

LIFE HISTORY OF CAPELIN (*MALLOTUS VILLOSUS* (MÜLLER, 1776)) AND DIETARY  
OVERLAP WITH ARCTIC COD (*BOREOGADUS SAIDA* (LEPECHIN, 1774)) IN THE  
CANADIAN ARCTIC

by

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## Abstract

Capelin (*Mallotus villosus* (Müller, 1776)) is an important marine forage fish species that typically inhabits sub-Arctic and temperate circumpolar waters. Capelin have recently been reported in greater abundance in Arctic regions, and are considered an indicator for warming climate in the northern marine ecosystem. The goal of this thesis is to examine intrinsic factors among capelin populations, and whether niche overlap among sympatric capelin and Arctic cod (*Boreogadus saida* (Lepechin, 1774)) will affect the abundance and persistence of capelin in the Arctic as temperatures continue to rise. Life history comparisons of capelin from two Arctic regions (Western Beaufort Sea, Cumberland Sound) relative to a sub-Arctic population (Newfoundland) show that body size, body condition, growth rate and age-at-maturity vary among these regions. Life history characteristics that are adapted to northern environments and increasing temperatures will allow the presence and persistence of this species to increase in the Arctic. The consequence of increased abundance of capelin in the Arctic environment could be competition between capelin and Arctic cod, an Arctic species within a similar dietary niche. Stomach contents indicated that both species feed primarily on calanoid copepods and this result was corroborated with high dietary overlap in isotopic bivariate space (carbon and nitrogen stable isotopes). The occurrence of capelin is expected to increase in the Arctic with rising temperatures, thus adaptation in life history traits in capelin specific to each region may facilitate increased abundance and persistence, and possibly contribute to competitive pressure on Arctic cod. Potential competition will be particularly important in nearshore and shelf habitats where shifts in availability of intermediate trophic level taxa will influence diet and distribution of key predators such as beluga, sea birds, and anadromous fishes. As the Arctic environment changes with climate shifts, newly adapted or dispersed species from sub-Arctic systems are expected to drive shifts in ecosystem structure and function in the marine environment.

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## Thesis Format and Manuscript Claims

This thesis is presented in manuscript format, with a general introduction (Chapter 1), Chapters 2, 3 and 4 written with an abstract, introduction, methods, results, discussion, and references, and finally a synthesis discussion (Chapter 5). Chapter 3 has been published in the special issue “Ecology of Arctic Gadids” in Polar Biology. The student contributions to Chapter 3 are provided below.

### CHAPTER 3

McNicholl, D.G., Walkusz, W., Davoren, G.K., Majewski, A.R. and Reist, J.D. 2015. Dietary characteristics of co-occurring polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) in the Canadian Arctic, Darnley Bay. Polar Biology. doi: 10.1007/s00300-015-1834-5. Published online: 27 November 2015.

D. McNicholl formulated the research questions, designed and performed the sub-sampling of fish stomachs, analysed the data, and wrote the manuscript. W. Walkusz assisted with taxonomy of stomach contents and provided advice and input at each stage. Fishes were collected and provided by A.R. Majewski, whom also provided revisions in the manuscript’s final stages. G.K. Davoren and J.D. Reist provided advice and revisions throughout the development of the manuscript.

## **Chapter One. General Introduction**

The ubiquitous effects of climate change are considered to be significant and accelerated in the Arctic (Reid and Beaugrand 2012). Arctic terrestrial, freshwater and marine ecosystems are experiencing dramatic changes in response to warming climate (Prowse et al. 2009; Reist et al. 2006). The oceanographic processes influenced by the extent, seasonality, and duration of sea ice play a pivotal role in habitat structure for species with sympagic-specific adaptations. Direct changes in temperature and indirect changes in habitat (e.g., reduction of sea ice) pose challenges for ice-associated organisms (Laidre et al. 2008), but may facilitate range expansions of sub-Arctic species restricted to warmer, open water (Moore and Laidre 2006). The reduction in duration and extent of seasonal sea ice is expected to increase primary production and facilitate habitat change in favour of sub-Arctic species (Post et al. 2009). Indeed, northward expansion of sub-Arctic fishes has been observed throughout the Arctic (Dunmall et al. 2013; Rose 2005) together with shifts in energetic pathways and an increase in niche overlap between Arctic and sub-Arctic species (Orlova et al. 2009). To predict and understand the structure of Arctic marine systems in the future, these changes must be further investigated.

Life history traits (e.g., growth, age of sexual maturity) and the extent of phenotypic plasticity among sub-Arctic biota will determine if these species can successfully inhabit Arctic environments. Ultimately, the successful persistence of sub-Arctic species in the Arctic will depend on their growth, survival and reproductive success in this habitat and whether they can successfully integrate into the existing and new trophic structures. Arctic fishes are particularly sensitive to ambient temperature and different species and life history stages within species will respond differently to changes in temperature (Christiansen et al. 1997). At the population-level, responses will depend on both genetic variation through adaptation and phenotypic variation in

response to environmental pressure. Within species, variation may also be evident between populations at the centre of a species distribution relative to those at range limits (Sexton et al. 2009). The reaction norm of a species dictates the response of a phenotype to continuous variation of an environmental factor, with the response being influenced by the upper and lower tolerance limits, typically referred to as the plasticity of an organism (Woltereck 1909). Reaction norms have important implications for the life history variation of a species, including adaptation or mal-adaptation to a particular environment (Stearns 1989). Evolutionary and ecological changes are thus facilitated by reaction norms within a species and their physiochemical responses to the surrounding environment (Dobzhansky 1951).

The niche of a species is shaped by environmental and biological factors in multi-dimensional space (Hutchinson 1957) and is an inter-related reflection of the ecological and evolutionary history of the species (Soberón 2005). The abiotic conditions that determine the potential geographic range of a species represent its fundamental niche, but that range is often further limited to regions with favourable biological interactions. These interactions determine the ability of a species to maintain populations (Soberón 2005) and, thus, they represent the realized niche space of a species. The realized niches and respective tolerances among co-occurring species are closely associated with the availability of resources. For instance, when food resources are limiting, competition may arise among species occupying a similar dietary niche at the same trophic level. One outcome of this interspecific competition is competitive exclusion, where one species out-competes another. Coexistence, however, can be achieved by partitioning resources, but resource partitioning is limited by the flexibility of each competing species to shift foraging strategies and dietary resources, especially the least competitively dominant species.

Arctic and sub-Arctic species respond to annual climate variation and realized niches are expected to shift in response to changing climate and its impact on temperature and availability of prey. The specific responses of these species to warmer years can be used to infer how the ecosystem and the biotic interactions within it may respond to climate change trends. As a result dietary shifts have occurred among key Arctic predators, such as beluga (*Delphinapterus leucas*), sea birds and anadromous fishes, in response to fluctuations in availability and distribution of mid-trophic level prey taxa (Dempson 2002, Gaston et al. 2003).

In the sub-Arctic marine system, capelin, *Mallotus villosus* (Müller, 1776), are an excellent indicator of marine climate conditions (Dunbar 1983) and have been described as a “sea canary” for a warmer Arctic scenario (Rose 2005). Shifts in the distribution of capelin in response to changing temperatures (Rose 2005) or increased appearance of capelin in the diets of Arctic predators (Gaston et al. 2003) both imply present ecosystem change in the Arctic.

### *Biology of capelin*

Capelin is a pelagic, schooling fish of the family Osmeridae and is abundant in sub-Arctic waters in the Northern Hemisphere. They are notably abundant in the Barents Sea, Alaskan Gulf, Iceland Sea, Bering Sea and off the coast of Newfoundland and Labrador. Capelin are short-lived, small fish typically <200 mm in length. They mature at age 2-4 and rarely exceed age 5+ (Gjøsæter and Loeng 1987; Huse 1998). Spawning occurs demersally on beaches or in deeper water (Carscadden et al. 2013b). This species typically undergoes extensive migrations to spawn and to access offshore feeding grounds. Capelin serve as an energy-rich prey source to predators in near-shore and offshore environments. Capelin play an important ecological role by



transferring energy from lower trophic levels (e.g., zooplankton) to upper trophic level predators such as marine mammals, seabirds and piscivorous fishes (Carscadden and Vilhjálmsson 2002). Accordingly, understanding the factors that influence the distribution and life history of capelin in marine systems is important for understanding overall ecosystem structure and function and potential shifts associated with climate variability and change.

Temperature influences the distribution of capelin (Carscadden et al. 2013a) and specifically limits the ability for populations to persist in polar waters. It is unknown if capelin can overwinter in sub-zero temperatures, but they are known to occur in waters with temperatures as low as  $-1.5^{\circ}\text{C}$  (Carscadden et al. 1989). To persist in Arctic water, capelin must avoid freezing by a combination of behavioural and biochemical means. Capelin tolerate temperatures near  $0^{\circ}\text{C}$  by avoiding ice or areas of ice formation (Raymond and Hassel 2000), but high mortality due to freezing still poses a significant risk (Templeman 1965). As a result, capelin are typically found south of ice edges (Carscadden et al. 2013a), and appear to prefer temperatures between  $-1^{\circ}\text{C}$  and  $3^{\circ}\text{C}$  (Ingvaldsen and Gjøsæter 2013). Other osmerids produce an antifreeze protein (Ewart et al. 1992), which prevents freezing in Arctic waters during the winter. Capelin do not produce this antifreeze protein, but do produce significant quantities of trimethylamine oxide in their blood during the winter (Raymond and Hassel 2000). High concentrations of this compound contribute significantly to the winter freezing point depression of cold-acclimatized osmerids (Raymond 1994). Thus, capelin may have adaptations that facilitate occupancy of Arctic habitats particularly as those may shift towards sub-Arctic conditions with climate change.

Capelin are considered to be highly mobile, due to their long distance migrations over their lifespan as well as large scale distributional shifts with small changes in temperature (Rose

2005). Indeed, within the last decade a general northward shift of large stocks (i.e., Barents Sea, Iceland and Newfoundland) has been observed in response to increasing temperatures and reduced ice cover (Ingvaldsen and Gjøsæter 2013; Rose 2005). These northward shifts in distribution are attributed to the direct effects of temperature, coupled with the indirect effects related to zooplankton abundance. Such changes in prey availability have resulted in extreme population fluctuations documented in recent capelin stock assessments for the Barents Sea (Hop and Gjøsæter 2013). Shifts in capelin distribution are expected to occur globally, but are predicted to be the most significant in the Arctic (Carscadden et al. 2013a). The reduction of sea ice is expected to increase annual primary production in the Arctic Ocean (Arrigo et al. 2008), which will increase the abundance of secondary consumers preyed upon by capelin (Moore and Laidre 2006). Therefore, shifts in the abundance and distribution of capelin into the Canadian Arctic are expected to influence trophic dynamics at the mid-trophic level and have a significant impact on future ecosystem structure and function. In the Canadian Arctic, it has been suggested that an increase in temperature coupled with the reduction of sea ice may serve as good predictors for shifts in distribution of capelin (Gaston et al. 2003).

Capelin generally display an r-selected life history strategy, thus are prone to substantive population fluctuations, and variation in reproductive success among year classes. Capelin typically exhibit a single spawning (semelparous) strategy, but repeat spawning (iteroparous) strategies are also observed, although at low frequencies (Christiansen et al. 2008, Maxner et al. 2016). The proportion of iteroparous and semelparous capelin in a population is important for population dynamics, because repeat-spawning individuals enhance population stability in a highly variable habitat (Schaffer 1974; Resetarits 1996). Fecundity of capelin varies due to intrinsic factors such as length (Gjøsæter and Monstad 1973; Penton and Davoren 2008), age

(Winters 1971) and population density (Galkin and Kovalev 1975). Male capelin are generally larger than females but have greater post-spawning mortality (91%; compared to 49-75% in females; Shackell et al. 1994). Female capelin that survive post-spawning will continue to grow and spawn in subsequent years (Christiansen et al. 2008).

Maturing capelin typically segregate from stocks of immature individuals during the winter in offshore pelagic water (Carscadden et al. 2013b) as their gonads develop prior to summer spawning. During the spring, mature capelin migrate inshore to spawn on beach or deep-water sediments. Spawning locations are selected based on substrate size and temperature (Davoren et al. 2008). Optimal spawning temperatures are between 4°C and 7°C (Penton and Davoren 2013), but spawning can occur within a temperature range of 2°C - 12.0°C (Templeman 1948). Recent observations indicate that capelin can move between beach and deep-water spawning habitats when temperatures within a habitat fall outside the optimum range (Davoren 2013), but simultaneous use of deep-water and beach spawning habitats has also been observed (Nakashima and Wheeler 2002). Once eggs are released, they adhere to substrate during development and depending on temperature will hatch 15-50 days later (Frank and Leggett 1981; Pethon 1994). Larval capelin will disperse offshore from nearshore spawning sites by wind-forced surface currents or advection (deYoung et al. 1994). Mean temperature in surface waters (0-20 m) positively influences recruitment success of capelin during the first six months of their pelagic existence (Carscadden et al. 1989). In this upper surface layer, the abundance of larval capelin depends on temperature in combination with production of copepod nauplii (Cooney 1986), which are the primary prey taxa for larval capelin once exogenous feeding by the larval capelin begins.

Factors known to significantly influence capelin growth include temperature (Gjøsæter and Loeng 1987), prey availability (Gjøsæter et al. 2002), and interspecific competition among co-occurring fishes (Orlova et al. 2009). Zooplankton abundance significantly affects capelin stock size across all capelin age classes (Gjøsæter 1999), which are closely correlated with the abundance of zooplankton from the previous autumn (Gjøsæter et al. 2002). Sex-specific life history strategies are observed in mature male and female capelin resulting in sexual dimorphism. Capelin growth increases between winter and spring, and is greatest among larger individuals capable of consuming later-stage energy rich zooplankton (O'Driscoll et al. 2001). The relationship between foraging area and growth is regarded as a function of temperature and is associated with a general increase in capelin length (Gjøsæter and Loeng 1987). Back-calculated estimates of growth in Greenland capelin have also indicated that the average size increases with latitude and temperature (Hedeholm et al. 2010).

Few studies have investigated capelin in the Canadian Arctic and their role in local ecosystem function. The occurrence of capelin in the western Arctic (Beaufort Sea) and eastern Arctic (Baffin Island, NU) has been considered rare or sporadic (Carscadden and Vilhjálmsson 2002), but recent evidence and traditional ecological knowledge suggest that capelin may be more abundant than previously documented. Weak genetic barriers exist between Pacific capelin and those in the western Arctic (Præbel et al. 2008), and these two populations are likely more closely related than either one is with Atlantic populations. Although genetic barriers also exist among Atlantic populations of capelin, these populations are believed to be more closely related among themselves than to populations of Pacific origin (Præbel et al. 2008). It is uncertain, however, if capelin in the eastern Arctic represent isolated populations relative to those in Newfoundland or Greenland. It is possible that the present populations of capelin in the

Canadian Arctic are distinct from those in sub-Arctic regions. It remains unclear, however, if these individuals remain in the Arctic year-round or if these populations are annually replenished by individuals that have dispersed from southern locations.

Migrations from either Hudson Bay or the northern Pacific Ocean to the Beaufort Sea and Amundsen Gulf would require traveling a minimum 2000 km (from the Chukchi Sea) while following the coastline. In the Bay of Fundy, capelin have migrated as far as 1200 km to spawn, apparently in response to temperature (Frank et al. 1996). The ability for capelin to complete a migration from the Chukchi Sea to the Beaufort Sea is currently unknown. Another possibility is that they persist in the Beaufort Sea area year-round. In the Barents Sea, capelin are known to descend into demersal water (50 m) on coastal slopes to overwinter in temperatures between 2°C to 4°C and exhibit minimal activity (Ozhigin and Luka 1985). It remains unknown if capelin persist year-round, however, temperatures above 0°C may be found in this region in the Beaufort Sea, in a water layer of Atlantic origin (approximately 300 m depth). Aggregations of other forage fishes, such as Arctic cod, have been observed in this layer during the winter (Geoffroy et al. 2011).

Overall, the combination of an r-type life history strategy, high potential for dispersal, and ability to migrate substantive distances is favourable for capelin to colonize newly available habitat. Indeed, capelin are already present in the Arctic ecosystem, and their abundance and distribution may be expected to increase, faster based on their previously observed responses to changing temperature increases (Rose 2005), and their prominence in the marine food web that has increased in recent decades (Dempson et al. 2002; Gaston et al. 2003).

### *Co-occurrence of capelin and Arctic cod*

Arctic cod, *Boreogadus saida* (Lepechin, 1774), is an abundant forage fish species found throughout much of the Arctic Ocean and are closely associated with sea ice. Similar to capelin, Arctic cod are a planktivorous, mid-trophic level species that occupies a similar trophic niche. This sympagic species is dependent on ice throughout its lifecycle, particularly for reproduction and early development. This species has evolved antifreeze glycoproteins that lower the freezing point of their tissues below that of the ambient water temperature. Thus, Arctic cod occur regularly in temperatures as low as  $-1.9^{\circ}\text{C}$  (DeVries 1971). Arctic cod are relatively small ( $< 300$  mm) and short-lived fish (Scott and Scott, 1988), rarely exceeding five years of age (Bradstreet et al. 1986).

Similar to capelin, Arctic cod transfer energy between lower and upper trophic levels and serve as an abundant food source exploited by top predators such as beluga whales, seals, Arctic seabirds and anadromous fishes. An increase in abundance of capelin in the Arctic will likely result in dietary shifts among marine predators away from Arctic-adapted prey taxa towards capelin as a primary prey taxa (Gaston et al. 2003), as Arctic species are expected to decline. The likelihood that capelin could replace Arctic cod as a primary forage fish is uncertain. Should this occur, there would be important ramifications for the food web because it is likely that capelin would display greater fluctuations in abundance and availability than do Arctic cod, particularly in the coastal environment (Hop and Gjøsaeter 2013).

Presently, few studies have focused on the co-occurrence of capelin and Arctic cod and the conditions under which it occurs. Temperature and sea ice normally separate these species from one another, with capelin being restricted to relatively warmer, open waters, whereas Arctic cod are associated with ice in colder waters (Hop and Gjøsaeter 2013). However, these species do

co-occur, for example, in the marginal ice zones in the Barents Sea (Hop and Gjørseter 2013).

The extent of spatial overlap between these capelin and Arctic cod in the Canadian Arctic throughout the year is unknown.

### *Potential for competition*

In terms of potential dietary overlap, in regions where they co-occur, capelin and Arctic cod both prey upon marine invertebrates and typically occupy the third level of trophic webs (Hop et al. 2002). Arctic cod are considered generalist feeders throughout their life with a diet composed of copepods, amphipods, mysids and euphausiids (Bradstreet et al. 1986; Lønne and Gulliksen 1989; Walkusz et al. 2011; Christiansen et al. 2012). In the coastal Beaufort Sea, the diet of demersal Arctic cod is dominated by copepods, mysids and amphipods (Walkusz et al. 2013). The diet of age +0 Arctic cod (<80 mm standard length) was composed primarily of copepods, while the diet of those between the ages 1-4 displayed higher diversity (Walkusz et al. 2013). Although Arctic cod are strongly associated with sea ice, their fatty acid signatures suggest they rely on pelagic prey as opposed to ice-associated invertebrates (Graham et al. 2014). Thus, pelagic prey are considered to be a more important dietary source for Arctic cod. Like Arctic cod, capelin rely on secondary production, but the consumption of prey items varies according to body size, location and season (O'Driscoll et al. 2001; Davoren 2013). In the Barents Sea, a comparison of diet between co-occurring capelin and Arctic cod indicated that even though both species used zooplankton sources, there was some difference in feeding preference between them, regardless of size class. Arctic cod fed primarily on copepods (i.e., 49.6% for cod 130-150 mm long and 31.9% for 210-270 mm) whereas the diet of capelin was dominated by copepods (56.5% for capelin <120 mm long) and euphausiids (51.7% for capelin >120 mm; Hop and Gjørseter 2013). Elsewhere, mature and juvenile capelin exhibit different

feeding behaviour due to body size and the size of their available prey (Carscadden et al. 2001), and typically display different migration patterns while feeding (Fauchald et al. 2006). When Arctic cod and capelin co-occur, capelin appear to have a lower body condition (up to 40% reduction of fat content, Orlova et al. 2009) potentially due to the combined effects of competition and maintaining physiological functioning under stressful environmental conditions. Immature capelin have also been observed switching to prey sources with lower energetic value (i.e., chaetognaths; arrow worms) when co-occurring in regions dominated by Arctic cod (Orlova et al. 2009). Overall, the effect of climate-induced change on the availability of preferred prey types, may increase inter-specific competition as conditions become more favourable for sub-arctic-adapted species. As Arctic conditions shift in response to climate change, it may be assumed that not only the occurrence and abundance of these two forage fish species will change, but also their interactions may change reflecting changes in the availability of preferred prey types. Investigation of capelin biology in the Arctic is the theme of this thesis to underpin future studies of potential responses to climate variability and change.

### *Thesis objectives*

This thesis examines the variation in life history characteristics of capelin in the Canadian Arctic and the potential for competition with Arctic cod based on dietary overlap. The spawning ecology of capelin together with interactions among co-occurring species will influence capelin abundance and persistence in the Arctic, and likely affect the trophic structure in Arctic regions. Specifically, I quantified and compared the life history traits of spawning capelin from two Arctic populations and one sub-Arctic population to determine whether body size, condition, age-at-maturity and growth differed among these regions (Chapter 2). Stomach content analysis was then conducted on co-occurring immature capelin and Arctic cod in the Canadian Beaufort



Sea to identify primary prey taxa consumed and the extent of dietary overlap, as well as whether diet varied among size classes within each species (Chapter 3). Lastly, to quantify the extent of dietary overlap of these two species over a longer temporal and spatial scale, I used stable isotope analysis (Chapter 4). By examining intrinsic factors (e.g., life history traits) that influence population dynamics and dietary overlap, which illustrates the potential for competition between these species when they co-occur, I provide a greater understanding of the current role of capelin in Canadian Arctic ecosystems, and how shifts in their abundance may influence ecosystem structure and function in the future.

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## **Chapter Two. Life history characteristics and spawning ecology of Capelin in the eastern and western Canadian Arctic.**

### **Abstract**

Life history trait variation within a species promotes regional-specific strategies that optimize fitness in a particular environment. Capelin (*Mallotus villosus* (Müller, 1776)) is an important forage fish species in circumpolar, sub-Arctic waters. In the sub-Arctic waters they are a primary prey source for marine predators and represent a critical link among trophic levels. This species is typically considered a sub-Arctic species, but undergoes pronounced geographical and ecological shifts in response to changes in temperature, and, thus, is expected to increase in abundance and persistence throughout Arctic regions as marine conditions warm. We compared the life history characteristics (length, body condition, age and growth) of spawning male capelin from the Arctic (eastern Canadian Arctic (Pangnirtung Fjord, NU) and western Canadian Arctic (Darnley Bay, NT)) and a sub-Arctic location (Newfoundland) sampled during July 2014. Capelin were smallest in the western Arctic (mean  $\pm$  SE;  $147.0 \pm 0.8$  mm) relative to those from Pangnirtung Fjord ( $180.25 \pm 2.0$  mm) and Newfoundland ( $177.0 \pm 2.5$  mm); however, body condition (Fulton's K) was lowest in Newfoundland ( $5.7 \pm 0.06$ ) relative to those from Pangnirtung Fjord ( $6.1 \pm 0.06$ ), and Darnley Bay ( $6.1 \pm 0.07$ ). The age structure of spawning males suggested that Newfoundland capelin reach sexual maturity at a younger age than individuals in Arctic populations. Mixed-effect models indicated that first year growth was highest for Newfoundland capelin relative to both Arctic populations, but Pangnirtung and Newfoundland capelin reached similar lengths by age  $\geq 4$ , whereas Darnley Bay fish were smaller. These regional differences suggest that each population may respond differently to shifts in temperature and availability of prey as climate changes, and thus impact foraging availability

and rate of growth. A greater understanding of habitat use and diet at the early life history stages, along with information on ages of sexual maturity, are necessary to further evaluate how capelin abundance and persistence will respond to the warming marine ecosystems in Arctic regions.

## **Introduction**

Local adaptation to environmental conditions across latitudinal gradients is often expressed as variation in growth, age and reproductive strategies within a species (Leggett and Carscadden 1978). Populations at the edge of a species' distribution may experience greater variation in survival and reproduction in environments due to extreme seasonality (e.g., temperature, foraging availability), relative to populations in the center of their distribution (Sexton et al. 2009). Variation in life history traits may therefore allow marginal populations to persist in environments where favourable habitat may be sparse or limiting (Schaffer 1974; Resetarits 1996; Schindler et al 2010). Divergent environmental conditions experienced by geographically distinct local populations may result in the adaptation of region-specific life history strategies among populations within a species (Carroll et al. 2007; Jørgensen et al. 2007; Hutchings and Fraser 2008). Population-specific adaptations to latitudinal differences or phenotypic plasticity due to differences in temperature (Beverton 1987) both contribute to region-specific life history variation within species, which may include slower growth, larger body sizes (Bergmann 1847), later maturation (Charnov and Berrigan 1991), and a greater allocation towards reproduction than growth (Blanck and Lamouroux 2006) in populations at higher latitudes.

Forage fishes in marine ecosystems are the primary energetic linkages between planktivorous species at the lower trophic levels and higher-level predators (Gjørseter and Loeng

1987, Hassel et al. 1991, Gjøsæter et al. 2002). Capelin (*Mallotus villosus*) is a small osmerid fish found throughout northern latitudes and is a dominant forage fish in sub-Arctic ecosystems. Capelin have a circumpolar, temperate distribution (Carscadden et al. 2013) and are found to a lesser extent in Arctic environments, such as the Beaufort Sea (McNicholl et al. 2015) and embayments associated with Baffin Island (Ulrich 2013). Genetic variation among capelin throughout their circumpolar distribution indicates that Pacific and Atlantic-associated populations are genetically distinct and Newfoundland stocks are distinct from those in the northeast Atlantic (Præbel et al. 2008). It is unclear, however, if capelin stocks within the northwest Atlantic are distinct from one another or how such differences may contribute to variation in life history traits. Capelin are generally small (<200 mm; Loeng 1989), short-lived (rarely exceeding age 6+; Gjøsæter and Loeng 1987; Huse 1998), and are typically semelparous (i.e., spawn once and die), although some repeat spawning occurs among beach-spawning females of some populations (Burton and Flynn 1998; Christiansen et al. 2008). The capelin spawning population is typically characterized by fluctuations in abundance with high variation in year-class strength (Gjøsæter 1998; Carscadden et al. 2013). Capelin are known to exhibit pronounced variation in geographical distribution at both larval and adult life stages in relation to large-scale shifts in temperature (Rose 2005). Regime shifts towards a warmer climate are inducing a shift in abundance and persistence of capelin in some areas, such that they are becoming more prominent in northern ecosystems (Dempson et al. 2002; Gaston et al. 2003). Dietary shifts among predators in such environments will likely alter foraging behaviour and may have implications related to availability of capelin as a prey source. Shifts in forage fish structure in Arctic ecosystems are likely to engender profound effects on overall energetics and trophic patterns.

The aim of this study is to compare life history characteristics of mature spawning capelin among coastal regions in the eastern (Pangnirtung) and western (Darnley Bay) Canadian Arctic and one sub-Arctic region (Newfoundland) in the context of regional environmental differences. Specifically, we investigated if region influenced somatic body condition, growth (i.e., length-at-age) and age-at-maturity. As otoliths record fish growth (Hedeholm et al. 2010), thus length-at-age was back-calculated from otoliths allows for retrospective growth comparisons among the regions. We predict that based on the oceanographic differences (e.g., temperature), life history traits (i.e., length, condition, age-at-maturity) of capelin will vary between the eastern and western Arctic, as well as with latitude between Arctic (Pangnirtung Fjord and/or Darnley Bay) and sub-Arctic (Newfoundland). The environmental conditions (e.g., colder temperature, shorter open water season) associated with Arctic locations were expected to result in lower growth rates and size in Arctic populations relative to the sub-Arctic population. Overall, this study provides insight as to how these populations may change in geographic occurrence and relative abundance under the scenario of a warmer Arctic.

## **Methods**

### *Study sites*

Capelin were sampled in three geographically distinct regions during July, 2014 (Fig 2.1). The sampling locations were categorized as Arctic or sub-Arctic based on whether upper water layers (<100 m) are of polar or non-polar origins (Dunbar 1953). In the western Arctic, Darnley Bay (Northwest Territories) is closely linked by oceanographic processes with the adjacent Amundsen Gulf and is considered to be Arctic in nature. The maximum depths within the bay

are <200 m; however, depth increases from the mouth of the bay into the Amundsen Gulf. Landfast ice forms in Darnley Bay forms each fall, and breakup occurs in the spring (late June), at which time it also receives freshwater discharge of the Hornaday and Brock Rivers. Sea surface temperature during the open water season is generally between 5 and 10 °C.



**Fig. 2.1** Locations (solid circles) where mature capelin were collected during the summer (July) of 2014.

In the eastern Arctic, Pangnirtung Fjord (Nunavut) has complete landfast ice cover each winter, similar to Darnley Bay, but this region is also substantially affected by circulation of Atlantic



water masses in Baffin Bay and Davis Strait. The fjord is a glacial trough (160 m maximum depth) that is separated from Cumberland Sound and Baffin Bay by four shallower sills extending across the width of the fjord. The fjord receives glacial discharge from the Penny Ice Cap. At the regional scale, Panguit Fjord is influenced by the cold (-1.8 to 1.8 °C; Bailey 1957), south-flowing, Baffin Island Current. It is also affected by circulation of warmer Atlantic water masses in the Baffin Bay and Davis Strait (Dunbar 1951; 1968).

In the eastern North American sub-Arctic, the northeast coast of Newfoundland is subject to oceanographic characteristics that are influenced by both the warmer North Atlantic current and colder south-flowing Labrador Current. The Labrador Current forms a cold (<0 °C) intermediate layer along the continental shelf between depths of 50 to 240 m (Petrie et al. 1988); however, capelin are commonly found at depths >240 m where temperatures are above 0 °C (Mowbray 2002). Sea ice forms on the northeastern coast of Newfoundland; however, it is likely that capelin in this region are less restricted by the formation of ice than may be seen at the higher latitudes.

### *Capelin sampling*

In coastal Darnley Bay, nearshore fishes were sampled at two field sites, Bennett Point (69.72845°N; 124.08906°W) and Brown's Harbour (70.12051°N; 124.38951°W) using demersal gill nets with a variety of mesh sizes (20 m panels with 1.3 cm, 2.5 cm mesh and 60 m panels of 2.5 cm and 3.8 cm mesh), and trap nets (fyke design; 1.7 m deep; 15.2 m wings) with 1.25 cm knotless nylon mesh. Gill nets and trap nets were deployed at multiple locations representative of various habitat types (e.g., cobble, silt and sand substrates). The depth and duration of net

deployments were recorded at each location, and loggers (Hobo conductivity Pro V2 logger) deployed on the nets continuously collected temperature and salinity data at 30 s intervals. Mature capelin collected were measured for body mass (g), and total, standard and fork-lengths (mm) in the field and then immediately frozen.

In Pangnirtung Fjord (66 14.021°N, 65.73.684°W), mature capelin were sampled at beaches among intertidal rocks during low tide using a dip net (38 cm diameter; 0.32 cm mesh). Fish were sampled each day they were observed near shore and frozen immediately. Near-surface aggregations of immature capelin collected during July 2015 were used to supplement the data on age-length relationships. Temperature was collected as point measurements using a YSI probe each time capelin were collected in shallow intertidal waters. On the northeast coast of Newfoundland, mature capelin were sampled at one beach spawning site (Anchor Brook; 49 22.934 °N, 53 43.785 °W) using a dip net (38 cm diameter, 0.32 cm mesh) and one deeper water (17 m) spawning site (49 14.1134 °N, 53 26.225 °W) using a purse seine (26 x 146 m, 0.21 cm mesh). Each sample consisted of 200 capelin (males and females combined), which were collected haphazardly from the larger netted sample and frozen immediately. Temperature was recorded using loggers deployed throughout the spawning period (42K Hobo Water Temperature Pro V2 Loggers) and set to record data each hour at a beach and deep-water site.

### *Laboratory processing*

Mature and immature capelin were thawed and total length (mm), body mass (g) and gonad mass (g) were recorded together with sex and macroscopically determined maturity stage (1=immature, 2=maturing, 3=ripe, 4=partially spent, 5=spent; see Flynn et al. 2001 for details).

For Newfoundland capelin, body mass, gonad mass and otoliths were examined for a subsample of up to two fish per sex per 5 mm length category (range: 100-195 mm) in each sample. Total length of capelin sampled in Pangnirtung and Newfoundland was determined after fish were thawed, therefore thawed lengths were corrected for shrinkage by multiplying by a factor of 1.03 (Winters 1982; O'Driscoll et al. 2001). Otoliths were removed and stored dry.

Age was determined by counting the number of translucent bands, representative of decreased winter growth (Gjøsæter, 1985; Hedeholm et al. 2010). Dried sagittal otoliths were placed on a black background, sulcus side down, immersed in water and illuminated with reflected light. Photographs were taken of each otolith under 2x and 5x magnification. All otoliths were aged by two independent readers, and otoliths were not used in further analyses if discrepancies occurred between readers. For otoliths from confidently aged individuals, we used image analysis software (Image-J) to measure increment widths ( $\mu\text{m}$ ) from the center of the otolith (i.e., core) to the outer edge of the first translucent zone and then to the outer edge of each translucent zone along a line perpendicular to the annuli, following Hedeholm et al. (2010). Increments in all otoliths were measured twice by the same reader blindly and otoliths were discarded from analyses if measurements differed by  $>10\%$ .

### *Data Analyses*

To compare life history characteristics of mature male capelin among the three regions, somatic body condition was quantified as a modified version of Fulton's K (Carscadden and Frank, 2002) using the following formula:

$$K = \{[\text{total body weight (g)} - \text{gonad weight (g)}] / (\text{total length (cm)})^3\} \times 10^3$$

Length-at-age was back-calculated using the following equation from Campana (1990):

$$L_a = L_c + (O_a - O_c)(L_c - L_i)(O_c - O_i)^{-1}$$

where  $L_a$  is the length at a given age,  $L_c$  is the length at capture,  $O_a$  is the otolith radius length at a particular age,  $O_c$  is the radius length at capture, and  $L_i$  and  $O_i$  are the respective biological intercepts. The biological intercept was set at a total fish length of 35 mm and an otolith radius of 0.08 mm determined from Gjøsæter (1999). Prior to back-calculation, a linear relationship between otolith radius and total fish length was assessed to ensure the otolith-fish length relationships displayed a linear relationship (Appendix A).

Analysis of variance (ANOVA) compared body condition and length-at-age of mature male capelin among the three regions, followed by Tukey HSD post hoc tests. If assumptions for normality and homogeneity of variance were not met, non-parametric tests were used. The mixed-effects model developed by Weisberg (2010) was applied to compare growth-at-age (i.e., annual otolith increment width) among regions and ages, while accounting for random effects (individual and inter-annual variation in growth). The mixed effects model also includes an interaction term and is summarized in the following formula:

$$y_{cka} = i_a + h_{c+a-1} + Y_{ck} + (ih)_{a,c+a-1} + f_{ck} + e_{cka}$$

where  $y_{cka}$  is the  $a$ -th annular increment for the  $k$ -th fish from year-class  $c$ . The fixed-effects include:  $i_a$ , the annular increment for year of life  $a$ ;  $h$ , the effect of environment for year class  $c$  of age  $a$ ;  $Y_{ck}$ , a variable used to represent a fish found in a particular region for the  $k$ -th fish in a year class  $c$ . The parameter includes an interaction term for age,  $(ih)_{a,c+a-1}$ , with region. The parameter,  $f_{ck}$  represents the random effect with zero mean variance  $\sigma_f^2$  for the  $k$ -th fish of year class  $c$ . Finally  $e_{cka}$  is assumed to be independent of errors with mean zero and common variance. Linear models without the interaction terms were calculated using restricted maximum likelihood estimation and were compared using Akaike information criteria (AIC) to determine the best model for describing increment growth, as reflected by otolith increments.

## Results

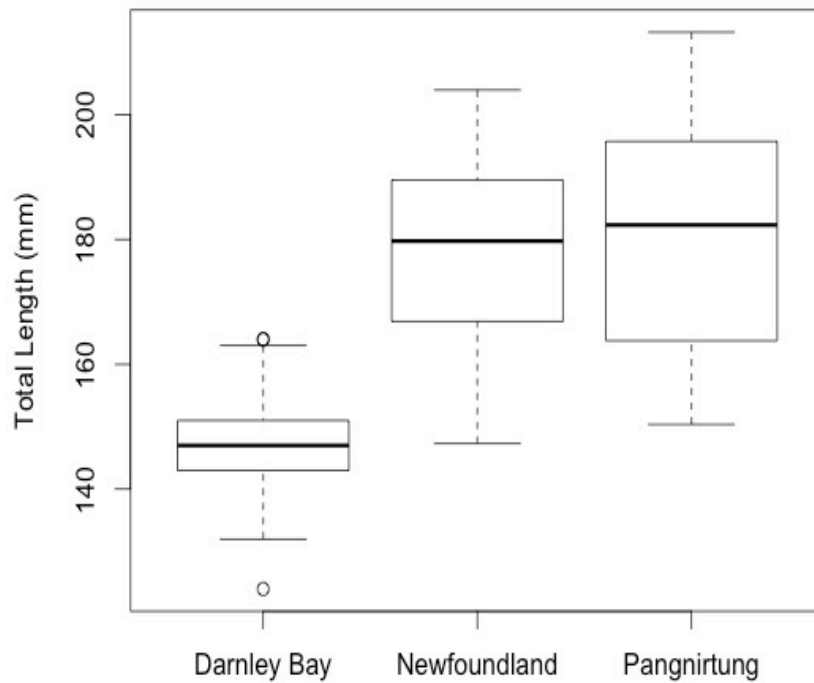
In all three regions, mature capelin were collected where capelin eggs were observed adhered to sediment. In Darnley Bay, the proportions of spent and ripe males were similar, whereas captured females were primarily spent (Table 2.1). Capelin eggs observed adhered to the sediment and net at one site, were determined to be in early developmental stages. Capelin in Pangnirtung Fjord were collected at intertidal spawning sites, whereas capelin in Newfoundland were collected at both one beach and one deep-water spawning site. Male capelin collected in Pangnirtung and Newfoundland were primarily spent, whereas female capelin collected in Newfoundland were primarily ripe.

Temperatures observed during spawning were lower in Darnley Bay relative to those in Pangnirtung and Newfoundland; however, these temperatures were based on limited observations (Table 2.1) and, thus, statistical tests were not conducted.

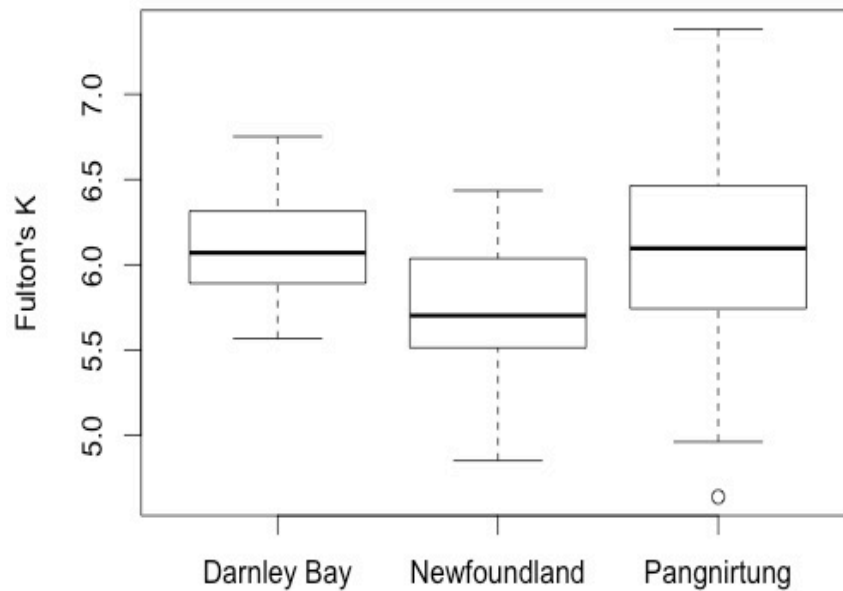
<b>Table 2.1</b> Mature capelin collected during July 2014 from Darnley Bay (trap net), Pangnirtung Fjord and the northeast coast of Newfoundland (dip net). Proportions of spent and ripe individuals were obtained from a randomly selected subset of Darnley Bay (n= 73). All individuals captured in Pangnirtung Fjord and Newfoundland were used in analysis. Only spent and ripe individuals are expressed as percentages; maturity of remaining individuals could not be determined. Mean temperature for each location was determined for dates indicated in brackets. Note that M refers to males, while F refers to females.			
	Darnley Bay	Pangnirtung Fjord	Newfoundland
Date Range	July 14 – 25	July 7-10	July 7 – 18
N (M; F)	273 (91; 178)	75 (74; 1)	74 (36; 38)
Temperature Range (°C)	-0.4 to 5.8 (July 14)	5.5 to 5.9 (July 10)	0.9 to 10.9 (July 7; Beach) 2.5 to 6.2 (July 18; Deep-water)
% Ripe (M; F)	(44%; 11%)	(23%; -)	(14%; 61%)
% Spent (M; F)	(47%; 81%)	(76%; -)	(78%; 21%)
Spawning Habitat	Beach	Beach	Beach / Deep-water

Life history characteristics of mature male capelin were compared among the three regions to avoid potential sex biases associated with the low number of females collected in Pangnirtung Fjord (n=1; Table 2.1). Kruskal-Wallis non-parametric tests were used, as total length did not meet the assumption of normality. Total length of mature males differed significantly among the three regions ( $X^2 = 130.0$ ,  $p < 0.0001$ ; Fig. 2.2), and Dunn's post hoc tests indicated that Darnley Bay males were smaller (mean  $\pm$  SE,  $147.0 \pm 0.8$  mm) relative to those from Pangnirtung Fjord ( $180.25 \pm 2.0$  mm;  $Z = -10.6$ ,  $p \leq 0.0001$ ) and Newfoundland ( $177.0 \pm 2.5$  mm;  $Z = -7.8$ ,  $p \leq 0.0001$ ). The total length of Newfoundland and Pangnirtung Fjord males, however, did not differ significantly ( $Z = -0.6$ ;  $p = 0.3$ , Fig. 2.2). Body condition (modified Fulton's K) differed significantly among regions ( $F_{2,128} = 8.0$ ;  $p \leq 0.001$ ; Fig. 2.3). Tukey HSD post hoc tests indicated that somatic condition in Newfoundland ( $5.7 \pm 0.06$ ) capelin was significantly than those in

Pangnirtung Fjord ( $6.1 \pm 0.06$ ;  $p=0.001$ ) and Darnley Bay ( $6.1 \pm 0.07$ ;  $p=0.003$ ); however, there were no differences between males from Pangnirtung Fjord and Darnley Bay ( $p=0.9$ ).



**Fig. 2.2** Comparison of total lengths among mature, male capelin collected in Darnley Bay (n=91), Newfoundland (n=36) and Pangnirtung (n=74) during July, 2014. Whiskers represent maximum and minimum values (excluding outliers, represented by small circles), the bottom of the box represents the lower quartile and the top represents the upper quartile, and the median is indicated by the bold line through each plot.

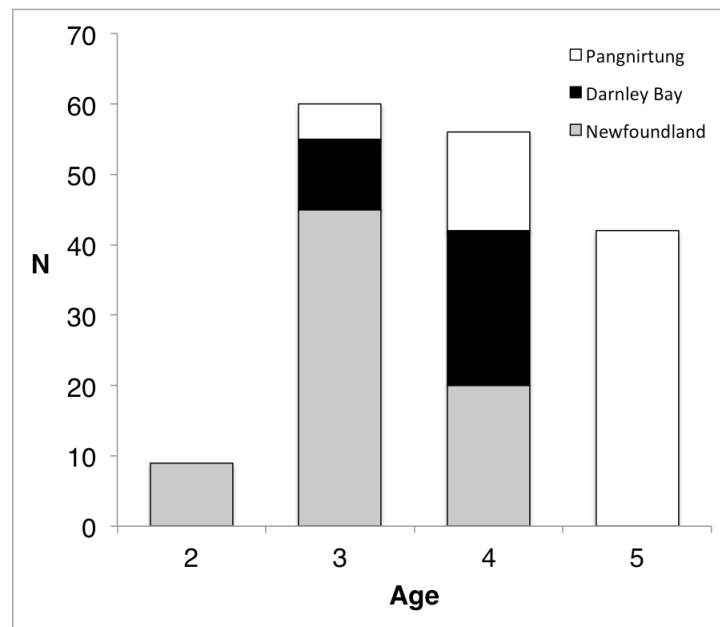


**Fig. 2.3** Comparisons of body condition (modified Fulton's K) among mature, male capelin collected in Darnley Bay (n=91), Newfoundland (n=36) and Pangnirtung Fjord (n=74) during July, 2014. Whiskers represent maximum and minimum values (excluding outliers represented by small circles), the bottom of the box represents the lower quartile and the top represents the upper quartile, and the median is indicated by the bold line through each plot.

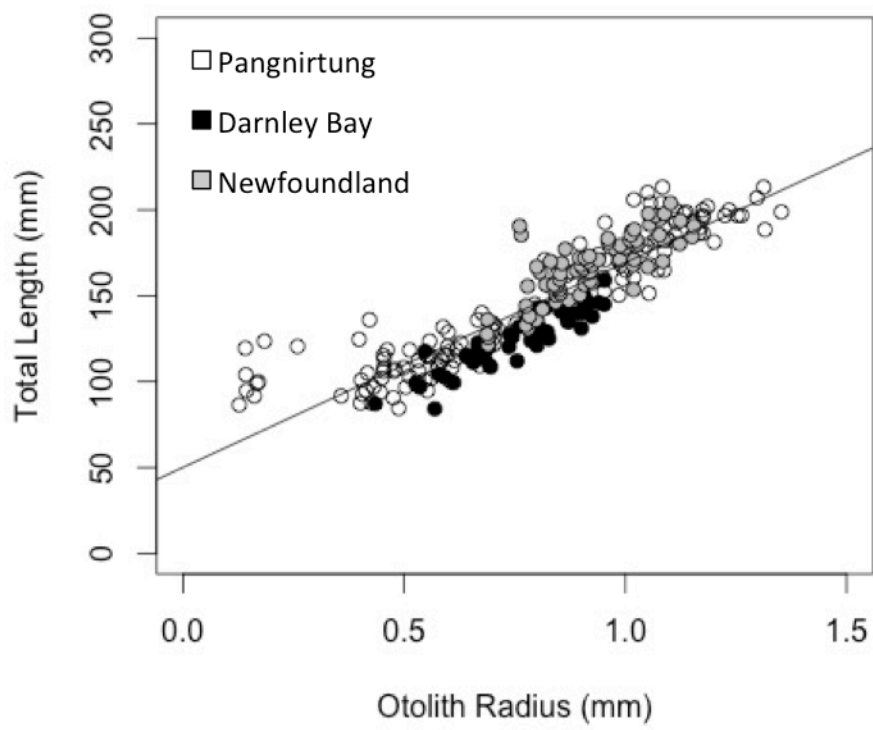
The age of mature male and female capelin sampled over all locations ranged from 2+ to 5+; however, age 2+ spawners were only sampled in Newfoundland, whereas only age 5+ spawners were sampled in Pangnirtung Fjord. Darnley Bay fishes were primarily age 3+ but some age 4+ individuals were also observed (Fig. 2.4). There were significant positive linear relationships of fish length and otolith radius over all regions (linear regression,  $F_{1,268} = 1053$ ,  $r^2 = 0.80$ ,  $p \leq$



0.0001; Fig. 2.5), and within each region (Darnley Bay:  $F_{1,55} = 260$ ,  $r^2 = 0.83$ ,  $p \leq 0.0001$ ; Pangnirtung Fjord:  $F_{1,137} = 751.8$ ,  $r^2 = 0.85$ ,  $p \leq 0.0001$ ; Newfoundland:  $F_{1,72} = 116.1$ ,  $r^2 = 0.62$ ,  $p \leq 0.0001$ ), validating the use of back-calculations to estimate length-at-age using a biologically determined intercept method (Campana 1990). Some variation occurred at early stages of growth, namely among individuals from Pangnirtung Fjord. This relationship was also examined using a polynomial fit, and explained a similar amount of variance as did the linear fit (Appendix A).



**Fig. 2.4** Frequency of mature, male capelin that were confidently aged among age classes collected from Newfoundland (n=74), Darnley Bay (n=32) and Pangnirtung Fjord (n=61) during July 2014.

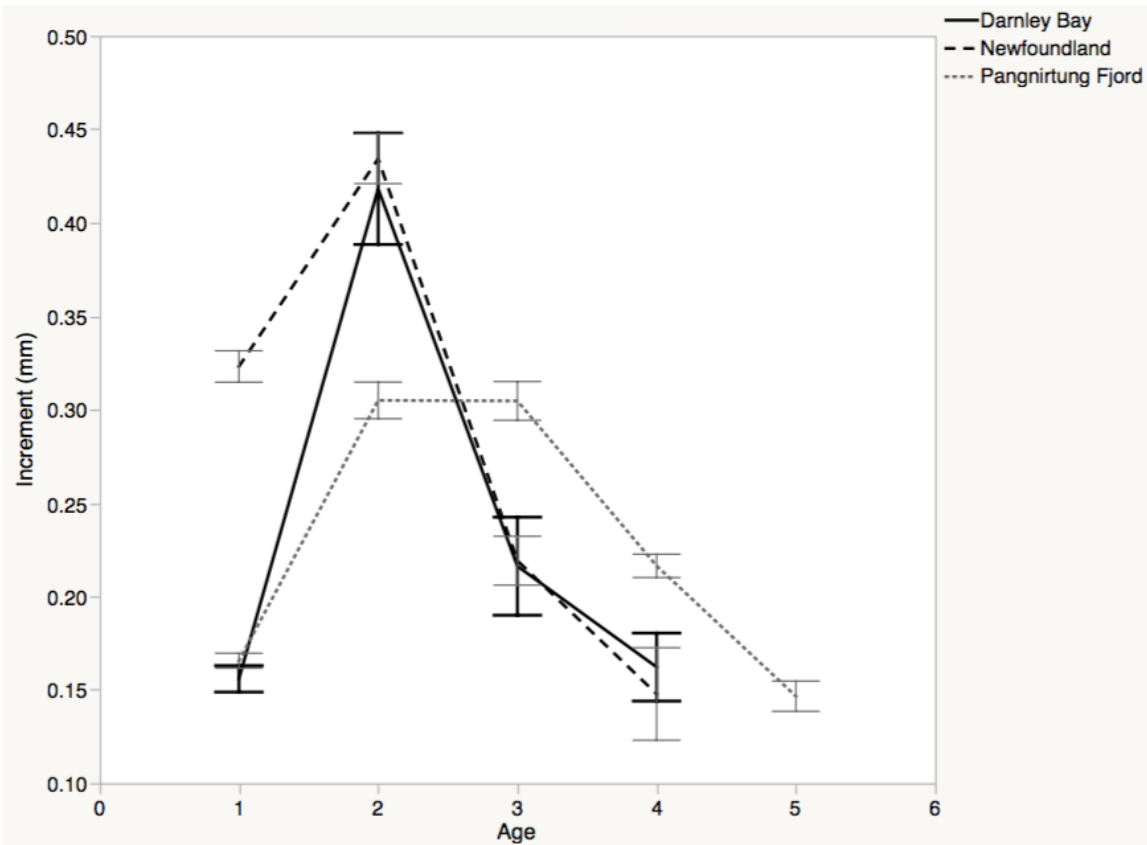


**Fig. 2.5** The relationship between total fish length and otolith radius for capelin (males and females) collected in Darnley Bay ( $n=60$ ;  $r^2=0.85$ ), Pangnirtung Fjord ( $n=139$ ;  $r^2=0.85$ ) and Newfoundland ( $n=74$ ;  $r^2=0.62$ ). Juveniles collected within Darnley Bay in 2013 ( $n=28$ ) and within Pangnirtung Fjord in 2015 ( $n=78$ ) were included in this analysis to provide a wider length range.

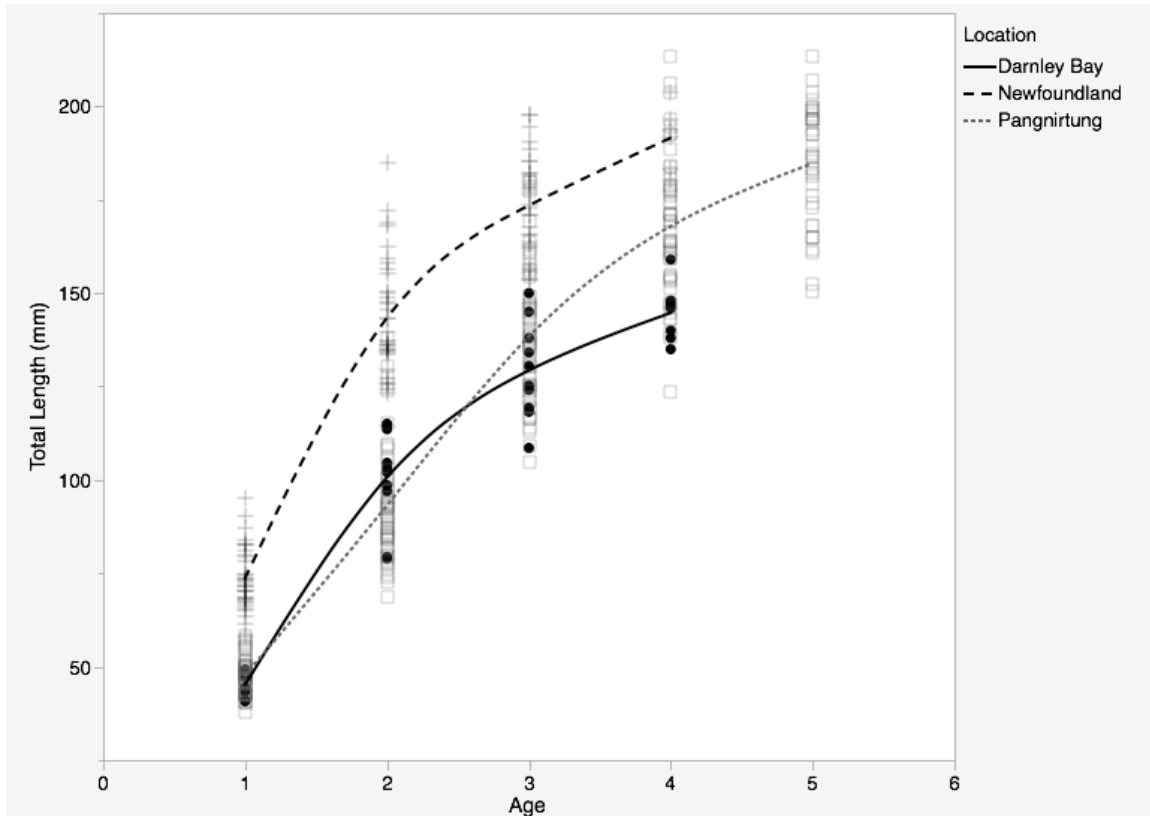
The best model (i.e., lowest AIC value) describing annual growth of capelin included region, age and an interaction term between age and region, when controlling for variation among individuals and years (Table 2.2).

<b>Table 2.2</b> The annular increment of growth of male capelin for a particular year class is determined from the following mixed effects models, where random effects are shown in parentheses. The interaction term is indicated with (*). Akaike information criterion (AIC), delta AIC ( $\Delta$ AIC), and log likelihood (logLik) are shown for each model.				
Model Parameters	AIC	logLik	$\Delta$ AIC	P value
growth = intrinsic growth + region + age + region*age (year + individual)	-993.7	511.9	0.0	<0.0001
growth = intrinsic growth + region + age (year + individual)	-850.7	434.3	143.1	<0.0001
growth = intrinsic growth + age (year + individual)	-819.8	416.9	174.0	<0.0001

This model indicated that growth (i.e., width of annular otolith increment) differed significantly among regions ( $F_{3,327} = 123.4$ ,  $p < 0.0001$ ) and ages ( $F_{3,40} = 110.4$ ,  $p < 0.0001$ ), and that there was a significant interaction between age and region ( $F_{6,40} = 31.0$ ,  $p < 0.0001$ ). Growth of age 0+ fish was highest in Newfoundland compared to that in Darnley Bay ( $t_{320} = -6.5$ ,  $p < 0.0001$ ) and Pangnirtung Fjord ( $t_{320} = 11.3$ ,  $p < 0.0001$ ), but growth of remaining ages was similar in Darnley Bay and Newfoundland (Fig. 2.6). Although 0+ fish growth was similar in Darnley Bay and Pangnirtung Fjord, fish from Pangnirtung had much lower growth at age 1+ than did those from Darnley Bay ( $t_{320} = 3.8$ ,  $p < 0.01$ ). There was no significant difference in growth between age 2+ and 3+ fish ( $t_{320} = -5.3$ ,  $p < 0.001$ ), however, resulting in Darnley Bay fish being the smallest size-at-age relative to fish from the other two regions at ages  $\geq 2+$  (Fig. 2.7).



**Fig. 2.6** Mean ( $\pm 1$  SE) otolith increment widths for each age of male capelin captured while spawning in Darnley Bay, Newfoundland and Pangnirtung Fjord during July 2014.



**Fig. 2.7** Back-calculated length-at-age of male capelin collected in Darnley Bay (•; n=10), Newfoundland (+; n=36) and Pangnirtung Fjord (□; n=59) for each age. Observed length-at-age relationships are shown in Appendix A.

## Discussion

The differences in young-of-the-year growth between Arctic and sub-Arctic capelin in this study suggest that divergent life history strategies exist among Canadian capelin populations. First-year growth was lower in both Arctic regions (i.e., Pangnirtung Fjord, Darnley Bay) relative to the sub-Arctic region. Higher growth at older ages (>3+) by capelin in Pangnirtung Fjord, however, resulted in larger maximum lengths compared to the western Arctic and similar maximum lengths to those of the sub-Arctic (i.e., Newfoundland). Although growth-at-age was

similar for Darnley Bay and Newfoundland populations, lower first-year growth in Darnley Bay resulted in a smaller mean size of capelin relative to both Atlantic populations. Lower first-year growth in both Pangnirtung and Darnley Bay may result from environmental pressure due to colder temperature that restricts the availability of foraging habitat (e.g., duration of open water season) of young-of-the-year. If foraging habitat for capelin in both Arctic regions is limited by sea ice in their first summer, smaller mean size at the end of the first year relative to that for Newfoundland capelin may be due to lower prey availability or higher competition among larval fishes.

The capelin in Newfoundland displayed lower somatic body condition relative to both Arctic regions. Lower somatic body condition may be due to the earlier sexual maturity of Newfoundland fish, evidenced by the presence of spawning two-year olds, whereas age 2+ spawners were absent in Arctic regions. Indeed, Newfoundland capelin spawning at an earlier age may allocate high amounts of energy towards gonadal development leaving reduced energy reserves in the body relative to capelin spawning later in life (Pangnirtung or Darnley Bay). Interestingly, males collected in Pangnirtung Fjord were composed primarily of age 4+ and 5+ spawners, which is suggestive of delayed maturation, assuming there is a low probability of repeat spawning for males (Christiansen et al. 2008). It is unclear if these populations differ in parity, but life history theory predicts that iteroparity is correlated with longer-lived organisms (Clutton-Brock 1984), suggesting that an iteroparous life history may be favoured in Pangnirtung capelin. Further studies are required to clarify whether such differences exist. Colder temperatures also delay maturation of gonads (Carscadden et al. 1997), which might explain delayed maturation in Pangnirtung Fjord and Darnley Bay. Therefore, fish in Arctic ecosystems may experience delayed maturation relative to sub-Arctic populations in response to a colder

environment and/or more seasonal variation in prey abundance (Blanck and Lamouroux 2006). It is unclear why the same pattern in growth was not observed in Darnley Bay, but this might be related to differences in prey availability, sea ice dynamics, or competition among co-occurring fishes.

For the Newfoundland and Pangnirtung populations in this study, there was a trend toward slower growth and later maturation at higher latitudes relative to lower latitudes. This result supports our prediction that high latitude populations would reach a smaller asymptotic length than would capelin from a lower latitude (e.g., Newfoundland). Similarly, capelin from Labrador, at intermediate latitude in the North Atlantic, exhibit slower initial growth resulting in a larger maximum length and greater proportion of older individuals, relative to more southern Newfoundland population (Winters 1982). This trend of increased average capelin size at higher latitudes has also been observed in western Greenland (Hedeholm 2010). Previous studies have identified the Labrador Current as a driver of lower mean growth and a larger final maximum size (Templeman 1948; Winters 1982) among capelin north of Newfoundland. It is possible that the cold, south-flowing Baffin Island Current has a similar effect on Pangnirtung Fjord capelin as it does on Labrador capelin, resulting in Pangnirtung capelin being unable to reach a higher maximal length than lower latitudes. The influence of these cold water masses may affect the growth rate of capelin (Hedelholm et al. 2010) as well as the availability and abundance of prey (Daase et al. 2015). Residing year-round in the Cumberland Sound-Pangnirtung Fjord region may favour a slow-growing, later-maturation life history strategy that is adapted to a shorter summer foraging period and Arctic water masses.

Limited gene flow on the northern margins of this species' geographical distribution may also contribute to life history variation among populations (Eckert et al. 2008). Such variation

may reflect life history trait evolution in each region that may also affect the ability of each population to respond to and tolerate environmental changes. Whether genetic differentiation exists between Pangnirtung Fjord and Newfoundland populations of capelin remains uncertain, but as sub-Arctic populations shift northward with increasing ocean temperatures, the potential for these populations to mix becomes greater. Migration to a marginal population (i.e., Pangnirtung Fjord) from a central population (i.e., Newfoundland) can increase genetic variation and facilitate adaptation to newly established habitat (Levins 1968; Barton 2001). Genetic differentiation is weak between capelin from the Beaufort Sea and the northeast Pacific but is higher between Pacific and Atlantic populations (Praebel et al. 2008). This suggests that Alaskan and Darnley Bay capelin have greater genetic similarity relative to the Atlantic populations. Genetic diversity among populations at the northern edge of this species' distribution may contribute to differences in growth and age-at-maturity and suggest potential adaptation to an Arctic environment.

Shifts in the distribution of capelin throughout the northern hemisphere are closely correlated with temperature change (Rose 2005) and historic range shifts have led to regional life history strategies (Vilhjálmsón 1994, Carscadden and Vilhjálmsón 2002). Higher condition among Arctic capelin, relative to those in Newfoundland, is an indication of successful persistence and may imply potential for colonization in newly available habitat beyond the current northernmost range of the species' distribution. As population dynamics of capelin within each region will vary according to growth rates and age-at-maturity (Hjermann et al. 2004), further understanding of the life history traits in high latitudes is critical to assess how capelin populations may respond to shifts in oceanographic conditions and prey availability with climate change. Further research is required on life history traits between central and marginal



populations of capelin, and how their adaptive responses may differ as range shift occurs. The findings of this study suggest that sub-Arctic populations and populations in the eastern and western Arctic will respond differently to environmental changes. This will likely lead to altered ecosystem function and structure, potentially at higher trophic levels (Hjermann et al. 2002).

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### **Chapter Three. Dietary characteristics of co-occurring Arctic cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) in the Canadian Arctic, Darnley Bay.**

#### **Abstract**

Reduction in sea ice due to climate change is expected to have a negative impact on habitat availability for Arctic marine fishes and induce range expansion of species from southern environments. Such an effect will likely be observed in the abundance of Arctic cod, *Boreogadus saida* (Lepechin, 1774), as well as interspecific interactions of this intermediate-level trophic taxon, particularly in more southerly fringing seas in the Arctic. Arctic cod and capelin, *Mallotus villosus* (Müller, 1776), are pelagic, planktivorous forage fishes, which occupy similar dietary niches and are the primary prey of marine predators. Co-occurring Arctic cod and capelin were collected at seven stations in Darnley Bay, NT, during August 2013. Standard length (SL), used as a proxy for age, suggested that Arctic cod (mean  $\pm$  1 SD: 71.1  $\pm$  10.3 mm) were predominantly age 1+ and capelin (96.2  $\pm$  13.4 mm) were mostly age 2+. Stomach content analyses indicated that both species fed extensively on calanoid copepods (*Calanus hyperboreus*, *C. glacialis*, *Metridia longa*) and amphipods (*Themisto libellula*). There was high dietary overlap between capelin and Arctic cod, evidenced by Schoener's index (0.80). Additionally the quantity of dietary items, biomass and energetic content consumed differed among size classes in both capelin (SL, 70.5–132.0 mm) and Arctic cod (SL, 42.1–114.4 mm). This study illustrates that the diets of these sympatric forage fishes in an Arctic ecosystem are very similar, indicating a high potential for interspecific competition as the sub-Arctic capelin expands its range into Arctic regions with climate change and if prey abundance becomes limited.

## Introduction

Direct effects of climate change on increased seasonal variability and the extent of sea ice are expected to have a significant impact on the availability of prey for marine organisms (Laidre et al. 2008; Prowse et al. 2009). As a result, indirect effects of climate warming on marine systems are expected to resonate through each trophic level with respect to bottom-up and top-down interactions (Beaugrand 2003; Parmesan 2006; Drinkwater et al. 2009). Local temperature regimes will impact marine fish at the individual level by influencing metabolic rate, reproduction and growth (Pörtner 2002; Swalethorp et al. 2014). Of particular concern are pelagic forage fish species, primarily Arctic cod (*Boreogadus saida* (Lepechin, 1774)) and capelin (*Mallotus villosus* (Müller, 1776)), considering that they play an integral role in transferring energy between upper (e.g., predatory fishes, seals, sea birds) and lower trophic levels (e.g., copepods) in the Arctic (Bradstreet et al. 1986; Welch et al. 1992; Orlova et al. 2009). These two forage species are expected to respond differently to a warming climate (Hop and Gjøsæter 2013). For instance, climate change may facilitate further range expansion of sub-Arctic capelin (Moore and Laidre 2006) and may lead to thriving populations of capelin where it is currently present. In contrast, sympagic-adapted species such as Arctic cod will be negatively affected by loss of habitat and reduced recruitment (Laidre et al. 2008). This will likely result in changing species interactions, including the restructuring of resource use among species with overlapping species ranges (Parmesan 2006), and shifts in the functional role of these species.

In the Arctic marine environment, Arctic cod and capelin rely heavily on the distribution and abundance of planktonic assemblages to sustain their energetic requirements for growth, reproduction and persistence in Arctic waters. Both Arctic cod and capelin prey upon zooplankton and typically occupy the third level of the trophic web (Hop et al. 2002). In the

Beaufort Sea, Arctic cod feed mainly on calanoid copepods and amphipods (Walkusz et al. 2013), but the diet of co-occurring capelin is unknown. The availability of copepods in the Beaufort Sea is closely associated with timing of ice break up and algal blooms (Forest et al. 2008). Studies in the Barents Sea and eastern Canada indicate that capelin primarily consume copepods, amphipods and euphausiids (O'Driscoll et al. 2001; Dalpadado and Mowbray 2013). Prey composition also changes as both species grow (e.g., Arctic cod, Walkusz et al. 2013; capelin, O'Driscoll et al. 2001; Dalpadado and Mowbray 2013), with smaller fish typically consuming smaller prey (e.g., copepods), while larger individuals consume larger prey (e.g. amphipods, euphausiids) as gape size increases (Walkusz et al. 2013). This suggests that diets of these two species are similar, leading to a high potential for interspecific competition as range overlap increases or capelin abundance increases with climate change.

The goal of this paper is to determine the potential for competitive interactions between Arctic cod and capelin by quantifying the dietary overlap of co-occurring individuals of both species in the high Arctic. We also compare the abundance, biomass and energetic content of prey taxa consumed by each species with respect to size. We predict that (1) the diet of both species will overlap, (2) the most abundant zooplankton taxa (i.e., calanoid copepods) will be the primary prey type consumed, and (3) the prey types consumed will differ among size classes in both species. This baseline information is essential to determine the potential for capelin to compete with or even to replace Arctic cod in a warmer Beaufort Sea scenario, and what that would mean for ecosystem structure and function throughout the Arctic.

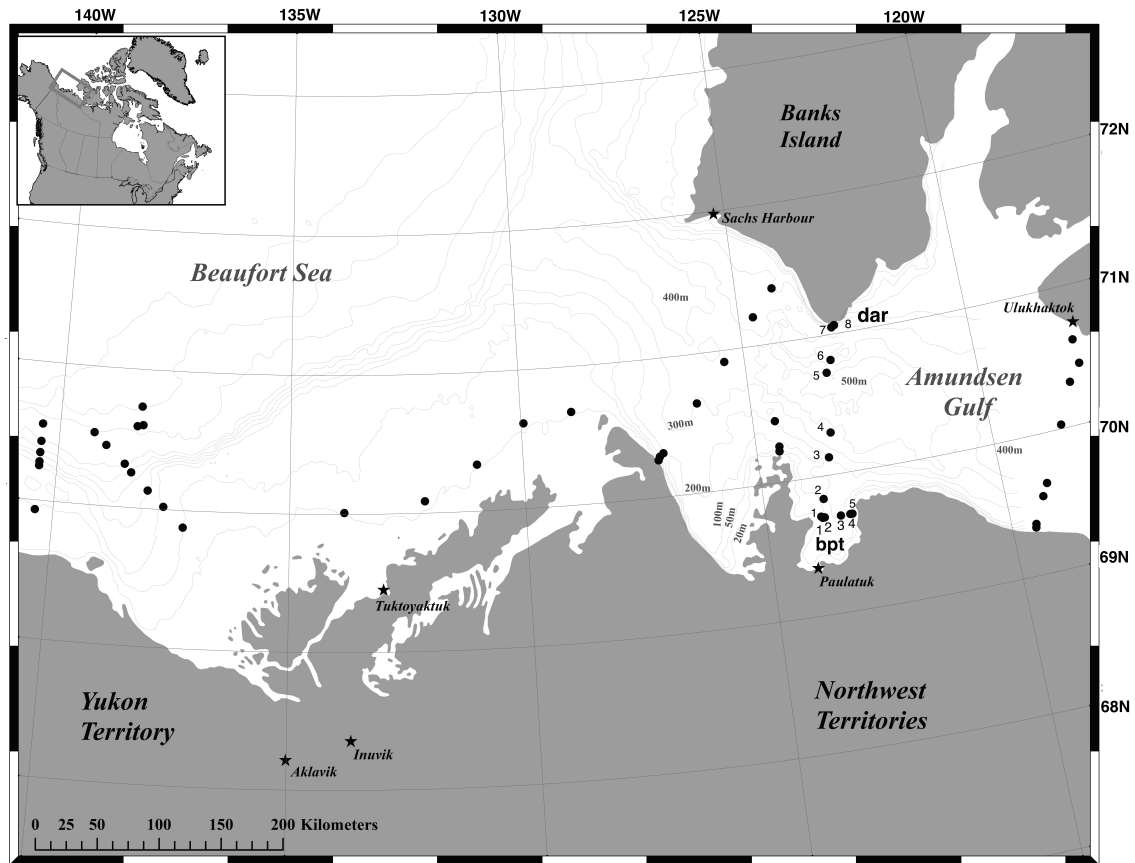
## Methods

### *Field sampling*

Capelin and Arctic cod were sampled aboard the *F/V Frosti* in Darnley Bay, Northwest Territories (NT), on 4–6 August 2013 (approximately 10.5 h of daylight) as a component of the Beaufort Sea Regional Environmental Assessment (BREA) Marine Fishes Project. This assessment was designed to determine the composition of fishes in relation to habitat parameters and associated biota in the offshore and nearshore environments in the Canadian Beaufort Sea region, including Amundsen Gulf (Fig. 3.1). Co-occurring capelin and Arctic cod were collected from seven stations in Darnley Bay (Table 3.1). Stomach content analyses were restricted to three 75-m stations (bpt\_04, bpt\_05 and dar\_02) to minimize confounding influences of dietary differences associated with depth resulting from small-scale spatial variation of zooplankton assemblages. Fish were collected primarily with a modified Atlantic Western IIA bottom trawl (22.86-m head rope, 21.23-m footrope with a 1.27-cm (0.5 in) mesh cod-end and intermediate liner) at each station (Cosmos-Swan and Isaac-Kidd mid-water trawls were also deployed at some stations). Bottom tow time at each station was limited to 20 min with a target speed set at 2.9 knots. Environmental data were collected using a Seabird SBE-9plus conductivity, temperature and depth (CTD) probe, mounted on a 12-bottle rosette, which was deployed prior to each tow. Immediately after sampling, the fork length (from snout to inside fork of caudal fin; mm) of each fish of both species was determined and individuals were flash-frozen at -50 °C. Individuals from each species were sub-sampled for diet analysis by sorting fish by fork length and roughly selecting every second capelin (47 % of total catch; n=164) and every third Arctic cod (39 % of total catch; n=257) to represent the full size range sampled.

### *Stomach content analysis*

Approximately 2 months after the cruise, frozen fish were thawed and standard length (mm) recorded in the laboratory (from snout to end of caudal peduncle). Individuals sub-sampled for diet analysis were examined under a dissecting scope to determine sex and maturity, and then stomachs were removed from the oesophagus to the pyloric sphincter. To prevent damage to the stomach contents, pyloric caecae remained intact until removal under a higher-magnification dissecting scope. All items found in each stomach were identified to the lowest possible taxonomic level, typically to species. For copepods, developmental stages of larger species were determined from stage-one copepodite (CI) to stage-six copepodite (adult female, AF; male, AM). *Calanus* species (*C. glacialis* and *C. hyperboreus*) were identified based on the prosome length for the study area, according to Walkusz et al. (2010). Diet items other than copepods were measured to the nearest 1 mm, in most cases as a total length. Finally, stomachs and contents were preserved in 70 % ethanol for future reference.



**Fig. 3.1** Map of the BREA Marine Fishes Project study area, with sampling stations completed during the 2013 survey indicated (black circles). Co-occurring capelin and Arctic cod were collected along the dar and bpt transects, indicated with station numbers. Capelin were not captured at any stations other than the dar and bpt transects; Arctic cod were captured at all stations

<b>Table 2.1</b> Stations where capelin and Arctic cod co-occurred, along with the number of fish collected at each station (number subsampled shown in parentheses) and environmental parameters.								
Station	Depth (m)	Time (hr:min)	Lat. (°N)	Long. (°W)	Temp. (°C)	Salinity	Arctic cod (n)	Capelin (n)
bpt_02	75	15:44	69 42.02	123 46.05	-1.06	32.06	78	30
bpt_03	125	1:08	69 41.91	123 26.47	-1.21	32.26	208	126
bpt_04	75	16:15	69 41.89	123 14.43	-1.05	32.06	215 (96)	82 (76)
bpt_05	75	20:56	69 41.94	123 11.78	-0.48	30.37	248 (116)	45 (44)
dar_01	40	19:52	69 42.19	123 49.14	0.21	29.54	82	8
dar_02	75	13:13	69 50.42	123 43.63	-1.34	32.50	186 (45)	44 (44)
dar_03	200	19:19	70 7.49	123 29.58	-1.41	33.68	116	9

### *Data analyses*

A number of metrics were used to describe the dietary composition of each species. First, we used relative abundance (%) of each prey type found in the stomachs. Second, as stomachs contained primarily digested material, biomass was calculated by multiplying the abundance of each prey taxon by published taxon-specific mass (mg DW) (for details, see Walkusz et al. 2013). Third, the total biomass for each taxon was then converted to energetic content (kJ/mg DW) by multiplying published energy density values for each taxon (see Walkusz et al. 2013 for details).

To estimate the extent of dietary overlap between co-occurring Arctic cod and capelin, we calculated the Schoener's index of dietary overlap at each station and also averaged among

the three stations. This index was chosen because it most accurately measures overlap over the range of potential overlap (Davies et al. 1981; Wallace 1981) between two co-occurring species on a scale from 0 (no overlap in dietary items) to 1 (complete overlap) using the following formula:

$$\alpha = 1 - 0.5 \left( \sum |p_{xi} - p_{yi}| \right)$$

In this equation,  $\alpha$  denotes Schoener's index which is calculated from the proportion of prey type  $i$  in the diet of predator  $x$  ( $p_{xi}$ ) and the proportion of prey type  $i$  in the diet of predator  $y$  ( $p_{yi}$ ).

Schoener's index values of  $\geq 0.6$  generally reflect high overlap (Barluenga et al. 2006). In addition, the dietary diversity of each species (over all individuals at all stations) was calculated using the Shannon–Wiener index which combines the relative abundance of each prey type ( $i$ ) and the total number of prey types consumed by each species ( $p_i$ ), expressed in the following formula:

$$H' = - \sum (p_i)(\log_2 p_i)$$

This index provides a quantitative measure of the dietary breadth or diversity of each species. The measures of dietary overlap and diet diversity were qualitatively examined and compared, respectively, between species.

We used Chi-square tests of independence to statistically compare the frequency of prey taxa primarily consumed (*C. hyperboreus*, *C. glacialis*, *M. longa*) between Arctic cod and capelin. Two-way analysis of variance on rank-transformed data was conducted to compare the mean energetic content and mean prey length (mm) consumed per individual between capelin and Arctic cod, with station included as a random effect.



To determine whether the mean abundance, biomass and energy of consumed dietary items differed among fish size classes within each species, both predator species were divided into 10-mm size classes. Size classes were determined using pooled data from all three stations to provide a large enough sample size to adequately test among different lengths.

Prior to statistical tests, normality and homogeneity of variance were tested using Shapiro–Wilk and Levene’s tests, respectively. If data did not meet the assumptions, Kruskal–Wallis and Dunn’s nonparametric tests were conducted. If data met the assumptions, an ANOVA with Tukey HSD post hoc tests was conducted.

## **Results**

The majority (98.6 %) of all capelin collected in 2013 were captured using the benthic trawl within Darnley Bay, with few individuals caught at other stations in the Amundsen Gulf area (Table 2.1). In total, Arctic cod ( $n = 650$ ) and capelin ( $n = 348$ ) were found to co-occur at seven stations, with the highest number of both species caught at stations located along the 75- and 125 m-depth contours (Table 2.1). Covering the entire size range for both species, 164 capelin (Fig. 3.2) and 257 Arctic cod were sub-sampled from three stations for dietary analysis (Fig. 3.3).

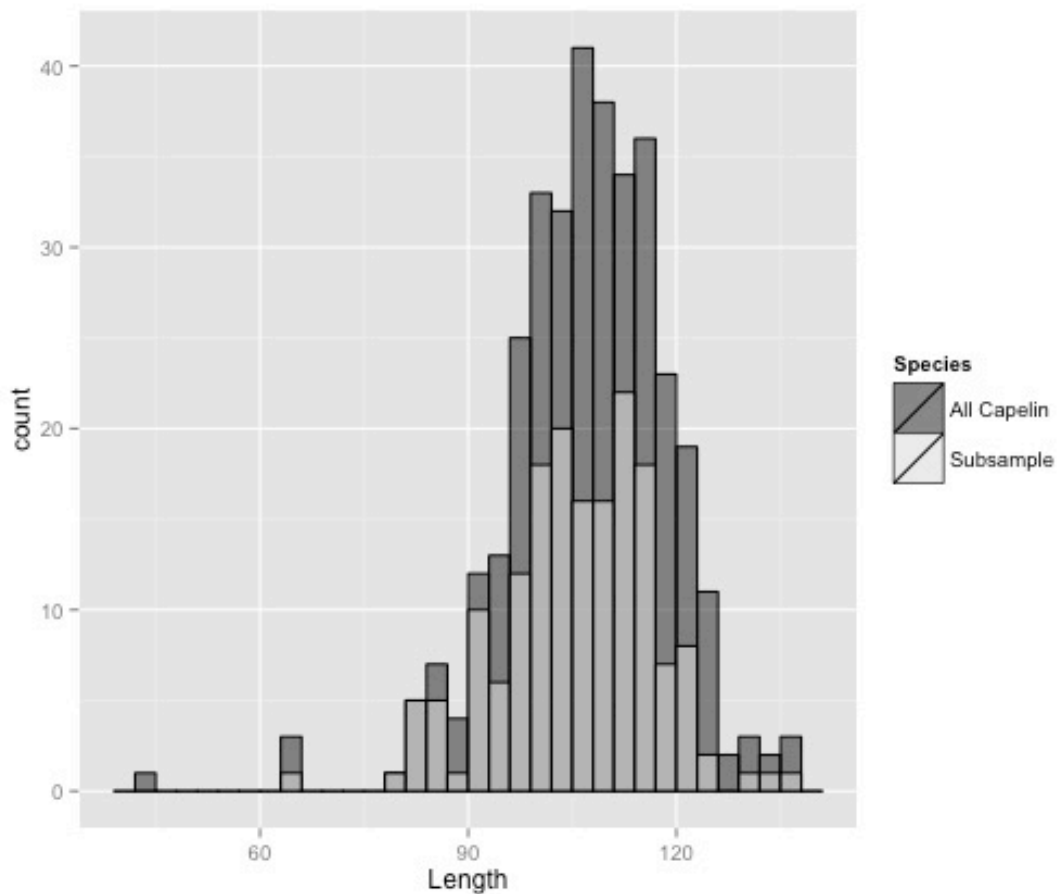
Among the sub-sampled individuals, Arctic cod ranged from 42 to 114 mm (fork length; Fig. 3.3) and were divided into five size classes (i.e., <60, 60–69, 70–79, 80–89 and >90 mm), whereas capelin ranged from 70 to 132 mm (Fig. 3.2), resulting in six size classes (i.e., 70–79, 80–89, 90–99, 100–109, 110–119 and >120 mm). Capelin were larger ( $\bar{x} \pm \text{SD} = 96.2 \pm 13.4$  mm) than Arctic cod ( $\bar{x} = 71.1 \pm 10.3$  mm) over all individuals caught, as was the case for fishes sub-sampled for stomach content analysis (capelin:  $96.9 \pm 11.3$  mm,  $n = 164$ ; Arctic cod:  $70.6 \pm$

9.7 mm, n = 257; Fig. 3.2).

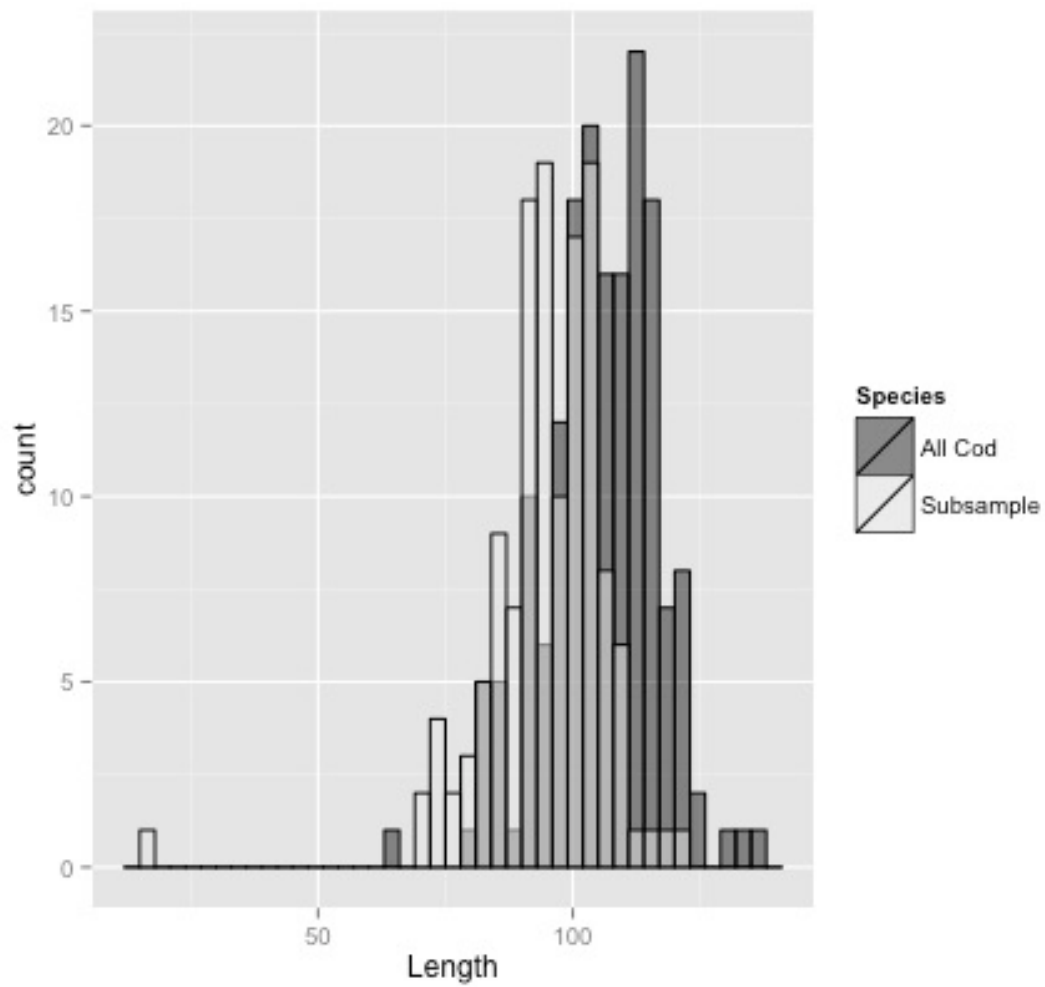
Calanoid copepods (particularly *C. hyperboreus*, *C. glacialis* and *M. longa*) were the primary prey types consumed by capelin and Arctic cod (Fig. 3.4). The majority of *Calanus* consumed by both species were adult females (91.6 and 96.7 %, for *C. hyperboreus* and *C. glacialis*, respectively), while other developmental stages were consumed much less frequently. Rare prey types in diets of both species, hereafter referred to as ‘other’ prey types, included copepods (*Paraeuchaeta glacialis*, *Pseudocalanus* spp., *Jashnovia tolli*, *Oithona similis*, *Microcalanus* spp., *Aetideidae*), amphipods (*Themisto libellula*, *Themisto abyssorum*, *Apherusa glacialis*, *Ampelisca macrocephala*), euphausiids (*Thysanoessa raschii*), mysids (*Mysis oculata*), cumaceans, larval decapods, pteropods (*Limacina helicina*), chaetognaths (*Eukrohnia hamata*) and appendicularians. The biomass (mg DW) and energy (kJ) consumed by both forage fishes were dominated by two copepod species, *C. hyperboreus* and *C. glacialis* (Fig. 3.4). Adult female *C. hyperboreus* contributed the greatest proportion of total biomass and total energy consumed by both species, as this prey type is larger relative to other copepods (Walkusz et al. 2010).

There was high dietary overlap between capelin and Arctic cod, evidenced by a high (i.e., >0.6) Schoener’s index when all three stations were pooled ( $\alpha = 0.80$ ) as well as within each station (bpt\_04  $\alpha = 0.86$ ; bpt\_05  $\alpha = 0.92$ ; dar\_02  $\alpha = 0.79$ ). Diet diversity was also similar between the two fish species, based on the Shannon–Wiener index (capelin,  $H' = 1.9$ ; Arctic cod,  $H' = 2.0$ ). Despite these similarities, the frequency of the four primary prey types consumed (i.e., *C. hyperboreus*, *C. glacialis*, *M. longa*, other) differed significantly between capelin and Arctic cod ( $\chi^2_3 = 381.9$ ,  $p < 0.0001$ ,  $N = 7639$ ), with *M. longa* being consumed more by capelin (35 %) relative to Arctic cod (17 %; Fig. 3.3). In addition, mean ( $\pm$ SD) prey length over all prey types

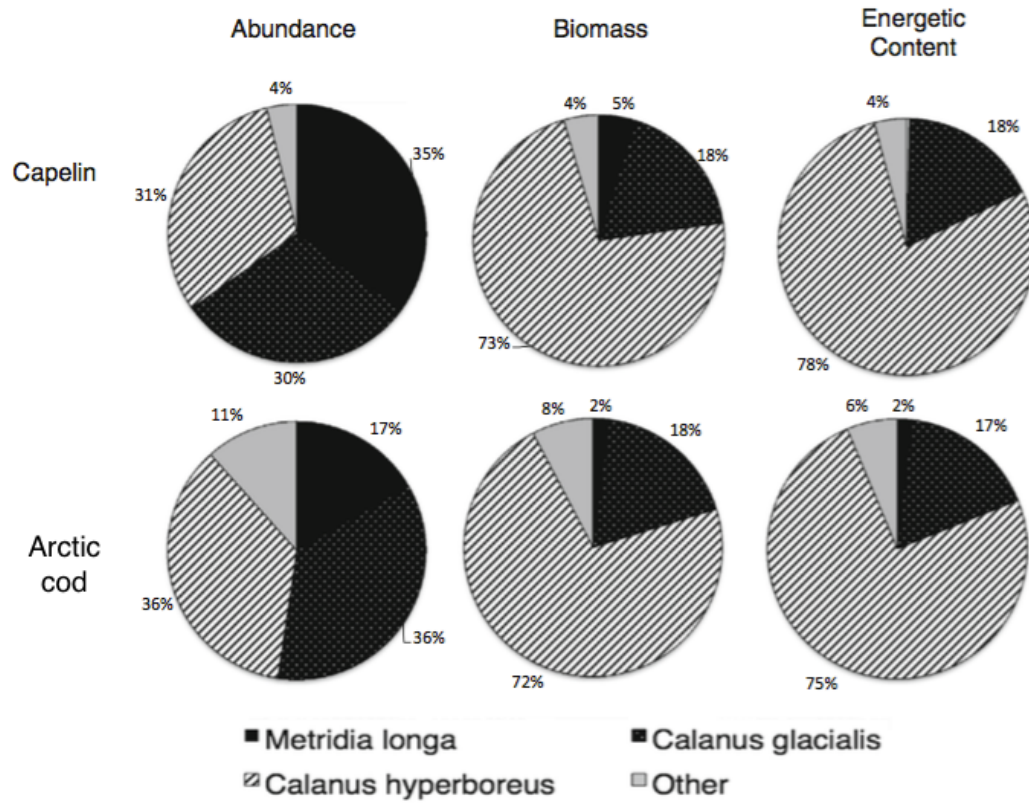
consumed was significantly smaller in capelin ( $5.0 \pm 1.1$  mm) relative to Arctic cod ( $5.4 \pm 9.6$  mm;  $F_{1,416} = 7.11$ ,  $p < 0.01$ ), and the mean energy of stomach content consumed by each species also differed (capelin:  $0.8 \pm 0.7$  kJ; Arctic cod:  $1.1 \pm 1.3$  kJ;  $F_{1,416} = 7.63$ ,  $p < 0.01$ ).



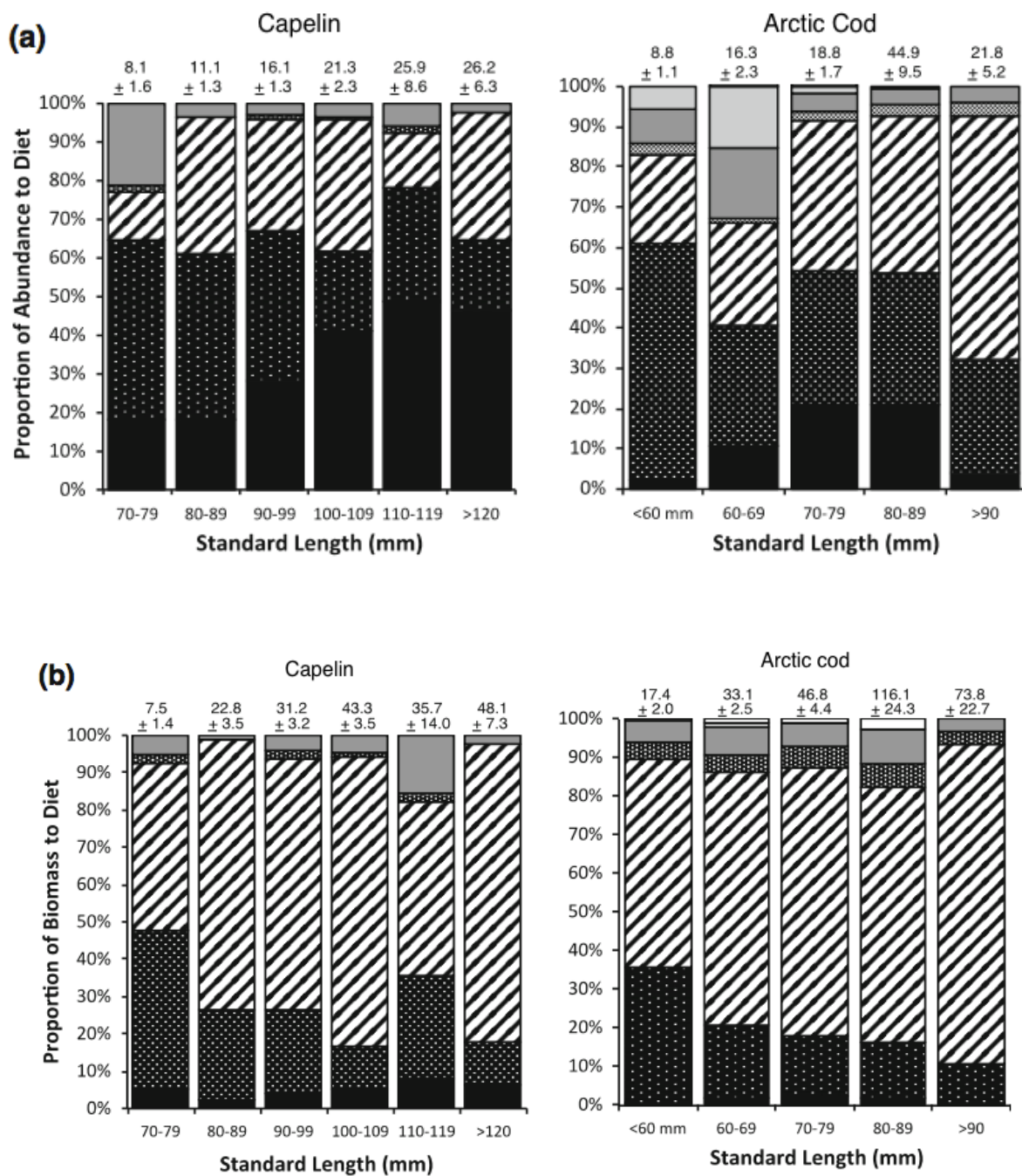
**Fig. 3.2** Fork length of all capelin (n=348) and subsampled individuals (n=164) in Darnley Bay during August, 2013.

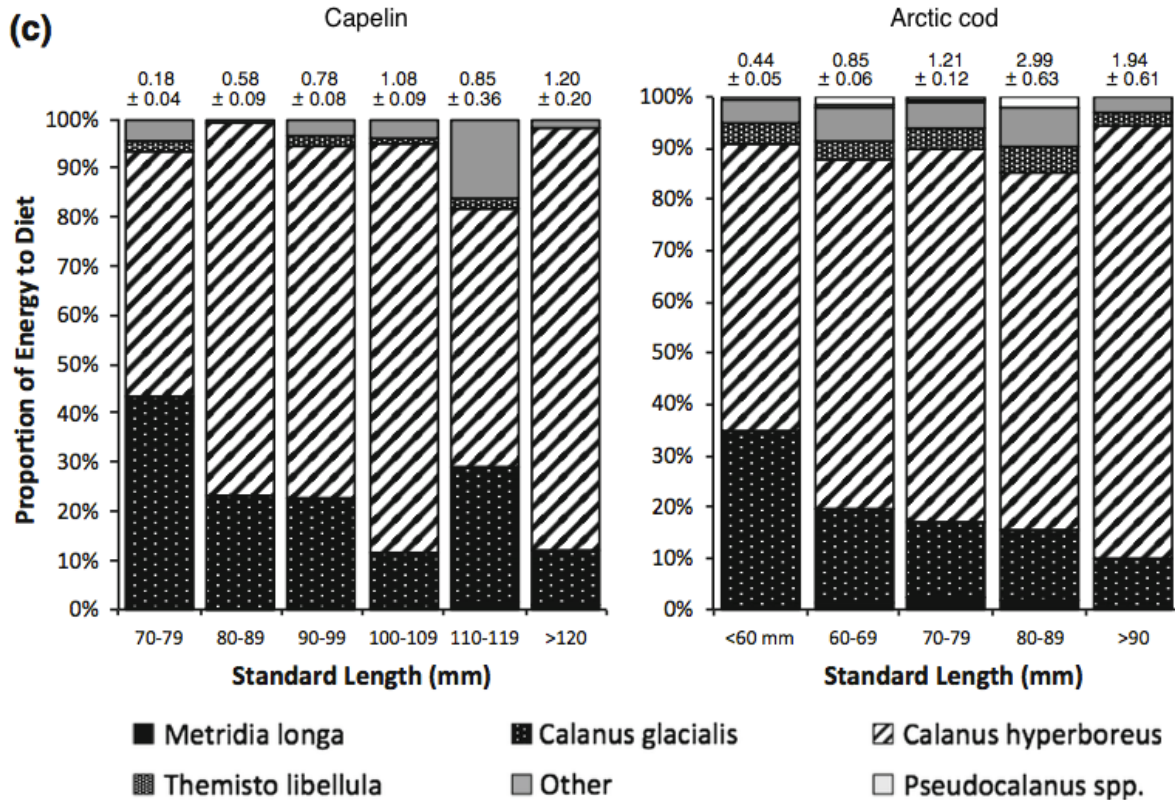


**Fig. 3.3** Fork length of all Arctic cod (n=650) and subsampled individuals (n=257) in Darnley Bay during August, 2013.



**Fig. 3.4** Relative abundance (% by number) of prey types found in capelin (n=164) and Arctic cod (n=257). Percentage of mass (mg dry weight) consumed by prey type for capelin and percentage of energy consumed (kJ) by prey type.





**Fig. 3.5** Percentage by number of prey types consumed by Arctic cod and capelin across size classes. The mean ( $\pm$ SE) percentage of a) prey items, b) mean mass (mg DW) and c) mean energetic content ( $\text{kJ mg}^{-1}$  DW) of all prey items in the stomachs of fish within each size range is indicated at the top of the respective column.

Kruskal–Wallis tests for one-way analysis of variance along with nonparametric post hoc tests revealed differences in the number of prey items, biomass and energetic content consumed among size classes within each species. The total number of prey items consumed differed significantly among the size classes within Arctic cod (prey items:  $X^2 = 23.1$ ,  $p < 0.0001$ ; Fig. 3.5) and capelin (prey items:  $X^2 = 27.3$ ,  $p < 0.0001$ ; Fig. 3.5). Biomass and energetic content

differed among size classes for Arctic cod (biomass:  $X^2 = 29.0$ ,  $p < 0.0001$ ; energetic content:  $X^2 = 29.1$ ,  $p < 0.0001$ ; Fig. 3.5) and capelin (biomass:  $X^2 = 40.1$ ,  $p < 0.0001$ ; energetic content:  $X^2 = 36.9$ ,  $p < 0.0001$ ; Fig. 3.5). Significantly different size classes are identified in Table 3.2.

<b>Table 3.2.</b> Size classes, which exhibited significant differences in post hoc tests from stomach content analyses. Size classes that were significantly different ( $p < 0.05$ ) indicated by A for relative abundance (n) and B for mean biomass (mg DW) are listed below (pairs $p < 0.0001$ are indicated by **). Results for mean energetic content were identical to those for biomass in both Arctic cod and capelin.							
Species	Size Class (mm)	70-79	80-89	90-99	100-109	110-119	>120
Capelin	70-79			A B	A B		A B
	80-89				A B		A
	90-99	A B					
	100-109	A B	A B				
	110-119						
	>120	A B	A				
Arctic cod	Size Class	<60	60-69	70-79	80-89	>90	
	<60			B	A B	B	
	60-69				A B		
	70-79	B					
	80-89	A B	A B				
	>90	B					



## Discussion

The overlapping occurrence of capelin and Arctic cod was unique to Darnley Bay, relative to other stations sampled throughout the Beaufort Sea. Nearshore, demersal Arctic cod have been observed throughout the Beaufort Sea (Walkusz et al. 2013) and are generally composed of 1+ and 2+ age classes (Benoit et al. 2008; Rand and Logerwell 2011). Based on length as a proxy of age in previous studies, Arctic cod in this study are considered to be in the +1 age class (Walkusz et al. 2013) and capelin between ages 1+ and 2+ (Winters 1982). This suggests that we sampled primarily juveniles, or pre-reproductive individuals (Gjørseter and Loeng 1987; Moulton and Tarbox 1987). As the majority of stomachs contained prey, this supports the importance of foraging for the early life history stages of both species during the open-water season. Interestingly, assemblages of Arctic cod were found during the winter in neighbouring Franklin Bay in the deeper portion (>180 m) of the halocline (-1.4 to 0.3 °C, salinity 33.0–34.8), but unlike fish sampled in our study, the majority of cod had empty stomachs, an occurrence that is believed to be associated with spawning (Benoit et al. 2008).

Our findings indicate that Arctic cod and capelin rely primarily on copepods in the Beaufort Sea, as observed in other regions (e.g., Ajiad and Gjørseter 1990; O’Driscoll et al. 2001). Generally, both species relied on *C. hyperboreus* and *C. glacialis* and had similar proportions of prey types in their diets, with the exception of *M. longa*. These copepods have the greatest relative abundance during summer–autumn in the coastal Amundsen Gulf in response to open-water algal blooms, although abundance is considerably variable (Daase et al. 2013). In investigating overlap dietary overlap under the sea ice, Renaud et al. (2011) demonstrated minimal overlap (Schoener’s diet overlap <0.4) and low potential for interspecific competition among co-occurring Arctic cod, juvenile Atlantic cod (*Gadus morhua*) and haddock

(*Melanogrammus aeglefinus*) in Svalbard waters. In contrast, here we found extensive overlap between Arctic cod and capelin, which supports the potential for interspecific competition between these forage fishes as they occupy the same dietary niche.

The mean energetic content consumed differed between capelin and Arctic cod, and cod consumed larger prey items in spite of having a shorter SL on average. This was likely due to a combination of different gape morphologies of the two species, in which Arctic cod have been known to consume larger prey than co-occurring fishes with a smaller gape (Robb and Hislop 1980) and the greater contribution of less energetically rich prey, such as *M. longa*, to the capelin diet.

Arctic cod diets here were primarily composed of copepods, differing from benthic-associated Arctic cod in the Barents Sea, which relied on ‘non-copepod’ prey (i.e., amphipod, *Apherusa glacialis*; Renaud et al. 2011). Although the composition of mesozooplankton assemblages in Darnley Bay was not measured, copepods (*C. glacialis* and *C. hyperboreus*) accounted for 94.5–99.2 % of the total observed abundance in zooplankton catches in neighbouring Franklin Bay during winter (Benoit et al. 2008). It is therefore possible that Darnley Bay has a similar assemblage dominated by *C. hyperboreus* and *C. glacialis* that supports the diet of Arctic cod and capelin.

Both Arctic cod and capelin ate lipid-rich prey, but due to the physiology of Arctic cod, they are potentially limited by low rates of gastric evacuation rather than prey abundance (Hop and Tonn 1998). Where Arctic cod co-occur with capelin in the Beaufort Sea, capelin may have higher foraging capabilities should zooplankton assemblages shift towards smaller prey taxa (such as *M. longa*). However, more efficient consumption would be dependent on faster rates of

gastric evacuation, which are currently unknown for capelin in an Arctic environment. The caloric consumption of demersal Arctic cod in the Beaufort Sea has been observed as high as  $1510 \text{ J day}^{-1}$  (Walkusz et al. 2013) in the field to  $716 \text{ J day}^{-1}$  (Hop et al. 1997) in a controlled laboratory setting. Hop et al. (1997) estimated gastric evacuation time to be approximately 51 h in this controlled experiment. In relation to the caloric content consumed, Arctic cod are considered to be efficient converters of energy from zooplankton (approximately 80 %), yet exhibit slow rates of growth ( $0.25 \text{ \% body weight day}^{-1}$ ) for individuals in 1+ and 2+ age classes (Hop et al. 1997). In order to maximize growth in the juvenile age classes, diets based on *Calanus* spp. have been shown to promote faster growth (Hop et al. 1997), most likely due to greater energetic content of these energy-rich copepods in comparison with other taxa. Although gastric evacuation time is slow for Arctic cod, they display high absorption efficiency of energy when digesting their prey (Hop et al. 1997). During summer, capelin produce more digestive enzymes (Gildberg 1978) and they may be capable of evacuating their guts at greater rates than Arctic cod, provided that their evacuation time is less. In the Barents Sea, juvenile capelin exhibited a reduction in body condition by approximately 40 % (Orlova et al. 2009), which was believed to be the result of competitive pressure by Arctic cod. However, Orlova et al. (2009) did not compare these fishes at equivalent life history stages, and it is therefore unknown whether juvenile Arctic cod will exhibit the same competitive pressure with capelin. The individuals observed in Darnley Bay provide a unique comparison between juveniles in the same location and indicate that there is a high potential for competition between the two species.

This study shows that the number of prey items consumed is related to the length of each fish (Scharf et al. 2000; Dalpadado et al. 2009; Graham et al. 2014). In this study, the type of prey consumed was assumed to be associated with fish length, and likely gape size, as previous

studies have indicated that these factors are linearly related (Scharf et al. 2000). The Arctic cod observed are probably too small to eat larger prey items (such as *T. libellula*) when we assume that these individuals are age 1+ and increased consumption of amphipods has been shown to occur at age 2+ (Walkusz et al. 2013). Similarly to capelin, individuals in this study relied heavily upon *Calanus spp.*, however, no significant diet shift towards larger prey was observed with body size. Although there was no increase in the consumption of amphipods across size classes, individuals >70 mm in both species consumed more lipid-rich *C. hyperboreus* than individuals <70 mm. Smaller fishes therefore relied more on smaller prey taxa (i.e., *M. longa* and *Pseudocalanus spp.*) despite the lower relative energetic content of these prey species.

We predict that the increased temperature and ice-free conditions in the Arctic are expected to favour pelagic ecosystems (Falk-Petersen et al. 2007) and as a result, food availability for forage fishes is expected to change. Significant ecological reorganization of calanoid copepods in the Arctic, with respect to abundance and diversity, will likely occur in response to changing climate (Beaugrand 2003; Falk-Petersen et al. 2007). Timing of algal blooms in high latitudes may influence reproduction and occurrence of copepods and therefore influence the availability of prey for forage fishes (Daase et al. 2013). Changes in the composition of planktonic assemblages may result in assemblages dominated by smaller zooplankton species (Pomerleau et al. 2014) which will impact foraging of capelin and Arctic cod, and potential competition may result in displacement or segregation into sub-optimal habitats. Competitive foraging pressure from capelin alone is unlikely to have a significant impact on Arctic cod (Hop and Gjørseter 2013). However, we suggest that loss of multiyear sea ice, combined with shifts in the composition of zooplankton, and northward expansion of other sub-Arctic species, will exert negative effects on the population of Arctic cod. This includes loss

of spawning habitat, seasonal variation in availability of prey and an increased threat of sub-Arctic colonizing species. If these same shifting conditions positively influence capelin populations, changes in the abundance may ensue, thus affecting the entire structure of the ecosystem.

In the Canadian Arctic, it has been estimated that Arctic cod are responsible for up to 93 % of the energy transferred from zooplankton to pelagic vertebrates including marine mammals (i.e., beluga, bowhead whales and seals), sea birds and piscivorous fishes (Welch et al. 1993). The impacts of food availability on the juvenile cohort of Arctic cod not only will be felt in the level of recruitment in the future population, but will resonate through the upper trophic levels which rely heavily upon the availability of Arctic cod as a primary prey source. Although the majority of the Arctic cod population occurs offshore (Geoffroy et al. 2015; Majewski et al. 2015), the energetic contribution of nearshore forage fishes to coastal habitats is considered to be a significant energetic link to coastal predators (Loseto et al. 2009). Therefore, assemblages of forage fish in coastal embayments, such as Darnley Bay, play an important role in ecosystem structure and energy transfer (Carscadden and Viláhljlmsson 2002; Loseto et al. 2009). Fishes with the greatest foraging plasticity in response to changing climatic conditions will have greater success in response to changes in composition and abundance of prey availability in a warmer Arctic marine environment.

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## **Chapter Four: Isotopic niche metrics and effect of lipid extraction on stable isotope signatures of co-occurring capelin (*Mallotus villosus*) and Arctic cod (*Boreogadus saida*).**

### **Abstract**

Climate change is expected to drive shifts in abundance and distribution of marine forage fishes and induce dietary overlap among sub-Arctic and Arctic species. Stable isotopes  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were used as a proxy to establish dietary niche and overlap between co-occurring, immature capelin (*Mallotus villosus*) and Arctic cod (*Boreogadus saida*) collected in the western Arctic, Darnley Bay NT, during August 2013. Stable isotope values were obtained from muscle tissue to describe the range of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , and produce niche metrics (standard area ellipses and total area) using Stable Isotope Bayesian Ellipses in R (*SIBER*) in bivariate space. Diet overlap was calculated using *nicheRover*, as the probability of one species being found within the niche region of the other. Additionally,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, niche metrics, and extent of overlap were compared between lipid-extracted and non-extracted muscle tissue of capelin and Arctic cod. The effect of lipid extraction influenced the values of  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and C:N ratio in Arctic cod, but only  $\delta^{13}\text{C}$  in capelin tissue. Lipid extraction influenced the interpretation of dietary niches and extent of overlap between co-occurring species, such that overlap of capelin within the niche of Arctic cod increased (53.0% to 89.7%) when lipids were extracted. This study suggests the use of lipid-extraction to standardize  $\delta^{13}\text{C}$  values when assessing dietary niches and extent of overlap between co-occurring fishes that differ in lipid content. Extent of dietary overlap between capelin and Arctic cod in the western Arctic suggests there is a high potential for competition between immature fishes, which may have significant implications for growth and reproduction in subsequent years as climate warms and conditions become less favourable for Arctic-adapted species.

## Introduction

The ubiquitous effects of climate change are expected to cause dramatic shifts in the ecological niches used by organisms in the Arctic marine ecosystem. Increased temperature and loss of sea ice have had a pronounced influence on the seasonality of lower trophic level prey (Falk-Petersen et al. 2007; Laidre et al. 2008; Prowse et al. 2009), and the extent of available habitat for mid-trophic level species. Range expansions of sub-Arctic species from southern environments may result in overlapping niches with Arctic and sub-Arctic marine species at high latitudes, owing to similar requirements for shared resources, thus possibly leading to interspecific competition (Beaugrand 2003; Parmesan 2006; Drinkwater et al. 2009; Falardeau et al. 2013). Overall, the combined effects of habitat loss, shifts in prey availability, and increased competition are expected to have a negative effect on polar-adapted species in the marine food web.

Arctic cod, *Boreogadus saida* (Lepechin, 1774), and capelin, *Mallotus villosus* (Müller, 1776), are pelagic forage fishes that occupy similar dietary niches in Arctic and sub-Arctic ecosystems (Hop and Gjørseter 2013; Walkusz et al. 2013; McNicholl et al. 2015). Both are planktivorous species, with short-term dietary reconstruction through stomach content analyses revealing that both species feed primarily on calanoid copepods at high latitudes when disjunct (Hop and Gjørseter 2013) as well as when co-occurring (Orlova et al. 2009; McNicholl et al. 2015). These species differ in their adaptations to cold environments, with Arctic cod being closely associated with sea ice and persisting at sub-zero temperatures through the production of antifreeze glycoproteins, whereas capelin are primarily associated with the sub-Arctic marine environment and are unable to persist year-round at temperatures below zero. Therefore, these species are predicted to have different responses to a warming ocean climate, where warming

may promote increased abundance and distribution of capelin in Arctic ecosystems (Hop and Gjøsæter 2013), whereas cod survival declines in response to limited sea ice (Fortier et al. 2006) and substantive changes in prey availability (Falk-Petersen et al. 2007). Northward range expansion of Atlantic capelin has been observed in recent years in response to marine shifts in ocean temperature. This trend is expected to continue as temperatures rise (Drinkwater 2005; Rose 2005; Stenevik and Sundby 2007). Similarly, capelin have been documented in the Beaufort Sea within embayments or in the nearshore environment, where they co-occur with immature Arctic cod, which are found in the highest abundance at depths <100 m (Geoffroy et al. 2015). Together, this information suggests that competition between these two fish species is likely and will be the most pronounced in the coastal environment within Arctic ecosystems.

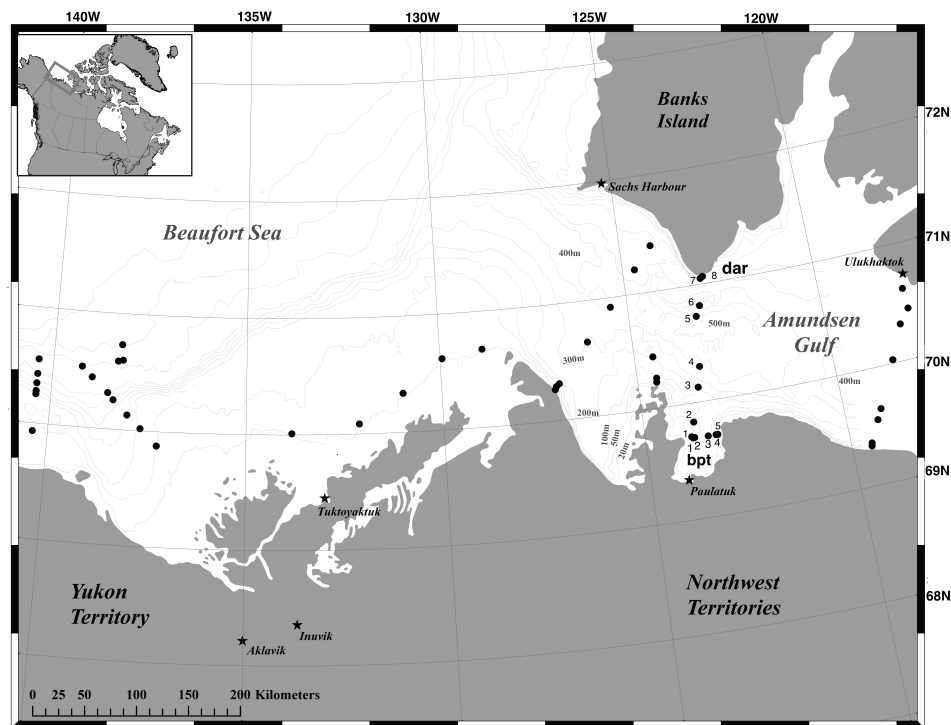
Although stomach content analyses provide valuable information on recently consumed prey, this method of diet reconstruction may not reflect prey items that differ in rates of digestion, and only reflects diets over relatively short temporal scales (approximately 24 hours). Stable isotope values obtained from muscle tissue, however, provide dietary information integrated over longer periods and reflect niche breadth (Layman et al. 2007; Jackson et al. 2011). Stable isotopes,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , are effective markers of dietary source and trophic position, respectively, in ecological studies (Peterson and Fry 1987; Post 2002), and are useful tools for describing the extent of dietary overlap between co-occurring species (Swanson et al. 2015). Intrinsic factors such as life history, sex and reproductive status are known to influence  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in high latitude fishes (Michaud et al. 2013). This is likely due to varying tissue lipid content across these intrinsic factors in addition to differences in diet. Lipids are carbon-depleted, and thus, lipid-rich fish will tend to have lower  $\delta^{13}\text{C}$  relative to less lipid-rich fish, simply reflecting the difference in lipid content. Therefore, previous studies suggest lipid

extraction is necessary for valid comparisons among lipid-rich fish (Sotiropoulos et al. 2004; Cherel et al. 2011). As there is a strong correlation between lipid content and C:N ratio, lipid-rich tissues are often indicated by a C:N >3.5 (Mintenbeck et al. 2008). Differences in tissue lipid content between species can influence the proportion of lipids and protein composition of the consumer, and subsequently, the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (Tiezen et al. 1983; Focken and Becker 1998; Pinnegar and Polunin 1999; McCutchan et al. 2003). Therefore, such factors must be considered and standardized when comparing the isotopic niches between species.

The purpose of this study is to examine the long-term (30-40 days) dietary overlap of co-occurring immature Arctic cod and capelin, using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  as long-term dietary markers. Indeed, stable isotope ratios of carbon and nitrogen from fish sampled in the summer reflect dietary sources synthesized into muscle tissue during the spring feeding period (Perga and Gerdeaux 2005; 20-40 d, Heady and Moore, 2012). This work thus complements our previous characterization of short-term diet of capelin and cod based on stomach contents analysis (see Chapter 2; McNicholl et al. 2015). Long-term trophic niche overlap for co-occurring immature Arctic Cod and capelin was examined by describing niche metrics and assessing the extent of overlap in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in bivariate, isotopic space. Range of stable isotope ratios, niche metrics, and extent of overlap, will be the basis of inferences for the foraging strategies of these species and the potential for competition, should resource availability change. We predict that these species will share a similar dietary niche, and thus exhibit substantive dietary overlap, evidenced by  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in bivariate space. An additional aim of this study is to compare  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values derived from lipid-extracted and non-extracted muscle tissues in immature capelin and Arctic Cod to determine whether time-consuming lipid extraction is necessary when comparing dietary overlap of these two species.

## Methods

Immature capelin and Arctic cod were sampled aboard the F/V Frosti in Darnley Bay, Northwest Territories (NT), on 4–6 August 2013 (approximately 10.5 h of daylight) as a component of the Beaufort Sea Regional Environmental Assessment (BREA) Marine Fishes Project (Fig. 4.1). This assessment was designed to determine the composition of fishes in relation to habitat parameters and associated biota in the offshore and nearshore environments in the Canadian Beaufort Sea region, including Amundsen Gulf.



**Fig. 4.1** Map of the BREA Marine Fishes Project study area, with sampling stations completed during the 2013 survey indicated (black circles). Co-occurring capelin and Arctic cod were collected along the dar and bpt transects, indicated with station numbers. Capelin were not captured at any stations other than the dar (station 2) and bpt (station 3,4,5) transects; Arctic cod were captured at all stations.



Fish were collected with a modified Atlantic Western IIA bottom trawl (22.86-m head rope, 21.23 m footrope with a 1.27 cm (0.5 in) mesh cod-end and intermediate liner) at each station (Cosmos-Swan and Isaac-Kidd mid-water trawls were also deployed at some stations). Bottom tow time at each station was limited to 20 min with a target speed set at 2.9 knots. Co-occurring capelin and Arctic cod were collected from seven stations along two transects in and near Darnley Bay. Capelin were not collected at any other stations, whereas Arctic cod were captured at all stations (Fig. 4.1). Capelin and cod selected for diet analysis were selected from three stations at 75-m (bpt\_04, bpt\_05 and dar\_02; Fig. 4.1), from which 348 capelin and 650 Arctic Cod were sampled.

Immediately after sampling, the fork length (from snout to inside fork of caudal fin; mm) of each fish was determined and individuals were stored at -20 °C. Individuals from each species were selected for stable isotope analysis by sorting fish by fork-length and selecting every 15<sup>th</sup> fish, to represent the full size range sampled for capelin (n=30; 70 to 132 mm) and Arctic cod (n=30; 42 to 114 mm).

Sub-sampled fish were later thawed for processing, including removal of stomachs and a sub-sample of left dorsal muscle tissue. Muscle samples were placed in 118 mL whirl-paks and freeze dried for 48 hours (LABCONCO-FreeZone 4.5). Dried tissues were then homogenized using a ceramic mortar and pestle. Homogenized samples were transferred into 20 mL glass scintillation vials for storage. Samples were weighed ( $400 \pm 10 \mu\text{g}$ ) and duplicate samples were prepared for every 10<sup>th</sup> sample. For the same sub-sample, lipids were extracted from ~100 mg of the homogenized tissue using the cold cyclohexane (C<sub>6</sub>H<sub>12</sub>) method (Cherel et al. 2010). This method removes neutral lipids, including triacylglycerols and wax esters, but leaves structural lipids intact, thus minimizing variation associated with life history or reproductive status

(Chouvelon et al. 2014; Elliott and Elliot 2016). If supernatant still held the colour of the tissue after extraction, lipid extraction steps were repeated to ensure that supernatant successfully extracted all neutral lipids.

All samples were analyzed for stable carbon and nitrogen isotopes using a continuous flow isotope ratio mass spectrometer (Thermo-Delta 5 Plus) equipped with a Costech elemental analyzer at the Freshwater Institute, Winnipeg. Stable isotope ratios are expressed in delta ( $\delta$ ) notation, defined as the deviation from a standard reference material in parts per thousand (‰).  $\delta^{13}\text{C}$  results are relative to Vienna Pee Dee Belemnite (VPDB) whereas  $\delta^{15}\text{N}$  results are relative to atmospheric air. Both values are calculated using the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where X is  $^{13}\text{C}$  or  $^{15}\text{N}$ ,  $R_{\text{sample}}$  is the ratio ( $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ ) in the sample while  $R_{\text{standard}}$  is the ratio in the standard. Standard deviations of repeated measurements of certified reference materials (USGS 40 and 41) were  $< 0.1\text{‰}$  for  $\delta^{13}\text{C}$  and  $< 0.16\text{‰}$  for  $\delta^{15}\text{N}$ . The standard deviation of repeated measurements of an in-house standard was  $< 0.1\text{‰}$  for  $\delta^{13}\text{C}$  and  $< 0.11\text{‰}$  for  $\delta^{15}\text{N}$ . Prior to statistical analysis, standard deviations determined from duplicate samples were  $< 0.08\text{‰}$  for  $\delta^{13}\text{C}$  and  $< 0.07\text{‰}$  for  $\delta^{15}\text{N}$  for both species, and within the acceptable range for direct comparison (Hobson and Schell 1998).

### *Statistical Analyses*

The values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , together with C:N ratios were calculated from the mass fraction of stable isotopes for each sample. To examine the influence of lipid extraction when comparing dietary overlap of two species, non-extracted and extracted  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were

compared from the same individuals. Non-parametric Mann-Whitney U tests were used to compare species, while extraction methods were compared using Wilcoxon signed rank tests because the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values did not meet the assumptions of parametric tests (i.e., normality and homogeneity of variance).

To evaluate the isotopic niche metrics of co-occurring immature Arctic cod and capelin, the total area of convex hulls and standard ellipse areas (SEA) for each species as boundaries describing isotopic niche space were calculated (Jackson et al. 2011) using stable isotope Bayesian ellipses in R (SIBER). Total areas (TA) of the convex hulls were calculated from the outermost values on the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  bi-plot, whereas SEAs were calculated within the convex hulls to measure isotopic niche space (Jackson et al. 2011, Guzzo et al. 2013, Swanson et al. 2015). The SEA contains 40% of the data points, and is considered to be more robust to varying sample sizes and the influence of outliers relative to the area of the convex hull (Batschelet 1981; Jackson et al. 2011). Correction for small sample size was not applied to these ellipses, given that samples sizes of  $n \geq 30$  provide a more constant value of SEA (Jackson et al. 2011).

Probability of overlap was calculated using the *nicheRover* package, rather than *SIBER*, to produce a pairwise probability of overlap based on one species occurring within the niche of another. Although SEA and TA provide valuable information about isotopic niches in bivariate space, they lack directionality when calculating overlap (i.e., overlap of one species' niche within the other, rather than total overlap; Swanson et al. 2015). *NicheRover* calculates the extent of overlap between two species using niche region ( $N_R$ ), defined as a specific region in which a species has a 95% probability of being found in bivariate space using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. This overlap was then calculated as a probability (95%) of Arctic Cod occurring in the  $N_R$  of capelin, as well as the converse probability of capelin occurring within the  $N_R$  of Arctic Cod. Stable

isotope data were assessed for multivariate normality using probability plots prior to analysis, and fit the assumption of normality.

## Results

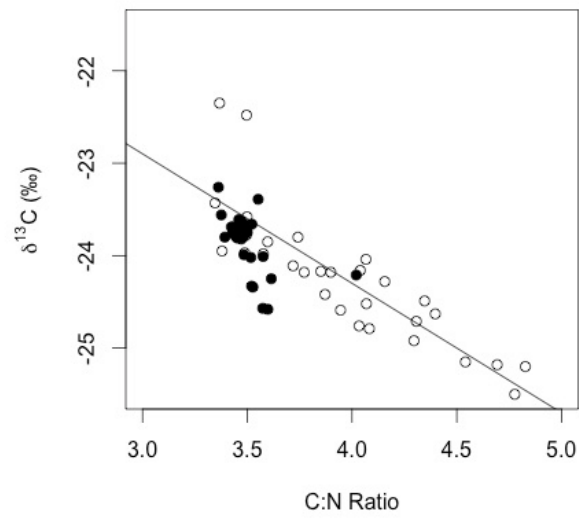
Among sub-sampled capelin, 53% were male, 37% were female and the remainder were unknown sex. Among sub-sampled Arctic cod, all were immature with undeveloped gonads and, therefore, their sex could not be determined.

Muscle samples with and without lipid extraction differed in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  within both capelin and Arctic cod (Table 4.1). For non-extracted tissues, mean  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and C:N values differed between species.  $\delta^{13}\text{C}$  values were lower for Arctic cod relative to capelin ( $W=219.5$ ;  $p=0.001$ ) and showed a greater range than for capelin (-25.5 to -22.3‰; -24.6 to -23.3‰, respectively). Arctic cod also had higher C:N ratios ( $W=723$ ;  $p<0.0001$ ).  $\delta^{15}\text{N}$  ranges in both species suggest they fall within similar trophic positions (13.0 to 14.5‰ for capelin; 13.2 to 14.6‰ for Arctic cod), but overall  $\delta^{15}\text{N}$  values were significantly higher for capelin relative to Arctic cod ( $t(57)=4.1$ ;  $p<0.05$ ).

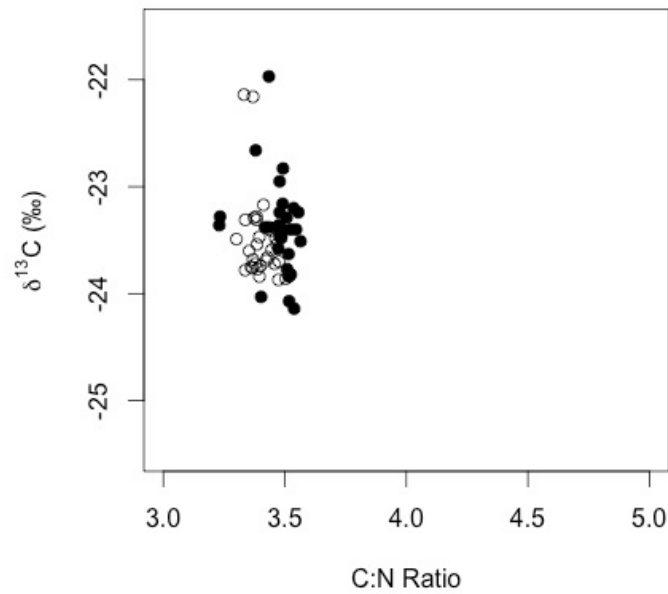
<b>Table 4.1</b> Mean +/- SD total fish length, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and C:N ratio for co-occurring capelin (n=30) and Arctic Cod (n=30) collected in Darnley Bay, NWT, during the summer of 2013. Significant differences ( $p<0.05$ ) between lipid extracted and non-extracted muscle within each species was found through paired t-tests, and Wilcoxon signed-rank tests used to examine differences between species are indicated in bold.					
Species	Total Length (mm)	Extraction Method	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C:N
Arctic Cod	86.6 +/- 11.9	None	-24.2 +/- 0.7	13.6 +/- 0.4	4.0 +/- 0.4
		Neutral	<b>-23.5 +/- 0.4</b>	<b>13.7 +/- 0.4</b>	<b>3.4 +/- 0.1</b>
		None	-23.9 +/- 0.1	13.9 +/- 0.4	3.5 +/- 0.1
		Neutral	<b>-23.4 +/- 0.4</b>	14.0 +/- 0.4	3.5 +/- 0.1
Capelin	107.5 +/- 11.0	None	-23.9 +/- 0.1	13.9 +/- 0.4	3.5 +/- 0.1
		Neutral	<b>-23.4 +/- 0.4</b>	14.0 +/- 0.4	3.5 +/- 0.1

Lipid extraction influenced  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and C:N values obtained for Arctic cod, but only  $\delta^{13}\text{C}$  values in capelin tissue (Table 4.1). Arctic cod tissues decreased in  $\delta^{13}\text{C}$  values and decreased in C:N ratio as a result of lipid extraction. Although lipid extraction influenced  $\delta^{13}\text{C}$  in capelin, the overall ratio of C:N was unaffected. Among non-extracted tissues (Fig. 4.2a) there was a weak relationship between  $\delta^{13}\text{C}$  and the ratio of C:N for capelin ( $F_{1,27}=10.36$ ;  $r^2=0.15$ ;  $p=0.003$ ) and a substantive relationship for Arctic cod ( $F_{1,28}=71.95$ ;  $r^2=0.72$ ;  $p<0.0001$ ). When tissues were lipid-extracted (Fig. 4.2b), the relationship between  $\delta^{13}\text{C}$  and the ratio of C:N was absent for capelin ( $F_{1,28}=1.58$ ;  $r^2=0.05$ ;  $p=0.22$ ) and Arctic cod ( $F_{1,28}=3.16$ ;  $r^2=0.10$ ;  $p=0.09$ ). The range of  $\delta^{13}\text{C}$  values for capelin (-24.1 to -22.0‰) and Arctic cod (-23.9 to 22.1‰) were more similar after extraction, yet a less pronounced shift in the range of the values was observed for  $\delta^{15}\text{N}$  (capelin 13.1 to 14.7‰; Arctic cod 13.0-14.7‰). The mean C:N ratio was higher ( $W=140$ ;  $p<0.0001$ ) in non-extracted tissue than in extracted Arctic Cod tissue (Table 4.1); however, once lipids were extracted from tissues this ratio was significantly higher in capelin ( $t(57)=3.96$ ;  $p<0.001$ ) than in Arctic cod.

Based on the standard area ellipses, Arctic cod had a wider isotopic niche in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  bivariate space than did capelin for non-extracted (Fig. 4.3a,b) tissues. When examining non-lipid extracted muscle, the isotopic niche of Arctic cod (SEA=0.81, TA=3.01) was larger than that of capelin (SEA=0.30, TA=0.98). When lipids were extracted, however, the isotopic niche decreased for Arctic cod (SEA=0.48, TA=1.7), becoming more similar to capelin (SEA=0.41, TA=1.4). The lipid-extraction method standardized isotope values for both species, allowing dietary overlap to be evaluated on a common basis.

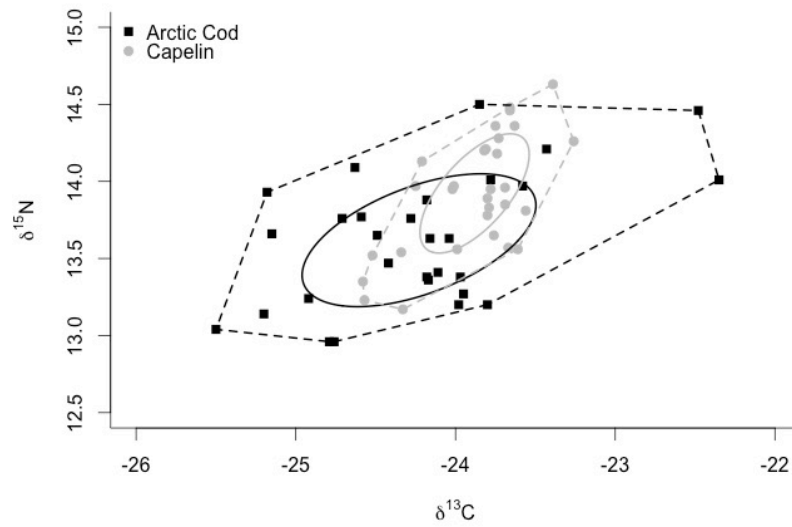


a)

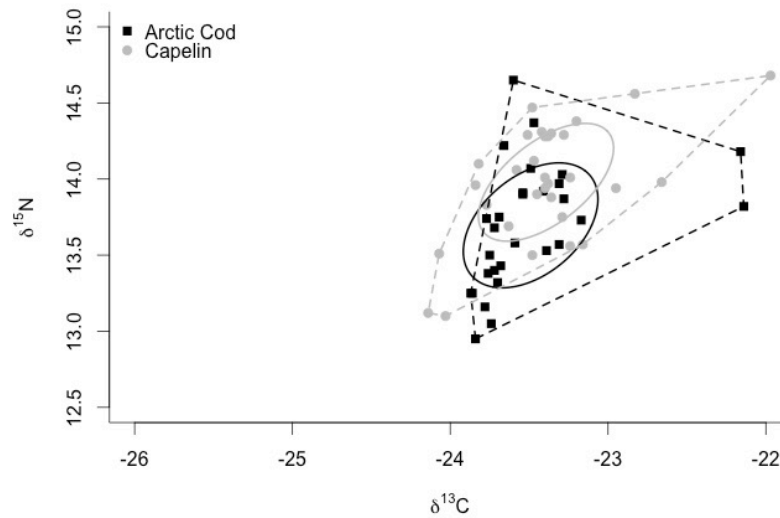


b)

**Fig. 4.2** Relationship between  $\delta^{13}\text{C}$  and the carbon:nitrogen (C:N) ratio in a) non lipid-extracted, and b) lipid-extracted muscle tissue from capelin (black; n= 30) and Arctic cod (white; n=30) sampled during the summer of 2013 in Darnley Bay.



a)



b)

**Fig. 4.3** The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of a) non-lipid-extracted, and b) lipid-extracted muscle tissue from Arctic Cod (black) and capelin (grey) collected in Darnley Bay during the summer of 2013. Standard ellipse areas (SEA) are indicated by the solid lines; convex hulls or total area (TA) are indicated by the dashed lines.

Density plots for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  indicated no substantive violation to the assumption of normality, but lipid extraction reduced skew of posterior distributions produced for Arctic cod (Appendix). Probabilistic niche overlap metrics (%) estimated that Arctic cod had a 82.6% probability of occurring within the  $N_R$  of capelin, and capelin had a 89.7% probability of occurring within the  $N_R$  of Arctic cod. This was contrary to what was found for non-extracted tissues where the probability of cod occurring within the  $N_R$  of capelin was 53.0%, and there was a 94.7% probability of capelin occurring within the  $N_R$  of Arctic cod.

## Discussion

Although life history, sex and reproductive status were similar for both species, the effect of lipid content on  $\delta^{13}\text{C}$  was enough to influence the interpretation of dietary overlap between these co-occurring fish species. The greater range in  $\delta^{13}\text{C}$  values from non-extracted cod tissue suggested that cod use a greater variety of prey from coastal and pelagic sources than do capelin, whose  $\delta^{13}\text{C}$  values suggest they are either restricted to a particular foraging area or rely primarily on prey items associated with the inshore (Cherel et al. 2011; Giraldo et al. 2015). In contrast, stomach content analysis on the same fish illustrated high dietary overlap (McNicholl et al. 2015). This discrepancy may be interpreted as differences in the short-term (stomach contents) diet versus long-term (stable isotope) inferred diet of both species. Although capelin generally had higher  $\delta^{15}\text{N}$  values, the difference between species was less than the average trophic fractionation value (3.40‰) and therefore these species were not considered to be feeding at different trophic levels (Minagawa and Wada 1984; Post 2002). When carbon-depleted lipids were extracted, however, the range of  $\delta^{13}\text{C}$  values for Arctic cod decreased, resulting in a much higher diet overlap with co-occurring capelin. Therefore, lipid-extraction resulted in the isotopic



dietary metric supporting the conclusions from stomach content analysis that co-occurring capelin and Arctic cod occupy a similar dietary niche and display a high potential for competition.

Lipid extraction had a higher influence on stable isotope ratios of Arctic cod than on capelin. This influence on stable isotopes ratios is likely due to cod muscle containing more lipid than capelin, evidenced by the negative trend between  $\delta^{13}\text{C}$  and C:N ratio in cod tissue as well as the higher range in C:N ratios. Low  $\delta^{13}\text{C}$  values are consistent with tissues with high lipid content, undergoing little or no isotopic fractionation and, therefore, are less enriched in  $^{13}\text{C}$  (Hare et al. 1991; Fantle et al. 1999; McMahon et al. 2010). Although capelin and Arctic cod are energetically rich and store considerable quantities of lipid in their body tissues, there is variation between species in how these lipids are digested and stored (Henderson and Tocher 1987; Tocher 2003). Because these fishes differ in their physiological adaptations to an Arctic environment (i.e., antifreeze protein production in cod), it is likely these fishes also differ in long-term lipid storage in muscle and allocation of lipids (Tocher 2003). For instance cod may be more efficient than capelin at digesting lipids by bile-activated lipase produced by pyloric caecae with concomitant higher storage of lipids in the liver (Gjellesvik 1991) relative to capelin. Regardless of the factors leading to differential lipid content in muscle tissues of these two fish species, lipid-extracted tissues must be used to compare the diet and dietary overlap of these species using carbon stable isotopes to eliminate biased values due to high lipid content in Arctic cod and variation between individuals within species. The change in the degree of overlap of standard area ellipses, and reduced skew in posterior distributions of the probability of overlap between cod and capelin, both illustrate the importance of diet comparisons using lipid extracted relative to non-extracted tissues.

The use of stable isotopes as a proxy for dietary niches in this study confirms that the extent of dietary overlap between cod and capelin is high during the open-water season. The probabilities of cod occurring within the niche of capelin, and capelin within the niche of cod, were high (83-90%) based upon results from lipid-extracted tissues. These results are consistent with stomach content analysis of the same cod and capelin from Darnley Bay, where both species fed primarily on calanoid copepods such as *Calanus hyperboreus* and *C. glacialis* (McNicholl et al. 2015). The combination of stomach contents and stable isotopes from this study indicate that cod and capelin feed on similar prey taxa, and within similar temporal and spatial scales respectively. Although stomach content analysis indicated high dietary overlap with respect to prey taxa consumed (Schoener's index= 0.80), mean energetic content of the diet was higher for Arctic cod, potentially explaining its higher lipid content. It is unknown however, if competitive pressure exists in the pelagic Beaufort Sea, or the extent of dietary overlap between adult capelin and Arctic cod. Competition between adult Arctic cod and juvenile capelin in the Barents Sea resulted in a 40% reduction in condition among capelin (Orlova et al. 2009). In the Beaufort Sea, adult Arctic cod (>100 mm standard length) are generally found on the continental shelf (350-500 m; Majewski et al. 2015), whereas adult capelin have only been observed in high abundance near-shore (McNicholl unpublished data). Arctic cod exhibit a transition to larger prey with depth, such that smaller cod feed primarily on smaller prey taxa (Walkusz et al. 2013; Majewski et al. 2015). In Franklin Bay, NT, smaller (<100 mm standard length) Arctic cod were observed at depths <180 m performing diel vertical migrations (Benoit et al. 2010). This is potentially a strategy to avoid competition or cannibalism with larger adult cod known to occupy the mesopelagic layer (Rand et al. 2013; Majewski et al. 2015). If intraspecific competition and predation drive juvenile cod into coastal embayments or the pelagial layer, there

is a greater potential for competition in the coastal environment between juvenile cod and capelin. Capelin feed primarily on copepods as juveniles and adults (Vesin et al. 1981) and are not known to consume other fishes or cannibalize smaller size cohorts. It is possible that differences in gape morphology restrict capelin to smaller planktivorous prey taxa (Robb and Hislop 1980), and make it unlikely that capelin would exhibit competitive pressure on immature Arctic cod. In Darnley Bay, immature capelin and Arctic cod were only collected by a benthic trawl, and may therefore be exhibiting similar diel vertical migrations as in the neighbouring Franklin Bay. The extent of diet overlap between these species throughout the year remains uncertain, but feeding is expected to be greatest during the summer open-water season.

Competitive pressure among immature forage fishes will influence summer growth and reproductive success in subsequent years as a greater allocation of energy is required towards reproduction during the adult life history stage. Understanding how prey availability will shift in a warmer Beaufort Sea scenario is required to predict how these forage fishes and their interactions may be influenced by climate change. Environmental drivers that increase primary production and zooplankton abundance nearshore may be more favourable for fishes which have a life history associated with the coastal environment, such as capelin whose isotopic range is consistent with that of coastal Beaufort Sea fishes (Giraldo et al. 2015). Immature fishes of both species are consuming similar prey in the coastal environment at a life history stage that requires high growth if they are to successfully spawn in the subsequent year. Therefore, a shift in prey availability in coastal embayments, such as Darnley Bay, may not only influence interspecific competition but growth and condition of a particular year-class. It is uncertain if these fishes may be able to use different habitats or prey types if abundances become limiting, or if the effect of competition will influence these species when they co-occur. High dietary overlap, shown in

stomach contents (Hop and Gjøsæter 2013; McNicholl et al. 2015), in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ranges, and in bivariate isotopic space (this study), suggest that a high potential for competition exists between immature individuals of both species. Further studies are required to compare niche regions of cod and capelin across all life history stages, in addition to other forage fishes occupying the Arctic coastal environment (i.e., Pacific Sandlance (*Ammodytes hexapterus* (Pallas, 1814)) to best assess habitat use among fishes, and ecosystem structure in a dynamic marine environment. Shifts in the abundance of prey items for these forage fishes and potential for competition will influence energetic linkages between trophic levels and engender re-organization of ecosystem structure in the Arctic environment (Carscadden and Vilhjálmsson 2002; Loseto et al. 2009). Further studies are required that examine dietary niches and ecological factors influencing stable isotopes as the Arctic environment continues to change with climate.

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## Chapter Five. Synthesis Discussion

The examination of life history traits among populations and the interactions among co-occurring species are essential for describing the ecological niche of capelin in Arctic ecosystems. Capelin populations in the Canadian Arctic differ in condition, age-at-maturity and growth (Chapter 2) and, thus, will likely respond differently to climatic shifts, relative to those in the sub-Arctic. Responses are also expected to differ between the western and eastern Arctic, evidenced by larger body size and older, spawning males in Pangnirtung Fjord relative to those in Darnley Bay. The variation in life history traits illustrated at the northern limit of this species' distribution will likely contribute to their capacity to adapt to conditions of the edges of their distributional range and persist in two very different but highly variable environments. As climate changes, the extent of suitable habitat for capelin and other sub-Arctic species is expected to increase, thereby facilitating increased abundance of populations in Arctic regions as well as emigration of individuals originating from sub-Arctic stocks. Because regional-specific life history strategies influence annual survival and reproductive rates of individual fish, population dynamics will likely differ among the regions. Mixing of populations that differ in life history traits increases the capacity for this species to persist in the Arctic and colonize newly available habitat, the use of which were previously limited by environmental conditions (e.g., temperature, sea ice extent). The substantive variation observed in first year growth between Arctic and sub-Arctic populations may influence life history traits (e.g., age-at-maturity), and contribute to differences in the spawning ecology among Arctic populations. Future studies are required to examine the factors influencing growth and mortality of young-of-year capelin, and potential of iteroparity among females to further assess population dynamics in the Arctic environment.

The high extent of dietary overlap suggests a strong potential for competition between capelin and Arctic cod, should prey availability and seasonality shift with warmer temperatures. Stomach content analysis between co-occurring immature capelin and Arctic cod indicated that both species rely primarily on calanoid copepods (e.g., *Calanus hyperboreus* and *C. glacialis*) and significant overlap exist in diets (Chapter 3). Within species, mean abundance, biomass and energetic content consumed varied among size classes as larger individuals consumed a greater variety of prey. Stable isotope analysis, representative of diet integrated over the course of spring foraging, provided further support for potential competition between capelin and Arctic cod based on values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Chapter 4). The combined effect of shifts in zooplankton community composition and competitive pressure from capelin are expected to exert negative pressure on growth and survival of juvenile Arctic cod (Hop and Gjørseter 2013). Future studies that examine the extent of overlap throughout the year in relation to the amount of available prey are necessary to determine if interspecific competition is actually occurring between these mid-trophic level species.

The stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) values differed when lipids were extracted from tissues from capelin and cod (Chapter 4), such that the range of  $\delta^{13}\text{C}$  in lipid-rich Arctic cod tissue decreased with extraction. This therefore increased the extent of inferred dietary overlap of Arctic cod with sympatric capelin. Lipid-extraction is advised as a means to standardize  $\delta^{13}\text{C}$  values, when comparing the diets of fishes that differ in lipid content. Future studies that examine differences in  $\delta^{13}\text{C}$  values in fishes differing in lipid content within species (i.e., life history, sex) and among species, would provide valuable information to better understand trophic structure in the Arctic marine food web.

As the abundance of Arctic cod is expected to decline with changing climate, it remains uncertain if capelin may fulfill the role as a primary prey source for Arctic marine predators. Recent studies examining the diet of Thick-billed Murres (*Uria lomvia*) and Arctic char (*Salvelinus alpinus*) have indicated dietary shifts towards capelin, relative to Arctic prey taxa (i.e., Arctic cod, amphipods) among Arctic and sub-Arctic locations (Dempson et al. 2002; Gaston et al. 2003; Ulrich, 2013). Coastal predators are expected to display similar shifts in diet in other regions of the Canadian Arctic as sub-Arctic prey, such as capelin or sand lances (*Ammodytes spp.*), become more abundant in response to warming climate (Hop and Gjøsæter 2013). Dietary studies examining such predators in the future would indicate possible range shifts among sub-Arctic forage fishes, and implications for foraging behaviour and success of marine predators. Although capelin serve as a primary prey source in coastal environments, populations of capelin may exhibit substantive fluctuations in abundance and will likely become a highly variable prey source for predators.

Overall, this thesis has shown that the life history characteristics of capelin differ across the Canadian Arctic, as well as in relation to sub-Arctic populations, and capelin in these regions exhibit high dietary overlap with co-occurring Arctic cod. These results contribute to understanding the role of capelin in ecosystem structure and function among trophic levels. As climate changes and the populations of Arctic cod are expected to decline, capelin is expected to increase in abundance and persistence, and may occupy a similar ecological role as Arctic cod in coastal environments in the Arctic as global temperature continues to rise.

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## Appendix A

### *Growth Validation*

Otolith radius in relation to total length was examined using a polynomial fit for all fishes ( $F_{2,267} = 646.6$ ,  $r^2 = 0.83$ ,  $p < 0.0001$ ). This relationship provided a strong fit relative to a linear regression used for growth validation ( $F_{1,268} = 1053$ ,  $r^2 = 0.80$ ,  $p = < 0.0001$ ; Fig. 4.5), therefore based on an  $r^2$  value  $> 0.60$  (Hedeholm et al. 2010) this trend was considered an appropriate validation of fish length in relation to otolith radius in capelin.

### *Mixed Effects Model Pairwise Comparison*

(Beaufort Sea (B), Pangnirtung Fjord (P), Newfoundland (N))

```
> lsmeans(n5, pairwise~age*region, adjust="tukey")
```

```
lsmeans(n5, pairwise~age*region, adjust="tukey")
```

```
$lsmeans
```

age	region	lsmean	SE	df	lower.CL	upper.CL
1	B	0.186311	0.02741627	15.36	0.12799230	0.2446297
2	B	0.423531	0.02668502	14.84	0.36659813	0.4804639
3	B	0.189713	0.02696604	15.01	0.13224138	0.2471852
4	B	0.133475	0.03139530	24.44	0.06873924	0.1982102
1	N	0.338362	0.02064364	5.28	0.28614395	0.3905799
2	N	0.415647	0.02060681	5.27	0.36348258	0.4678115
3	N	0.191046	0.02237018	6.58	0.13745642	0.2446348
4	N	0.119082	0.03293670	29.13	0.05173144	0.1864323
1	P	0.186133	0.02011578	4.65	0.13322737	0.2390385
2	P	0.333372	0.02066561	4.86	0.27977980	0.3869644
3	P	0.314133	0.01960968	4.34	0.26131406	0.3669509
4	P	0.190423	0.02025101	4.78	0.13763132	0.2432147

Confidence level used: 0.95

```
$contrasts
```



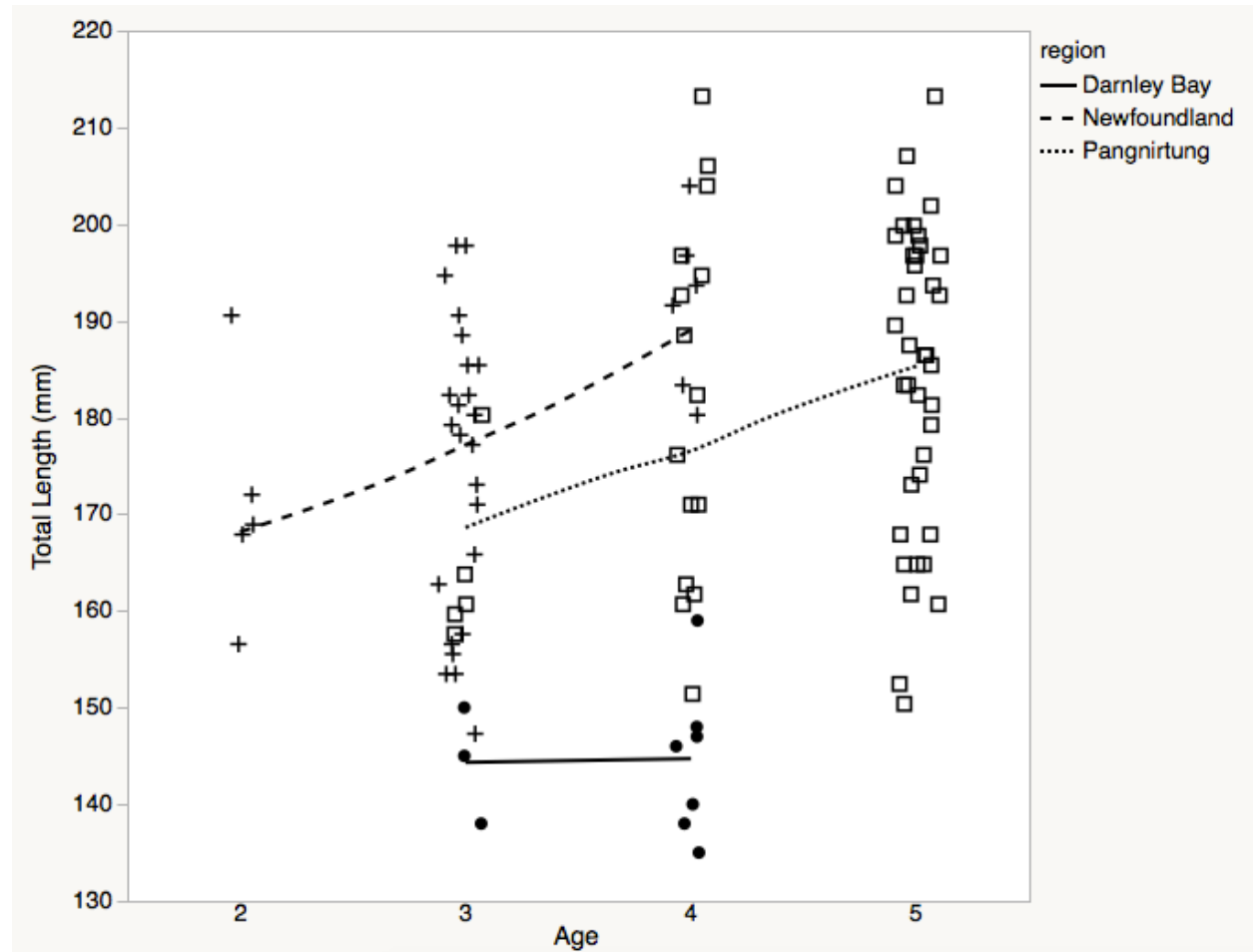
contrast	estimate	SE	df	t.ratio	p.value
1,B - 2,B	-0.237219999	0.02979499	276.55	-7.962	<.0001
1,B - 3,B	-0.003402277	0.03175360	294.05	-0.107	1.0000
1,B - 4,B	0.052836295	0.03624658	318.43	1.458	0.9506
1,B - 1,N	-0.152050881	0.02365537	368.75	-6.428	<.0001
1,B - 2,N	-0.229336033	0.02597456	342.32	-8.829	<.0001
1,B - 3,N	-0.004734607	0.02855289	278.12	-0.166	1.0000
1,B - 4,N	0.067229152	0.03759812	298.01	1.788	0.8234
1,B - 1,P	0.000178074	0.02297536	368.08	0.008	1.0000
1,B - 2,P	-0.147061075	0.02163272	366.34	-6.798	<.0001
1,B - 3,P	-0.127821457	0.02352722	364.99	-5.433	<.0001
1,B - 4,P	-0.004111980	0.02607417	324.13	-0.158	1.0000
2,B - 3,B	0.233817723	0.02971303	284.84	7.869	<.0001
2,B - 4,B	0.290056294	0.03458796	327.52	8.386	<.0001
2,B - 1,N	0.085169118	0.02272100	367.17	3.748	0.0110
2,B - 2,N	0.007883966	0.02358340	368.98	0.334	1.0000
2,B - 3,N	0.232485392	0.02638145	343.15	8.812	<.0001
2,B - 4,N	0.304449152	0.03599234	344.57	8.459	<.0001
2,B - 1,P	0.237398073	0.02190743	368.01	10.836	<.0001
2,B - 2,P	0.090158924	0.02406926	361.71	3.746	0.0111
2,B - 3,P	0.109398542	0.02163372	366.34	5.057	<.0001
2,B - 4,P	0.233108019	0.02349983	366.95	9.920	<.0001
3,B - 4,B	0.056238572	0.03262653	306.45	1.724	0.8561
3,B - 1,N	-0.148648604	0.02511995	357.25	-5.918	<.0001
3,B - 2,N	-0.225933757	0.02272375	367.20	-9.943	<.0001
3,B - 3,N	-0.001332330	0.02401239	368.98	-0.055	1.0000
3,B - 4,N	0.070631429	0.03410811	366.81	2.071	0.6439
3,B - 1,P	0.003580350	0.02505465	347.85	0.143	1.0000
3,B - 2,P	-0.143658798	0.02601518	313.04	-5.522	<.0001
3,B - 3,P	-0.124419180	0.02391100	363.36	-5.203	<.0001
3,B - 4,P	-0.000709703	0.02182203	366.71	-0.033	1.0000

4,B - 1,N	-0.204887176	0.03062359	323.68	-6.691	<.0001
4,B - 2,N	-0.282172328	0.02863920	364.81	-9.853	<.0001
4,B - 3,N	-0.057570902	0.02657920	366.62	-2.166	0.5754
4,B - 4,N	0.014392857	0.03521399	366.01	0.409	1.0000
4,B - 1,P	-0.052658222	0.03043928	311.36	-1.730	0.8531
4,B - 2,P	-0.199897370	0.03143096	275.42	-6.360	<.0001
4,B - 3,P	-0.180657752	0.02927516	336.65	-6.171	<.0001
4,B - 4,P	-0.056948275	0.02814578	365.77	-2.023	0.6772
1,N - 2,N	-0.077285152	0.01727913	295.80	-4.473	0.0007
1,N - 3,N	0.147316274	0.02095743	263.82	7.029	<.0001
1,N - 4,N	0.219280033	0.03220387	327.28	6.809	<.0001
1,N - 1,P	0.152228955	0.01346132	367.04	11.309	<.0001
1,N - 2,P	0.0049898060	0.01580429	350.78	0.316	1.0000
1,N - 3,P	0.0242294241	0.01353324	368.26	1.790	0.8225
1,N - 4,P	0.1479389012	0.01738128	314.94	8.511	<.0001
2,N - 3,N	0.2246014263	0.01795895	309.64	12.506	<.0001
2,N - 4,N	0.2965651855	0.03031843	366.84	9.782	<.0001
2,N - 1,P	0.2295141068	0.01698366	322.46	13.514	<.0001
2,N - 2,P	0.0822749580	0.01865384	253.91	4.411	0.0009
2,N - 3,P	0.1015145762	0.01564156	355.86	6.490	<.0001
2,N - 4,P	0.2252240532	0.01371140	367.30	16.426	<.0001
3,N - 4,N	0.0719637592	0.02836938	356.61	2.537	0.3207
3,N - 1,P	0.0049126805	0.02074135	219.70	0.237	1.0000
3,N - 2,P	-0.1423264682	0.02208499	172.50	-6.444	<.0001
3,N - 3,P	-0.1230868501	0.01909204	263.43	-6.447	<.0001
3,N - 4,P	0.0006226269	0.01706183	351.74	0.036	1.0000
4,N - 1,P	-0.0670510787	0.03202792	293.96	-2.094	0.6278
4,N - 2,P	-0.2142902274	0.03298190	256.40	-6.497	<.0001
4,N - 3,P	-0.1950506093	0.03092072	321.10	-6.308	<.0001
4,N - 4,P	-0.0713411323	0.02985586	362.71	-2.390	0.4159

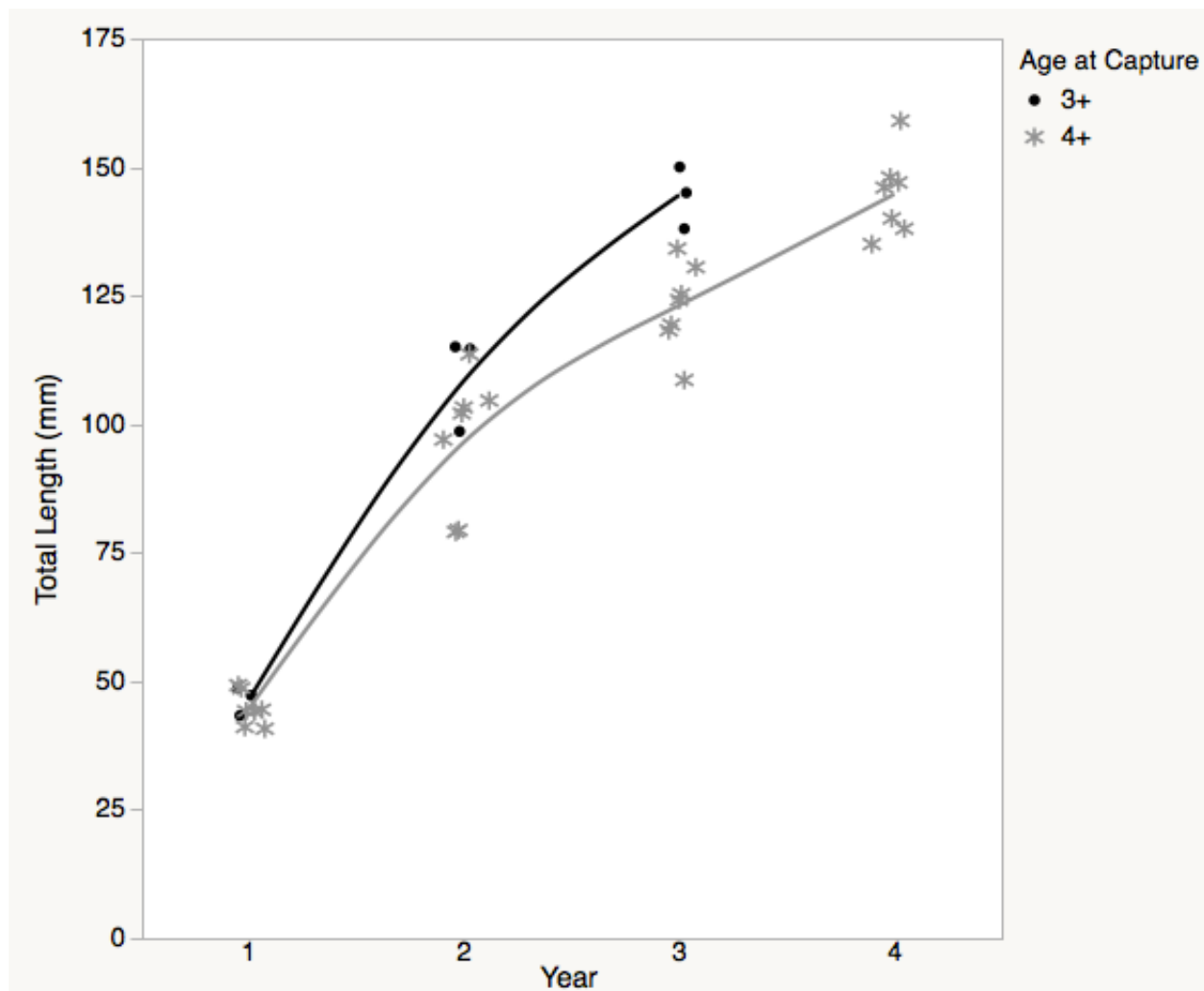
1,P - 2,P	-0.1472391488	0.01500972	268.01	-9.810	<.0001
1,P - 3,P	-0.1279995306	0.01186128	279.83	-10.791	<.0001
1,P - 4,P	-0.0042900536	0.01734404	276.47	-0.247	1.0000
2,P - 3,P	0.0192396181	0.01579279	260.51	1.218	0.9871
2,P - 4,P	0.1429490951	0.01862766	213.58	7.674	<.0001
3,P - 4,P	0.1237094770	0.01575035	301.02	7.854	<.0001

P value adjustment: tukey method for comparing a family of 12 estimates

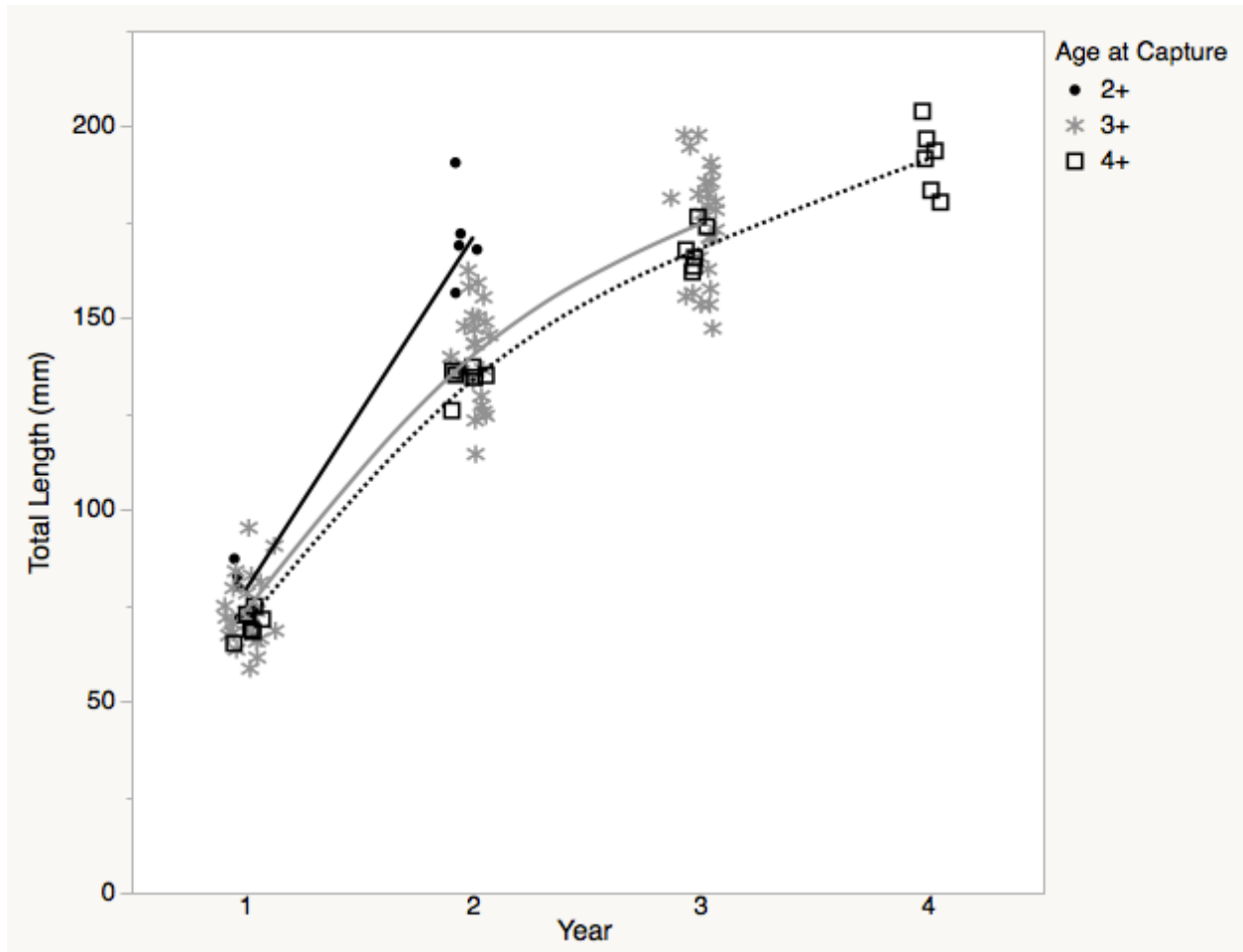
<b>Table A1</b> Mean total length at age among capelin from Darnley Bay, Pangnirtung Fjord and Newfoundland determined from back-calculation.							
Age at Capture	Region	N	Total mean length at capture +/- SE	Back calculated mean length (mm) at age			
				+1	+2	+3	+4
2	Newfoundland	5	171.9 +/- 5.5	77.4 +/- 2.7	-	-	-
3	Darnley Bay	3	144.3 +/- 3.5	46.4 +/- 1.6	109.4 +/- 5.4	-	-
	Newfoundland	25	173.5 +/- 3.0	72.1 +/- 1.7	136.5 +/- 2.4	-	-
	Pangnirtung	5	164.4 +/- 4.1	63.0 +/- 6.2	133.9 +/- 8.6	-	-
4	Darnley Bay	7	144.7 +/- 3.0	44.6 +/- 1.3	97.0 +/- 5.0	122.9 +/- 3.2	-
	Newfoundland	6	191.6 +/- 3.6	68.9 +/- 1.4	130.5 +/- 1.6	163.5 +/- 2.3	-
	Pangnirtung	15	182.2 +/- 4.9	47.6 +/- 0.8	93.3 +/- 3.2	142.2 +/- 4.9	-
5	Pangnirtung	39	184.8 +/- 2.5	46.2 +/- 0.7	86.1 +/- 1.5	128.6 +/- 2.0	157.9 +/- 2.4
<b>Average Back-Calculated length (mm)</b>							
Darnley Bay				45.1 +/- 1.0	100.7 +/- 4.1	122.9 +/- 3.2	-
Newfoundland				72.3 +/- 1.3	135.3 +/- 2.0	163.5 +/- 2.3	-
Pangnirtung Fjord				47.3 +/- 0.6	91.1 +/- 1.9	132.4 +/- 2.1	157.9 +/- 2.4



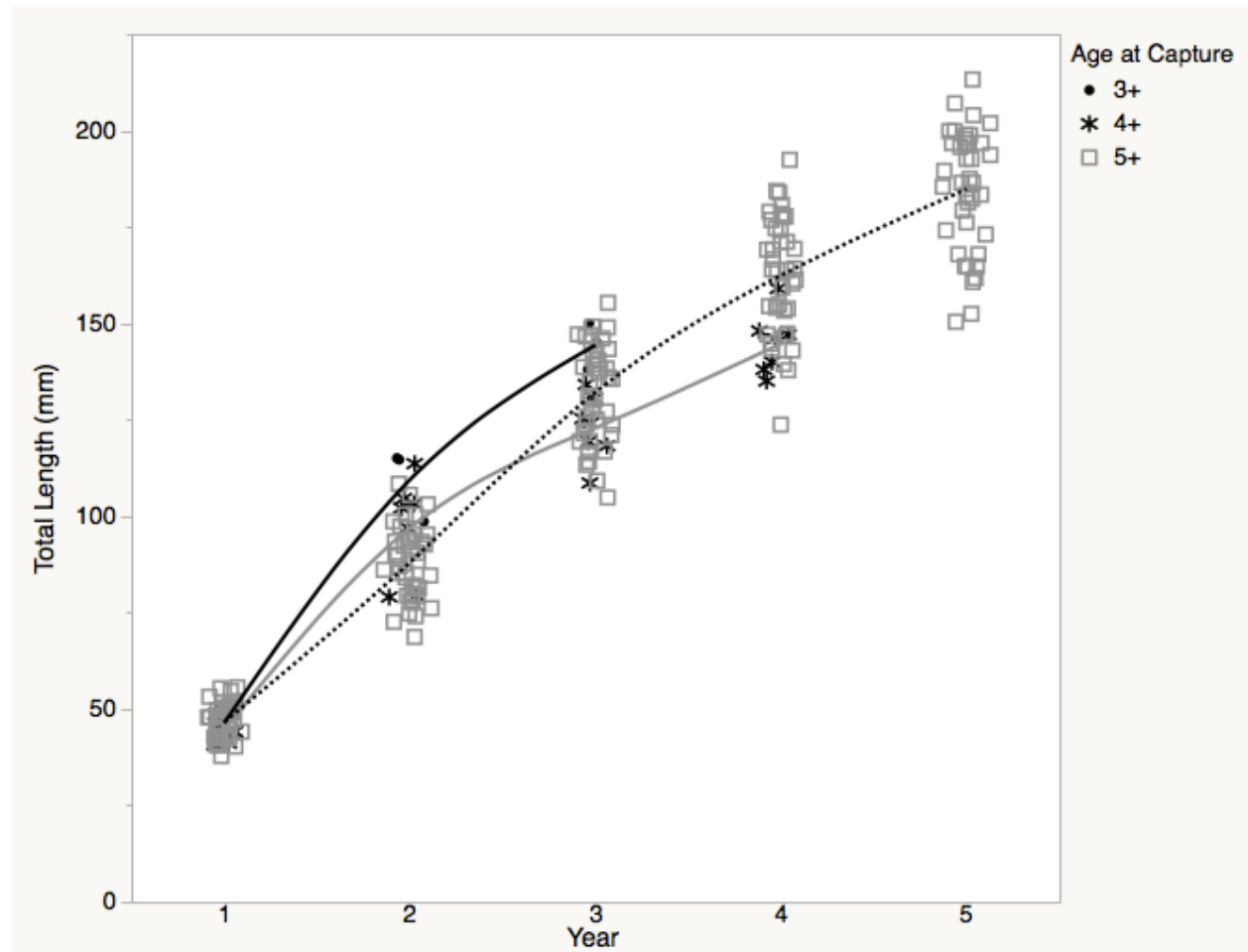
**Fig. A1** Observed total lengths (mm) at age of male Capelin collected in Darnley Bay (•; n=10), Newfoundland (+; n=36) and Pangnirtung Fjord (□; n=59) for each age.



**Fig. A2** Back-calculated length-at-age of male capelin, which spawned at age 3+ (n=3; black) and age 4+ (n=7; grey) collected in Darnley Bay, July 2014



**Fig. A3** Back-calculated length-at-age of male capelin, which spawned at age 2+ (n=5; black), age 3+ (n=25; grey) and age 4+ (n=6; dashed) collected in Newfoundland, July 2014.



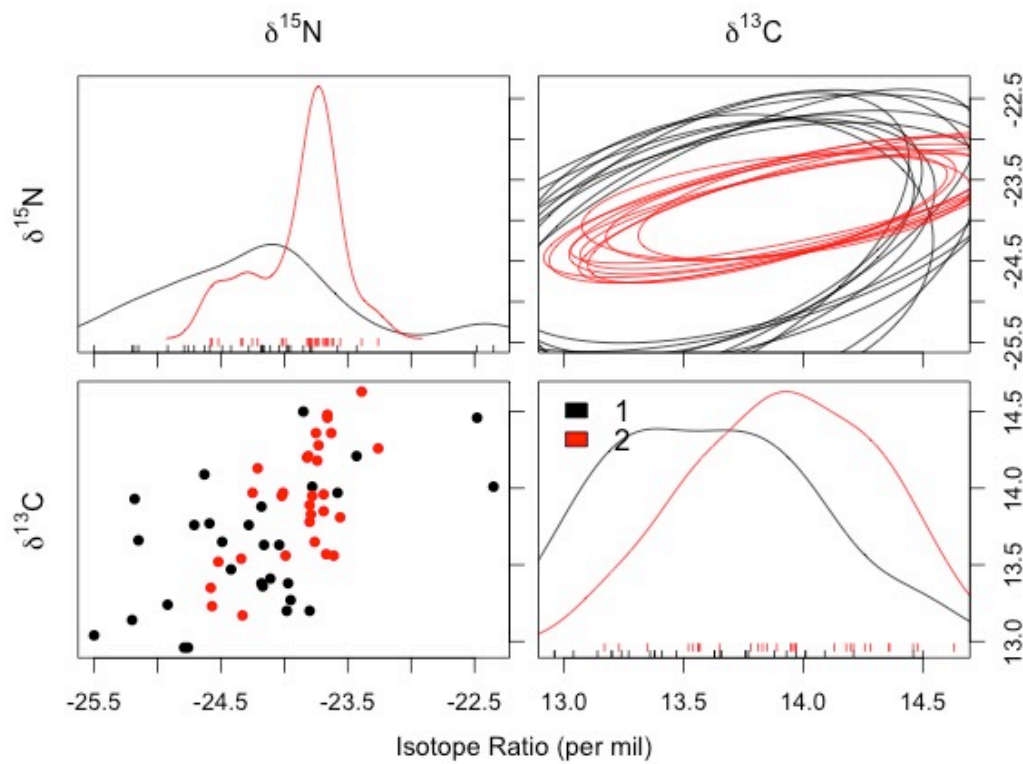
**Fig. A4** Back-calculated length-at-age of male capelin, which spawned at age 3+ (n=5; black), age 4+ (n=15; dashed) and age 5+ (n=39; grey) collected in Newfoundland, July 2014.

## Appendix B

Probability of overlap calculated in the *nicheROVER* package in R (version 3.2.2) including script and posterior distributions produced as  $\alpha = 95\%$ . Package details are found at:

<https://cran.r-project.org/package=nicheROVER>

### *Niche Overlap – Non-Extracted*



**Fig. B1** Ten elliptical projections chosen at random of  $N_R$  for Arctic cod (red) and capelin (black). One-dimensional density plots (lines) are drawn for each stable isotope, and two-dimensional scatterplot of the raw data. Density plots and ellipses were drawn using stable isotope values obtained from tissues without lipid extraction.



### *nicheROVER Overlap calculation*

```
# niche overlap plots for 95% niche region sizes
```

```
nsamples <- 15000
```

```
fish.par <- tapply(1:nrow(overlap), overlap$Code, function(ii) niw.post(nsamples = nsamples, X  
= overlap[ii, 2:3]))
```

```
# Overlap calculation. use nsamples = nprob = 10000 (1e4) for higher
```

```
# accuracy. the variable over.stat can be supplied directly to the
```

```
# overlap.plot function
```

```
over.stat <- overlap(fish.par, nreps = nsamples, nprob = 15000, alpha = c(0.95, 0.99))
```

```
# The mean overlap metrics calculated across iterations for both niche
```

```
# region sizes (alpha = .95 and alpha = .99) can be calculated and displayed
```

```
# in an array.
```

```
over.mean <- apply(over.stat, c(1:2, 4), mean) * 100
```

```
round(over.mean, 2)
```

```
, , alpha = 95%
```

	Species B	
Species A	1	2
1	NA	52.88
2	94.78	NA

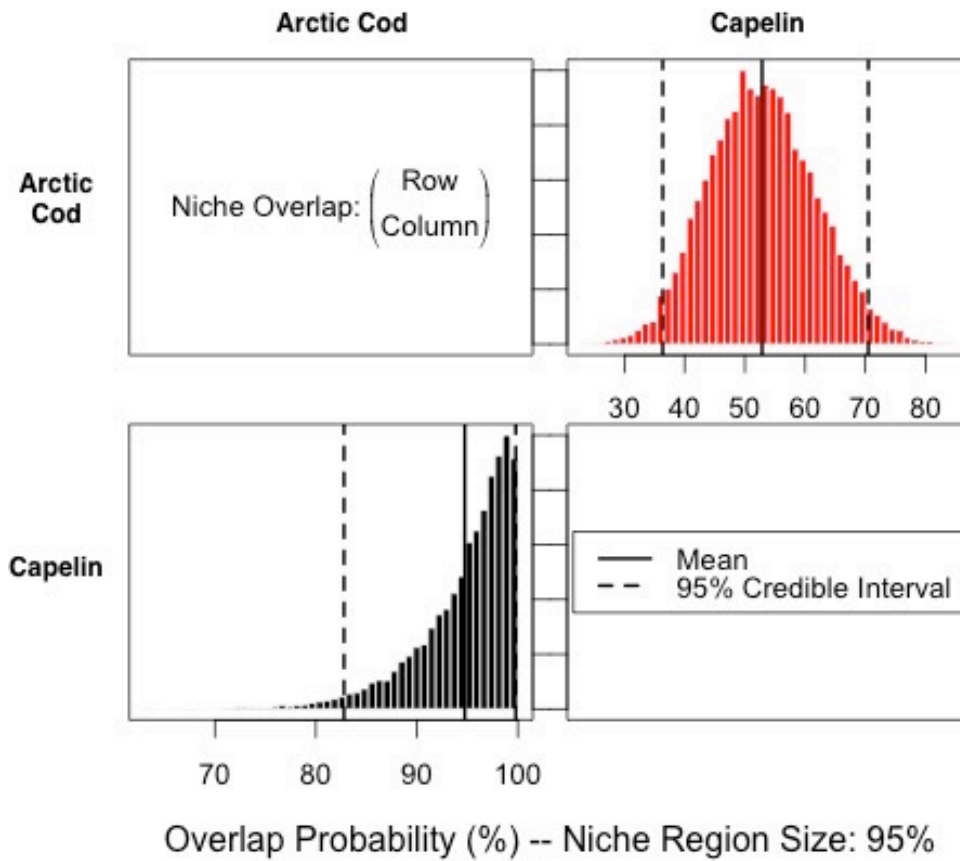
```
, , alpha = 99%
```

	Species B	
Species A	1	2
1	NA	66.54
2	98.42	NA

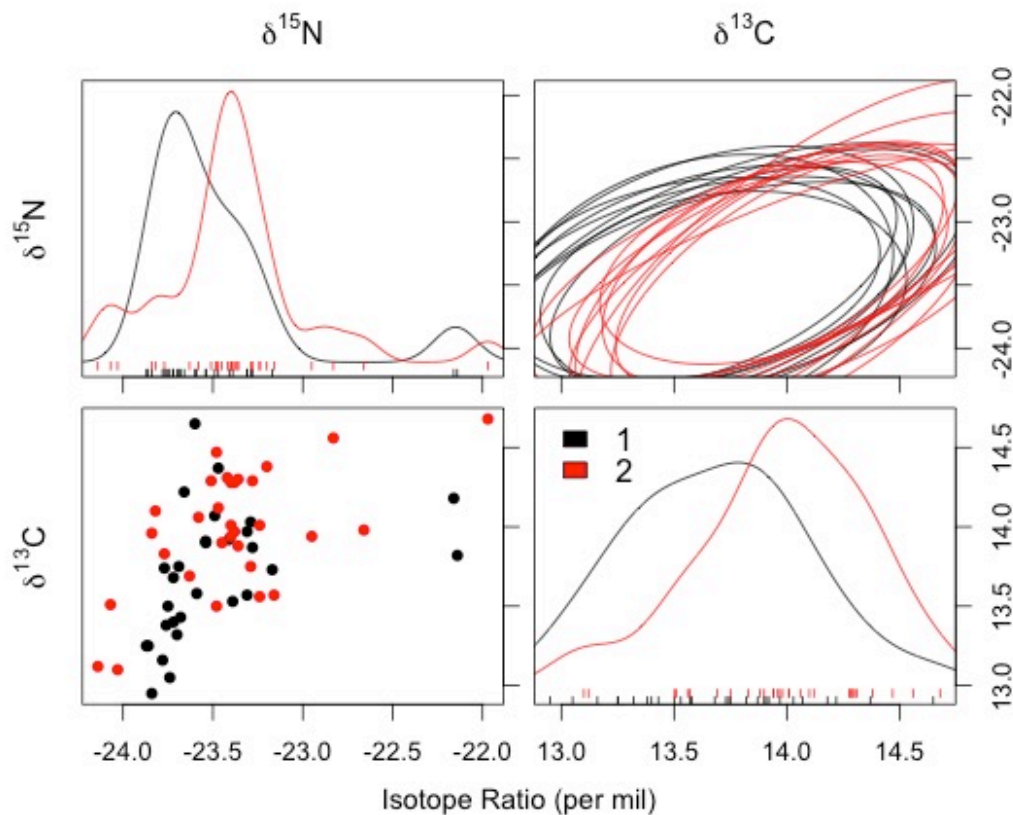
```

clrs <- c("black", "red") # colors for each species
over.stat <- overlap(fish.par, nreps = nsamples, nprob = 15000, alpha = 0.95)
overlap.plot(over.stat, col = clrs, mean.cred.col = "black", equal.axis = TRUE,
             xlab = "Overlap Probability (%) -- Niche Region Size: 95%")

```



**Fig. B2** Posterior distribution of probabilistic niche overlap for Arctic Cod (black) and Capelin (red).  $N_R$  is specified as a 95% probability of species displayed in rows overlapping onto columns. Posterior means and 95% credible intervals are displayed in black.



**Fig. B3** Ten elliptical projections chosen at random of  $N_R$  for Arctic cod (red) and capelin (black). One-dimensional density plots (lines) are drawn for each element, and two-dimensional scatterplot of the raw data. Density plots and ellipses were drawn using stable isotope values obtained from lipid-extracted tissues.

*nicheROVER overlap calculation*

# niche overlap plots for 95% niche region sizes

`nsamples <- 15000`

`fish.par <- tapply(1:nrow(overlap), overlap$Code, function(ii) niw.post(nsamples = nsamples, X = overlap[ii, 2:3]))`

# Overlap calculation. use `nsamples = nprob = 10000 (1e4)` for higher

```
# accuracy. the variable over.stat can be supplied directly to the
# overlap.plot function
```

```
over.stat <- overlap(fish.par, nreps = nsamples, nprob = 15000, alpha = c(0.95, 0.99))
```

```
# The mean overlap metrics calculated across iterations for both niche
# region sizes (alpha = .95 and alpha = .99) can be calculated and displayed
# in an array.
```

```
over.mean <- apply(over.stat, c(1:2, 4), mean) * 100
round(over.mean, 2)
```

```
, , alpha = 95%
```

	Species B	
Species A	1	2
1	NA	82.58
2	89.74	NA

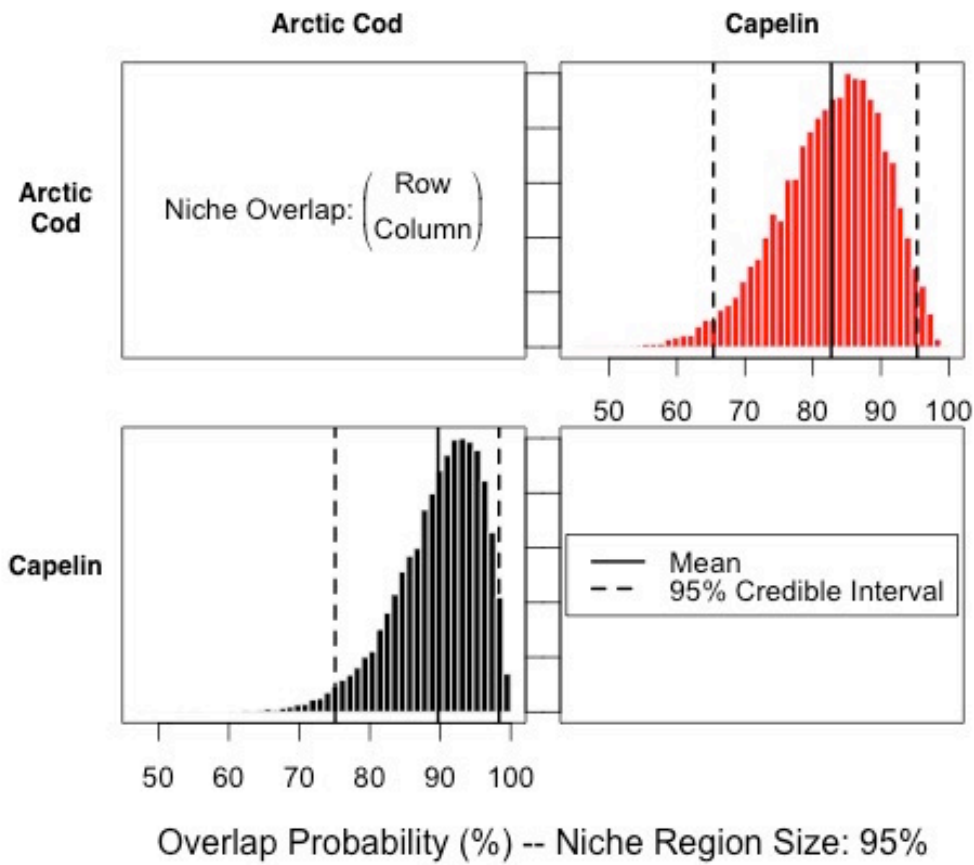
```
, , alpha = 99%
```

	Species B	
Species A	1	2
1	NA	92.37
2	96.46	NA

```
clrs <- c("black", "red") # colors for each species
```

```
over.stat <- overlap(fish.par, nreps = nsamples, nprob = 15000, alpha = 0.95)
```

```
overlap.plot(over.stat, col = clrs, mean.cred.col = "black", equal.axis = TRUE, xlab = "Overlap
Probability (%) -- Niche Region Size: 95%")
```



**Fig. B4** Posterior distribution of probabilistic niche overlap for Arctic Cod (black) and capelin (red).  $N_R$  is specified as a 95% probability of species displayed in rows overlapping onto columns. Posterior means and 95% credible intervals are displayed in black.