

# Climate change-related shifts in species interactions and diet in an Arctic marine ecosystem

by

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## Thesis Abstract

In the Arctic, climate change is accelerated relative to other areas, and temperate species are becoming increasingly able to occupy regions that were previously unsuitable. For example, capelin (*Mallotus villosus*) have become abundant in Cumberland Sound (CS) in recent decades. During the same period, migratory harp seals (HS; *Pagophilus groenlandicus*) have become very abundant in CS during the summer. Coincident with these changes, a decline in the abundance of native, ice-obligate ringed seals (RS; *Pusa hispida*) has been reported. The consequences of these changes to the CS ecosystem have not yet been fully studied. The objectives of this thesis, therefore, were to (1) examine size-dependent and inter-annual variation in capelin diet and isotopic niche characteristics in CS to determine how capelin fit into the food web and (2) to determine the degree to which ringed and harp seals overlap in their diet and isotopic niche. Results indicated inter-annual variation in capelin diet, perhaps related to the timing of spawning in relation to sampling date. Generally, small capelin appeared to specialize on small copepods (primarily Clausocalanidae), while larger capelin were more varied and consumed a greater proportion of large prey types (primarily *Calanus hyperboreus* and amphipods) with increasing size. Results also indicated a high potential for dietary overlap between ringed and harp seals, with both species consuming many of the same prey types and having high isotopic niche overlap when both are occupying CS; however, differences in isotopic signatures and prey size and composition (RS: 66.7% invertebrate; HS: 67.2% fish) suggest partitioning of resources and foraging locations, perhaps related to greater dive capabilities of harp seals. Overall, my thesis findings have provided a baseline against which future studies on the impacts of northward range shifts of temperate species in the Arctic may be compared, offering new insight into a complex ecosystem and providing information that may be of importance when drafting management plans under changing Arctic conditions.

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## Chapter 1: General Introduction

It is well documented that the global surface temperature of Earth is rising and has been for some time (IPCC 2014). This rise, however, has been most pronounced in the last several decades, with each of the last three decades having been successively warmer than any preceding it since 1850 (IPCC 2014). Reports now indicate that, in the Northern Hemisphere, the period from 1983-2012 was likely the warmest 30-year period to occur in the last 1400 years (IPCC 2014). It is projected that by the end of the 21<sup>st</sup> century, the average global surface temperature may be ~1.5°C warmer than in 1850 (IPCC 2014). Unsurprisingly, global ocean temperatures have risen simultaneously (Roemmich *et al.* 2015), with the upper 75 m of ocean warming by 0.11°C (0.09-0.13°C) per decade between 1971 and 2010 (IPCC 2014). While the surface of the ocean exhibits the greatest temperature change, there has been some degree of warming across all depths over the last several decades (IPCC 2014, Roemmich *et al.* 2015). Although these changes in average global surface and ocean temperatures may seem trivial, the predicted impacts of future climate warming are far-reaching and are already being observed. These changes include sea level rise (Church and White 2011, Albert *et al.* 2016), extreme weather events (Moore *et al.* 2015, Deng *et al.* 2016, Nakamura *et al.* 2016) and species invasions and extinctions (Franco *et al.* 2006, Malcolm *et al.* 2006, Thomas 2010).

In the Arctic, climate change is occurring at an accelerated rate relative to other regions (IPCC 2014). Consequently, the effects of decreased sea ice and warmer conditions are of increasing concern (Kovacs *et al.* 2011). With such environmental changes, conditions are allowing more-temperate associated species to shift or expand their ranges northward and thrive in areas that were previously unsuitable (Wassmann *et al.* 2011). While many of the consequences of species range-shifts are not yet known, changes to species interactions are a

likely consequence that may have drastic ecosystem-wide effects (Kortsch *et al.* 2015, Frainer *et al.* 2017). When a new species enters an area (or becomes significantly more abundant than it was previously), it interacts with species already occupying the system. The ecological niche of one species – defined as the range of all conditions that support the vital activities of a species or population (Hutchinson 1957, Alley 1982) – might overlap or coincide with the ecological niche of another species. The competitive exclusion principle, as propounded by Hardin (1960), states that if two non-interbreeding populations occupy the same ecological niche and are sympatric, one population will be displaced by the other, although this is not always the case. When no competitive interactions occur, it may be because the new species occupies a “vacant” ecological niche, or because resources are abundant. If, alternatively, resources are limiting, competitive interactions will result (Schoener 1983). This can lead to one species shifting its niche to reduce or eliminate direct competition (e.g. a generalist consumer that is able to consume different resources, or to restrict the number of resources it uses), known as niche partitioning (George and Hadley 1979), or in one species outcompeting the other at obtaining resources, potentially leading to competitive exclusion, whereby one species is forced out of the system (through extinction or extirpation; Hardin 1960, Bøhn *et al.* 2008).

With range shifts occurring throughout the world (Parmesan and Yohe 2003, Root *et al.* 2003, Hickling *et al.* 2006), it is increasingly important to understand how ecosystem structure and function may be altered, which may partially depend on the trophic level at which species are entering and being displaced from systems. Low-trophic species entering or becoming abundant in a system results in changes to prey density, and can lead to competitive interactions, both with other low-trophic level species, and with high-trophic generalists that feed at multiple trophic levels. Such changes to prey density may, consequently, result in predator dietary

switching (Greenwood and Elton 1979, Gendron 1987). As a result, negative impacts on predator fitness can occur if the new prey item is of lower nutritional quality than the native one, or it possesses features that prevent consumption by predators (Cruz-Rivera and Hay 2000, Kirsch *et al.* 2000, Litzow *et al.* 2002). Alternatively, if the organism shifting its range is a predator, then competition might arise with native predators (Bøhn *et al.* 2008) and prey populations might be negatively impacted by increased predation pressure (Eby *et al.* 2006, Amundsen *et al.* 2009). Hence, the continued study of species range shifts and subsequent changing species interactions will be important to increase our understanding of the impacts of ecosystem changes related to human activity and climate change.

## Study area and species

Cumberland Sound is located along the eastern coast of Baffin Island, just below the Arctic circle. It receives water from both Arctic and Atlantic currents, and reaches a maximum depth of ~1400 m (Bedard *et al.* 2015). Numerous marine top and near-top predators inhabit Cumberland Sound at some point throughout the year, including beluga (*Delphinapterus leucas*), ringed seals (*Pusa hispida*), Arctic charr (*Salvelinus alpinus L.*), narwhals (*Monodon monoceros*), harp seals (*Pagophilus groenlandicus*), Greenland shark (*Somniosus microcephalus*), Greenland halibut (*Reinhardtius hippoglossoides*), Arctic skate (*Amblyraja hyperborean*), and numerous seabirds (Diemer *et al.* 2011, McKinney *et al.* 2012). Pagnirtung Fjord, along the northeast side of Cumberland Sound, is shallower, reaching a maximum depth of ~160 m; it has long intertidal zones (up to 500 m near Pagnirtung), a shallow sill at the mouth, and is ~43 km in length (Gilbert 1978).

Capelin is a forage fish species and acts as an important energetic link between lower trophic levels (i.e. plankton) and higher trophic levels (i.e. seabirds, Carscadden *et al.* 2002;

piscivorous fishes, Orlova, *et al.* 2009; and marine mammals, Tucker *et al.* 2009). Capelin is a small pelagic fish, generally reaching a length of 130-200 mm (up to a maximum of about 250 mm; Carscadden and Vilhjálmsón 2002, Hop and Gjørseter 2013). It has a lifespan of about 5-7 years, reaching sexual maturity between ages 2 and 5, at which point it spawns in large aggregations on beaches or at deeper water sites (Davoren 2013). While capelin are generally considered a sub-Arctic species, as they do not possess antifreeze proteins to prevent freezing in Arctic conditions (Osuga and Feeney 1978), they are now known to be abundant in northern regions where they were historically sparse: in Hudson Bay and Ungava Bay, capelin increased in the diet of thick-billed murres from the early 1980s to late 1990s (Gaston *et al.* 2003, Carscadden *et al.* 2013); in 2004 and 2005, locals in Frobisher Bay and Cumberland Sound reported capelin as unusually abundant (Carscadden *et al.* 2013); and in Lancaster Sound, capelin were observed in thick-billed murre feeding studies in 2000-2003 for the first time since the study began in 1975 (Carscadden *et al.* 2013). Whether this is a true shift in range, or simply the result of warmer temperatures now allowing capelin populations to thrive in these areas, is not known, but there is evidence of a correlation between capelin range expansions and changes in sea surface temperature (Ozhigin and Luka 1985, Ozhigin and Ushakov 1985, Frank *et al.* 1996, Rose 2005, Huse and Ellingsen 2008). Further, capelin have been known to expand their distribution in warm years, and contract it in colder years (Ozhigin and Luka 1985). As such, it seems likely that the large shifts in capelin distribution seen in the last several decades are related to climate change.

Because of the importance of forage fishes for marine predators, any change to forage fish species composition and abundance could serve as an early warning sign of subsequent changes to predator populations. The ringed seal, a predator that is resident to Cumberland

Sound, and the harp seal, a predator that migrates annually between the North Atlantic and the Arctic, both consume capelin in Cumberland Sound (Yurkowski *et al.* 2016; personal observation of harp seal aggregations near capelin-rich areas). Interestingly, reports indicate that harp seals have become more abundant since the mid-1990s (DFO 2011) and are now very abundant in Cumberland Sound and Pangsirtung Fjord, although it is believed that harp seal populations have recently stabilized (Hammill *et al.* 2015). Coincident with this increase in harp seals has been a decrease in ringed seal numbers in recent decades (Diemer *et al.* 2011). While it is difficult to draw any conclusions as to the cause of these changes, considering the numerous possible pressures acting on these populations (e.g., hunting, ocean warming, disease, pollution, natural population cycles, etc.), it is possible that shifts in the composition of available forage fishes is a factor. In fact, changes to harp seal diet in relation to changing forage fish composition have been reported in the past, and harp seals may attempt to maximize capelin consumption by timing their northward migrations to coincide with the later spawning times of capelin in northern locations (Beck *et al.* 1993).

## Study Context and Objectives

As a result of temperate species moving northward, competition is predicted to arise with endemic species, and food resources may be more spatially and temporally dispersed due to warming conditions and reduced sea ice (Kovacs *et al.* 2011). Moore and Huntington (2008) predicted that with decreasing sea ice in the Arctic, seasonally migrant species may infiltrate Arctic habitats and take advantage of extended foraging periods, thus increasing interspecific competition with ice obligate species that occupy the region year-round. In Cumberland Sound, this competition may arise between endemic ringed seals and seasonally-migrant harp seals (high trophic level), and between polar cod (*Boreogadus saida*) and recently-abundant capelin (mid

trophic level). In the Barents Sea, almost complete dietary overlap was shown between ringed and harp seals captured during October of 1994 and 1995, though there seemed to be a difference in the size of prey consumed (Wathne *et al.* 2000). Similarly, in the Western Canadian Arctic, high dietary overlap occurs between capelin and polar cod (McNicholl *et al.* 2016). The impacts of changes such as these are not fully known, but dietary switching of pinnipeds has been observed as a result of changes in prey composition. During the 1980s, capelin were the dominant prey for harp seals in the north Atlantic (Beck *et al.* 1993), but after the 1980s, when polar cod biomass began to increase (whether due to competition or other factors), harp seals shifted their diet toward polar cod (Lawson *et al.* 1998).

In marine systems, it is often impossible to conduct observational studies to determine whether competition may arise between species. As such, various dietary metrics are used (Pierce and Boyle 1991). To directly examine the diet of seals and capelin for the present study, stomach content analyses were used. Although stomach content analysis is an important method for identifying prey consumed, it can be limited by the brief feeding period that it represents (i.e. fast digestion rates and empty stomachs when organisms have not recently fed) and biased toward hard-shelled prey items and by rare feeding events (Hyslop 1980, Matley *et al.* 2015). For this reason, I used stable isotope analyses to complement stomach contents, as stable isotopes provide a long-term average of a consumer's feeding location ( $\delta^{13}\text{C}$ ; DeNiro and Epstein 1978) and trophic position ( $\delta^{15}\text{N}$ ; DeNiro and Epstein 1981). Based on isotopic turnover rates in seal tissues (Tieszen *et al.* 1983, Vander Zanden *et al.* 2015), I used muscle to represent longer-term diet, representative of the time period prior to sympatry, and liver to represent shorter-term diet, during ringed and harp seal sympatry. For capelin, only muscle tissue was used.

The objectives of this thesis were to (1) determine where capelin fit in the Cumberland Sound food web by examining their diet and isotopic niche characteristics, and (2) determine the degree to which ringed and harp seals overlap in their diets as well as in their isotopic niches. Specifically, I quantified capelin diet and isotopic niche characteristics among size classes and across two study years, and briefly discussed the dietary similarities between Pangnirtung Fjord capelin and forage fishes from other Arctic and sub-Arctic regions (Chapter 2). By determining capelin diet in this northern part of their range, where they are now more abundant than previously, I provide a baseline against which future studies can be compared and help to disentangle the complex role that capelin may play in the Cumberland Sound/Pangnirtung Fjord food web. Additionally, I used stomach contents and stable isotope analyses to quantify ringed and harp seal diets and isotopic niche characteristics in Cumberland Sound, and determined the amount of stomach content and isotopic niche overlap between seal species (Chapter 3). I provide insight into the ecological interactions between ringed and harp seals that might have resulted, and might continue to result, from increased abundance of harp seals in Cumberland Sound. Given the importance of ringed seals for Inuit subsistence, it is necessary to assess whether or not harp seals have the potential to act as a competitor. As previous research using stable isotope analysis has shown that ringed seals in Cumberland Sound have not changed drastically with regard to their isotopic niche since the 1990s (Yurkowski *et al.* 2016), changes to ringed seal diet in relation to harp seal abundance can still be discerned. Information gleaned from this research will be of value when drafting management plans for Arctic species in the context of continued warming and environmental and biological changes.

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## Chapter 2: Inter-annual and size-dependent diet of capelin (*Mallotus villosus*) in the Eastern Canadian Arctic

### Abstract

Under warmer conditions and reduced sea ice in the Arctic, temperate species are able to expand their ranges and thrive in northern regions where they were historically rare or absent. Capelin (*Mallotus villosus*) is a typically sub-Arctic forage fish that has become abundant in some regions of the Canadian Arctic in recent decades. In Pangnirtung Fjord, Nunavut, capelin presence is now well documented, but its foraging ecology in this location is not yet well known. As such, the objective of this research was to use stomach contents and stable isotopes to examine inter-annual and size-dependant diet of capelin sampled in Pangnirtung Fjord. Results varied inter-annually and indicated that the diet of mature capelin is influenced by the timing of spawning in relation to sampling date. Generally, capelin up to ~120-140 mm, most of which were immature, appeared to specialize on small copepods (primarily Clausocalanidae), while larger capelin were more varied in their diet. With increasing size of adult capelin, the contribution of large prey types (primarily *Calanus hyperboreus* and amphipods) to the diet increased. In addition, capelin diet was broadly similar to the diets of forage fishes in other Arctic regions, suggesting high dietary overlap with other forage fishes in Cumberland Sound, such as polar cod (*Boreogadus saida*). This information begins to fill an important knowledge gap with regard to the trophic role that capelin plays in the Canadian Arctic, and provides an important baseline against which future dietary studies of planktivorous fish in the Canadian Arctic may be compared.

## Introduction

Climate change is occurring at an accelerated rate in the Arctic. With melting sea ice, albedo is reduced, further accelerating melt and warming the ocean (Holland *et al.* 2006, IPCC 2014). As a result of a warmer ocean and a longer open-water period, temperate species are now able to extend the northern margins of their range and thrive in regions in which they were rare or absent in recent history (Moore and Huntington 2008, IPCC 2014). This change in species composition and abundance can have effects throughout the ecosystem and impact trophic interactions (Post *et al.* 2009).

An example of a temperate species that has become abundant in Arctic regions is capelin (*Mallotus villosus*), a small (< 250 mm; Hop and Gjørseter 2013a), short-lived (5-7 years) forage fish species. Sexual maturity occurs between ages 2 and 5, after which capelin spawn at beaches or deep-water sites (15-40 m; Davoren 2013), which are primarily determined by suitable temperature and sediment size ranges (Penton and Davoren 2012, Crook *et al.* 2017). Capelin act as an important energetic link between lower trophic levels (i.e. plankton) and higher trophic levels (i.e. predators), and, thus, are important prey for seabirds (Carscadden *et al.* 2002), piscivorous fishes (Orlova *et al.* 2009), and marine mammals (Tucker *et al.* 2009). Capelin abundance has increased in regions of the Canadian Arctic, where this species was historically sparse. Evidence includes increasing capelin in the diet of thick-billed murres from the early 1980s to late 1990 in Hudson Bay and Ungava Bay (Gaston *et al.* 2003, Carscadden *et al.* 2013) as well as in Lancaster Sound during 2000-2003 (Carscadden *et al.* 2013). Additionally, locals in Frobisher Bay and Cumberland Sound reported capelin as unusually abundant in 2004 and 2005 (Carscadden *et al.* 2013). Whether this is a true shift in range, or simply the result of warmer conditions allowing capelin populations to thrive, is unclear. There is evidence that capelin were

historically found in these regions, although rare (Carscadden *et al.* 2013), but capelin are also known to expand their range in warmer years (Ozhigin and Luka 1985, Ozhigin and Ushakov 1985, Frank *et al.* 1996, Rose 2005, Huse and Ellingsen 2008).

Regardless of the mechanism, high abundances of capelin in the eastern Canadian Arctic are relatively recent and comparatively little research has been conducted on capelin in these regions relative to other regions. With higher abundances in the ecosystem, capelin may be able to outcompete other species if resources are limited. High dietary overlap has been shown between capelin and other forage fishes, such as polar cod, in the western Canadian Arctic (McNicholl *et al.* 2016), and in other Arctic regions (Barents Sea, Hop and Gjørseter 2013). In addition, capelin may be an important consumer of pelagic zooplankton and has been shown to cause significant reductions in zooplankton biomass in the Barents Sea (Hassel *et al.* 1991). Capelin has also been found to be important food for predators in the eastern Canadian Arctic, namely Cumberland Sound (harp seals, Chapter 3; belugas, Marcoux *et al.* 2012; ringed seals, Yurkowski *et al.* 2016). Without knowing the diet of capelin in Cumberland Sound, however, it is difficult to draw any conclusions with regard to the effects that capelin may have on local ecosystems and energy flow in Arctic food webs. The objective of this research is to investigate size-dependent capelin diet in Pangnirtung Fjord, Cumberland Sound (Baffin Island, Nunavut). This information will provide insight into capelin life history and will be useful for future studies aiming to quantify functional roles of capelin and other species, thus allowing a greater understanding of the Cumberland Sound food web. It will also allow a better understanding of the potential for competition between capelin and other species in the fjord (e.g. Arctic charr, polar cod) and will be helpful for assessing the potential impact of capelin on prey species.

## Methods

### *Biological Sampling*

In both 2015 and 2016, fieldwork commenced on June 18. Upon arrival to the field site, beaches in and around Pangnirtung were checked 2-3 times daily (morning, noon/early afternoon, and evening) for indications of capelin presence. Beaches and intertidal zones were patrolled by two observers, who examined rock, sand, and algal substrate to check for adhered eggs. Water was observed from the beaches as well as any nearby high points (e.g. nearby hills and large boulders) to determine whether fish were present nearby offshore. When boat drivers were available, observations were made from small boats (5-6 m long) within the Fjord (Fig. 2.1).



Figure 2.1: Sampling locations within Pangnirtung Fjord in 2015 and 2016. The large yellow shaded region indicates the area surveyed for capelin and eggs. The darker, smaller shaded area indicates the region close to the Pangnirtung townsite where most capelin were sampled, with an exception being the orange point, indicating the location where immature capelin were sampled in 2016.

All spawning capelin were sampled on or near spawning sites within Pagnirtung Fjord, Nunavut during June-July, 2015 and 2016. In 2015, spawning occurred most-commonly on typical sandy substrate in the intertidal zone and near a stream outlet, but also on boulders. In 2016 spawning sites were typically boulders in the Pagnirtung harbour or intertidal zone during low tide, and there was minimal evidence of beach spawning in this location. In the harbour in 2016, capelin also spawned on the side of the steel wharf. In this location, no sandy substrate was present, and spawning appeared to occur exclusively on the rock and wharf surfaces. Toward the head of the fjord, evidence of spawning was present in 2016, and eggs were primarily adhered to large boulder surfaces, with some evidence of spawning in the sand between boulders. Boulders showed scour marks where eggs appeared to have been scraped off, leading us to hypothesize that spawning here likely occurred when ice was still present. Capelin in 2016 did not appear to spawn in the same locations as they did in 2015. Samples of immature (age 0+) capelin were collected nearshore from small boats within the fjord in both years. Up to 200 capelin per sampling event were collected using a dip net (38 cm diameter; 0.32 cm mesh). A total of 16 samples of spawning capelin were collected in 2015 (2785 individuals), whereas 9 samples of spawning capelin were collected in 2016 (1487 individuals). Two samples of immature capelin (400 individuals) were collected in 2015, while one sample was collected in 2016 (332 individuals). All samples were frozen at  $-20^{\circ}\text{C}$  within one hour of capture and stored until further analysis.

Capelin were thawed and, for each fish, total length (snout to tip of tail, mm), sex, and maturity were recorded. Maturity was determined macroscopically on a 5-point scale by examining the gonads, where 1 = immature, 2 = maturing, 3 = ripe, 4 = partially spent, and 5 = spent (Flynn *et al.* 2001). All immature fish were primarily  $< 140$  mm in total length and, thus,

we were unable to determine their sex. Up to 2 fish per sex from each predetermined 5 mm length category (e.g. 150-154 mm, 155-159 mm, etc.) were further subsampled. From subsampled fish, stomach fullness (~0%, ~25%, ~50%, ~75%, or ~100%; modified from Slotte *et al.* 2006) was recorded, and a 1-2 g sample of dorsal muscle (excluding skin) was removed and frozen for stable isotope analysis. Stomachs that appeared to contain some identifiable content were removed and stored in 95% ethanol. As capelin tend to cease feeding prior to spawning (Winters 1970) the number of preserved stomachs ranged from 0-20 per sample of adult capelin over both years; for juvenile fish, 30-40 stomachs per sample were preserved. Adult capelin sample sizes ranged from 93-200 in 2015, and from 8-200 in 2016; two immature capelin samples in 2015 were collected and contained 200 individuals each, while in 2016 a single sample of immature capelin was collected and contained 332 individuals.

### *Stomach Content Analysis*

Subsampled stomachs were selected for content analysis haphazardly from the larger subsample (2015:  $n=141$ ; 2016:  $n = 225$ ), while attempting to reach a minimum of ~10 samples per size class where possible. For less common size classes (i.e. very small or very large adult capelin), fewer stomachs were available, in which case  $n < 10$ . Stomachs were removed from ethanol and opened from the pyloric sphincter to the esophageal sphincter using a scalpel and forceps. Contents were scraped from the stomach lining using forceps and rinsed with 95% ethanol into a petri dish to ensure all prey items were collected. Once all contents were removed, empty stomach linings were discarded. Prey was identified under a dissecting microscope (Nikon SMZ-10) to the lowest taxonomic level and verified by an expert. All individuals of each taxonomic group were counted and then returned to ethanol for future reference. The length (head to tail, mm) of amphipods, mysids, euphausiids, and decapods were measured using an

ocular micrometer to obtain lengths for biomass conversions. Copepods were staged (CI to CIV female or male) and identified to species-level based on prosome length (Kwasniewski *et al.* 2003). Stomachs containing high numbers of small prey (in particular, *Pseudocalanus* spp.) were subsampled by diluting all stomach contents to a total volume of 50 mL in water, suspending organisms, and taking 1 mL quantities until ~200 organisms were counted. The number of individuals of each taxonomic group in the sample was then estimated using the following formula:  $N_E = \frac{V_t \times n_s}{V_s}$ , where  $N_E$  is the total estimated sample size,  $V_t$  is the total diluted sample volume (50 mL),  $V_s$  is the subsampled volume, and  $n_s$  is the number of individual prey in the subsample.

### *Stable Isotope Analysis*

Capelin were grouped into three size classes within each sex and year: 70-129 mm ('small'), 130-174 mm ('medium'), and 175-219 mm ('large') based on length-frequency histograms. Within each sex/size/year category, 20 muscle samples per adult size class (i.e. medium, large) were selected for stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope analysis and 30 immature (i.e. small) fish from 2016 were selected. Sample selection was semi-haphazard, as we attempted to select an even spread of samples across the range of available fish lengths. Capelin muscle tissue was freeze-dried at approximately  $-50^\circ\text{C}$  for 48 h, and dried samples were then homogenized using a mortar and pestle. Lipids were extracted using a 2:1 chloroform:methanol solvent. Homogenized tissue was placed into a 10 mL tube with 5 mL of solvent, mixed, and placed in a  $30^\circ\text{C}$  water bath overnight. Each sample was then vortexed for 30 s and centrifuged at 2000 rpm for 3-4 min. The supernatant, containing the solvent and the extracted lipids, was then discarded. The remaining tissue pellet was mixed with an additional 5 mL of chloroform:methanol, vortexed, centrifuged, and decanted the same as in the previous

step. The remaining tissue pellets were then left in a fumehood overnight to allow the solvent to evaporate. This dry, lipid-extracted muscle was re-homogenized and  $400 \pm 10 \mu\text{g}$  was weighed into  $3.5 \times 5$  mm tin capsules. Samples were run using a Thermo-Delta 5 Plus continuous flow isotope ratio mass spectrometer equipped with a Costech elemental analyser at the Freshwater Institute in Winnipeg, Manitoba to obtain  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were measured against Vienna Pee Dee Belemnite and atmospheric nitrogen standards, respectively, using the following formula:  $\delta^x E = \left( \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \right) \times 1000$ , where  $^x E$  refers to  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$ , and  $R$  refers to the ratio of heavy to light isotopes of element  $E$  in either the sample or the standard. Duplicates were run every 10 samples to ensure precision of measurements. Standard deviations for these replicates were  $<0.07\text{‰}$  for  $\delta^{13}\text{C}$  and  $<0.06\text{‰}$  for  $\delta^{15}\text{N}$ .

### *Data Analysis*

The isotopic niche breadth of each size/sex/year grouping was quantified using the *SIBER* package (Jackson *et al.* 2011) in R version 3.4.3 using standard ellipse area corrected for small sample sizes (SEAC). The SEAC represents  $\sim 40\%$  of points and is considered a bivariate mean plus standard deviation, representative of the core population. The 95% prediction ellipse includes  $\sim 95\%$  of points and we considered this more representative of the sampled population as a whole. Niche breadth was calculated using 95% ellipses, and overlap among size/sex/year groups was calculated using the following formula:

$$\% \text{ overlap} = \frac{\text{overlap area}}{\text{area of harp niche} + \text{area of ringed niche} - \text{overlap area}} \times 100 .$$

From stomach contents, dietary composition was quantified using prey abundance and prey biomass. Abundance was determined for each stomach by counting (or estimating; see above) the number of individuals of each prey type. Biomass was calculated for each stomach by

multiplying taxon-specific dry biomass values for each prey type by the number of individuals counted as in Walkusz *et al.* (2013). Diets were not converted to energy content, as McNicholl *et al.* (2016) found minimal differences in dietary composition when converting dry biomass to energy content for capelin and polar cod sampled in the western Canadian Arctic. Diet composition was calculated using the following metrics:

$$\text{Frequency of Occurrence: } FO = \frac{\# \text{ stomachs containing prey } j}{\text{total \# stomachs}} \times 100$$

$$\text{Percent Abundance: } A = \frac{\# \text{ of individual specimens of prey } j}{\text{total \# of specimens of all prey types in stomach } y} \times 100$$

$$\text{Percent Biomass: } B = \frac{\text{biomass represented by prey } j}{\text{total biomass of prey in stomach } y} \times 100$$

where  $j$  represents prey taxa, and  $y$  represents the individual capelin stomach. Frequency of occurrence is a single number representing the percentage of stomachs in which each prey item occurred. Percent abundance and biomass were calculated per stomach and means were calculated across all individuals in each size/sex/year group separately.

## Results

Ice conditions differed between study years. Ice break-up at capelin spawning sites near Pangnirtung occurred by June 20-21, 2015, although ice was still present near the head of the fjord. In 2016, ice break-up did not occur until June 30-July 1, with ice breaking up and moving out from the head of the Fjord into Cumberland Sound, and the entire Fjord clearing by June 30 - July 1. Interestingly, capelin were first observed at similar dates in both years. In 2015, despite ice cover throughout the fjord, near-shore spawning capelin were first observed on June 18, which initiated sampling that continued over ~1 month (June 18 - July 20), resulting in 18 samples ( $n$  range: 93-200). In 2016, capelin were first observed sporadically on June 17, as dead

ripe or spent individuals in the intertidal zone at low tide, as well as sparse eggs on boulders and algae in the intertidal zone. Spawning capelin, however, were not observed until ice break-up ~2 weeks later, after which they were sampled for ~2 weeks (June 30 - July 13), resulting in 10 samples ( $n$  range: 8-200). Of all adult fish sampled in 2015, 86.7% were males and 13.3% were females; in 2016, 79.3% of adult fish were males and 20.7% were females. Of all females caught, 40.5% were ripe, and 59.5% were spent; 16.5% of males were ripe and 83.5% were spent.

### *Stable Isotopes*

Outliers in the stable isotope dataset were removed (2016 immature:  $n = 1$ ; 2016 medium males:  $n = 2$ ) based on Q-Q plots to meet the underlying assumptions of parametric statistics. A three-factor MANOVA on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  identified significant differences among sizes ( $F_{2,178} = 34.1, p < 0.0001$ ), between sexes ( $F_{1,178} = 7.5, p = 0.0007$ ), and between years ( $F_{1,178} = 69.1, p < 0.0001$ ), with interactions between size and sex ( $F_{1,178} = 4.1, p = 0.018$ ), sex and year ( $F_{1,178} = 4.3, p = 0.014$ ), and size, sex, and year ( $F_{1,178} = 5.7, p = 0.0038$ ). Similarly, a three-factor ANOVA on  $\delta^{13}\text{C}$  showed significant differences among sizes ( $F_{2,178} = 47.6, p < 0.0001$ ) and between years ( $F_{1,178} = 106.0, p < 0.0001$ ) but not between sexes ( $F_{1,178} = 0.31, p = 0.5760$ ), with interactions between size and year ( $F_{1,178} = 4.07, p = 0.045$ ) and between sex and year ( $F_{1,178} = 8.6, p = 0.004$ ). Post-hoc analysis revealed that large females, medium males, and large males differed in  $\delta^{13}\text{C}$  between years ( $p = 0.011, 0.0005, \text{ and } < 0.0001$ , respectively), but medium females did not ( $p = 0.071$ ). In 2015, the only significant difference in  $\delta^{13}\text{C}$  between size and sex groups was between medium males and large females ( $p = 0.036$ ). In 2016, small immature fish differed in  $\delta^{13}\text{C}$  from all other size classes ( $p$  values  $< 0.0001$ ), and medium males differed from large males ( $p < 0.0001$ ). All other size/sex comparisons within years were not significant ( $p >$

0.05). For  $\delta^{15}\text{N}$ , a three factor ANOVA indicated significant differences among size classes ( $F_{2,178} = 53.0, p < 0.0001$ ), between sexes ( $F_{1,178} = 14.2, p = 0.0002$ ), and between years ( $F_{1,178} = 21.6, p < 0.0001$ ), with interactions between size and sex ( $F_{1,178} = 5.8, p = 0.017$ ) and between size, sex, and year ( $F_{1,178} = 8.5, p = 0.004$ ). Post-hoc analysis revealed that large males differed in  $\delta^{15}\text{N}$  between years ( $p = 0.009$ ), but medium males, medium females, and large females did not ( $p = 1.000, 0.057, \text{ and } 1.000$ , respectively). In 2015, there were no significant differences in  $\delta^{15}\text{N}$  between any size and sex groups. In 2016, small immature fish differed significantly from medium males ( $p < 0.0001$ ), large males ( $p < 0.0001$ ), and large females ( $p < 0.0001$ ), while medium males differed from medium females ( $p = 0.002$ ). No other size/sex groups differed significantly.

The isotopic niche breadth of capelin appeared to be generally broader in 2016 relative to 2015 (Table 2.1) and shifted to lower values for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Fig. 2.2). Ellipses of each size/sex category appeared to be clustered together in 2015, evidenced by higher proportional overlap (Table 2.1). In contrast, ellipses of different size and sex categories from 2016 were more separated with lower overlap (Table 2.1). Overall, niche breadth also varied among size/sex groups (Fig. 2.2, Table 2.1), with medium females having the broadest niche, followed by medium males in both years (Fig. 2.2, Table 2.1).

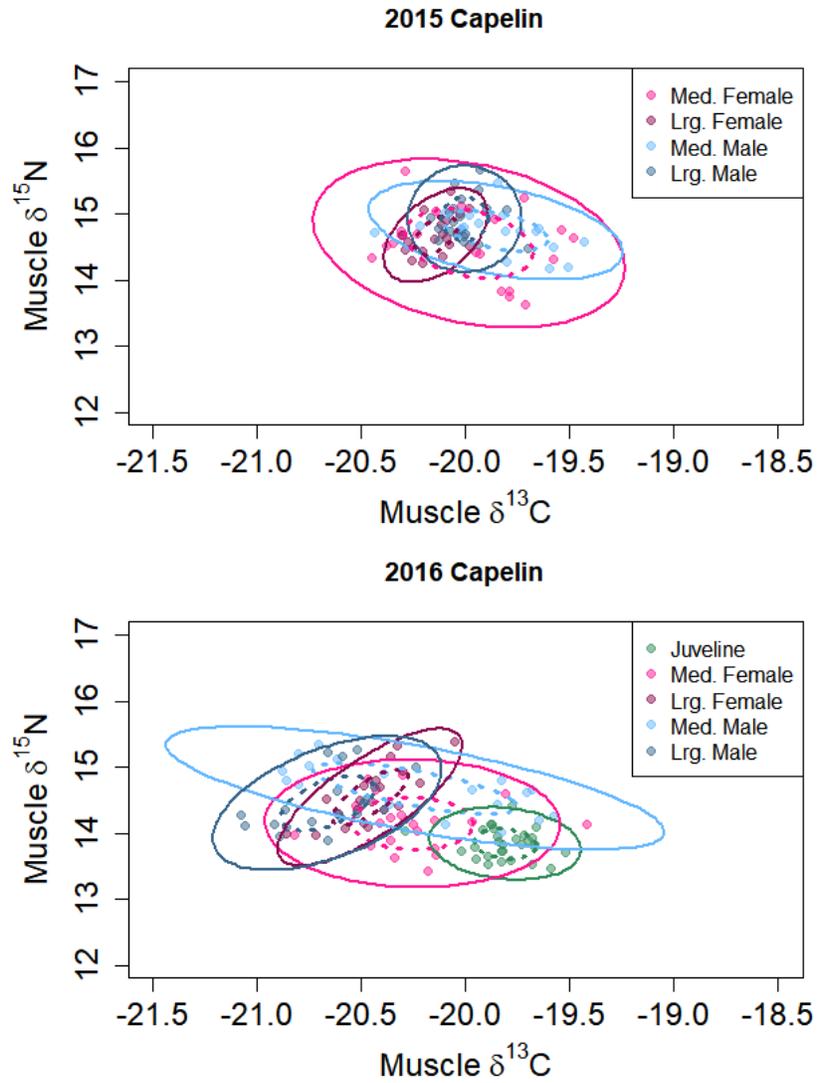


Figure 2.2: Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotopic standard ellipse (dashed line) and 95% prediction ellipses (solid line) of lipid-extracted muscle from small (70-129 mm), medium (130-174 mm) and large (175-219 mm) male and female capelin, sampled in Pangnirtung Fjord during June-July, 2015 and 2016.

Table 2.1: The proportion of overlap of the 95% prediction ellipses (gray shading) and SEAC (standard ellipses corrected for small sample size; blue shading) between size/sex categories of lipid-extracted muscle from small (70-129 mm), medium (130-174 mm) and large (175-219 mm) male and female capelin, sampled in Pangnirtung Fjord during June-July, 2015 and 2016. Ellipse sizes (95% ellipse area and SEAC; %<sup>2</sup>) are indicated by the darker shaded boxes along the diagonal.

			2015				2016				
	95% EA	SEAC	Medium Female	Medium Male	Large Female	Large Male	Medium Female	Medium Male	Large Female	Large Male	Immature
2015	Medium Female	3.03	0.51	0.30	0.17	0.17	0.11	0.34	0	0	0.01
	Medium Male	0.45	1.35	0.23	0.05	0.29	<0.0001	0.09	0	0	<0.0001
	Large Female	0.17	0.26	0.52	0.09	0.10	0.04	0.17	0	0	0
	Large Male	0.24	0.44	0.41	0.73	0.12	<0.0001	0.06	0	0	<0.0001
2016	Medium Female	0.44	0.23	0.18	0.17	2.27	0.38	0.06	0.06	<0.0001	0.22
	Medium Male	0.48	0.37	0.18	0.18	0.35	2.62	0.44	0.16	0.08	<0.0001
	Large Female	0.22	0.18	0.20	0.15	0.33	0.20	1.00	0.17	0.20	0
	Large Male	0.21	0.11	0.06	0.06	0.33	0.27	0.53	1.58	0.26	0
	Immature	0.21	0.08	0.02	0.05	<0.0001	0.11	<0.0001	<0.0001	<0.0001	0.64

### *Stomach Contents*

A total of 206 capelin stomachs were subsampled and used for analyses (2015:  $n = 100$ ; 2016:  $n = 106$ ). Of the stomach subsamples in each year, the majority were from male fish (2015: 63.1%; 2016: 81.6%) with fewer from females (2015: 36.9%; 2016: 18.4%). For both years, capelin  $\geq 140$  mm were generally ripe or spent, whereas fish  $< 140$  mm were mostly immature (Fig. 2.3). Overall, ripe fish were 45.9% female and 54.1% male; spent fish were 19.8% female and 80.2% male. Capelin stomachs from 2015 had more contents (i.e. higher stomach fullness) than stomachs from 2016 (Fig. 2.3).

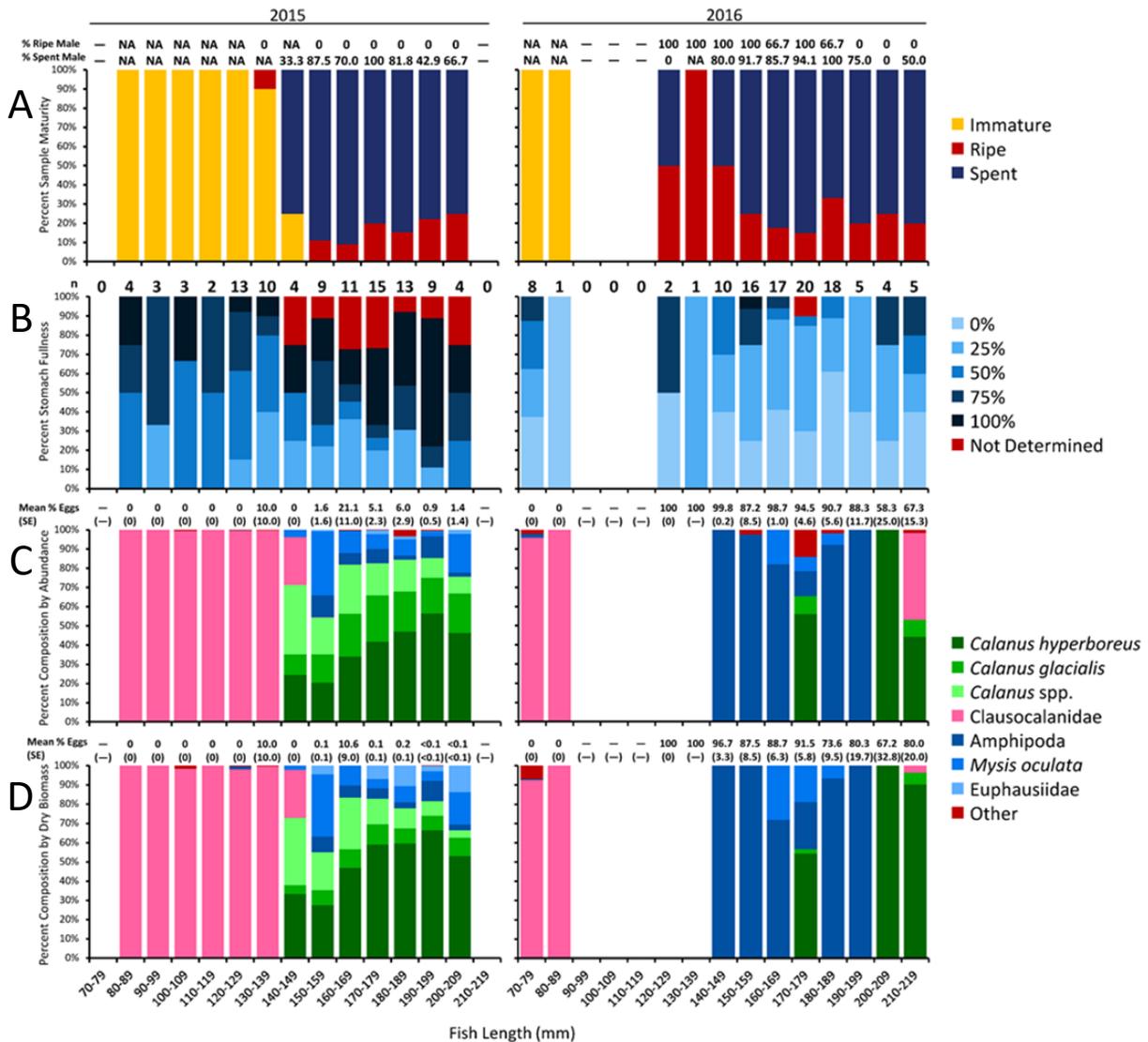


Figure 2.3: Maturity composition (a), percent stomach fullness (b), percent composition by abundance (c), and percent composition by dry biomass (d) of capelin (males and females combined) sampled in Pangnirtung Fjord, Nunavut during June-July, 2015-2016. Numbers above columns indicate (a) the percentage of fish in the respective column that were ripe or spent males, (b) sample sizes for each size grouping, and (c and d) mean ( $\pm$ SE) percent egg composition.

A total of 23 prey taxa were identified in the stomachs of capelin. Prey taxa were grouped into 8 prey categories: *Calanus hyperboreus*, *Calanus glacialis*, *Calanus* spp., Clausocalanidae, Amphipods, *Mysis oculata*, Euphausiids, and other. *C. hyperboreus* found in stomachs were primarily late-stage individuals (56.4% CV, 41.8% CVI female, and < 2% other), and this varied between study years (2015: 58.6% CV, 39.6% CVI female, and < 2% other; 2016: 1.2% CV,

96.3% CVI female, and 2.5% other). *Calanus glacialis* were also primarily late-stage individuals overall (68.7% CV, 28.8% CVI female, < 3% other), and this varied between study years as well (2015: 69.5% CV, 27.9% CVI female, and < 3% other; 2016: 93.3% CVI female and 6.7% CI-CIV). Based on body size, individuals grouped into *Calanus* spp. were likely late-stage *C. hyperboreus* or *C. glacialis*, but this could not be confirmed due to their highly digested state. Clausocalanidae contained *Pseudocalanus* spp., *P. acuspes*, and *Microcalanus* spp. Although 99.9% were classified as *Pseudocalanus* spp, this may be an overestimation, as most of these were highly digested. Amphipods were primarily *Apherusa glacialis* (41.7%) and *Themisto libellula* (54.9%), but *Omisimus glacialis*, *Omisimus* spp., and Gammaridae were also found. Amphipod composition also differed between years, with 2015 amphipods composed of 66.5% *T. libellula* and 33.5% *A. glacialis*, while 2016 were composed of 78.3% *A. glacialis*, 2.2% *T. libellula*, and 19.6% other amphipods. Euphausiids were usually identified to family level only, but a few individuals were identified as *Thyanoessa inermis*. Prey grouped into “Other” included *Calanus finmarchicus*, *Metridia longa*, *M. lucens*, Decapod larvae, *Aglantha* spp., Ctenophora, Ostracoda, and Chaetognatha. *C. finmarchicus* were only found in 2015 and were almost exclusively late-staged (39.5% CV, 58.6% CVI, and 1.9% CIV). Of the *Metridia* species observed, 97.9% were *Metridia lucens*. Capelin eggs were also often found in stomachs (Table 2.2). These were excluded from diet descriptions (Fig. 2.3), as our primary goal was to examine dietary links within the food web. Additionally, capelin eggs were most often loose and not clumped together, suggesting that they may not have been actively consumed from the substrate on which they were deposited (Slotte *et al.* 2006, Bone and Davoren in press).

Table 2.2: Percent frequency of occurrence of common prey types found in capelin stomachs collected in Pangnirtung Fjord, Nunavut during June-July of 2015-2016. Darker shades indicate higher frequencies of occurrence: ■ 90+, ■ 66-89, ■ 41-65, □ 21-40, □ 1-20, and □ 0%.

Length Category (mm)	<i>Calanus hyperboreus</i>	<i>Calanus glacialis</i>	<i>Calanus</i> spp.	Clausocalanidae	Amphipoda	<i>Mysis oculata</i>	Euphausiidae	Capelin Eggs	Other
<b>2015</b>									
70-79	-	-	-	-	-	-	-	-	-
80-89	0	0	0	100	0	0	0	0	0
90-99	0	0	0	100	0	0	0	0	0
100-109	0	0	0	100	0	0	0	0	33.3
110-119	0	0	0	100	0	0	0	0	0
120-129	0	15.4	15.4	100	7.7	0	0	0	15.4
130-139	0	0	0	90	0	0	0	10	40
140-149	50	50	75	25	0	25	0	0	0
150-159	55.6	66.7	55.6	11.1	33.3	44.4	11.1	11.1	0
160-169	72.7	63.6	36.4	0	27.3	18.2	0	72.7	9.1
170-179	100	86.7	93.3	0	66.7	33.3	26.7	46.7	6.7
180-189	92.3	92.3	92.3	0	46.2	53.8	15.4	38.5	15.4
190-199	100	100	77.8	0	44.4	55.6	11.1	33.3	11.1
200-209	100	75	75	0	50	25	25	25	0
210-219	-	-	-	-	-	-	-	-	-
<b>2016</b>									
70-79	0	0	0	100	25	0	0	0	25
80-89	0	0	0	100	0	0	0	0	0
90-99	-	-	-	-	-	-	-	-	-
100-109	-	-	-	-	-	-	-	-	-
110-119	-	-	-	-	-	-	-	-	-
120-129	0	0	0	0	0	0	0	100	0
130-139	0	0	0	0	0	0	0	100	0
140-149	0	0	0	0	10	0	0	100	0
150-159	0	0	0	0	12.5	0	0	87.5	6.3
160-169	0	0	0	0	11.8	11.8	0	100	0
170-179	5	5	0	0	10	15	0	100	5
180-189	0	0	0	0	33.3	5.6	0	94.4	5.6
190-199	0	0	0	0	20	0	0	100	0
200-209	25	0	0	0	0	0	0	75	0
210-219	20	20	0	20	0	0	0	100	20

In both years, small/immature capelin most frequently consumed Clausocalanidae, which were present in nearly all stomachs of fish <120-140 mm but were rarely present in capelin  $\geq$ 120-140 mm (Table 2.2). For fish  $\geq$ 140 mm, inter-annual differences in prey types consumed were observed, with 2015 fish most frequently consuming *Calanus* copepods, and slightly less frequently consuming amphipods, mysids, and euphausiids (Table 2.2). In contrast, capelin  $\geq$ 140 mm in 2016 rarely consumed *Calanus* copepods, and more commonly consumed amphipods, mysids, and euphausiids (Table 2.2). Overall, common prey types were far less frequently consumed in 2016 than in 2015, with 2016 capelin stomachs frequently containing only capelin eggs (Table 2.2). Other prey appeared to be sporadically consumed in both years by several size classes, with no obvious patterns (Table 2.2).

In 2016, capelin eggs made up a higher proportion, by abundance and biomass, of stomach contents for all size categories than in 2015 (Fig 2.3). In 2016, 84.9% of stomachs were composed primarily (~80% or more) of eggs (abundance), and all were from fish >120 mm. Of the remaining stomachs, 11.3% contained no eggs and 3.8% contained varying amount of eggs (3-42%). Overall, capelin eggs made up  $95.5 \pm 1.7\%$  of contents consumed in stomachs containing eggs in 2016. In 2015, 3% of stomachs were composed primarily (~80% or more) of eggs (abundance), whereas 74% contained no eggs, and the remaining 23% had varying amounts of eggs (0.66-35%). Overall, capelin eggs made up  $19.8 \pm 5.8\%$  of contents in 2015 stomachs containing eggs, and all were from fish >130 mm.

Non-egg prey appeared to differ in composition between 2015 and 2016, though common prey types (i.e., calanus copepods, mysids, and amphipods) were present in both years (Table 2.2; Fig. 2.3). In both 2015 and 2016, Clausocalanidae (in particular, *Pseudocalanus*) comprised the highest percent abundance in stomachs of capelin < 140 mm, whereas diet became more

varied in larger capelin. In 2015, capelin generally appeared to consume more of the larger copepods (mainly *C. hyperboreus*) by abundance and by biomass with increasing size (Fig. 2.3). In 2016, fish  $\geq 140$  mm primarily consumed amphipods, with some length categories also consuming large amounts of *C. hyperboreus* by abundance and mass (Fig. 2.3).

When broken into broader length categories to match stable isotope size categories, similar trends were observed (Fig. 2.4), with small, immature fish primarily consuming Clausocalanidae in both years. In 2015, medium and large capelin became more varied in their diet, though *C. hyperboreus* contributed the greatest proportion. Trends were similar for abundance and biomass, but became more pronounced with conversion to biomass (Fig. 2.4). In 2016, medium capelin consumed primarily amphipods by abundance, with the diet of large males and females becoming more varied. Upon conversion to biomass, amphipods replaced Clausocalanidae and *C. hyperboreus* was the dominant prey for large males, while *C. hyperboreus* remained dominant in the diet of large females (Fig. 2.4).

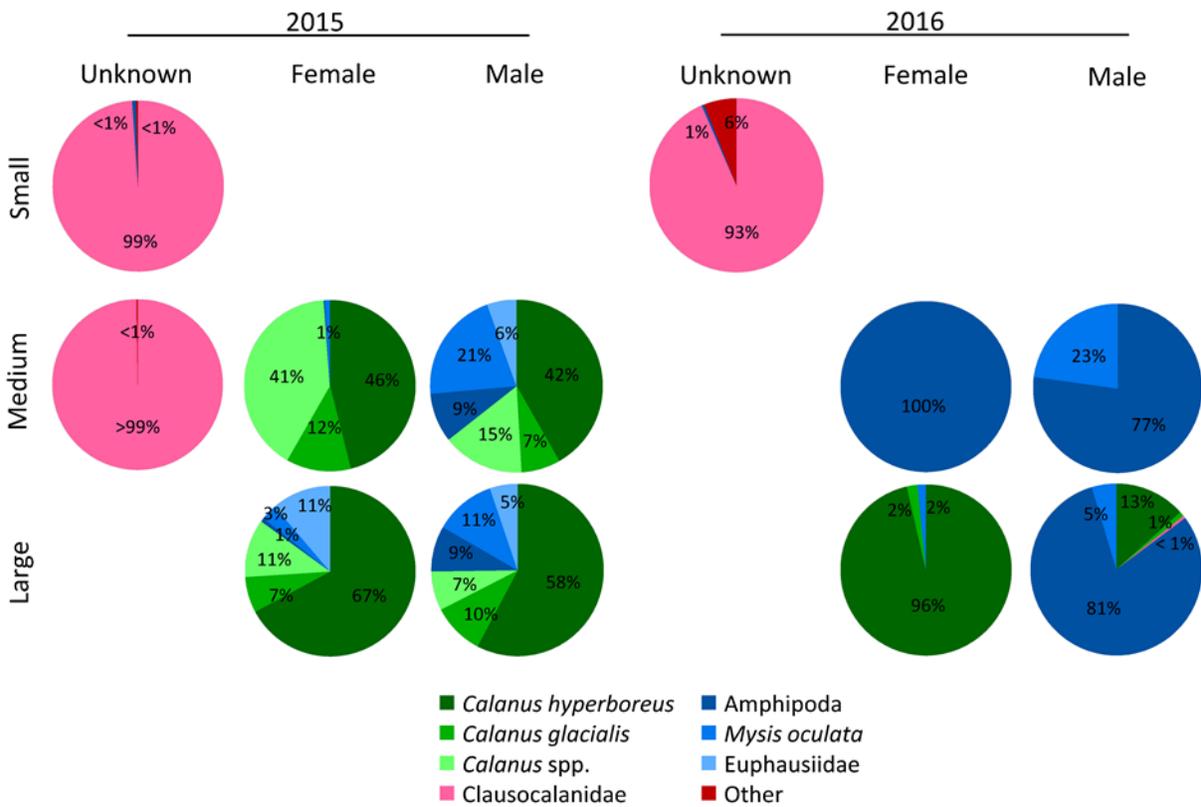


Figure 2.4: Diet composition by mean dry biomass of small (70-129 mm), medium (130-174 mm) and large (175-220 mm) capelin collected in Pangnirtung Fjord, Nunavut during June-July, 2015-2016.

## Discussion

Overall, capelin diet varied inter-annually and by size. Capelin appear to undergo an ontogenetic shift in their foraging ecology, as evidenced by dietary and isotopic niche differences between size classes of fish. Small, immature capelin (2015: < 140 mm; 2016: < 120 mm) fed almost exclusively on Clausocalanidae in both years, which, together with their relatively narrow isotopic niche breadth and low  $\delta^{15}\text{N}$ , suggested a fairly specialized diet on small copepods. In 2015, mature fish ( $\geq 140$  mm) had a more varied diet, being primarily composed of larger copepods (*C. hyperboreus*) with decreased amounts of smaller copepods, amphipods, mysids, and euphausiids with increasing fish size. Stable isotopes mirrored these trends, with a broad niche breadth for medium-sized adults but a narrowing for larger fish, suggesting a greater

degree of dietary specialization as body size increased. This trend in isotopic niche size was true in both years. Given the wider size categories used for stable isotopes, it could be suggested that the broader isotopic niche breadths for medium capelin might reflect a transitional signature, composed of a mixture of some capelin that consume small prey types and other capelin that consume larger prey types. However, in both years, most medium-sized capelin were beyond the 120-140 mm range where diet appeared to change based on stomach contents. Furthermore, in one case (medium males in 2015), all fish were  $\geq 146$  mm, and this group still had a broader isotopic niche width than large fish, suggesting that this was not an artefact of capelin size range, but rather a true reflection of their more varied diet. Trends in dietary composition in 2016 were less obvious, as most stomachs had minimal contents, which were primarily composed of capelin eggs. Of the non-egg prey present, amphipods dominated the diet of most size groups from 140-200 mm, beyond which the diet was primarily composed of *C. hyperboreus*. Stable isotopes supported a more varied diet in 2016, with niche breadth being generally broader for each size category than in 2015. In addition, there appeared to be minor dietary differences between sexes in both years, with female fish having slightly less varied stomach contents and narrower niche breadths than males. In general, capelin diet in our study was broadly similar to capelin diet from other regions (Huse and Toresen 1996, O'Driscoll *et al.* 2001, Dalpadado and Mowbray 2013, McNicholl *et al.* 2016), with common prey types found in our study being similarly common in other studies, and larger prey types increasing in percent contribution to diet with body size (Huse and Toresen 1996, O'Driscoll *et al.* 2001, McNicholl *et al.* 2016).

The amount of prey in the stomach as well as the dietary composition of mature capelin (i.e. >140 mm) within similar size classes differed between study years. Non-empty capelin stomachs were primarily comprised of capelin eggs in 2016 but not in 2015. This difference

could be attributable to later sampling relative to spawning in 2016 compared to 2015. Although sampling of spawning capelin started on the first ice-free day in Pangnirtung (June 30-July 1) in 2016, there was evidence of spawning (i.e., dead capelin and sparse eggs scattered on boulders and algae in the intertidal zone) starting on June 17 before spawning fish were observed and accessible for sampling near-shore. In contrast, spawning capelin were observed and sampled prior to the first ice-free day in 2015 (June 18). If capelin began spawning two weeks prior to sampling in 2016, while they were sampled immediately at the start of spawning in 2015, this could explain the lower stomach contents and higher proportion of capelin eggs in stomachs in 2016 relative to 2015. Indeed, capelin cease feeding during spawning (Winters 1970). Males generally remain at spawning sites for several weeks (Winters 1970, Davoren 2013), presumably to mate with multiple females, during which time they often cannibalize their own eggs (Slotte *et al.* 2006, Davoren and Bone in press). Therefore, a longer residence time of capelin at spawning sites prior to sampling in 2016 compared to 2015 might explain the higher proportion of capelin eggs in stomachs in 2016 relative to 2015, as well as the higher proportion of males sampled at spawning sites in this study and others (Slotte *et al.* 2006, Maxner *et al.* 2016). Interestingly, capelin eggs found in stomachs in the present study were, in most cases, not numerous and were not clumped (indicating that they may not have been fertilized) and rarely were pebble/sand particles found, suggesting that these eggs might have been incidentally consumed in most cases rather than actively cannibalized (Slotte *et al.* 2006).

For mature fish, the composition of non-egg prey also differed between years. Mature capelin in 2015 consumed *Calanus* copepods, with smaller proportions of mysids, amphipods, and euphausiids, whereas in 2016 they primarily consumed amphipods, with smaller proportions of *Calanus* copepods, mysids, and euphausiids. The presence of ice in the fjord two weeks later

in 2016 relative to 2015 might have resulted in a higher availability of ice-associated prey, which is indeed supported by the higher composition of sympagic amphipods, particularly *Apherusa glacialis* (78.3%; Poltermann 2000) in 2016 relative to 2015 (33.5%); in contrast, the earlier date of ice break up in 2015 compared to 2016 might have resulted in a greater availability of lipid-rich pelagic prey, in particular *Calanus* copepods (Hirche 1997, Kosobokova 1999), in 2015. Copepods and amphipods differ in their isotopic compositions (Pomerleau *et al.* 2016), therefore further explaining interannual differences in isotopic niche. Shifting diets, paired with different ice conditions between years, possibly affecting prey availability and isotopic baselines (Post 2002), seem to have resulted in a broader, more varied isotopic niche breadth in spawning adult capelin between years. The generally broader isotopic niche breadth in 2016 compared to 2015 may have been related to the higher consumption of amphipods as well as to the higher consumption of capelin eggs, which are similar in their isotopic signature to capelin muscle (Crook 2015).

Dietary differences with increasing fish size were observed. In particular, capelin up to ~140 mm, most of which were immature, consumed almost exclusively small prey types (namely Clausocalanidae) and had the smallest isotopic niche. Larger fish ( $\geq 140$  mm) were mature and consumed larger and more varied prey types, which was reflected in their broader niche breadth relative to immature capelin. As mature fish increased in size, prey types remained fairly similar, but the largest size classes became more specialized on larger prey, evidenced by a higher percentage of larger copepods (*C. hyperboreus*) in 2015 and amphipods in 2016, as well as a narrowing of capelin isotopic niche. Interestingly, while most adult capelin in 2016 consumed mostly amphipods, the two largest size classes consumed primarily *C. hyperboreus* by mass. While *A. glacialis* (the most commonly-consumed amphipod in 2016) can be much larger than

*C. hyperboreus*, measured specimens from stomachs in 2016 were never greater than 10.5 mm, only slightly larger than *C. hyperboreus* (5.1-6.8 mm prosome length). In addition, *C. hyperboreus* is higher in energy density (25.0 kJ/g; Kosobokova 1980) than *A. glacialis* (19.7 kJ/g; Weslawski *et al.* 1994), indicating that it might be more beneficial to feed on *C. hyperboreus* than on small *A. glacialis*. Alternatively, however, the observed change from amphipods to copepods could simply be a reflection of the small sample size of capelin in the largest size classes in 2016 ( $n \leq 5$ ). Overall, similar findings to ours were noted in the western Canadian Arctic (McNicholl *et al.* 2016), with capelin consuming more larger copepods (*C. hyperboreus*), while simultaneously consuming less smaller prey types, such as *C. glacialis*, small amphipods and *Metridia* spp, as they increased in size. Similarly, O'Driscoll *et al.* (2001) found that larger capelin consumed a higher proportion of larger copepods and a lower proportion of smaller copepods compared to smaller capelin. These size-related dietary differences support ontogenetic niche shift theory, which states that individuals in size-structured populations will shift and exploit several niches as they grow throughout their lifetime (Werner and Gilliam 1984). This ontogenetic shift in niche likely results from gape size limits when fish are small (Schmitt and Holbrook 1984), and allows larger, less gape-limited individuals to minimize competition with other members of their species and meet growing energetic requirements throughout their development. The increased dietary composition of large, lipid-rich *C. hyperboreus* in the diet of larger capelin may increase their net energy gain, as they are able to consume fewer large prey items rather than many small prey items (Charnov 1976). Previous studies on marine planktivorous fishes have demonstrated that fish will select prey of the size predicted by optimal foraging models to maximize their net energy intake, and optimal prey increased in size as fish size increased (Mittelbach 1981).

Compared to other forage fishes present in Pagnirtung Fjord and Cumberland Sound, capelin diet is likely very similar. Although other fish species were not sampled, capelin have been shown to overlap in dietary composition with polar cod in other Arctic regions (Orlova *et al.* 2009, Hop and Gjørseter 2013, McNicholl *et al.* 2016) as well as herring (Huse and Toresen 1996). When cod and capelin co-occur, they have high dietary overlap (McNicholl *et al.* 2016), suggesting that this is likely the case in Cumberland Sound. In particular, capelin and polar cod have been shown to both consume *Calanus* copepods, amphipods, euphausiids, and other crustaceans (Orlova *et al.* 2009, Hop and Gjørseter 2013, McNicholl *et al.* 2016). Additionally, some prey types consumed by Arctic charr (*Salvelinus alpinus L.*) in Cumberland Sound (Ulrich 2013) overlapped with prey consumed by capelin, in particular amphipods, euphausiids, and copepods. This suggests that capelin may compete with smaller Arctic charr when consuming primarily invertebrate prey under limited prey conditions. As such, the recent increases in capelin abundance in Cumberland Sound may have negative implications for other planktivorous species in the system, especially given that capelin are capable of rapidly depleting zooplankton abundance (Hassel *et al.* 1991), which would limit prey abundance. Overall, this could result in a higher likelihood of displacing other forage fishes, such as polar cod, upon which certain predator species (e.g. ringed seals) rely as their main fish prey in Cumberland Sound (Chapter 3). In turn, however, high abundances of capelin may have positive impacts on other predators in the region known to consume capelin, such as harp seals (Chapter 2), belugas (Marcoux *et al.* 2012), and even large/mature Arctic charr (Ulrich 2013).

This study provides valuable insights into capelin foraging ecology in Pagnirtung Fjord and Cumberland Sound, despite limitations with regard to the timing of sampling (i.e. during a time when capelin are known to cease feeding). Inter-annual differences highlighted that the

Cumberland Sound ecosystem is highly complex and variable, and conclusions can differ markedly between study years. In the future, it would be valuable to conduct more dietary analyses based on fish sampled multiple times throughout the year to gain a greater understanding of how capelin diet shifts both seasonally and annually, thus allowing for better-informed management decisions as temperate species distributions and abundance continue to shift into Arctic regions in response to climate change.

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## Chapter 3: Diet and isotopic niche overlap between two phocid seals in the Canadian Arctic

### Abstract

The continual warming of the climate and the ocean is allowing for the northward expansion of species ranges and distributions into Arctic regions where they were historically sparse or absent. In Cumberland Sound in the Canadian Arctic, research has shown that recent decades have seen an increase in the forage fish capelin, and a concurrent increase in migratory harp seals during the summer months; concomitantly, locals have reported reductions in resident ringed seal numbers. There remains, however, a deficiency in research related to the consequences of these ecosystem changes, thus leaving the potential effects on ringed seals, an important species for Inuit subsistence, relatively unknown. To address this deficiency, we examined both long- and short-term foraging of ringed and harp seals to determine whether or not harp seals might be potential competitors for ringed seals. Stable isotope analyses of muscle and liver, in combination with stomach content analysis, were used to assess diet before and during the time when ringed and harp seals are sympatric in Cumberland Sound. We determined that while there is a high overlap in prey species utilized while seals are sympatric, examination of prey size and isotopic niche position revealed that seals may partition prey resources and foraging habitats within Cumberland Sound, reducing the degree of realized niche overlap. With climate change and range shifts predicted to continue into the future, results from this study may provide valuable information when making management decisions for Cumberland Sound ringed and harp seal populations.

## Introduction

A continually-warming climate (IPCC 2014) is allowing northward shifts in species distributions (Parmesan and Yohe 2003, Root *et al.* 2003, Hickling *et al.* 2006). In the Arctic, climate-related ecosystem changes are occurring at an accelerated rate relative to more temperate regions (Kovacs and Lydersen 2008, IPCC 2014). Moore and Huntington (2008) predicted that with decreasing Arctic sea ice, seasonally-migrant temperate species will utilize Arctic habitats in greater numbers and for longer periods during the extended open-water season. As a result of temperate species moving northward, interspecific competition with ice obligate species is predicted to arise, and food resources may be more spatially and temporally dispersed as a result of warming conditions and reduced sea ice, which will exacerbate competitive interactions (Kovacs *et al.* 2011). Competition may result when the ecological niches – defined as the range of all conditions and resources that support the vital activities of a species or population (Hutchinson 1957, Alley 1982) – of two species overlap. The competitive exclusion principle (Hardin 1960) states that if two non-interbreeding populations occupy the same ecological niche and are sympatric, the two populations will not be able to coexist. Therefore, range expansions of temperate species to Arctic regions have the long-term potential to lead to the extinction, extirpation, or displacement of one or more Arctic species. With species distributional shifts predicted to increase in the future (IPCC 2014), it is increasingly important to understand how climate-induced distributional changes may impact endemic organisms and their ecosystems.

Over the last several decades, there have been changes in the presence and abundance of capelin (*Mallotus villosus*) in the Arctic (e.g. McNicholl *et al.* 2018). Capelin are an important pelagic forage fish for many predators, including seabirds (Carscadden *et al.* 2002), piscivorous fishes (Orlova *et al.* 2009), and marine mammals (Tucker *et al.* 2009) and, thus, provide an

essential linkage between low (e.g. plankton) and high (e.g. predators) trophic levels in temperate systems. While generally considered a sub-Arctic species, as they do not possess antifreeze proteins to prevent freezing in Arctic conditions (Osuga and Feeney 1978), capelin have recently been reported to be abundant in northern regions where they were historically sparse (Carscadden *et al.* 2013). For instance, capelin increased in the diet of thick-billed murres in Hudson Bay and Ungava Bay from the early 1980s to late 1990 (Gaston *et al.* 2003, Carscadden *et al.* 2013) and was first observed in their diet in Lancaster Sound during 2000-2003 (Carscadden *et al.* 2013). Additionally, locals in Frobisher Bay and Cumberland Sound reported capelin as unusually abundant in 2004 and 2005 (Carscadden *et al.* 2013), which was shortly before the time they appeared in the diet of Arctic charr (Ulrich 2013, Yurkowski *et al.* 2017). Harp seals, which migrate seasonally from their temperate winter range, have exhibited large increases in numbers during the open-water period in Cumberland Sound, Nunavut in recent decades (DFO 2011, Hammill *et al.* 2015). As almost complete dietary overlap has been shown between endemic ringed seals and harp seals in other regions where polar cod (*Boreogadus saida*) is the preferred prey (e.g. Barents Sea; Wathne *et al.* 2000), competition for resources may arise between these two seal species within Cumberland Sound.

The objective of this study was to assess the possibility for competition between ringed and harp seals during the open water season in Cumberland Sound, Nunavut, Canada (65°42'03.9"N 66°19'21.5"W) from 2008-2016 by examining their foraging ecology. Specifically, we investigated ringed and harp seal dietary composition and isotopic niche breadth and overlap. Dietary composition was determined using stomach contents, which offer a snapshot of seal diet within a matter of hours before death (Pierce and Boyle 1991). Since stomach contents offer only a short-term glimpse at diet, we paired stomach content analysis

with stable isotope analysis, which measures isotopic ratios of  $^{13}\text{C}:^{12}\text{C}$  and  $^{15}\text{N}:^{14}\text{N}$  and is used as a proxy for long-term ecological niche (Boecklen *et al.* 2011, Ben-David and Flaherty 2012). We hypothesized that, because ringed and harp seals are closely related predators that forage similarly, they, therefore, occupy a similar ecological niche. We predicted that during the open water season in Cumberland Sound, when both species are sympatric, stomach content and isotopic niche overlap would be high, suggesting use of the same resources and a high potential for competition under resource-limited conditions. Previous stable isotope research on ringed seals in Cumberland Sound has shown that ringed seals have not changed drastically since the 1990s with regard to their isotopic niches (Yurkowski *et al.* 2016b). As such, we believe we are still able to examine ringed seal diet in a natural state that has not yet been altered by the presence of harp seals in the system. This research will, therefore, act as an important baseline for studies examining interactions between ringed and harp seal in the future. In addition, the results from this research will provide insight into the effects of climate change-related species distributional shifts on ringed seals and other endemic higher trophic level species in the Canadian Arctic.

## Methods

### *Biological Sampling*

All ringed and harp seal samples were collected by Inuit beneficiaries from Pangnirtung, Nunavut as part of their subsistence hunt, mainly during the open-water period (May-November) in 2008-2016 (see Appendix A, Table 1 for breakdown of yearly sample sizes). Seals were collected in Cumberland Sound as well as in Pangnirtung Fjord and sampled immediately after capture by hunters. Stomachs were removed by cutting above the esophageal sphincter and below the pyloric sphincter, and samples of liver and dorsal muscle were taken. Additionally,

capelin were sampled using dipnets during spawning in June-July of 2015 and 2016 (see Chapter 2). All seal and fish tissue samples were frozen at  $-20^{\circ}\text{C}$  and shipped to the Freshwater Institute (Winnipeg, MB), where they were stored at  $-30^{\circ}\text{C}$  until analysis.

Overall 65 stomachs, 85 muscle samples, and 86 liver samples were collected from ringed seals during the open-water season in 2008-2011 and 2015-2016. From harp seals, 18 stomachs, 27 muscle samples, and 36 liver samples were collected. The discrepancies observed between tissue sample sizes within each seal species resulted from differences in sampling activities by hunters and from var researcher needs at the time of sampling. Seals were aged by counting the annual growth layer groups in the cementum of the lower right canine tooth from each seal. Notably, there was a difference in the age distributions among captured ringed and harp seals; ringed seals were primarily immature individuals, either pups or juveniles, whereas harp seals were mainly adults, with only six seals below the age of 10 (Fig. 3.1). During data exploration, a natural separation of seals aged 0, 1-4, and 5+ was found. While some authors state that 6+ is the age at maturity (Holst *et al.* 1999 and references within), others have more recently estimated 5+ (Krafft *et al.* 2006, Quakenbush *et al.* 2011). For the purposes of this study, seals of age 5 and above were considered “adults”.

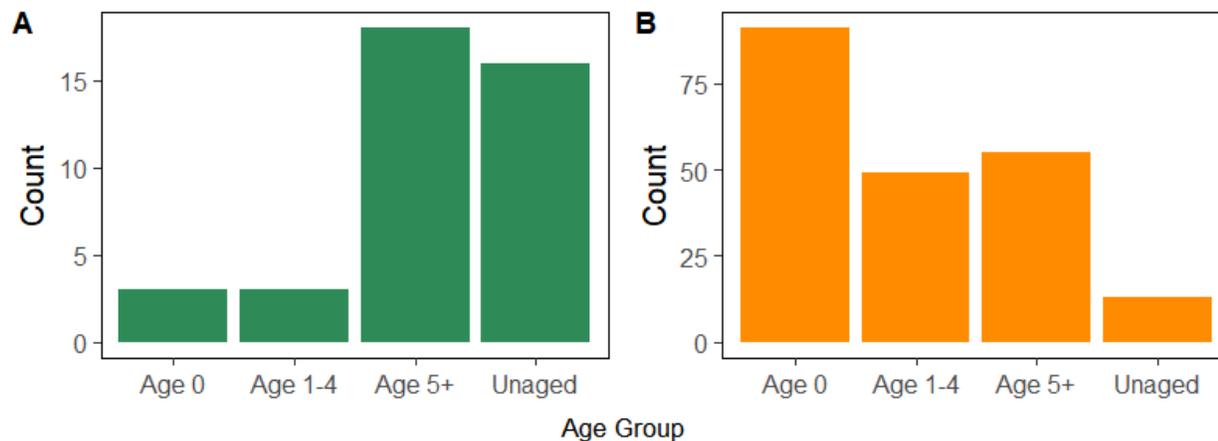


Figure 3.5: Frequency distribution of harp (A) and ringed (B) seal samples represented by different age groups. Seals were sampled in Cumberland Sound between May and October from 2008-2016. Note that the scale on the y-axes differ because sample sizes differed between seal species (n=37 harp; n=204 ringed).

### *Stable Isotope Analysis*

Both muscle and liver tissues of ringed and harp seals were used for stable isotope analysis, as they differ in their turnover rates and, consequently, represent different periods of averaged seal diet. Muscle has a slower turnover rate than liver, with an isotopic half-life in the range of ~100-150 days (Vander Zanden *et al.* 2015). As such, muscle likely represents the averaged diet of seals both before and during the open water period, and, thus, before the summer period when harp seals arrive in Cumberland Sound. Liver has a faster turnover rate than muscle, representing the averaged diet over several weeks to a couple of months (Tieszen *et al.* 1983), thus providing an indication of diet when both seal species are sympatric in Cumberland Sound.

All seal muscle and liver samples were prepared for stable isotope analysis by freeze-drying at -50°C for 48 h and homogenizing using a mortar and pestle. Lipids were extracted using a 2:1 chloroform:methanol solvent (Yurkowski *et al.* 2016a, 2016b). Ratios of  $^{13}\text{C}:^{12}\text{C}$  and  $^{15}\text{N}:^{14}\text{N}$  (denoted  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively) were measured using a Thermo Finnigan Delta<sup>Plus</sup> mass spectrometer and an elemental analyzer at the Chemical Tracers Lab at the Great Lakes

Institute for Environmental Research (University of Windsor).  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were measured against Pee Dee Belemnite and atmospheric nitrogen standards, respectively, using the following formula:  $\delta^x E = \left( \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \right) \times 1000$ , where  $^x E$  refers to  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$ , and  $R$  refers to the ratio of heavy to light isotopes of element  $E$  in either the sample or the standard. Triplicates were run every 10 samples to ensure precision of measurements, and precision was determined to be 0.1‰ for both liver and muscle  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

### *Stomach Content Analysis*

Seal stomachs were removed from the freezer 1-2 days prior to analysis to ensure adequate time to thaw in a refrigerated room. Stomachs were then cut open and all contents were rinsed through five nested sieves (4000, 2000, 500, 250, and 125  $\mu\text{m}$ ). Otoliths, squid beaks, fish remains, and any other non-invertebrate prey items were removed from the sample, identified, and counted. Otoliths from stomach contents were identified to the lowest taxonomic level possible. Those that were too digested to identify were considered to be from previous feeding events and were omitted from further analyses to reduce biases associated with overestimating prey with hard parts in stomach content analysis. Otoliths of the two most-commonly consumed fish species, polar cod and capelin, were photographed using an Olympus SZX7 microscope and length was measured using ImageJ software. Total otolith length ( $\mu\text{m}$ ) was measured as the greatest distance across the otolith surface. Total lengths of otoliths of less common taxa (Cottidae, Liparidae, and Cyclopteridae) were measured using an ocular micrometer.

The remaining invertebrate prey items were placed into a 500 mL splitter until an estimated 200 organisms were present. These organisms were then identified to the lowest taxonomic level possible given partial digestion and counted. In most cases, invertebrates were highly digested, and intact individuals were rare. For this reason, invertebrates were identified

and counted using only the tails, as this would most reliably represent the number of individuals present before digestion. These count data were then used to estimate total numbers of invertebrate prey in the stomach using the following formula:  $N_{Ej} = N_{sj} \times 2^m$ , where  $N_{Ej}$  is the estimated number of prey type  $j$  in the sample,  $N_{sj}$  is the number of prey item  $j$  in the subsample, and  $m$  is the number of times the sample was split. After obtaining counts for all taxa in each stomach, those numbers were multiplied by published taxon-specific masses, as in Walkusz *et al.* (2013), to estimate prey biomass. There was a small number (<0.0005% by number) of unidentifiable invertebrates which were omitted from biomass and energy content analyses, as we were unable to calculate reliable biomass or energy content values without knowing their identity. Stomachs containing no contents, or minimal amounts of worms and/or unidentifiable content, were considered empty and omitted from analyses, but still counted in total sample sizes.

Analysis of stomach contents revealed many different prey taxa in the stomachs of ringed (n = 23 taxa) and harp seals (n = 10 taxa). As some invertebrate taxa were represented in small numbers (range: 1-30 individuals per stomach) and/or were present only in a few stomachs (e.g. ~200 individuals occurring in a single stomach), invertebrate prey were grouped into three major taxonomic groups: amphipods, mysids, and euphausiids. *Themisto libellula* was the most commonly-occurring amphipod (85% by number), *Mysis oculata* was the most commonly-occurring mysid (96% by number), and Euphausiids were not identified to the species level. Invertebrates grouped into the “mysid” category were *Mysis oculata*, *Boreomysis arctica*, and unidentified Mysidae. The “amphipod” category included *Themisto libellula*, *Onisimus littoralis*, *Onisimus edwardsii*, *Gammarus wilkitzkii*, *Gammaracanthus loricatus*, *Eusirus holmii*, *Apherusa glacialis*, Gammaridae, Hyperiididae, and Lyanassidae. Prey grouped into the “other invertebrates”

category were Copepoda, Decapoda, Crangonidae, Hippolytidae, *Gonatus fabricii*, unidentified squid, and unidentified echinoderms. As “other invertebrates” accounted for <1% of total prey by number, they were omitted from abundance, biomass, and energy content analyses, and included only in frequency of occurrence analyses. Therefore, abundance, biomass, and energy content analyses are only reported for commonly-occurring (i.e. not rare) prey types. The most commonly-occurring fish species found in seal stomachs were capelin (*Mallotus villosus*) and polar cod (*Boreogadus saida*). Other fish were identified to the families Liparidae (snailfish), Cottidae (sculpin), and Cyclopteridae (lumpsuckers) and grouped into “other fish”; representative species of these families were chosen for biomass and energy content analyses (*Liparis fabricii*, *Myoxocephalus Scorpius*, and *Cyclopterus lumpus*, respectively). We determined the issue of secondary prey (prey released from the stomachs of consumed fish during digestion; Pierce and Boyle 1991) inconsequential because invertebrate prey found in fish stomachs (Ogloff Chapter 2) were much smaller in body size than invertebrates found in seal stomachs.

### *Data Analysis*

Stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope values were analysed using the *SIBER* package (Jackson *et al.* 2011) in R version 3.4.3 to quantify isotopic niche breadth and overlap. Bayesian standard ellipse area ( $\text{SEA}_B$ ) was estimated for each species using  $10^5$  iterations, with a burn-in of  $10^4$ . The posterior distribution was thinned by 10, and 2 chains were run. The probability that a species’ niche was larger than the other was calculated by determining the percentage of all iterations in which the niche of ringed seals was larger than harp seals. Niche overlap was quantified using standard ellipse areas (SEA) – corrected for small sample sizes ( $\text{SEA}_C$ ) – which are considered a standard deviation around the bivariate mean. Niche overlap

was also quantified using the 95% ellipse area, which we considered more representative of each population as a whole. Overlap was calculated in three different ways: the percentage of ringed seal isotopic niche overlapped by harp seal niche (i.e. overlap area divided by the area of ringed seal niche); the percentage of harp seal isotopic niche that overlapped ringed seal niche (i.e. overlap area divided by the area of harp seal niche); and the percentage of the total niche space that is shared, using the following formula:

$$\% \text{ overlap} = \frac{\text{overlap area}}{\text{area of harp niche} + \text{area of ringed niche} - \text{overlap area}} \times 100 .$$

Note that overlap area is subtracted from the denominator to prevent double-counting of the overlap area, thus preventing underestimation of niche overlap.

Otolith measurements (total length) were used to estimate the length of fishes using published species-specific regression equations (Appendix A, Table 2). To assess whether the size of consumed fishes differed between ringed and harp seals, comparisons were made between the estimated lengths of fishes from the stomachs of both seals using Wilcoxon Rank-Sum tests, as the assumptions for parametric tests were not met. Fish biomass was estimated from these calculated lengths. Capelin mass was estimated using a quadratic regression equation obtained from capelin sampled in Pangnirtung Fjord during 2015 and 2016 (n=842; see Chapter 2). The masses of other fish species were estimated from published regression equations (Appendix A, Table 3). Wet mass was converted to dry mass (Appendix A, Table 4), and then to energy content (Appendix A, Table 5). For biomass and energy estimations, the number of otoliths was divided by two (+1 if there was an odd number), as otoliths are paired in fish.

To quantify the dietary composition from stomach contents of each seal species, we used the following metrics:

$$\text{Frequency of Occurrence: } FO = \frac{\# \text{ stomachs containing prey } j}{\text{total \# stomachs}} \times 100$$

$$\text{Percent Abundance: } A = \frac{\# \text{ of individual specimens of prey } j}{\text{total \# of specimens of all prey types in stomach } y} \times 100$$

$$\text{Percent Biomass: } B = \frac{\text{biomass represented by prey } j}{\text{total biomass of prey in stomach } y} \times 100$$

$$\text{Percent Energy Content: } E = \frac{\text{energy content represented by prey } j}{\text{total energy content of prey in stomach } y}$$

where  $j$  represents prey taxa, and  $y$  represents the individual seal stomach. Frequency of occurrence is a single number representing the percentage of stomachs in which each prey item occurred. The other three metrics were calculated per stomach and means ( $\pm$  SE) were calculated across all individuals for ringed seals and harp seals separately.

Dietary overlap of stomach contents between ringed and harp seals was calculated for percent abundance, percent biomass, and percent energy content separately using Schoener's Index (Schoener 1970):  $\alpha = 1 - 0.5(\sum |p_{xi} - p_{yi}|)$ , where  $p$  is the proportion of prey type  $i$  in the diet of predator  $x$  or  $y$  (ringed or harp seals, in this case). For this index, values represent proportion of overlap, where 0 suggests no overlap and 1 suggests complete overlap. Overlap is considered ecologically meaningful if  $\alpha \geq 0.60$  (Wallace 1981).

## Results

### *Stable Isotopes*

When all age classes were combined, ringed and harp seals differed significantly in muscle  $\delta^{13}\text{C}$  ( $W = 4099.5$ ,  $p < 0.0001$ ), muscle  $\delta^{15}\text{N}$  ( $W = 1689.5$ ,  $p < 0.01$ ), and liver  $\delta^{13}\text{C}$  ( $W = 4261$ ,  $p < 0.001$ ), but not in liver  $\delta^{15}\text{N}$  ( $W = 3309.5$ ,  $p = 0.634$ ). The 95% ellipse area was larger for ringed seals (muscle:  $9.49 \text{‰}^2$ ; liver:  $9.59 \text{‰}^2$ ) than for harp seals (muscle:  $6.94 \text{‰}^2$ ; liver:  $8.00 \text{‰}^2$ ) when considering seals of all ages. When comparing only adult (5+ years) seals of both

species, the 95% ellipse area was similarly larger for ringed seals (muscle: 10.28‰<sup>2</sup>; liver: 10.02‰<sup>2</sup>) than for harp seals (muscle: 5.37‰<sup>2</sup>; liver: 9.55‰<sup>2</sup>). When all ages were considered, SEA<sub>B</sub> was also larger for ringed seals (muscle: 1.07‰<sup>2</sup>; liver: 1.26‰<sup>2</sup>) than for harp seals (muscle: 1.57‰<sup>2</sup>; liver: 1.59‰<sup>2</sup>) in 94.2% and 85.0% of iterations for muscle and liver, respectively; for seals aged 5+ only, SEA<sub>B</sub> was larger for ringed seals (muscle: 0.39‰<sup>2</sup>; liver: 0.65‰<sup>2</sup>) than for harp seals (muscle: 1.86‰<sup>2</sup>; liver: 1.69‰<sup>2</sup>) in 100% and 99.7% of iterations for muscle and liver, respectively. Low sample sizes did not allow for niche size comparisons for seals aged 0 or aged 1-4 (Fig. 3.1). Because relationships did not change among age classes, stable isotope biplots are shown only for seals of all ages (Fig. 3.2). Regardless of the overlap measurement, the percent overlap was greater when ringed and harp seals were sympatric in Cumberland Sound (i.e. using liver) than when harp seals were in the southern part of their range or during their migration (i.e. muscle; Table 3.1). Additionally, overlap of harp seal niche on ringed seal niche was greater than ringed seal overlap on harp seal niche (Table 3.1).

Table 3.3: Isotopic niche overlap of ringed and harp seal muscle and liver tissue collected from seals hunted in Cumberland Sound during the open water period from 2008-2016. Standard ellipse here refers to the non-Bayesian SEA.

	<b>Standard Ellipse</b>	<b>95% Prediction Ellipse</b>
<b>MUSCLE</b>		
<b>% Shared area</b>	11.3	45.6
<b>% Ringed that overlaps harp</b>	17.6	54.2
<b>% Harp that overlaps ringed</b>	24.0	74.1
<b>LIVER</b>		
<b>% Shared area</b>	48.1	74.2
<b>% Ringed that overlaps harp</b>	59.5	78.1
<b>% Harp that overlaps ringed</b>	71.4	93.6

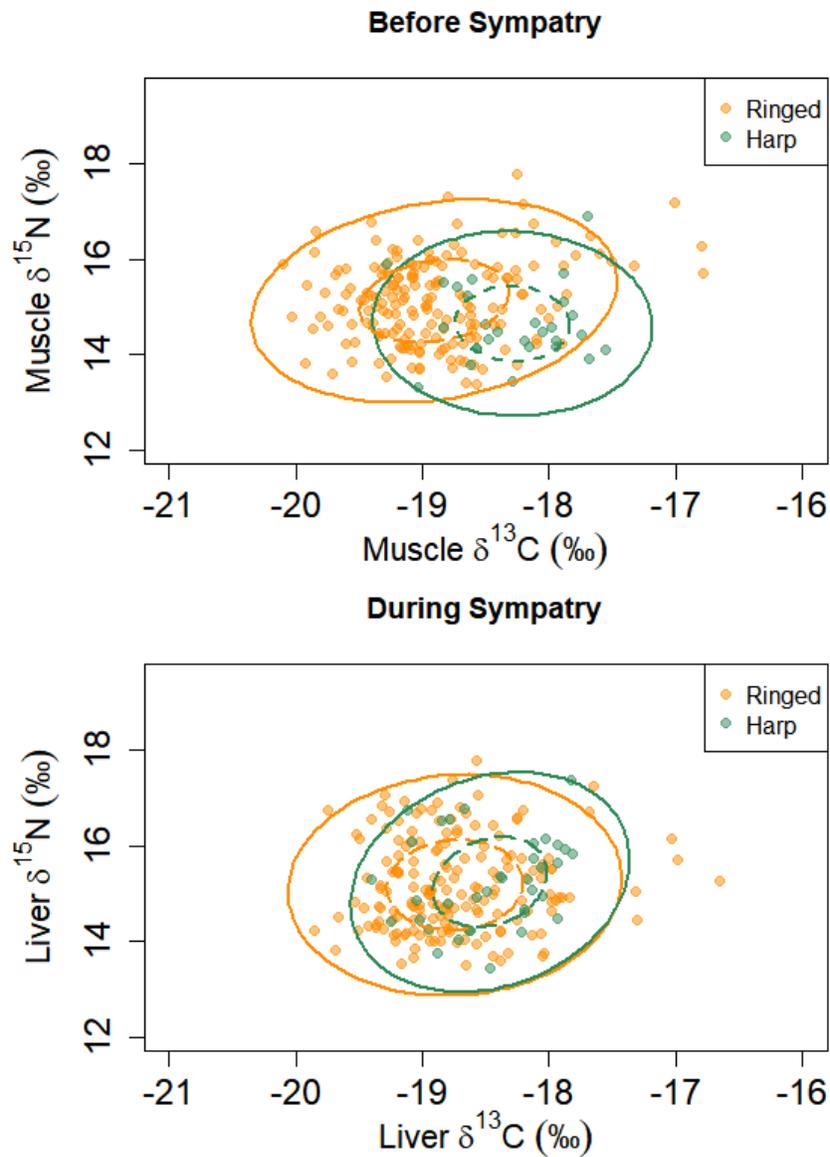


Figure 3.6: The carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotopic niches of ringed and harp seal muscle (left) and liver (right) tissues. Both standard ellipse (dashed line) and 95% prediction ellipses (solid line) are shown. Figure includes seals of all ages. Seals were hunted in Cumberland Sound during the open water period from 2008-2016.

## Stomach Contents

Of stomachs analysed, 15.9% of ringed seal stomachs were empty, and 5.0% of harp seal stomachs were empty. Ringed and harp seals both regularly consumed all of the common prey types (amphipods, mysids, euphausiids, polar cod, and capelin). Ringed seals, however, more commonly consumed rare prey types (e.g. squid and decapods; Fig. 3.3). Additionally, more ringed seal stomachs had amphipods, euphausiids, other invertebrates, and other fish, whereas harp seals appeared to consume capelin much more frequently than ringed seals. Both seals appeared to consume mysids and cod with similar frequencies. Comparable trends were observed between species across all age classes, as no notable differences in prey types in the diet were observed across age classes within each species (Fig. 3.3), though limited sample sizes made some age groups hard to compare (Fig. 3.1).

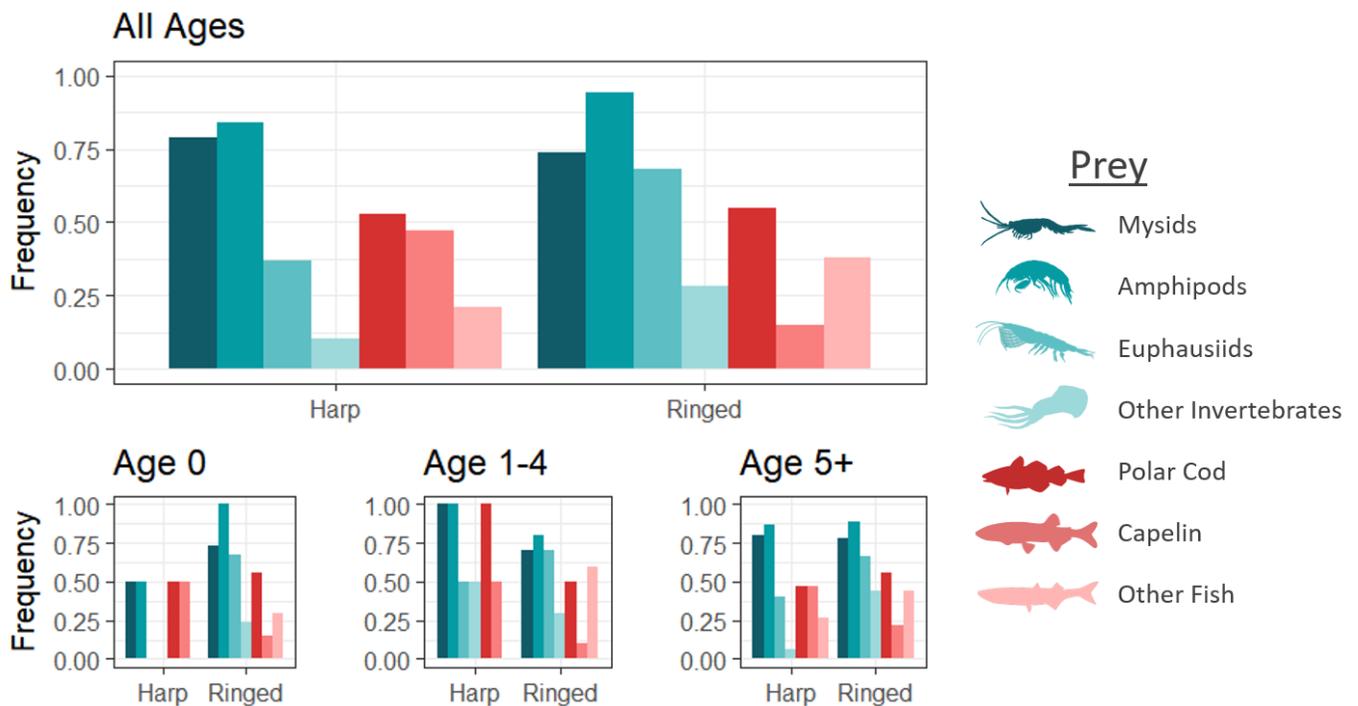


Figure 3.7: Frequency of occurrence of prey groups found in the stomachs of ringed (n=65) and harp (n=18) seals and within each age category sampled in Cumberland Sound during the open-water period from 2008-2016. Sample sizes of age categories per seal species are given in Fig. 1.

Both ringed and harp seals consumed a higher percentage by number of invertebrates (92.8% and 62.3%, respectively) than of fish (7.2% and 37.7%, respectively) when all ages were combined, but harp seals consumed a higher percentage of fish than did ringed seals (Fig. 3.4). Results were similar when seals were separated by age (Fig. 3.5). While ringed seals and harp seals consumed a similar percentage of euphausiids by number (20.3% and 25.1%, respectively), ringed seals consumed approximately double the percentage by number of amphipods and mysids (43.7% and 28.8%, respectively) compared to harp seals (21.8% and 15.4%, respectively; Figs. 3.4 and 3.5). In contrast, harp seals consumed nearly four times the percentage by number of polar cod (18.9% vs. 4.8%), and about 12 times the percentage by number of capelin (17.2% vs. 1.4%). For both seal species, polar cod were the most-consumed fish by number, though harp seals consumed similar amounts of capelin and polar cod (Figs. 3.4 and 3.5).

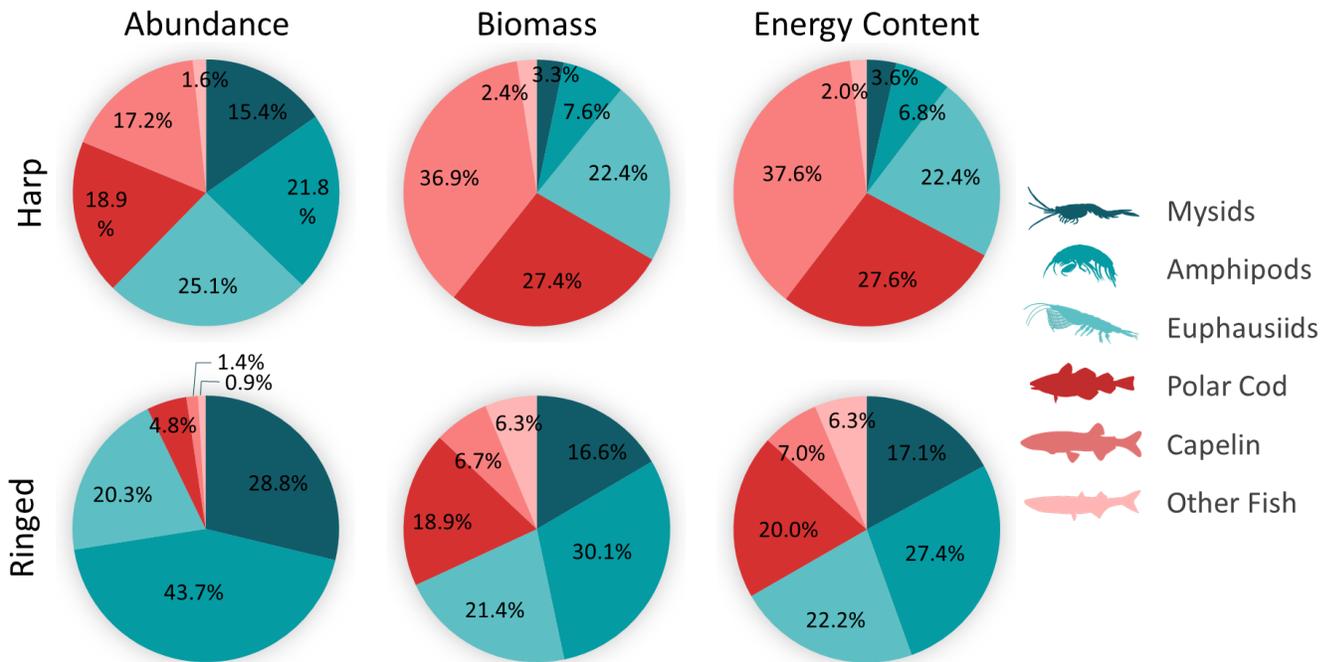


Figure 3.8: Mean percent composition of frequently-occurring prey from stomachs of ringed (n=65) and harp (n=18) seals captured in Cumberland Sound from 2008-2016 during the open water period. Seals of all ages are grouped. Percent of total average frequently-occurring diet is shown based on mean abundance (by number), mean dry biomass, and mean energy content.

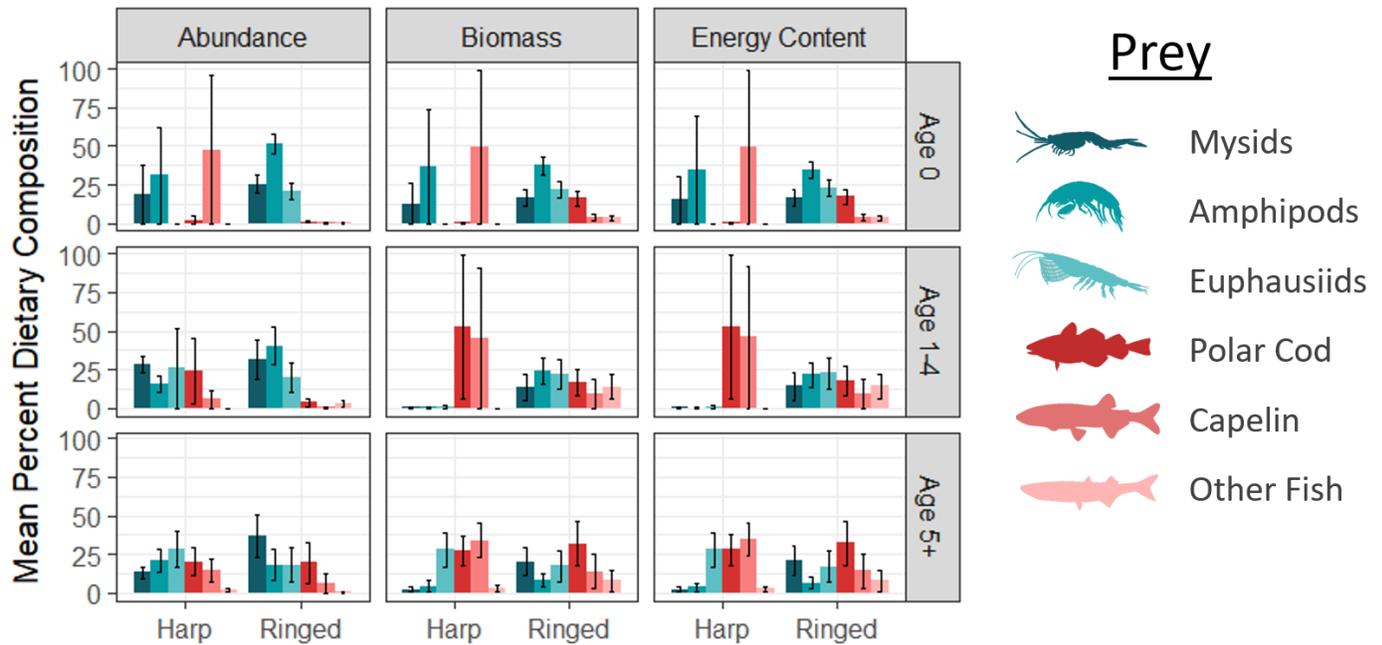


Figure 3.9: Mean ( $\pm$  SE) percentage composition of prey found in ringed and harp seal stomachs collected in Cumberland Sound during the open-water period from 2008-2016. Three dietary metrics are used to examine diet among seals of three different age groups. Sample sizes for age classes per seal species are given in Fig. 1.

Trends for percent composition by dry biomass were mirrored by energy content, revealing that fish contributed about two thirds of the overall biomass and energy within harp seal stomachs (66.7% and 67.2%, respectively) relative to invertebrates. This was not the case for ringed seals, whereby fish represented roughly one third of the biomass and energy (31.9% and 33.3%, respectively). Similar to prey abundance, ringed seals consumed more invertebrates by mass and by energy than did harp seals (Figs. 3.4 and 3.5). As expected, the representation of fish in the diet roughly doubled when using biomass and energy compared to abundance for harp seals, and roughly quadrupled for ringed seals, whereas invertebrates were less represented in the diet of both seals. Diets showed similar trends when all ages were combined within a species and when each species was separated into age classes (Figs. 3.4 and 3.5).

Harp seals consumed significantly larger capelin ( $W = 2413$ ,  $p < 0.0001$ ), polar cod ( $W = 14400$ ,  $p < 0.01$ ), and Liparidae ( $W = 1307$ ,  $p < 0.01$ ) relative to ringed seals (Fig. 3.6).

Comparisons between the sizes of Cyclopteridae consumed by ringed and harp seals were not reliable, as no harp seals and only one ringed seal consumed Cyclopteridae ( $n = 4$ ; mean =  $45.8 \pm 15.4$  mm). Similarly, while numerous ringed seal stomachs contained Cottidae ( $n = 116$ ; mean =  $41.9 \pm 25.5$  mm), only two harp seal stomachs contained Cottidae and, thus, comparisons could not be made. Schoener's Index for dietary overlap based on prey abundance was above the ecologically meaningful threshold of 0.60 only for seals aged 1-4 and 5+ (Table 3.2). Age 0 seals and seals of all ages showed lower overlap with regard to prey abundance. When considering prey biomass and energy content, Schoener's Index was ecologically meaningful only for seals aged 5+ and for all seals combined (Table 3.2).

Table 3.4: Schoener's Index of dietary overlap between ringed and harp seals captured in Cumberland Sound between 2008-2016 during the open-water period. Overlap values above or equal to 0.60 are considered ecologically meaningful and are indicated in bolded text.

Age Group	Schoener's Index		
	Abundance	Biomass	Energy Content
All Ages	0.51	<b>0.60</b>	<b>0.61</b>
Age 0	0.52	0.48	0.48
Age 1-4	<b>0.68</b>	0.28	0.29
Age 5+	<b>0.73</b>	<b>0.68</b>	<b>0.67</b>

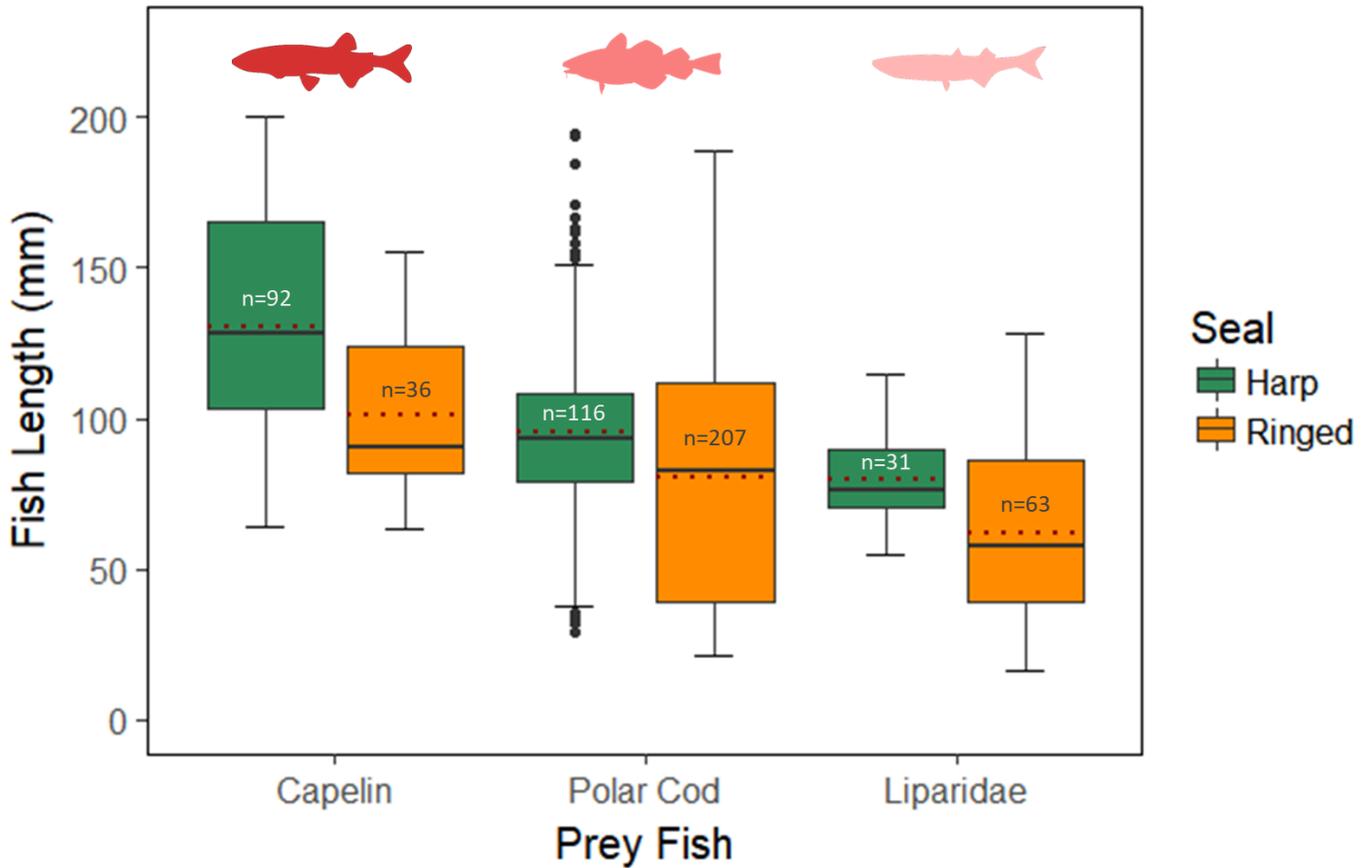


Figure 3.10: Boxplots showing maximum, minimum, median, and the first and third quartiles of the estimated lengths of prey fish found in the stomachs of ringed and harp seals captured in Cumberland Sound during the open-water period from 2008-2016. Outliers are indicated by dots outside of the range of the whiskers, the red dotted lines indicate the mean length of each fish type, and sample sizes for each fish type are denoted.

## Discussion

Co-occurrence of species can lead to competition, especially between closely related species (Hardin 1960); however, if resources are sufficiently abundant, species may segregate resources, thereby reducing the likelihood of competitive exclusion (Alley 1982). Results from our study indicated dietary niche differences between ringed and harp seals prior to sympatry (i.e. different muscle  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ), which was not surprising as each species likely had different prey types available and owing to potential differences in baseline stable isotopic ratios among regions. Once seals were sympatric in Cumberland Sound, however, both species

appeared to forage at a similar trophic position (i.e. no difference in liver  $\delta^{15}\text{N}$ ) and, overall stable isotopes and stomach content analysis indicated high dietary niche overlap, suggesting a high potential for competition. Although consuming many of the same prey species, harp seals consumed more fish and larger fish than ringed seals, suggesting partitioning of resources between species, thereby reducing the likelihood of direct competition.

Despite similarities in dietary composition when ringed and harp seals were sympatric, there were notable dietary differences. First, ringed and harp seals differed significantly in  $\delta^{13}\text{C}$  when sympatric. This implies that, while ringed and harp seals forage on similar prey species, their foraging locations differ, either by depth or habitat (e.g. inshore versus offshore), with the more depleted  $^{13}\text{C}$  in ringed seals suggesting that they feed more pelagically and harp seals more benthically (Hobson *et al.* 2002, Michener and Kaufman 2007), thereby diminishing the degree of realized dietary overlap. Differences in vertical foraging locations could be attributable to differences in dive capabilities between ringed and harp seals (Wathne *et al.* 2000), as body size is the main factor that limits dive depth (Lydersen *et al.* 1992, Kelly and Wartzok 1996). Harp seals (up to 1.7 m in length, ~130 kg; Lavigne 2009) have been recorded diving as deep as 568 m, though most dives are less than 300 m (Folkow *et al.* 2004). Alternately, ringed seals (1.3-1.5 m in length, up to ~100 kg; Hammill 2009) generally dive less than 50 m, although one adult male was recorded diving deeper than the 500 m maximum depth limit of the depth-recording instrument; the next-deepest dive in this study was 360 m (Born *et al.* 2004). Additionally, prey located deeper in the water column tend to be larger (Macpherson and Duarte 1991). These differences in body size and dive capabilities may allow larger harp seals to access prey that are not accessible to smaller ringed seals, possibly driving interspecific dietary differences. In support, stomach contents revealed that harp seals appeared to consume more fish, and fish of

larger size, than ringed seals. Similarly, harp seals in the Barents Sea consumed more fish (specifically polar cod) in the same size range as those collected at depths of about 250 m, while ringed seals mainly consumed smaller fish, in the same size range as those collected at 100-150 m (Wathne *et al.* 2000). Hoskins *et al.* (2017) also showed that the larger, deeper-diving Australian fur seal consumed significantly larger prey (fish, cephalopods, and crustaceans) than did the smaller, shallower-diving New Zealand fur seal.

Additionally, isotopic niche sizes differed between ringed and harp seals, with harp seal niche being smaller for both muscle and liver, suggesting a difference in the degree of dietary specialization between ringed and harp seals. This idea is supported by stomach contents, with harp seal diet composed primarily (two thirds) of capelin and polar cod, which are very similar in their isotopic signatures (Marcoux *et al.* 2012). Harp seals also appeared to exploit more of the resources within the isotopic niche of ringed seals than vice versa. This suggests the possibility of competitive asymmetry (Persson 1985), with ringed seals being potentially more affected by this interaction than harp seals. Generally, larger individuals or organisms have a competitive advantage over smaller competitors due to higher rates of resource exploitation and/or a greater physical ability to displace smaller competitors (Schoener 1983, Persson 1985, Law *et al.* 1997). Since harp seals (e.g. 130 kg; Lavigne 2009) are larger than ringed seals (e.g. 100 kg; Hammill 2009), harp seals might have a competitive advantage at exploiting 78.1% of ringed seal resources, whereby they are more successful at capturing common prey types than ringed seals. Competitive pressures by harp seals under resource-limited conditions could force ringed seals to shift their diet toward the resources represented by the other 21.9% of their isotopic niche. For example, harp seals, which consume more fish, might outcompete ringed seals for common fish prey (primarily polar cod), thus forcing ringed seals to supplement their diet with additional

invertebrate prey, which already make up the majority of their diet, or with other fish species, such as sculpin and snailfish, which already contribute about the same as capelin do to ringed seal diet. Given that these other resources appear to be nutritionally adequate, based on their high contribution to ringed seal diet, an ability of ringed seals to shift their dietary niche in response to competition (Alley 1982) would suggest a potential resilience of ringed seal populations to resource limitation.

Interestingly, fish consumption by ringed seals increased with age. The difference in fish consumption by abundance for age 0 seals appears to be strong enough to reduce the overall overlap below the ecologically meaningful threshold when all ages are grouped. Yet, despite potential dietary differences in young seals (i.e. < age 5), the trends in overlap seem to reflect the dietary metrics of the adults, especially for biomass and energy content. This suggests that young seals (i.e. age 0-4) forage differently and are less consistent in their dietary choices than adults, resulting in greater differences in prey composition between ringed and harp seals. Juvenile seals might forage opportunistically or still be learning to forage efficiently across the range of available prey resources. Younger ringed seals are known to make more dives and at shallower depths than adult ringed seals, indicating that young seals do not consume potential high-quality prey resources (often older/larger fish) deeper in the water column and that individual foraging trips from the ocean surface are likely less fruitful for young seals than for adult seals (Born *et al.* 2004). Similar trends have been shown for other pinnipeds, with young Galapagos fur seals (Horning and Trillmich 1997) and California sea lions (Weise and Costa 2007, Weise *et al.* 2010) making more frequent shallower, shorter dives than adults.

There were also differences in the composition of consumed fish species between ringed and harp seals. Most notably, while ringed and harp seals consumed many of the same fish

species, the frequency and amount of capelin consumed differed, with harp seals consuming more than five times the amount of capelin by energy than ringed seals (37.5 and 7.0%, respectively). Although prey availability and abundance were not quantified during this study, vast, near-shore spawning aggregations of capelin have been observed within Pangnirtung Fjord (present study; McNicholl *et al.* 2018). As such, it is unclear why ringed seals did not forage to a great extent on highly available capelin. Capelin are an important prey source for ringed seals in other regions (Siegstad *et al.* 1998, Chambellant *et al.* 2013), and are often the preferred forage fish for harp seals in regions where they coexist (Beck *et al.* 1993). Capelin are also comparable in energy density to polar cod, perhaps even slightly higher (Elliott and Gaston 2008), and in this study were generally larger, suggesting that capelin are able to provide adequate energy. A possible explanation for this could be differential digestibility between prey species for ringed seals. For example, harp seals digest capelin more efficiently than some cod species, halibut, and herring (Lawson *et al.* 1997). It is possible that ringed seals have similar variability in their digestive capabilities and are more efficient at digesting cod, their preferred fish (20% by energy) or invertebrate species. It is also possible that ringed seals might have simply not learned efficient search and capture techniques for capelin, given that capelin are relatively new (or at least newly-abundant) in the Cumberland Sound ecosystem (Carscadden *et al.* 2013). Harp seals, which regularly consume capelin, may do so cooperatively, as evidenced by large groups (Heithaus and Dill 2009, Diemer *et al.* 2011) of harp seals observed associated with capelin shoals in this study. In contrast, ringed seals are generally observed solitarily (Diemer *et al.* 2011), which likely suggests a solitary foraging strategy. These differences in foraging strategies and capelin consumption between ringed and harp seals could imply that group foraging is a more effective strategy for capelin capture that ringed seals have not learned, thus offering a

potential explanation for the lack of capelin in the diet of ringed seals. Cooperative foraging, perhaps by prey herding (Heithaus and Dill 2009), has been observed in other seals (Gottfried 2014), and may be an effective strategy for capturing certain prey types. With time, ringed seals might modify their foraging techniques to consume more capelin, especially considering that polar cod might become less abundant, essentially being replaced in Arctic ecosystems by capelin (Hop and Gjørseter 2013, Crawford *et al.* 2015).

In conclusion, results from this study highlight the importance of complementing stable isotope data with some additional dietary metric(s), as the two-dimensional nature of carbon and nitrogen stable isotope analysis cannot fully elucidate an animal's realized ecological niche. While stable isotope analysis offers valuable insight into long-term niche use, it lacks the fine-scale detail to determine realized ecological niches on its own. Furthermore, our results emphasize that dietary niche overlap can be overestimated (by both stomach content and stable isotope analyses) if prey size is not considered in addition to prey composition.

To further examine diet similarities between co-occurring ringed and harp seals, future studies using telemetry would be valuable, as telemetry data might reveal further aspects of ringed and harp seal foraging behaviour. For instance, telemetry data paired with dietary metrics could confirm differences in foraging depth, as well as determine the degree to which foraging differs spatially (i.e. inshore vs offshore, benthic vs pelagic) or temporally (i.e. time of day). This information would further our knowledge of seal foraging in Cumberland Sound, and could identify important foraging habitats for both ringed and harp seals. Despite the foraging differences between Cumberland Sound ringed and harp seals outlined in this study, however, the similarities in prey species consumed should not be ignored. With continued climate warming, ecosystem changes will intensify in Arctic systems (Kovacs and Lydersen 2008, IPCC

2014). If these changes are severe enough to significantly deplete or alter prey resources, or to further increase harp seal abundance beyond carrying capacity, there is a high potential for competition to arise between ringed and harp seals. In turn, this could have negative impacts on ringed seals, upon which indigenous communities depend for their subsistence.

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## Appendix A

Table 3A.1: Sample sizes of seal tissues sampled between 2008-2016 in Cumberland Sound, Nunavut.

Sampling Year	Stomach	Liver	Muscle
<b>HARP</b>			
2008	7	5	5
2009	2	-	-
2010	-	1	-
2011	-	1	-
2015	4	4	3
2016	7	9	9
<b>RINGED</b>			
2008	3	6	6
2009	8	5	5
2010	8	6	7
2011	-	14	14
2015	27	27	23
2016	17	17	15

Table 3A.2: Regression equations used to estimate body length, either fork length (FL) or total length (TL) (cm), from otolith length, OL (mm) of fish found in ringed and harp seal stomachs. Seals were captured in Cumberland Sound between 2008-2010 and 2015-2016 during the open water period.

Fish Taxa	Equation	R <sup>2</sup>	Reference
<i>Boreogadus saida</i>	FL=6.088+24.711(OL)	0.98	Lidster <i>et al.</i> 1994
<i>Mallotus villosus</i>	TL=11.726+56.221(OL)	0.96	Lidster <i>et al.</i> 1994
<i>Liparidae (Liparis sp.)</i>	TL=5.7414(OL) <sup>1.3634</sup>	0.83	Chambellant <i>et al.</i> 2013
<i>Cottidae (Myoxocephalus scorpius)</i>	TL=2.2271(OL) <sup>1.2493</sup>	0.83	Chambellant <i>et al.</i> 2013
<i>Cyclopteridae (Cyclopterus lumpus)</i>	TL=-9.95+34.84(OL)	0.86	Harkonen 1986

Table 3A.3: Regression equations used to estimate wet mass (WM; g) from body length (fork FL or total length TL) of fish found in ringed and harp seal stomachs. Seals were captured in Cumberland Sound between 2008-2010 and 2015-2016 during the open water period.

Fish Taxa	Equation	R <sup>2</sup>	Reference
<i>Boreogadus saida</i>	WM=0.0053(FL) <sup>3.042</sup>	0.96	Fey & Weslawski 2017
<i>Mallotus villosus</i>	WM=15.96-0.4451(TL)+0.003242(TL) <sup>2</sup>	0.93	Ogloff Chapter 2
<i>Liparidae (Liparis sp.)</i>	WM=0.0065(BL) <sup>3.1802</sup>	0.96	Chambellant <i>et al.</i> 2013
<i>Cottidae (Myoxocephalus scorpius)</i>	WM=0.0048*(TL) <sup>3.3420</sup>	0.98	Dolgov 1994
<i>Cyclopteridae (Cyclopterus lumpus)</i>	WM=0.000027(L) <sup>3.0811355</sup>	0.99	Gauthier <i>et al.</i> 2017

Table 3A.4: Percent moisture in prey fish taxa used to estimate dry mass (g) of fish found in ringed and harp seal stomachs. Seals were captured in Cumberland Sound between 2008-2010 and 2015-2016 during the open water period.

<b>Fish Taxa</b>	<b>Percent Moisture</b>	<b>Reference</b>
<i>Boreogadus saida</i>	83.5	Walkusz <i>et al.</i> 2012
<i>Mallotus villosus</i>	68.2	Lawson <i>et al.</i> 1998
<i>Liparidae (Liparis fabricii)</i>	86.0	Walkusz <i>et al.</i> 2012
<i>Cottidae (Myoxocephalus scorpius)</i>	76.3	Mace & Davis 1972
<i>Cyclopteridae (Cyclopterus lumpus)</i>	78.1	approximated based on values in Davenport & Kjorsvic 1986

Table 3A.5: Energy content of fish taxa found in ringed and harp seal stomachs. Seals were captured in Cumberland Sound between 2008-2010 and 2015-2016 during the open water period.

<b>Fish Taxa</b>	<b>Energy (kJ/g)</b>	<b>Reference</b>
<i>Boreogadus saida</i>	22.0	Elliott & Gaston 2008
<i>Mallotus villosus</i>	23.5	Elliott & Gaston 2008
<i>Liparidae (Liparis fabricii)</i>	18.4	Walkusz <i>et al.</i> 2012
<i>Cottidae (Myoxocephalus scorpius)</i>	20.9	Mace & Davis 1972
<i>Cyclopteridae (Cyclopterus lumpus)</i>	23.5	approximated based on values in Davenport & Kjorsvic 1986

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## Chapter 4: Synthesis and General Conclusion

Examination of diet and isotopic niche characteristics of capelin, ringed seals, and harp seals provided valuable insight into dietary linkages and species interactions within the Cumberland Sound food web. Results showed that capelin primarily consume small zooplankton. Small capelin (up to ~140 mm) consumed almost exclusively Clausocalanidae, and were primarily immature. Larger, mature capelin had a more varied diet, but became more specialized on larger species with increasing size. The diets of mature capelin varied between study years. Mature capelin in 2015 consumed a varied diet of *Calanus* copepods, mysids, amphipods, and euphausiids, but became more specialized on *Calanus hyperboreus* with increasing size. In 2016, mature capelin consumed mainly amphipods, with smaller amounts of copepods, mysids, and euphausiids, and patterns with increasing size were not obvious. These inter-annual differences are likely related to differences in sampling time between years relative to the start of spawning. In 2015, capelin were sampled at or near the beginning of spawning, while ice was still present in Pangnirtung Fjord; in 2016, however, there was evidence of spawning ~2 weeks before live capelin were observed and sampling could commence, which was not until ice had completely left Pangnirtung Fjord. As such, capelin stomachs from 2016 contained less content than those in 2015. In addition, the content that was present in 2016 was often capelin eggs, further supporting the idea that spawning had already begun before sampling, as capelin are known to cease feeding when spawning (Winters 1970). Isotopic niches of capelin differed between years as well, with 2016 niches being generally broader, perhaps due to a lack of recent feeding or to differences in the prey available to capelin prior to sampling between years. With the later date of ice break-up in 2016, the appearance of ice associated amphipods, mainly *Apherusa glacialis*, in the diet of capelin could help to explain inter-annual isotopic niche

differences. In contrast, the primarily copepod-based diet in 2015 might be related to the earlier date of ice break up, which might have allowed for increased presence of copepods, which feed in the water column, and differ in isotopic composition from amphipods (Pomerleau *et al.* 2016).

When comparing ringed and harp seal diets, results showed a high potential for competition to arise between species, as ringed and harp seal utilized many of the same prey types; however, examining the size of prey as well as isotopic niches seemed to suggest that realized ecological niches differed between seal species. Harp seals consumed a higher proportion of fish than did ringed seals, while ringed seals consumed more invertebrate prey, primarily zooplankton. In addition, the fish consumed by harp seals were significantly larger than fish consumed by ringed seals, and differed slightly in composition. While both seals consumed some proportion of the two major forage fish in the area (capelin and polar cod), ringed seals consumed almost exclusively polar cod and very few capelin, whereas harp seals consumed roughly equal amounts of capelin and polar cod. As well, stable isotopes showed that harp seals tended to feed slightly more benthically and had a narrower isotopic niche breadth. A narrower niche breadth suggests a more specialized diet, which is likely explained by the high dietary composition of capelin and polar cod, which are very similar in their isotopic composition (Marcoux *et al.* 2012). I hypothesize that the more benthic signature of harp seals may be related to their larger body size and greater dive capabilities relative to those of ringed seals (Born *et al.* 2004, Folkow *et al.* 2004), which is supported by the presence in the diet of larger fish, which often reside at greater depth (Macpherson and Duarte 1991). As such, it appears as though ringed seals and harp seals do not compete to a great degree, instead occupying slightly different ecological niches in Cumberland Sound, similar to conclusions drawn in the Barents Sea (Wathne *et al.* 2000).

Overall, given the similarity of capelin diet to the diet of other forage fish present in Cumberland Sound, primarily polar cod, it is possible that capelin may have negative effects on other species in the ecosystem. Capelin have been shown to significantly decrease zooplankton abundance in other Arctic regions (Hassel *et al.* 1991), thus potentially causing resource-limited conditions. Polar cod may, consequently, become threatened by resource-limited conditions and competition with capelin and other zooplanktivorous fish in Cumberland Sound, potentially causing them to experience population declines. In addition, zooplankton is the primary prey for ringed seals, so zooplankton depletion by capelin could have impacts on ringed seals as well. This means that capelin have the potential to negatively impact ringed seals, both as a direct competitor, and as a competitor of ringed seal prey. As generalists, it is possible that ringed seals could switch to consume capelin, but, presently, ringed seals do not appear to take advantage of seemingly high capelin biomass in Cumberland Sound. While it is not possible to draw conclusions as to why this might be, an absence of preferred fish prey for ringed seals, like polar cod, could have negative implications for fitness, especially if there is a physiological reason for a lack of capelin consumption, such as a lower digestibility (Lawson *et al.* 1997).

Although the recent increase in capelin abundance could be negative for ringed seals, it may be beneficial for harp seals. Harp seals are believed to consume capelin as their preferred prey in other regions and have been shown to time their northward migrations with capelin spawning to maximize capelin consumption (Beck *et al.* 1993). In addition, harp seals are able to digest capelin more efficiently than polar cod (Lawson *et al.* 1997). As such, it seems likely that harp seals benefit from high abundances of capelin in Cumberland Sound, and the coincident increases in both capelin and harp seal abundance in Cumberland Sound could be closely linked. If capelin do effectively replace polar cod in the Cumberland Sound ecosystem, evidence seems

to suggest that harp seals will still be able to thrive. Additionally, capelin may be an important resource for other predators in Cumberland Sound, including Arctic Charr (Ulrich 2013), belugas (Watts and Draper 1986, Dahl *et al.* 2000), and seabirds (Carscadden *et al.* 2002), as they are an abundant pulsed resource known to lead to predator hotspots in other regions (Davoren 2013).

In conclusion, it seems as though the recent shifts in the Cumberland Sound ecosystem have both positive and negative consequences. While increased capelin abundance may be positive for some predators, it may be detrimental to ringed seals, which are important for Inuit communities, both culturally and for subsistence. At this stage, it seems impossible to determine whether or not reported reductions in ringed seal numbers (Diemer *et al.* 2011) have been partially caused by concurrent changes to capelin (Carscadden *et al.* 2013) and harp seal (DFO 2011) abundance, though these changes appear to be plausible factors. Numerous other factors, however, are likely at play, including reduced sea ice, disease, hunting pressures, and natural population cycles. Therefore, continued research will be necessary to continue unravelling the mechanisms behind changes to ringed seal populations, especially under the continued influences of climate change.

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