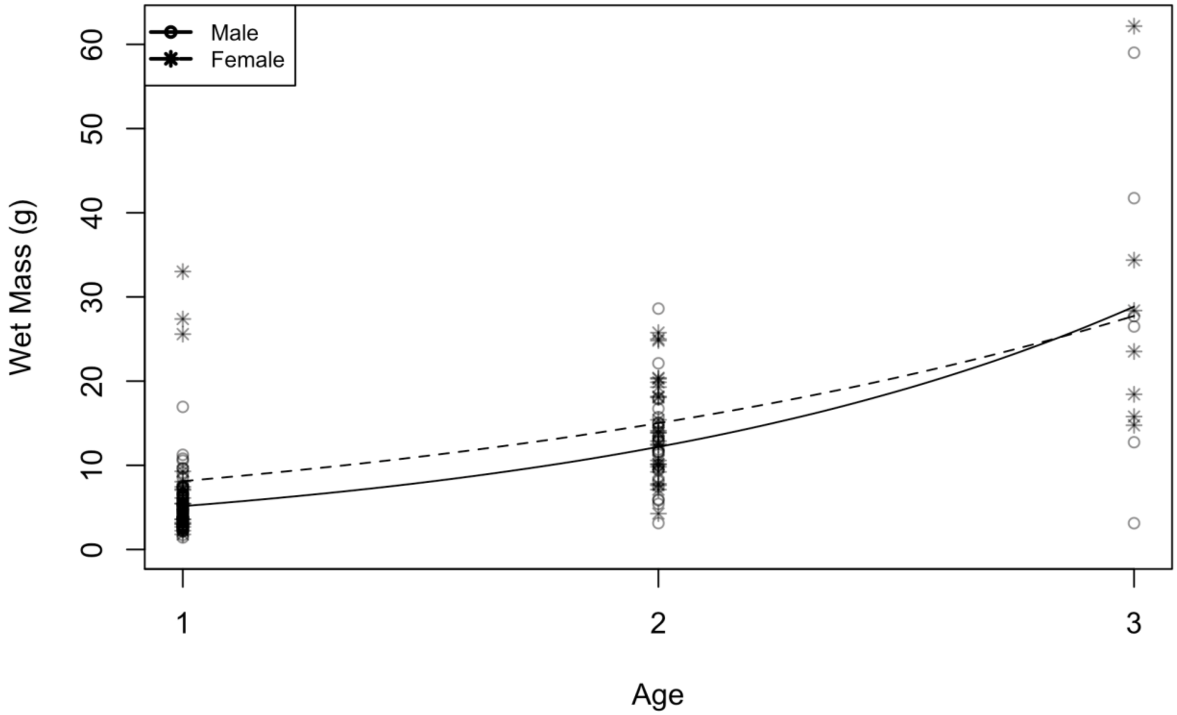

Figure 6.8 Arctic Cod growth as mass (g) by sex, fit to nonlinear models. There was no significant difference in the mass at age of male and female Arctic Cod in the Canadian Beaufort Sea (Figure 4.1b; Appendix F, Table 6.11).

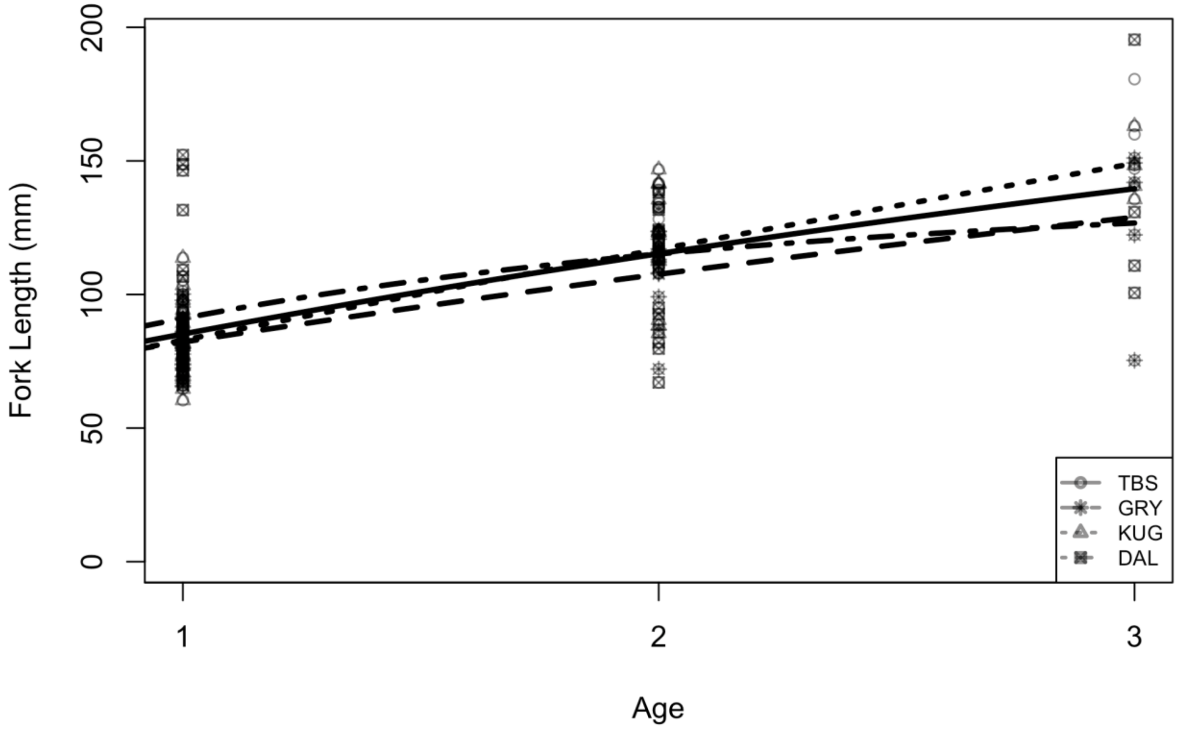

Figure 6.9 Arctic Cod growth as fork length (mm) by sampling transect, fit to nonlinear models. According to Kruskal-Wallis tests, there was no significant differences in length at age among transects in the Canadian Beaufort Sea (Figure 4.2a; Appendix F, Table 6.11).

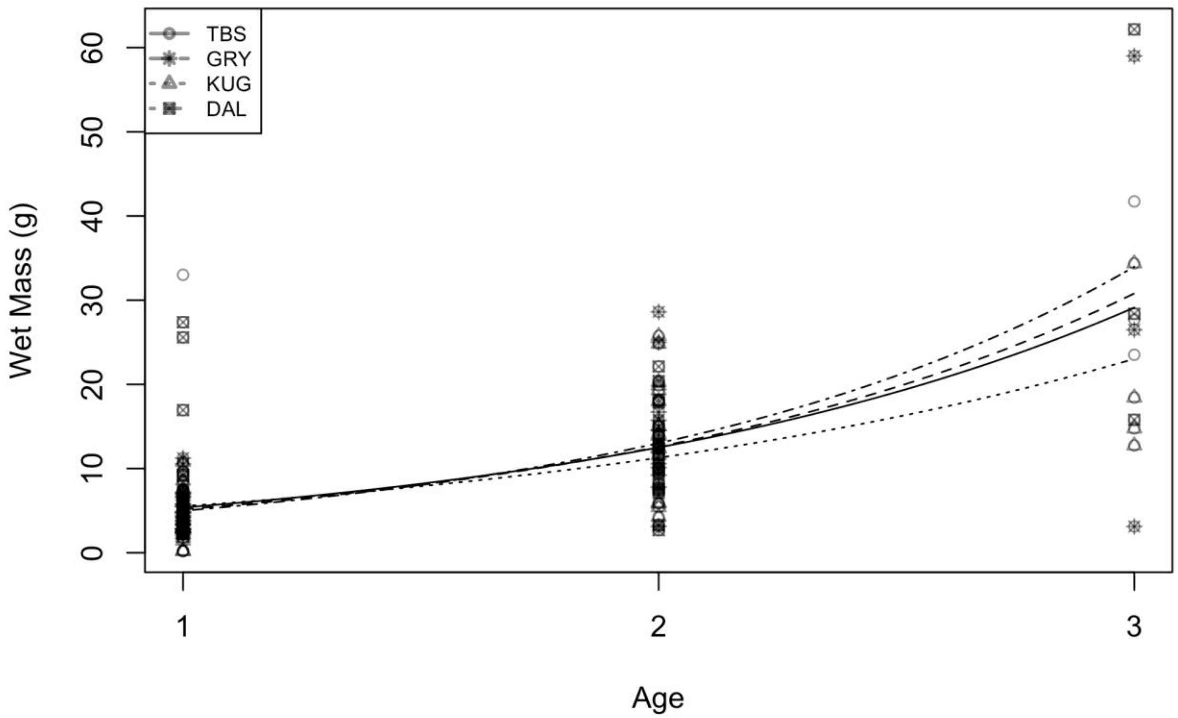

Figure 6.10 Arctic Cod growth as mass (g) by sampling transect, fit to nonlinear models. According to Kruskal-Wallis tests, there were no significant differences in Arctic Cod mass at age among transects in the Canadian Beaufort Sea (Figure 4.2b; Appendix F, Table 6.11).

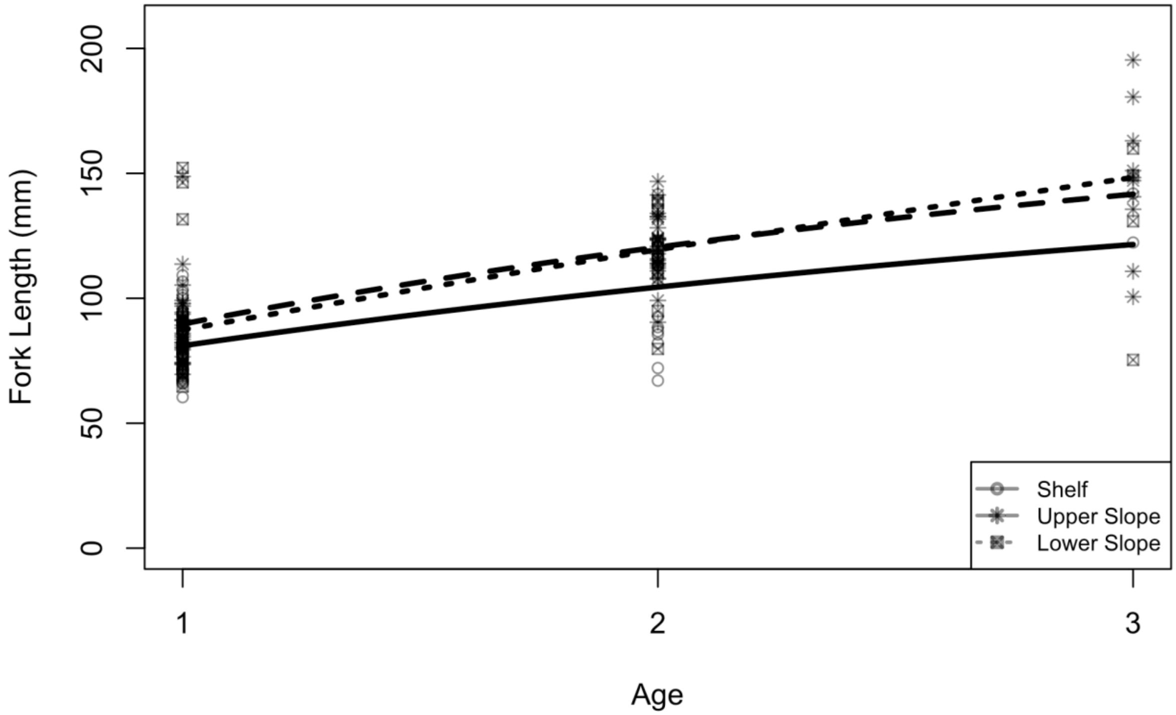

Figure 6.11 Arctic Cod growth as fork length (mm) by depth zone, fit to nonlinear models. According to Kruskal-Wallis tests, there were no significant differences in Arctic Cod length at age by depth zone in the Canadian Beaufort Sea (Figure 4.3a; Appendix F, Table 6.11).

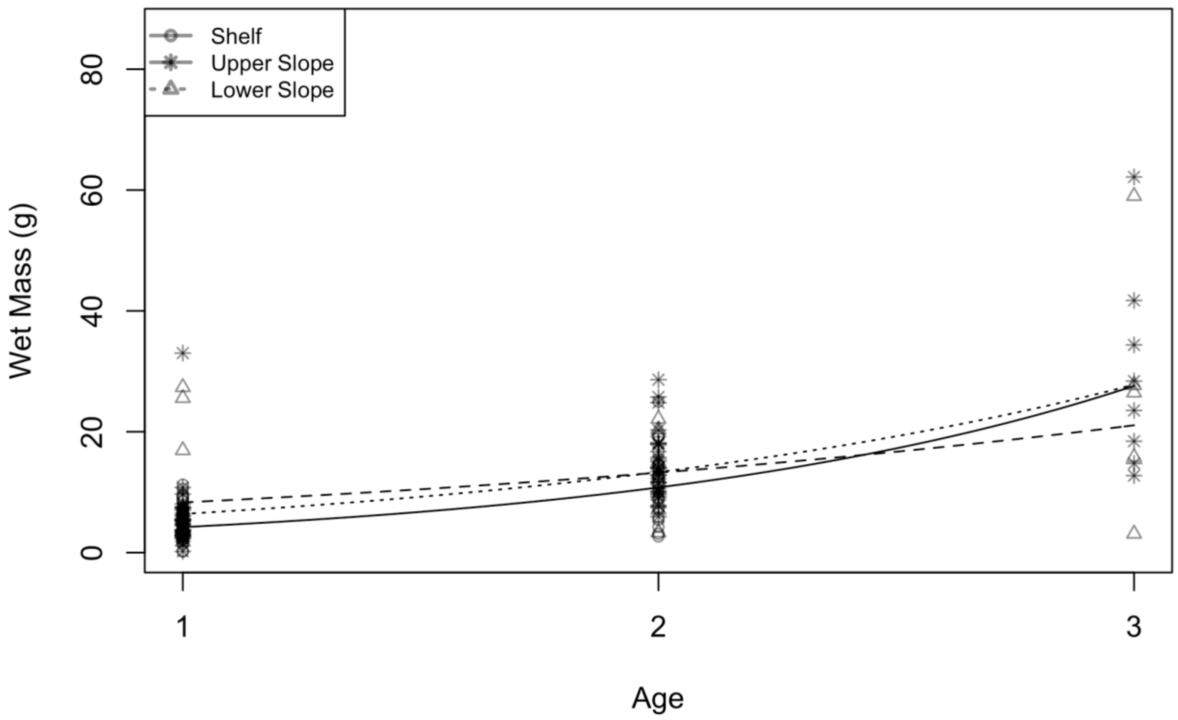

Figure 6.12 Arctic Cod growth as mass (g) by depth zone. According to Kruskal-Wallis tests, there was no significant difference in mass at age among depth zones in the Canadian Beaufort Sea (Figure 4.3b; Appendix F, Table 6.11).