The Ecology of Arctic Cod (*Boreogadus saida*) and Interactions with Seabirds, Seals, and Whales in the Canadian Arctic

by

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Abstract

This thesis investigates the foraging behaviour of Arctic cod (*Boreogadus saida*) and its predators during the summer in Allen Bay and Resolute Bay, Cornwallis Island, Nunavut, Canada. Major findings included the identification of Arctic cod, ringed seal (*Pusa hispida*), beluga (*Delphinapterus leucas*), and narwhal (*Monodon monoceros*) diet shifts in response to seasonal prey availability; calculation of isotopic diet-tissue discrimination factors for Arctic cod, ringed seals, and whales based on local tissue and stomach content sampling; and determination of cues that predators use to optimize foraging, such as the presence of schools. Additionally, I quantified seabird feeding and interspecific interactions such kleptoparasitism and found that black-legged kittiwakes (*Rissa tridactyla*) and northern fulmars (*Fulmarus glacialis*) captured cod directly but lost many to parasitic jaegers (*Stercorarius parasiticus*) and glaucous gulls (*Larus hyperboreus*). Finally, I determined that schools of cod were important prey sources for northern fulmars, glaucous gulls, and whales however non-schooling cod were a significant source for black-legged kittiwakes and ringed seals.

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Thesis Format and Manuscript Claims

This thesis is presented in a manuscript format. Chapter 2, 3, 4, and 5, and the Appendix are written in a manuscript style containing an Abstract, Introduction, Materials and methods, Results, and Discussion. All references (except in Appendix) are combined at the end of the thesis. The General Introduction and Chapter 1 introduce the overall theme and review pertinent literature. Findings of the thesis are summarized in Thesis Conclusions.

References to manuscripts, copyright permissions, and author contributions are as follows:

Chapter 2: Matley JK, Fisk AT, Dick TA. The biology and foraging ecology of Arctic cod (*Boreogadus saida*) in Allen Bay, Canada. This manuscript is in revision for submission to a peer-reviewed journal (to be determined). Jordan Matley collected the data, conducted the analyses, and wrote the manuscript, all with the participation and guidance of co-authors.

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Chapter 5: Matley JK, Crawford R, Dick TA. Summer foraging behaviour of shallow-diving seabirds and distribution of their prey, Arctic cod (*Boreogadus saida*), in the Canadian Arctic. This manuscript has been accepted by 'Polar Research' and is currently undergoing final revisions. Jordan Matley collected the data, conducted the analyses, and wrote the manuscript, all with the participation and guidance of co-authors. Author permission was obtained and submitted accordingly. Copyright permission was not required as Polar Research is an open-access journal and authors retain copyright.

Appendix: Matley JK, Crawford R, Dick TA (2012) Observation of common raven (*Corvus corax*) scavenging Arctic cod (*Boreogadus saida*) from seabirds in the Canadian High Arctic. Polar Biology 35: 1119-1122 doi: 10.1007/s00300-011-1148-1. Jordan Matley collected the data, conducted the analyses, and wrote the manuscript, all with the participation and guidance of co-authors. Author and copyright permission was obtained and submitted accordingly.

General Introduction

With the onset of summer, the Arctic marine environment is transformed. As the sea-ice melts, short intense blooms of phytoplankton supplement ice algae as the main base food sources for first-order consumers (Søreide et al. 2006) which in turn support organisms throughout the food web. The Arctic Ocean is one of the least productive ecosystems (Niemi et al. 2010), however during these times of proliferation, millions of top predators including seabirds, ringed seals (*Pusa hispida*), belugas (*Delphinapterus leucas*), and narwhals (*Monodon monoceros*) migrate to productive areas benefitting from the surplus of food. In the High Arctic, Arctic cod (*Boreogadus saida*) is the major prey item consumed and accordingly is a keystone species in the Arctic Ocean. Despite the significant ecological role, few studies examine how and why predators select Arctic cod. Similarly, research concerning the biology and foraging ecology of Arctic cod is sparse. Studying the interactions among ecologically significant Arctic organisms is increasingly important as the Arctic continues to face environmental changes. Without critical baseline information of life history and behaviour, such as habitat and prey selection, responsible management decisions will be more difficult and likely less effective.

Importance of Arctic cod

Arctic cod is the most frequent, numerous, and energetically profitable prey item that directly supports the millions of top consumers migrating to the Arctic seasonally (Bradstreet 1976; Bradstreet and Cross 1982; Hobson 1993). One Arctic cod provides equivalent energy as >1000 calanoid copepods (Bradstreet and Cross 1982) and is responsible for ~75% of the energy transferred between zooplankton and top consumers

(Welch et al. 1992). Welch et al. (1992), based on population estimates of consumers and their maintenance requirements, estimated 148,000 tonnes of Arctic cod are consumed by animals in the Lancaster Sound Region (LSR) annually. This is equivalent to over 5 billion individuals (using average weight of Arctic cod 33.4g (Welch et al. 1993)) and does not account for consumption by poorly studied organisms (e.g., sculpin). Consequently, it is not surprising Arctic cod is such an important prey item and provides a critical link between upper and lower trophic levels. Large scale population estimates of Arctic cod are rare because its commercial value is minimal. Nevertheless it is thought to be the most abundant fish in the Arctic (Ponomarenko 1968) with schools comprising millions of individuals (Crawford and Jorgenson 1996). Schooling is especially important to predators providing high energy potential at low foraging cost. Exploited schools result in large feeding aggregations including hundreds of whales and seals, and thousands of seabirds. For example, Welch et al. (1993) suggested that such events could lead to the consumption of 20 tonnes of Arctic cod daily in individual bays. With the limited data available, it is believed that schools contain the necessary biomass to support predators in the Canadian Arctic (Welch et al. 1992; Crawford and Jorgenson 1996). Although schools contain significant energy, the contribution of schooling and non-schooling Arctic cod to the diet is unknown.

Studying predator-prey interactions in the Arctic

Information on the interactions between predators and Arctic cod are temporally and spatially limited. For example, studies are infrequent in the Arctic and are usually restricted to the ice-free period. Additionally, research originates from various regions of the Arctic, many with different habitats and organisms, often making comparisons difficult. Much of our knowledge concerning foraging behaviour and predator-prey interactions in the Arctic Ocean are anecdotal and limited to nearshore waters and at the surface. Nevertheless, techniques exist to identify important food sources, as well as delineate behaviours of predator and prey. These approaches enable greater understanding of foraging for various habitats, locations, and at different times of the year.

The traditional method to investigate the interaction between predator and prey is to examine stomach contents. By identifying food directly, the relative importance of prey is determined with taxonomical accuracy. The size of prey can also be reconstructed with regressions, for example using the length of fish otoliths or cephalopod beaks (e.g., Laidre and Heide-Jørgensen 2005). Limitations to stomach analysis are numerous however and include: 1) it is only a snapshot of recent feeding. For example, Christiansen et al. (2005) showed that whole capelin (*Mallotus villosus*) became fully digested after 6 hours and otoliths were unidentifiable after an additional hour submerged in digestive solutions; 2) the presence of certain prey items in the stomach can be biased because body parts of organisms are digested at different rates. Indigestible materials such as chitinous beaks of cephalopods, crustacean carapaces, fish bones, and eye lenses are commonly the only remains found in stomachs (Finley and Gibb 1982). Consequently, organisms with hard or indigestible tissues are overestimated. In particular, cephalopod beaks appear to be retained in stomachs for extended amounts of time because they catch on the folds of the forestomach and are not evacuated (Santos et al. 1999); and 3) identification of stomach remains is difficult, especially for highly digested items. Despite the limitations, stomach content analysis provides a direct look at prey items and is a necessary step to validate other approaches (e.g., stable isotope analysis).

In the last several decades stable isotope analysis (SIA) has increasingly become a popular technique to examine food web structure as it provides a temporal and spatial view of dietary and energy pathways (Peterson and Fry 1987; Cabana and Rasmussen 1994; Vander Zanden and Rasmussen 1999). At present, it is a common method to examine the structure of food webs with hundreds of studies published throughout the world in all types of aquatic and terrestrial habitats (Layman et al. 2011). Stable isotopes are atoms with the same number of protons and electrons that do not decay and are more stable when the number of neutrons and protons are similar (Sulzman 2007). Isotopic composition (δ) is the common measurement and is presented as parts per thousand of an elemental sample compared to a standard as follows:

$$(1) \qquad \delta X = [(R_{sample} / R_{standard}) - 1] \text{ x } I0^3$$

where X represents ^{13}C, ^{15}N, or another isotope, and R is the corresponding ratio of sample to a standard (i.e. $^{13}C/^{12}C$, $^{15}N/^{14}N$). Therefore, the measurement of isotopic composition is a comparison of heavy isotopes to light isotopes. Positive δ values indicate that the sample has more heavy isotopes than the standard, while negative δ values indicate that the sample has less heavy isotopes than the standard (Peterson and Fry 1987). Physiological and biochemical processes cause fractionation which refers to the reactions that alter the ratio between heavy and light isotopes.

Stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are commonly used in ecology because they provide meaningful information on dietary pathways and food sources. The isotopic composition of carbon of consumers is similar to prey (<1‰ enrichment, Michener and Schell 1994), and nitrogen is typically 3‰ to 5‰ heavier in the consumer (Peterson and Fry 1987). Additionally, benthic food webs (i.e., derived from algae and detritus) are generally enriched in $\delta^{13}C$ signatures compared to pelagic food webs (i.e., derived from phytoplankton) (Hecky and Hesslein 1995; Hobson and Welch 1992a; Hobson et al. 1994; France 1995). These isotopic characteristics provide researchers with information on food sources, as well as position of consumers in the food web. Not only can specific habitats (e.g., littoral, profundal, and pelagic) in lakes and oceans be determined using SIA but also time-integrated estimates of diet. For example, since turnover rates are correlated to metabolic activity (Tieszen et al. 1983), different tissues can be used to elucidate temporal changes in isotopic composition of individuals. Of particular interest is using SIA to examine how seasonal changes (e.g., winter to summer in the Arctic) influence diet shifts and habitat selection.   With consistent or predictable fractionation through trophic levels, SIA has proven to be an incredibly useful tool in ecology. Nevertheless, SIA is intrinsically associated with many limitations or possible sources of error that should be understood prior to analysis and interpretation of results. Christiansen et al. (2012) listed that SIA can be confounded by: 1) methodology (Layman et al. 2011), 2) physiological and environmental processes (Sakano et al. 2005), 3) variation in isotope fractionation (Post 2002), 4) tissue-specific turnover rates (Dalerum and Angerbjörn 2005), 5) seasonality and 6) variations in particulate organic matter (Tamelander et al. 2009).

Other approaches that examine predator-prey interactions mainly investigate the behaviour of organisms in relation distribution, movement, and habitat. Hydroacoustics is defined as the use of underwater sound to detect, enumerate, and measure the distribution of living marine and freshwater resources and describe their habitat (Sullivan and Rudstam 2009). To summarize, energy (in the form of sound) is directed through the water at a designated frequency and intensity. Once the pulse of energy encounters an object such as a fish, part of this energy is reflected in the form of an echo and translated into an electrical signal which can be measured. Target strength is a measure of echo strength or the acoustic size of the object (or target) and is a major tool in hydroacoustic studies. For example, species-specific standardized equations are used to convert target strength into estimates of fish size. Similarly, various equations are used to calculate density and abundance of fish based on target strength. Measures of target strength are affected by a variety of factors such as fish orientation and depth (Sullivan and Rudstam 2009), highlighting the need for caution when interpreting findings. Other issues also require consideration. For example, detections close to the surface can be misleading because sound waves have not yet properly aligned, less water volume is sampled (i.e., sound travels as a conical beam), and fish may be changing behaviour in reaction to the vessel (Simmonds et al. 1992; Crawford and Jorgenson 1993). Also, dense schools make detection of individual fish and quantitative estimates difficult because of acoustic shading (Crawford and Jorgenson 1996). In most cases, the application of hydroacoustics does not directly examine interactions between predator and prey. For example, surveys provide high resolution of prey distribution but offer little information concerning predator behaviour. However, to understand the cues that encourage foraging or initiate feeding, it is important to examine the distribution, habitat, and movement of prey.

Direct observations also provide information concerning the foraging behaviour of predators and prey in the Arctic. These have proven particularly useful describing the importance of schooling fish such as Arctic cod to seabirds, seals, and whales in large feeding events. Since Arctic cod swim close to shore during the summer in visible aggregations, estimating the areal size of schools or the number of predators exploiting them is relatively easy (cf. Welch et al. 1993), but these are only fragmented accounts of highly detectable occurrences. They do not provide continuous and standardized reports that would represent more common and day-to-day foraging. Therefore, structured observation studies are needed to accurately delineate foraging behaviour and delve deeper than merely anecdotally discussing large feeding events. Further, density surveys provide meaningful information about population trends of predators such as seabirds and also serve to identify important habitats or foraging areas (Piatt et al. 2007). This is useful when attempting to quantify or describe interactions with prey.

Additional techniques provide insight on predator-prey interactions in the Arctic, however commonly they are only supplementary to the methods described above. Fatty acid analysis is increasingly being used to identify prey items because fatty acids transfer from prey to predator with little modification (Iverson et al. 2004). However, this analysis is not powerful at providing quantitative estimates of prey. Given the low diversity of prey in many parts of the Arctic, fatty acid analysis is not as useful as other ecosystems. Similar to stomach content analysis, fecal analysis of marine mammals has also been used although it is more common for larger marine mammals that are not regularly caught by hunters (e.g., mysticeti whales). The movement of predators have been determined using satellite tracking and time-depth recorders. This provides spatiotemporal distribution that can relate to available prey in certain habitats at different times of the year however prey items are not measured simultaneously. The acoustic behaviour of whales has been studied using recording devices (e.g., AURALs and CPODs) however direct interactions with prey while sampling are rare. Finally, traditional knowledge allows fragmented information of movement and foraging at the surface based on hundreds of years of observations. Each method described above has strengths and weaknesses however by combining approaches our ability to understand foraging decisions is stronger.

Rationale

With increasing concerns of climate change and human impact in the Arctic, it is important to understand how top predators associate and interact with prey in order to make responsible management decisions. For example, anthropogenic impacts could alter distribution and migration, increase contaminant and disease exposure, reduce habitat availability, increase competition, and decrease survival and recruitment of top predators (Learmonth et al. 2006). By learning how important prey items, such as Arctic cod, impact foraging behaviour we can begin to know how changes in resource availability will affect the distribution and movement of top predators. Similarly, by studying the biology and behaviour of Arctic cod we can extend our understanding of the Arctic food web and how factors such as season, habitat, and invertebrate distribution influence foraging.

The majority of predator-prey studies in the Arctic simply re-iterate that Arctic cod is an important food source, and few specifically examine the cues that initiate feeding or drive foraging behaviour. The aim of this thesis is to provide a broad and comprehensive examination of the interactions among top predators and Arctic cod using a variety of exploratory tools including, observations, density surveys, hydroacoustic sampling, stomach content analysis, and stable isotope analysis. For clarity and simplicity, the thesis is divided into four research chapters (Chapters 2-5) each concerning a particular research topic.

Research topics

Chapter 2 investigates the biology and feeding ecology of Arctic cod. Despite its ecological significance there is a lack of studies examining biological aspects that are key to reproductive success and survival. In particular, little is known of the interrelationship among growth, energy storage, and gonadal development. Two organs are critical in this regard and appear to control many aspects of the life history of Arctic cod. First, Arctic cod stores energy as lipids in the liver (Hop et al. 1997b). The liver is the largest visceral organ occupying as much as two thirds of the body cavity and providing access to reserve energy in times of need such as low food availability (Bain and Sekerak 1978). Second, gonad weight shows large seasonal variation as development to spawning approaches. For example, unripe gonads account for <5% of the body weight (Nahrgang et al. 2010) and ripe gonads account for ~50% of the body weight (Hop et al. 1995). Bain and Sekerak (1978) suggested that the energy for increased gonadal development towards spawning condition was mobilized from lipids in the liver. Hop et al. (1995) later found preliminary evidence for this in laboratory-reared Arctic cod, estimating that 40% of energy lost from liver (and muscle to a lesser extent) was incorporated into the gonads in ripe females. This highlights the importance of energy reserves for Arctic cod, in particular associated with reproduction. Foraging behaviour may also play a fundamental role in relation to energy allocation and warrants further investigation.

Ontogenetic niche shifts (i.e., changes in resource use with body size or age) are very common in animals and can affect how intra-specific individuals select resources (Werner and Hall 1988; Hammerschlag-Peyer et al. 2011). Hobson et al. (2002) cautioned pooling species in foraging studies due to ontogenetic changes and suggested more detailed species-specific analyses could greatly improve understanding of the Arctic marine food web. Although diet of Arctic cod has been thoroughly examined (at least during the summer), few studies have segregated prey selection based on size of individuals (and size of prey) and explored intra-specific dietary niche overlap. Fewer still have supplemented stomach content data with stable isotopes to provide a timeline of feeding, habitat, and intra-specific isotopic niche overlap. These types of studies are important because seasonal changes (e.g., break-up of ice) influence resource availability and may alter how Arctic cod selects habitat and prey.

As climate change continues to be a topic of concern for Arctic organisms, insight is needed on how long-term trends are affecting Arctic cod biology. This type of information is difficult to obtain because Arctic cod studies are rare and usually spatially distinct. However, Bain and Sekerak (1978) and Hop et al. (1997a) completed studies of the general biology (including diet) of Arctic cod captured from Allen Bay. This enables temporal comparison of Arctic cod biology without spatial variability and provides initial steps to exploring how a changing environment has affected a critical Arctic organism.

The purpose of *Chapter 2* was to supplement the few existing studies that examine multiple aspects of the biology and ecology of Arctic cod. The main hypothesis of *Chapter 2* was that Arctic cod demonstrate seasonal dietary shifts in response to changing prey distribution and availability. The main objective was to determine how seasonal changes and ontogeny affect the diet and foraging habitat of Arctic cod using stomach content analysis, and stable isotope analysis of liver and muscle tissues.

Chapter 3 investigates the foraging behaviour of marine mammals. Selection of prey by predators can provide important information about foraging ability and preference. In the Arctic, marine mammal prey selection is often driven by life history traits such as size and age (Finley and Gibb 1982, Lesage et al. 2001), as well as behavioural traits such as migration and habitat selection (Laidre and Heide-Jørgensen 2005, Loseto et al. 2008). Therefore, understanding how and why predators make foraging decisions can elucidate many aspects of their biology, but also that of prey. Belugas and narwhals complete seasonal migrations coinciding with the break-up and consolidation of ice. Few studies have attempted to examine diet and habitat of Arctic whales throughout these movements. Considering prey availability between summering and wintering areas is different, investigating the importance of different food items while travelling can serve to identify ecologically relevant organisms. For predators that remain in Arctic waters year-round, such as ringed seals, investigating seasonal diet shifts can provide useful information concerning prey availability and distribution.

The importance of Arctic cod to marine mammals during the summer has readily been demonstrated (e.g., Holst et al. 2001, Labansen et al. 2011). However, the role of schooling and non-schooling cod in the diet is more tenuous. Welch et al. (1992)

suggested that schools contain the necessary biomass to support predators because non-schooling cod are dispersed and abundances low. For example, the average standing biomass of non-schooling Arctic cod ($0.062g\cdot m^{-2}$) was 25 times less than the amount consumed by predators such as seabirds and marine mammals. Nevertheless, ringed seals appear to prefer non-schooling cod based on observations and stomach content analysis (i.e., otoliths at differential states of digestion; Bradstreet et al. 1986). More information using traditional (i.e., size extrapolation from otolith length) and more advanced techniques (i.e., hydroacoustics) are needed to determine the importance of Arctic cod schools to predators.

The purpose of *Chapter 3* was to investigate foraging behavior of top marine Arctic predators (i.e., beluga, narwhal, and ringed seal). The main hypothesis of *Chapter 3* was that Arctic cod compose a greater proportion of the diet of predators in the summer reflecting the availability of Arctic cod in nearshore waters. The main objective was to determine the importance of Arctic cod temporally and spatially for different age and sex classes using stomach content analysis, on-site observations, and stable isotope analysis of liver and muscle tissues.

Chapter 4 investigates the foraging behaviour of Arctic seabirds. Seabird population data are absent in many parts of the Canadian Arctic (Mallory and Fontaine 2004). Standardized density surveys provide a simple yet meaningful approach to quantify populations as it can delineate breeding colony trends and identify important foraging areas. Standardized surveys can also be used to quantify predatory interactions of shallow-diving seabirds in these ‘hotspot’ areas because interactions are readily visible and typically take place close to shore. Little is known about foraging decisions of shallow-diving seabirds despite that they consume more Arctic cod per individual than deep-diving birds, such as murres, in the Canadian Arctic (Welch et al. 1992, Mallory and Fontaine 2004). Therefore, it is unclear how different foraging strategies (e.g., type of dive and foraging flight time) differ between species. This type of information is particularly useful because it can aid to support or improve energy budgets and provides field-based estimates of prey consumption. Alternative foraging strategies, such as kleptoparasitism (food stealing) are not well documented especially in the High Arctic. Kleptoparasitism is considered a substitute foraging method when direct prey capture is more energetically demanding (e.g., Stempniewicz and Iliszko 2010). As a result, quantifying kleptoparasitism provides useful information about foraging costs, as well as the ability of different species to be successful food stealers.

Additionally, it is unclear how direct extrinsic factors, such as environment variables affect foraging behaviour in each species. In this regard, the role of sea ice is of particular interest because Arctic cod associate with it (Lonne and Gulliksen 1989; Crawford and Jorgenson 1996) and therefore can provide a proxy to prey behaviour. The behaviour of Arctic cod also influences seabird foraging, in particular because many seabirds are restricted to the water surface (e.g., <3m deep) for capturing prey. The role of Arctic cod schooling to influence foraging behaviour has only been described anecdotally (e.g., Welch et al. 1993, Crawford and Jorgenson 1996). Unsurprisingly, when large schools of Arctic cod are detected close to the surface they are exploited heavily by seabirds. However, these occurrences should only provide short-term energetic gains because they are relatively rare (see Table 1 in Welch et al. 1993). Therefore, non-schooling or dispersed individuals may also be important as a more consistent food source. Since seabirds demonstrate species-specific foraging patterns in response to prey (Elliott et al. 2008), the importance of schooling and non-schooling should also differ among species.

The purpose of *Chapter 4* was to explore the foraging behaviour of shallow-diving seabirds during the summer in Allen Bay. The main hypothesis of *Chapter 4* was that kleptoparasitism is an energy-efficient foraging strategy benefitting the species that are adept at it. The main objective was to quantify predatory interactions and determine the importance of Arctic cod schools as food sources using rigorous and standardized shore-based observations and vessel surveys.

Chapter 5 investigates the distribution of seabirds in relation to schools of Arctic cod. Distributional patterns of animals are strongly determined by prey conditions such as availability, density, behaviour, and composition of prey (Harper 1982; Croy and Hughes 1991; Davoren et al. 2003a). Therefore, not only does distribution elucidate spatial foraging behaviour of seabirds, it can also provide information concerning the behaviour of prey species. This interaction is critical to understand the importance of high density aggregations, such as Arctic cod schools, and their influence on predator-prey relationships.

An intuitive method to examine prey behaviour uses hydroacoustics because it provides a real-time, high resolution, and quantifiable view of distribution throughout the water column. Hydroacoustic research in the Arctic has focussed on the behaviour of cod in relation to size, age, depth, density, temperature, salinity, time of day, and presence of ice, prey and predators (e.g., Moulton and Tarbox 1987; Crawford and Jorgenson 1993, 1996; Benoit et al. 2008, 2010). Despite the wide applicability of hydroacoustics, there are many limitations and sources of bias that should be considered to effectively explain findings. Of particular concern are biases associated with detection of Arctic cod close to the surface including density and abundance estimates, and extrapolation of fish sizes. Without thoughtful consideration, findings may prove misleading and altogether wrong, highlighting the need for continuing technological and analytical advances.

Nevertheless, combining hydroacoustic surveys with simultaneous seabird surveys enables researchers to identify the cues that seabirds use to maximize foraging potential. Additionally, investigating the distribution of Arctic cod can reveal behavioural patterns related to schooling, such as feeding and protection from predators that have yet to be discovered. Finally, knowing where fish commonly aggregate provides useful information about habitat selection and potential foraging hotspots.

The purpose of *Chapter 5* was to study the behaviour of Arctic cod in a nearshore habitat and identify cues seabirds use to locate prey. The main hypothesis of *Chapter 5* was that prey condition (i.e., presence, density, abundance, and depth of Arctic cod schools) influences the distribution of predatory seabirds. The main objective was to determine the extent to which seabirds distribute in relation to Arctic cod schools using standardized observation and hydroacoustic surveys.

Chapter 1: Literature Review

1.1. Arctic cod

1.1.1. General biology

Arctic cod is a ubiquitous species throughout the Arctic that is small (<30cm), and short-lived (rarely 7 years), reaching maturity at 2-3 years (Bradstreet et al. 1986). It has a holarctic distribution and is found throughout the water column (Benoit et al. 2008; Gradinger and Bluhm 2004). It has a wide tolerance to temperature, salinity, and turbidity (Craig et al. 1982). Spawning in the Canadian High Arctic occurs in winter and buoyant eggs hatch just prior to open water (Bouchard and Fortier 2008). In other parts of Canada and the Arctic Ocean hatching begins in winter possibly resulting in predator-avoidance benefits (i.e., increased size) (Bouchard and Fortier 2011). Male gonadal development begins earlier (~August) than females (~December) and reach maximum size approximately two months before females (Hop et al. 1995). When ripe, gonadosomatic index (GSI; gonad weight/body weight x 100) is 47.7% and 29.7% for females and males, respectively (Hop et al. 1995). On average, ripe females consist of ~26 500 eggs with a diameter of 1.65mm (Hop et al. 1995). The liver of Arctic cod is lipid-rich and may serve as a storage organ for energy reserves (Bain and Sekerak 1978). Hop et al. (1995) showed a decrease in hepatosomatic index (HSI; liver weight/body weight) as spawning time approached (i.e., July-September: 5.4%, February: 1.2%) suggesting energy for gonadal development was drawn primarily from liver.

Growth is rapid compared to other Arctic species, especially when food availability is high (i.e., during the summer) (Hop and Graham 1995). Compared to temperate species, energy budgets indicate that growth is slow and seasonal, basal metabolism is low, and growth efficiency is high (Hop et al. 1997b). Arctic cod demonstrate slow gastric evacuation which may limit food intake when prey is abundant (Hop 1994), however a high diet assimilation (i.e., assimilation efficiency = 80%; Hop et al. 1997b) makes up for this deficiency. In general, Arctic cod life history is typified as an r-selected species due to its small size, short-life span, early maturity, high growth efficiency, and high mortality (Craig et al. 1982; Hop et al. 1997b). These traits are common for generalist consumers that are at risk of wide-spread deaths and therefore do not invest in long-term survival (Craig et al. 1982). The main diet of Arctic cod comprises mysids, amphipods, and copepods, although consumption of small fish and cannibalism has been reported (Bain and Sekerak 1978; Craig et al. 1982; Gradinger & Bluhm 2004). Despite the ecological significance of Arctic cod, only a few extensive studies have been completed concerning its biology (i.e., Bain and Sekerak 1978; Bradstreet et al. 1986).

1.1.2. Diet

Arctic cod are generalist and opportunistic consumers where food items typically reflect their foraging habitat. Copepods and amphipods are the most common prey items throughout its distribution (see Table 4 in Renaud et al. 2012). The importance of other prey items, such as mysids, appears to vary regionally and with season (Craig et al. 1982). Few studies have examined winter diet, but in ice-covered waters ice-associated amphipods dominate (Bradstreet and Cross 1982; Lønne and Gulliksen 1989). Diet in open water typically consists of calanoid copepods and hyperiid amphipods (Hop et al. 1997a; Renaud et al. 2012), both pelagic crustaceans. Prey selection is size-dependent, where smaller individuals consume smaller prey than large individuals. For example, the mean prey length of larval Arctic cod gradually increased as cod size increased in the Northeast Water Polynya (Michaud et al. 1996). Larger size classes also demonstrate size-dependent selection when divided into broad length categories (i.e., <30mm, 30-100mm, >100mm). For example, larvae (<30mm) primarily consumed phytoplankters and copepod nauplii, juveniles (30-100mm) consumed a greater proportion of copepodites and adult copepods, and finally adults (>100m) consumed larger prey such as amphipods near Cornwallis Island (Bain and Sekerak 1978). Similarly, fewer items are consumed as size increases (Walkusz et al. 2011).

Studies using stable isotopes to explore trophic structure and diet of Arctic cod are rare. Christiansen et al. (2012) compared the diet and stable isotopes of sympatric populations of Arctic cod and *Arctogadus glacialis* from two fjords in NE Greenland. Both diet and stable isotopes suggested a spatial segregation in feeding habitat where Arctic cod associated primarily with the pelagic food web. Pelagic habitat has also been demonstrated for Arctic cod in the North Water Polynya (see Fig. 1 in Hobson et al. 2002a). Isotope values of Arctic cod tend to place it at a trophic level of 3.6 (Hobson and Welch 1992a; Hobson et al. 2002a) which supports its role as a biological link between top predators and lower-level consumers. The limited data available indicates that as Arctic cod grow, there is a gradual change to more isotope-enriched diets (Christiansen et al. 2012). This highlights the need to separate samples of cod based on ontogenetic differences as most studies only sample a small number of cod with limited ranges in size (e.g., Hobson and Welch 1992a).

1.1.3. Distribution, habitat, and schooling behaviour

Reports of Arctic cod schooling behaviour are limited and many are anecdotal. Methods to document and quantify schooling of Arctic cod are restricted to observations, net sampling, and hydroacoustic sampling. Observations provide fragmented information and are only possible when schools are near the surface (<5m deep). Net sampling offers little information about schooling behaviour in real-time and can be size-biased. Hydroacoustics can sample a large volume of water and provides a cross sectional quantitative estimate of schools but it is difficult to sample an entire school. Hydroacoustic techniques have been used to study various components of the biology and ecology of Arctic cod. These studies focus on movements and determining quantitative estimates of density and abundance. Given the limited commercial interest, scientific hydroacoustic surveys provide the most informative accounts of their distribution and are integral to understand temporal changes in behaviour and abundance.

During the summer, Arctic cod frequent shallow bays as dispersed individuals (i.e. non-schooling) or in schools (Bradstreet et al. 1986; Welch et al. 1993). These schools consist of varying number of fish but can be very large and dense. For example, Crawford and Jorgenson (1996) estimated that the biomass of one school in Allen Bay, Nunavut was 45 000 tonnes with a surface area of approximately 31 hectares. In the same area in 1990, two large schools were estimated to contain a total of 900 million Arctic cod and were likely underestimated (Crawford and Jorgenson 1996; Niemi et al. 2010). The reasons Arctic cod aggregate in bays during the summer is not clear but one hypothesis is that Arctic cod are optimizing physiological performance by remaining in relatively warm waters (Crawford and Jorgenson 1996). Near Cornwallis Island and

Devon Island, Arctic cod were not detected in waters colder than -1.3°C during the summer (Crawford and Jorgenson 1996). By contrast, Craig et al. (1982) found that an increase in abundance of Arctic cod during late summer in Simpson Lagoon, Beaufort Sea, was partly due to increased salinity and not temperature. Arctic cod movements may also be influenced by feeding. Moulton and Tarbox (1987) showed that Arctic cod associate with temperature and salinity transition layers in near-shore regions of the Beaufort Sea, which are believed to concentrate zooplankton and other potential food items. The role of schooling to obtain food however has also been debated. Hop et al. (1997a) reported that adult schools were not actively feeding compared to individually dispersed fish and areas surrounding schools were depleted in prey. Prey items may therefore be a factor driving fish into bays but once there, they may be schooling for other reasons. On a local scale, the behaviour of schools is often affected by predatory pressure as seals and whales sometimes drive Arctic cod into shore where they become stranded and consumed by seabirds (Bradstreet et al. 1986; Finley et al. 1990; Welch et al. 1993). Severe weather conditions (Craig et al. 1982) and tide (Bain and Sekerak 1978) also cause mass stranding of Arctic cod on shore. The stranding of Arctic cod acts as a significant resource for predators and consequently a potential dietary 'hotspot' for scavengers. For example, I documented opportunistic common raven (*Corvus corax*) scavenging on Arctic cod that were discarded by seabirds after they exploited a shallow school (Appendix).

Arctic cod is commonly associated with sea-ice during the summer as a means of protection from predators and to feed on sympagic zooplankton (Bradstreet and Cross 1982; Joensen 2008). Crawford and Jorgenson (1993) found low abundance of Arctic cod when ice was present in Resolute Bay, suggesting they were hiding under it to reduce predation risk. However, under-ice surveys were not possible and predatory interactions were not studied. During an 11 month survey in Amundsen Gulf, Geoffroy et al. (2011) only detected schools of Arctic cod when ice was present, and ice thickness had no effect. By contrast, Bain and Sekerak (1978) noted that Arctic cod were abundant in Allen Bay during the summer when fast-ice was present but also when the bay was completely ice-free. Further, Bradstreet and Cross (1982) found that 91.1% and 62.5% of dry weight from offshore and inshore summer diets, respectively, were contributed by species that were not considered to be associated with ice. The inherent difficulty of measuring fish directly under the ice surface poses difficulties to accurately assess its role affecting movements and schooling behaviour.

During the winter, Arctic cod also school in large numbers however aggregations are detected in deeper water and at greater depths. In Franklin Bay, Beaufort Sea the standing biomass of Arctic cod between February and April was estimated to be 11.23 kg m^{-2} or 30.3 megatons (Benoit et al. 2008). During the densest aggregation, Benoit et al. (2008) reported a biomass of 0.25 – 2.67 kg m^{-3} which is less than coastal schools (e.g., 3.1 – 10.6 kg m^{-3}; Crawford and Jorgenson 1996). Similar to summer movements, Arctic cod appear to distribute during the winter in response to temperature gradients, predator-avoidance, and distribution of prey. For example, in Franklin Bay, Benoit et al. (2008) found that Arctic cod remained in the lower halocline (>140m deep) where the temperature was higher compared to shallower water. Similarly, Geoffroy et al. (2011) found that Arctic cod usually remained in the warm deep Atlantic Layer (>0°C) in the Amundsen Gulf, however some individuals occasionally moved into shallower and colder water. This diel vertical migration was synchronized with photoperiod potentially in response to prey movements (Geoffroy et al. 2011). Further, Benoit et al. (2010) argued that smaller Arctic cod moved upwards at night to feed to meet requirements due to low energetic reserves (i.e., small livers). Benoit et al. (2008) and Geoffroy et al. (2011) suggested a progressive migration into deeper water as daylight period increased was to avoid predation from seals.

1.2. Beluga and narwhal

1.2.1. General biology

Beluga and narwhal are gregarious animals typically travelling in familial or same-sex groups. Belugas are restricted to Arctic and sub-Arctic waters along the northern coasts of Canada, Norway, Russia, Alaska, and Greenland. The narwhal's range is more northern, primarily inhabiting waters off Canada and Greenland. The number of beluga and narwhal summering in Canadian waters is estimated to be approximately 120,000 and 80,000, respectively (Niemi et al. 2010). Belugas and narwhals are separated into several stocks based on genetic analysis, distribution, and traditional knowledge. Life history parameters such as size and age of maturity vary between sexes but both species, in general, have similar life history (Table 1). The diet is variable depending on seasonal and regional availability.

Beluga and narwhal migrate to the Canadian Arctic Archipelago during summer mainly from Baffin Bay, Jones Sound, the North Water polynya, and off the western coast of Greenland (Innes et al. 1996). In the Arctic, whales typically migrate along coasts to predictable locations, however little is known of the movements of individuals between winter and summer areas (Dietz et al. 2001). In the LSR, bays and deep water around Somerset Island, particularly in Peel Sound, are important locations where whales aggregate (Smith and Martin 1994; Innes et al. 1996). Movement through bays and close to shore may be related to water temperature, orientation, raising calves, moulting, protection from ice and predators, and feeding (St. Aubin et al. 1990; Richard et al. 2001; Loseto et al. 2006). Seasonal variation affects the timing of migration however movements are tightly coordinated with the break-up and consolidation of ice. As sea ice extent diminishes during the summer, beluga and narwhal closely follow ice-cracks and ice-leads as they move to productive waters. Alternatively they return to wintering areas as the sea-ice consolidates. Both whales associate strongly with sea ice and as a result often become entrapped, particularly narwhals. During the ice-free period, beluga and narwhal swim within the upper water column (<5m deep) approximately 40% of the time or more (Heide-Jørgensen et al. 1998, 2001) however they do make numerous dives to depths >100m presumably to feed. As whales migrate away from summering areas, there is a progression towards deeper and more frequent dives (Heide-Jørgensen et al. 1998).

Historically, beluga and narwhal were hunted for commercial purposes however presently only subsistence hunting by Inuit occurs. Each community has restrictions on the number of whales to be captured and likely does not exceed 1000 per year (DFO 2011). Nevertheless, whales face other human-related impacts such as distributional changes of prey and increased contaminant concentrations (Learmonth et al. 2006). Management of whale stocks is difficult because population data is lacking.

1.2.2. Diet

The diet of beluga and narwhal in the Arctic has been documented however data is sparse and often incomplete (see Table 1 in Lairdre and Heide-Jørgensen 2005). Lairdre and Heide-Jørgensen (2005) found Arctic cod and *A. glacialis* in 88% and 60% of narwhal stomachs (ignoring empty stomachs) from Inglefield and Melville Bay, Greenland, respectively. Around Bylot Island, Nunavut fish constituted 93% of wet weight of stomach contents with Arctic cod and Greenland halibut being the most important (Finley and Gibb 1982). Although *Gonatus fabricii* is a common prey item of narwhals, the relatively slow digestion rate of beaks and their high propensity to get caught along the forestomach overestimates numbers. Nevertheless, nearly all narwhals sampled from Uummannaq and Disko Bay, Greenland contained 'fresh remains' of both Greenland halibut (*Reinhardtius hippoglossoides*) and *G. fabricii* during the fall and winter (Lairdre and Heide-Jørgensen 2005). Finley and Johnston (1977), Bradstreet and Cross (1982), and Welch et al. (1992) reported that narwhal fed almost exclusively on Arctic cod in Creswell Bay, Pond Inlet, and Allen Bay, Nunavut, respectively.

The diet of belugas has been demonstrated to be very diverse including crustaceans, polychaetes, molluscs, tunicates, squid, Arctic cod, saffron cod, herring, whitefish, smelt, Arctic char, and sculpins, among others (Lowry et al. 1985). In Greenland and Russia Arctic cod, *A. glacialis*, and whitefish are the primary diet items; in the Canadian Arctic and Svalbard Arctic cod is the primary diet item; in sub-Arctic Canada capelin, sandlance, and benthic invertabrates are the primary diet items; and around Alaska saffron cod and shrimps are the primary diet items (NAMMCO 2004; Welch et al. 1992). Overall, the diet of beluga and narwhal vary at a regional scale reflecting the available prey items. Narwhals appear to be more specialist foragers relying on fewer diet items.

Based on $\delta^{13}C$ and $\delta^{15}N$, Hobson and Welch (1992a) suggested that beluga and narwhal sampled from the LSR fed more on invertebrates than previous stomach content analysis had determined. Similarly, Hobson et al. (2002) showed beluga and narwhal at lower trophic levels than a diet predominated by Arctic cod, suggesting squid or pelagic crustaceans are also important prey items in the North Water.

1.2.3. Interactions with prey

Beluga and narwhal commonly enter bays or move along the shoreline during the summer (Innes et al. 1996; Dietz et al. 2001; Richard et al. 2001). In part, these movements are thought to be related to foraging because Arctic cod aggregate in shallow bays (Richard et al. 2001). Large feeding aggregations of whales, seals, and seabirds are common close to shore when schools of Arctic cod are present. For example, Innes et al. (1996) observed a group of 400 and 250 belugas in Radstock Bay (31 July 1996) and Maxwell Bay (1 August 1996), Devon Island, Nunavut, respectively, aggregating near schools of Arctic cod. Hundreds of harp seals and seabirds were also observed feeding with the whales. The specific behaviour used by whales to capture prey is not well understood however echolocation and coordinated movements are likely used. For example, belugas work together to drive schools of Arctic cod into shallow water where escape is more difficult and stranding occurs (e.g., Welch et al. 1993).

Past research has shown that whales spend the majority of time near the surface while travelling along the coast but do frequently make deep dives (>500m) when aggregating in specific areas (Richard et al. 2001). These dives are believed to be related to feeding. Using fatty acid analyses, Loseto et al. (2009) demonstrated that smaller-sized belugas fed on smaller Arctic cod in shallow nearshore waters, while larger individuals consumed larger Arctic cod from the deep offshore in the Beaufort Sea. Further, Finley and Gibb (1982) commonly found deepwater fish (*A. glacialis*, Greenland halibut, and redfish) in the stomachs of male adults and not in other sex or age classes.

Habitat and dietary differences based on life history characteristics have been further demonstrated. For example, belugas harvested from Tuktoyaktuk fed more pelagically, whereas beluga from Paulatuk fed on terrigenous sources based on $\delta^{13}C$ levels (Loseto et al. 2008). Further, Loseto et al. (2008) found that both $\delta^{13}C$ and $\delta^{15}N$ were best described by the length of the whale, and therefore larger beluga fed at higher trophic levels. Similarly, Lesage et al. (2001) reported male belugas feeding at a higher trophic level than females in the Gulf of St. Lawrence based on $\delta^{15}N$. The size of prey items consumed however was not different among age and sex groups of narwhals around Pond Inlet, Nunavut (Finley and Gibb 1982).

There is contention as to whether whales reduce their feeding during the summer. Lairdre and Heide-Jørgensen (2005) suggested that due to a large occurrence of empty stomachs cetaceans such as beluga and narwhal face reduced productivity during the summer and as a result feed more heavily during the winter. However, an empty stomach may not be a reliable indicator of non-feeding. For example, Jobling and Breiby (1986) suggested that marine mammals feed intermittently and as a result an empty stomach may be common. Additionally, many fall/winter individuals were taken from offshore regions while summer individuals were caught nearshore (Lairdre and Heide-Jørgensen 2005).

The narwhals taken during this study were also collected from different locations and sample sizes across seasons were considerably different. Therefore comparing feeding regimes from different depths/habitats and locations is not necessarily indicative of differences in seasonal diets but of prey availability.

1.3. Ringed seal

1.3.1. General biology

Ringed seals are Arctic and sub-Arctic phocids that typically remain in ice-covered waters year-round. Contrary to beluga and narwhal, ringed seals are not strongly sexually dimorphic. Ringed seals also have shorter gestation times allowing them to reproduce annually (Table 1). Sexually mature individuals appear to prefer bays and fjords with stable ice, whereas subadults prefer water with less stable ice, such as polynyas (Teilmann et al. 1999). Females breed and pup on landfast ice and are extremely reliant on access to water for feeding and escape from predators. Approximately 2.5 million individuals are estimated to inhabit Canadian waters (Niemi et al. 2010). Although most ringed seals show area fidelity, some demonstrate long-range movement and changes in seasonal distribution (e.g., Heide-Jørgensen et al. 1992). Ringed seals do not usually forage in groups and larger individuals dive deeper exceeding 250m (Teilmann et al. 1999). Fish and crustaceans compose the majority of diet items.

1.3.2. Diet

The diet, and $\delta^{13}C$ and $\delta^{15}N$ values of ringed seals are variable among location, sex, and age. For example, immature seals in Grise Fjord, Nunavut fed primarily on the amphipod *Parathemisto libellula* in the summer, whereas Arctic cod and *A. glacialis* dominated the diet of adults (Holst et al. 2001). By contrast, both immature and mature individuals fed primarily on Arctic cod in Qaanaaq, Greenland (Holst et al. 2001). In sub-Arctic Hudson Bay adult ringed seals had higher $\delta^{15}N$ values compared to juveniles suggesting age-specific foraging behaviour (Young et al. 2010). The autumn diet in Northeast Greenland consisted primarily of *P. libellula*, while the spring diet consisted mainly of Arctic cod (Labansen et al. 2011). Dehn et al. (2007) showed that females captured in Barrow, Alaska consumed more fish and had higher $\delta^{15}N$ than males possibly due to spatial segregation or differential use of resources. Overall, the diet of ringed seals in the High Arctic is dominated by only a few species, including Arctic cod, pelagic amphipods, and mysids (Bradstreet and Cross 1982; Marcin 1994; Holst et al. 2001; Labansen et al. 2011).

1.3.3. Interactions with prey

Information associated with ringed seal foraging is primarily limited to the ice-free period. Ringed seals often show sex- and age- related resource partitioning and may be limited to the size and type of prey that can be captured or consumed. For example, dive depth is positively correlated with size (Teilmann et al. 1999), suggesting that deeper prey items are excluded from the diet of juvenile seals. Because Arctic cod are typically demersal, younger seals may exploit pelagic or ice-associated invertebrates to a greater extent. Similarly, large Arctic cod may aggregate deeper than smaller Arctic cod, excluding them from the diet of seals (Benoit et al. 2008). By contrast, Holst et al. (2001) found no difference in the size-selection of Arctic cod by adults and subadults in Grise

Fjord and Qaanaq. Bradstreet et al. (1986) found no size differences in relation to age, season, habitat, or year based on regressions from otolith size found in stomachs.

Based on $\delta^{15}N$, Hobson and Welch (1992a) estimated that ringed seals in Barrow Strait consumed only 54% Arctic cod in early summer and hypothesized that $\delta^{15}N$ values would increase in late fall in concordance with the nearshore movement of Arctic cod. When large feeding aggregations occurred, ringed seals seldom associated with schools or other predators (Bradstreet et al. 1986; Welch et al. 1993). Further, Bradstreet et al. (1986) indicated that the stomachs of those organisms feeding heavily on schools (i.e., harp seal, beluga, and narwhal) were typically full of fish showing the same degree of digestion, whereas ringed seals displayed fish at varying levels of digestion. Therefore, dispersed Arctic cod may be a more important source of prey for ringed seals than schooling cod.

1.4. Seabirds

1.4.1. General biology in Arctic

Each summer, millions of seabirds including dozens of species use the Canadian Arctic for breeding, feeding, moulting, and migration (Mallory & Fontaine 2004). Seabirds migrate to the Arctic in early summer and depart in early fall. Some species such as glaucous gulls (*Larus hyperboreus*) migrate from temperate coastal areas, while others such as northern fulmars (*Fulmarus glacialis*) and black-legged kittiwakes (Rissa *tridactyla*) migrate from the open ocean. Breeding and incubation periods vary among species but coincide with the break-up of ice and increase in primary productivity. Arctic seabirds usually nest on sea cliffs and parents alternate incubation shifts. Breeding sites are typically located near productive feeding areas, such as polynyas to maximize foraging efficiency while providing for chicks (Mallory and Fontaine 2004; Garthe et al. 2007). Usually seabirds reproduce annually or once every two years however mature birds may not reproduce if environmental conditions are unfavourable (e.g., lack of food). Population studies in the Arctic are rare and many estimates are based on surveys completed decades ago (e.g., Nettleship 1980; Hatch and Nettleship 1998). Mallory and Fontaine (2004) estimated approximately 10 million pairs of breeding seabirds in the Canadian Arctic. Additionally, hundreds of thousands of nonbreeding seabirds inhabit the Arctic (Mallory and Fontaine 2004).

1.4.2. Diet

Seabirds are mostly opportunistic and generalist consumers. As a result diet is varied but in the Arctic mainly includes amphipods (e.g., *T. libellula*), copepods (e.g., *Calanus glacialis*), and Arctic cod. Although the percent and frequency of occurrence of invertebrates is often higher than fish, the energetic contribution of Arctic cod is usually >75% of all items. For example, Bradstreet (1976) concluded that Arctic cod made up over 90% of the dry weight in the diet of black-legged kittiwakes in the LSR. Northern fulmars are opportunistic feeders relying on a wide variety of prey including squid, invertebrates, food scraps from hunters, and fish. Nevertheless, during chick-rearing, Arctic cod was a primary diet item in the LSR (Bradstreet 1976). Further, near Pond Inlet, Nunavut Bradstreet and Cross (1982) found that Arctic cod made up at least 78% of dry weight based on stomach content analysis. Glaucous gulls feed at high trophic levels often consuming chicks of other birds (Hobson 1993) or small mammals (Barry and

Barry 1990). The contribution of Arctic cod to the diet in the Arctic is not well known, however fish were a major part of the diet in the Beaufort sea (see Table 2 and 3 in Barry and Barry 1990). Additionally, when foraging distant from seabird colonies, glaucous gulls feed at lower trophic levels (i.e., on fish) (Gaston and Nettleship 1981).

Using stable isotopes, Hobson (1993) proposed that murres, fulmars, kittiwakes, and guillemots fed on higher proportions of lower trophic-level organisms (although Arctic cod was still important) than previous stomach content studies reported. Additionally, using SIA, Hobson (1993) suggested that black-legged kittiwake chicks were fed Arctic cod while adults consumed invertebrates.

1.4.3. Interactions with prey

Seabirds have diverse behavioural foraging strategies and physiological adaptations to obtain prey in the Arctic. Several species are able to make dives underwater >100m deep. For example, Croll et al. (1992) recorded a maximum dive depth for thick-billed murres (*Uria lomvia*) of 210 m and maximum dive duration was 224 sec. Murres have numerous adaptations to facilitate deep and prolonged dives such as high blood volume, and high hematocrit and haemoglobin levels (Croll et al. 1992). Many seabirds however are not adapted to deep-diving and must capture prey at-sea close to the surface. For example, the northern fulmar is capable of making shallow underwater dives (<3m deep), but they also feed by plunge diving and dipping their beaks at the surface (Hobson and Welch 1992b). Similarly, black-legged kittiwakes feed by surface dipping and plunge diving from air.

Breeding colonies are typically located near productive areas allowing seabirds to forage close to the colony. However, seabirds often travel long distances while foraging when local resources are deficient (Benvenuti 1998; Welcker et al. 2009). Maximum foraging ranges vary but can exceed 200km (Falk and Moeller 1995; Welcker et al. 2009). To find prey, seabirds use a variety of methods. Over small temporal and spatial scales, seabirds may use memory to return to the same food patch as the previous foraging bout (Davoren et al. 2003a). Additionally, seabirds use the behaviour of other individuals as a proxy to locate food patches locally (Davoren et al. 2003b). At larger scales, where food may not be persistent, individuals follow successful foragers to food patches or cue on the direction of their return from foraging (Gaston and Nettleship 1981; Buckley 1997). Seabirds also use environmental cues to find prey. For example, northern fulmars and black legged kittiwakes aggregate near tidal fronts where prey items are concentrated (e.g., Begg and Reid 1997). If food patches are unknown, seabirds appear to forage by following random flight patterns (Elliott et al. 2009).

Seabirds are faced with numerous search options. Ultimately the decisions they make affect energy expenditure and as a result the net gain is dependent on the prey consumed. Therefore to be profitable, energetically costly dives or search patterns should result in high energy prey acquisition. For example, pelagic prey tend to form large aggregations (Cotté et al. 2007) and require less energy to exploit, however more time is typically spent to find such items (Weimerskirch 2007). By contrast, benthic prey are fewer but due to habitat preferences are a reliable source of prey to locate (Davoren et al. 2003a). Elliott et al. (2009) found that benthic feeding thick-billed murres had higher underwater search times than pelagic feeding murres which conversely had higher above-water search times. Additionally, total trip time, flying time, number of flights, and number of dives increased with prey energy content. Foraging in productive nearshore areas like Allen Bay, Nunavut appears to benefit seabirds by reducing search effort and increasing encounters with prey. When Arctic cod are driven to the surface or nearshore by marine mammals, the areas become increasingly important at least on a short-term basis.

In addition to capturing prey directly from the water, an important foraging method used by marine birds is kleptoparasitism. It is the act of obtaining food from other individuals through harassment, intimidation, or physical harm. This form of foraging is thought to be an adaptive method to obtain food when resources are limited (Giraldeau and Caraco 2000). Consequently, many species are opportunistic kleptoparasites, while few species specialize as food stealers (Furness 1987a). Kleptoparasitism can be beneficial because often less energy is expended compared to capturing prey directly (Stempniewicz and Iliszko 2010). Parasitic jaegers (*Stercorarius parasiticus*) are adept food stealers and although they also capture prey directly, the majority of food is believed to come from kleptoparasitism (Furness 1987b). The success rate jaegers steal food varies but can be as high as 68% (Forssgren 1981), however rates as low as 10% are believed to be sufficient to make kleptoparasitism energetically profitable (Furness 1987b). Other birds, such as gulls (*Larus* spp.) are also proficient kleptoparasites. Furness (1987b) found that gulls (26%) were more successful at making a victim drop food then frigatebirds, jaegers, and skuas (19-23%). Nevertheless, gulls are opportunistic kleptoparasites and this behaviour is believed to only contribute a small amount to the diet.

1.4.4. Distribution of seabirds in relation to prey

High density aggregations of prey provide significant short-term benefits for predators such as seabirds by maximizing predator-prey encounters and minimizing search efforts (Davoren et al. 2003a). At a large spatial scale, seabirds concentrate on foraging in areas with predictable and abundant resources and avoid energetically costly search flights (Davoren et al. 2003b, Weimerskirch 2007). At a fine scale, foraging search patterns are not as clear, but stronger associations with aggregations of prey may result. For example, Davoren et al. (2003b) showed that murres associated more tightly with capelin in areas where schools were ephemeral versus persistent. Competitive interactions among conspecifics and cooperative foraging were also potential factors influencing predator distribution. The spatial scale at which seabirds locate prey is clearly important when studying distributional associations. In general, it appears that the location of resources at large or meso-scales are fairly predictable for seabirds, but at finer scales aggregations of prey are more difficult to locate (Weimerskirch 2007).

The ability to locate predictable resources strongly influences energy expenditure and has been correlated to decreased reproductive output. For example, South Georgia black-browed albatrosses typically have variable (and lower) breeding success compared to other colonies likely due to extremely variable krill availability (Croxall et al. 1997). Seabird breeding colonies are commonly located near productive habitats where energy allocated to foraging is low to allow for reproduction and parental care (Mallory and Fontaine 2004; Garthe et al. 2007). If local resources are depleted, seabirds forage distant from colonies where travel time between the colony and food patches, and foraging time within the food patch limit provisioning to offspring (Orians and Pearson 1979; Davoren et al. 2003a). Davoren and Montevecchi (2003) showed that murres foraging at greater distances in the Northwest Atlantic resulted in lower feeding rates for chicks and poorer fledgling condition. Therefore efficient ways to locate and associate with prey are important.

There are a few studies in polar waters that have compared the distribution of seabirds with prey using hydroacoustic techniques. Piatt et al. (1989) studied the distribution of seabirds near a major breeding colony in the southeastern Chukchi Sea. Large feeding flocks of murres and black-legged kittiwakes were observed over large aggregations (density $>15 \mathrm{g} \cdot \mathrm{m}^{-3}$) of fish, presumably Arctic cod. Additionally, fish were more abundant in coastal waters than offshore, which were correlated with seabird densities. Reproductive output may have been affected by low fish densities in later summer, as black-legged kittiwakes lost weight and fat stores and only had a 12% breeding success rate. Mehlum et al. (1996) also found a positive correlation between thick-billed murres and aggregations of fish in Svalbard near a large breeding colony. Specifically, there were much higher densities of foraging murres when dense aggregations of fish (presumably Arctic cod) and zooplankton were detected. By contrast, correlations between murres and dispersed echoes were weak. In the Southern Ocean, Heinemann et al. (1989) travelled along transects to simultaneously track predator and prey using visual and hydroacoustic observations. They discovered that species specializing in krill as a food resource were strongly correlated with swarms of krill whereas seabirds that consumed <50% krill were not correlated.

1.5. Stable isotopes

1.5.1. Introduction

Stable isotope analysis (SIA) is a popular technique to examine the structure and dynamics of food webs as it provides a temporal and spatial view of trophic relationships among organisms. Their application is widespread including studies concerning nutrient flow through food webs and ecosystems (Fry 2006), niche breadth and overlap (Hammerschlag-Peyer 2011), animal migration (Hobson 2009), and tracking contaminant flow (Atwell et al. 1998), among others. While novel analytical tools are currently being developed (i.e., Bayesian niche-width metrics; Jackson et al. 2011), much of the data is historically used to infer the relative position and importance of groups of organisms in the food web. Since it is difficult to obtain a complete suite of values for all diet items, especially in the Arctic, most studies rely on data from other studies (i.e., baseline values) that are temporally and spatially variable (Michener and Lajtha 2007). As it is difficult to obtain samples in remote areas some of the assumptions must be viewed with caution. Despite the limitations of SIA, there are more and more studies being conducted to which comparisons can be made. Further, standardization of techniques, equipment, and analysis throughout the last half-century has made comparisons more reliable.

1.5.2. What is a stable isotope?

Stable isotopes are atoms with the same number of protons and electrons that do not decay and exhibit varied reaction rates because the number of neutrons differ (Sulzman 2007). Stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are commonly used in ecology because they provide time-integrated information on feeding relationships and energy pathways in food webs (e.g., Peterson and Fry 1987; Cabana and Rasmussen 1994; Vander Zanden and Rasmussen 1999). Isotopic composition (δ) is most often presented as parts per thousand of an elemental sample compared to a standard presented as follows:

$$(1) \qquad \delta X = [(R_{sample} / R_{standard}) - 1] \text{ x } I0^{3}$$

where X represents ^{13}C, ^{15}N, or another isotope, and R is the corresponding ratio of sample to standard (i.e. $^{13}C/^{12}C$, $^{15}N/^{14}N$). Therefore, the measurement of isotopic composition is a comparison of heavy isotopes to light isotopes. Positive δ values indicate that the sample has more heavy isotopes than the standard, while negative δ values indicate that the sample has less heavy isotopes than the standard (Peterson and Fry 1987). These isotopic differences cause fractionation which refers to the reactions that alter the ratio between heavy and light isotopes. $R_{Standard}$ values are standardized reference materials of known and constant values. For example, the standards for nitrogen and carbon are often obtained from PeeDee limestone and nitrogen gas in the atmosphere, respectively (Peterson and Fry 1987).

1.5.3. Measuring stable isotopes

Typically, a small piece (~1g) of tissue is removed and dried in an oven or freeze-dryer. If organisms are small (e.g., zooplankton), the whole individual may be used. Once dry (i.e., 40°C to 70°C for 48 hours) tissues are crushed and ground prior to analysis. Lipids are commonly removed from the sample using a 2:1 chloroform/methanol solvent because lipids in tissues are depleted in ^{13}C compared to whole organisms and because the lipid content of animal tissue is considerably variable (Peterson and Fry 1987; Kling et al. 1992).

Stable isotope ratios are measured using a technique called isotope ratio mass spectrometry (IRMS). Mass spectrometers separate charged atoms or molecules based on their mass-to-charge ratio. There are four main components of IRMS including: *inlet system, ion source, mass analyzer, and ion detector*. Samples are introduced and converted to gas via the *inlet system* through capillary tubes to ensure no fractionation. Lighter isotopes separate and enter the mass spectrometer while heavier ones are left in a reservoir (Sulzman 2007). Two types of IRMS can be used for this process: dual inlet (DI-IRMS) and continuous flow (CF-IRMS). Replicate analysis is available using DI-IRMS thus increasing precision, while CF-IRMS allows different samples to be analyzed concurrently. In the *ion source*, electrons are accelerated by electrostatic potentials and introduced into an ionization box where they contact the sample gas. The resulting positively charged particles are repelled by an electrical field to form a thin beam (Sulzman 2007). This beam enters the *mass analyzer* and via a magnetic field lighter isotopes are separated from heavier isotopes and directed to the *ion detector*. The ion detector contains numerous Faraday cups, which are positioned to capture specific masses. The ion current that flows through them creates a voltage and a computer converts relative signal strength to a ratio, and a δ value relative to the standard (Sulzman 2007). To ensure analytical precision and accuracy, lab results are compared with international lab standards and often replicates are run on the same samples.

1.5.4. Application of nitrogen stable isotopes

Nitrogen is an important element for SIA because $\delta^{15}N$ tends to be enriched (3.4 ± 0.3‰) with each trophic transfer (Minigawa and Wada 1984). The reason for this is not fully understood however it is associated with isotopically light nitrogen (i.e., ^{14}N) being excreted in the urine of animals by deamination and transamination (Peterson and Fry 1987; Gannes et al. 1998). Retention of ^{15}N varies according to species, diet, and nutritional stress (Hobson and Montevecchi 1991). Nevertheless, $\delta^{15}N$ is useful when examining food webs because increases between 3‰ and 5‰ can be detected between predator and prey indicating successive trophic transfers based on diet (Peterson and Fry 1987). Despite the applicability of using ^{15}N data to study marine ecosystems and its robust nature (Post et al. 2002), the complexity of the nitrogen cycle and influence from multiple processes can result in ambiguous and unreliable results (Montoya 2007). Therefore a strong understanding of the behaviour of nitrogen in the environment is essential to properly interpret findings.

The natural abundance of ^{15}N in the marine system (and hence organisms) is determined by several processes bringing nitrogen into the ocean and moving it out. As a result the marine nitrogen cycle is very dynamic and in constant flux. Most marine autotrophs are unable to use molecular nitrogen N_2 as a substrate for growth and as a result dissolved inorganic nitrogen controls much of the isotopic composition of marine plankton (Montoya 2007). N_2-fixation and denitrification therefore play an important role adding and removing nitrogen from the environment (Brandes and Devol 2002). Typically N_2-fixing organisms are responsible for nitrogen isotopic variation, but excreted feces and detritus from organisms can also have an effect (Montoya 2007).

1.5.5. Application of carbon isotopes

Carbon fractionates minimally at each trophic transfer (<1‰) (Michener and Schell 1994). This is due to limited changes in the ratios of heavy to light isotopes during respiration, assimilation, and fixation (Peterson and Fry 1987; Vander Zanden and Rasmussen 1999). As a result, consumers retain the approximate ^{13}C of their food sources (DeNiro and Epstein 1978; Fry and Sherr 1984; Wada et al. 1993; France 1996; Harvey et al. 2002). This provides the potential to identify baseline prey items (e.g., ice algae or phytoplankton) and other organisms that consumed similar prey. The degree of fractionation however is not constant in all species and can be influenced by the diet and other factors. This variation can reflect differences in lipid or amino acid composition, turnover time in different tissues, and changes in turnover time due to selective feeding (Michener and Kaufman 2007). For example, organisms ingesting high protein diets tend to show isotopic carbon values reflecting the protein content while the whole item is represented in low protein diets (Ambrose and Norr 1993). Organisms fed high caloric and high fat diets also produce lower $\delta^{13}C$ values due to lipids being isotopically lighter than other biochemical components (Stephenson et al. 1986).

Pinnegar and Polumin (1999) found that several tissues in rainbow trout showed considerable isotopic variation due to changes in turnover rates. Metabolically more active tissues have quicker turnover rates and it is generally agreed that turnover is also affected by changes in body mass (Hesslein et al. 1993). Additionally, if diet changes temporally, $\delta^{13}C$ values will be affected. For migratory marine animals, it is difficult to assess whether carbon sources reflect local feeding or food from other sources. It is therefore advisable to sample several tissues to obtain a time-integrated view based on varying turnover rates (Michener and Kaufman 2007).

The power of ^{13}C is also strengthened because sources of carbon can be traced throughout the food chain (due to limited enrichment). In aquatic environments, benthic algae typically fractionate less during carbon fixation than phytoplankton resulting in more enriched signals (Vander Zanden and Rasmussen 1999). Similarly, benthic-pelagic coupling occurs where more organic deposits sink from the water column to the benthos enriching signals of benthic organisms (Hobson et al. 1995). In the Arctic, studying carbon pathways can be very informative because the two main food sources for all organisms (ice algae and pelagic phytoplankton) show distinct carbon signatures (Hobson et al. 2002a, Søreide et al. 2006). Therefore prey items, foraging location, and habitat can be determined using carbon isotopes.

1.5.6. Application of trophic level

Trophic level (or position) allows researchers to define the functional role of organisms and estimate the movement of energy in a food web (Post 2002). However, food webs involve complex interactions that are often difficult to detect or represent (i.e., omnivory). The use of stable isotopes is advantageous because it incorporates the assimilation of energy through the different pathways from primary producers to top consumers (Post 2002). Therefore complex interactions can be detected in an ecological community using SIA (Cabana and Rasmussen 1996). The simplest model for estimating the trophic level (TL) of a consumer is:

$$(2) \qquad TL = \lambda + (\delta^{15}N_{\text{secondary consumer}} - \delta^{15}N_{\text{base}})/\Delta_n$$

where λ is the trophic level used to estimate $\delta^{15}N_{base,}$ $\delta^{15}N_{secondary\ consumer}$ is measured directly, and Δ_n is the enrichment in $\delta^{15}N$ per trophic level (Post 2002). When consumers obtain nitrogen from multiple food sources, there is greater likelihood of spatial variation in $\delta^{15}N_{base}$ which must be accounted for (Post 2002). For example, fish that feed on organisms from the benthos and the water column will have multiple potential baseline signatures, each affecting trophic level calculations. To account for this heterogeneity, mixing models are used to estimate the affect of baseline signatures on trophic level. For a two-source food web, the trophic level is calculated as follows:

$$(3) \qquad TL = \lambda + (\delta^{15}N_{secondary\ consumer} - [\delta^{15}N_{base1} \text{ x } \alpha + \delta^{15}N_{base2} \text{ x } (1-\alpha)]/\Delta_n$$

where α is the proportion of nitrogen ultimately derived from the base of the first food web and assumes that mixing is linear. More complex mixing models exist to account for >2 food sources and/or habitats (Phillips 2001). For example, Bayesian statistics are increasingly being used to estimate contribution of different prey items to the diet (Moore and Semmens 2008). As the quantitative use of stable isotopes advances, difficult variables to measure, such as omnivory, trophic position, food chain length, and energy pathways can be estimated with greater accuracy and confidence (Vander Zanden and Rasmussen 2001).

1.5.7. Selecting the tissue to sample

A number of tissues have been used to examine stable isotopes, many of which show high variation within individuals and are less reliable than others (Peterson and Fry 1987). For example, Pinnegar and Polunin (1999) suggested the use of white muscle to elucidate fish trophodynamics since it was less variable than red muscle, liver, and heart in rainbow trout (*Oncorhyncus mykiss*). Isotopic variation within individuals occurs primarily during enzymatic pathways that fractionate stable isotopes after dietary uptake (Peterson and Fry 1987). For example, bone collagen and lipids in fat reserves were enriched (2‰ to 6‰) and depleted (2‰ to 8‰) in ^{13}C compared to diet items, respectively (Peterson and Fry 1987). Therefore it is imperative to use tissues that are consistently enriched or depleted versus the diet. Most commonly, muscle and liver are selected due to low variation compared to other tissues.

Since turnover rates of stable isotopes are tissue-dependent (Tieszen et al. 1983), the choice of tissue to analyze is important. Further, using several tissues from the same individual can provide time-integrated dietary information relating to migration, season, availability of prey, and habitat (Hobson et al. 1996). Muscle, liver, lung, kidney, heart, and spleen have all been used to examine the changes in isotopic composition that result due to metabolism (e.g., Hobson et al. 1996). Analysis of metabolically inactive tissues, such as whiskers, nails, baleen, skin, hair, and blood can also be used to study feeding patterns, as diet is reflected at times of growth (Hobson et al. 1996).

1.5.8. Isotopic baselines and variation

The use of ^{15}N and ^{13}C as time-integrated indicators of trophic level is highly dependent on the environment being studied. For example, variations of $\delta^{15}N$ in organisms at the base of the food web will affect consumers despite similar food chain lengths (Kline et al. 1993). Therefore, to compare $\delta^{15}N$ values in an ecosystem with precision, it is important to identify habitat variation and correct for $\delta^{15}N$. Without suitable baseline values, it is impossible to determine if $\delta^{15}N$ and $\delta^{13}C$ reflect changes in food web structure and carbon flow, or simply a variation in the base values (Vander Zanden and Rasmussen 1999). Organisms at the base of the food web, such as phytoplankton demonstrate large seasonal $\delta^{15}N$ variability and can be problematic. For example, Cabana and Rasmussen (1996) found that the $\delta^{15}N$ ranged between 1-13‰ in primary producers within the same lake. As a result, primary consumers such as unionid mussels (Cabana and Rasmussen 1996) are often used because they are less variable due to size and life-span.

1.5.9. Diet-tissue discrimination factors and turnover rates

The amount of fractionation (or discrimination) of isotope ratios between predator and prey is variable. This variation occurs in individuals, species, habitats, and can be affected by ontogeny (Gannes et al. 1998). When reconstructing diet, for example using mixing models, discrimination values for each predator-prey interaction are required. These models select the most likely prey item using the value selected. Consider a predator only consumes two prey items (item A and B), and is enriched by 2‰ and 3‰ for each item respectively. If the user selects a discrimination of 2.5‰ then we can expect an equal contribution from each prey in the diet. By contrast, if the user selects 2‰ or 3‰, the contribution will be mainly Item A or B, respectively. A common problem using stable isotopes to reconstruct diet is that reliable discrimination values do not exist. This is especially true in the Arctic because researchers study animals that are not easily sampled and cannot be examined in long-term or laboratory studies. Hobson and Welch (1992a) suggested an enrichment of 3.8‰ between predator and prey primarily based on the average difference between $\delta^{15}N$ of polar bears and their most common prey, ringed seals. Many studies have since used this value for every predator-prey transfer without significant support that other trophic levels or interactions occur similarly. Since this suggestion, only one study has meticulously examined Arctic marine animals and discrimination values. Hobson et al. (1996) calculated diet-tissue fractionation for $\delta^{15}N$ and $\delta^{13}C$ in captive harp, harbour, and ringed seals for numerous tissues. The seals were fed a consistent diet of herring for >2 years. $\delta^{13}C$ enrichment ranged from +0.6 to +3.2 and $\delta^{15}N$ ranged from +1.7 to +3.1 for all tissues. Similar studies are needed for other marine mammals in the Arctic, but also organisms at lower trophic levels (e.g., Arctic cod) to facilitate accurate discrimination factors throughout the food web to better reconstruct diet.

Future studies in aquariums or laboratories would not only provide data to help reconstruct diet more accurately, it could also provide time-integrated information about diet. Seasonal or temporal variation in food sources is important for understanding population dynamics (Reid et al. 1997). The ability to assess the timing of diet assimilation from isotopes of varying tissues is lacking. The reflection of prey in tissues is believed to be related to the turnover rate of each tissue because elemental turnover is related to protein turnover (Kurle and Worthy 2002). Tissues with increased metabolic activity (e.g., liver) represent more recent diet assimilation compared to tissues with reduced metabolic activity or those that are metabolically inactive (e.g., muscle and blood) (Hobson and Clark 1992). However, little experimental data has been collected to determine the timing and patterns of tissue turnover rates and isotope half-lives. The few studies that have experimentally manipulated diet to examine tissue turnover have almost exclusively used small mammals or birds (e.g., Tieszen et al. 1983; Hobson 1993). These authors suggested that tissue turnover in liver and muscle would be in order of days to months. Commonly these rates are applied to all animals in the Arctic with no experimental support. However, many rates of physiological processes are associated with body size (e.g., metabolic rate; Schmidt-Nielsen 1984) and larger animals, such as seals and whales may have slower turnover rates than those often used. If this allometric relationship holds, then reconstructing diet temporally becomes much more problematic without appropriate comparative data. Dalerum and Angerbjorn (2005) suggested the use of turnover rates from similar sized animals however these are non-existent for many large mammals. Knowledge of tissue specific turnover and fractionation is fundamental for meaningful interpretation of temporal patterns (Dalerum and Angerbjörn 2005) and requires more attention.

Overall there is a greater need for laboratory studies to understand the functional role of stable isotopes to reconstruct diet (Gannes et al. 1998). Comparative data is needed because metabolic and assimilation pathways differ (Gannes et al. 1998). For example, animals allocate nutrients in their diet differentially to specific tissues and body compartments (Tieszen and Fagre 1993). Consequently, tissues often reflect the isotopic composition of the nutrient component of the diet for which the tissue was synthesized and not the isotopic composition of the bulk of the diet (Gannes et al. 1998). For example, Ambrose and Norr (1993) showed that the composition of body protein in omnivores often reflects dietary protein. Similarly, animals assimilate dietary components with varying efficiency and may not reflect the whole diet item (Gannes et al. 1998). Stable isotope patterns in the field are linked to the biochemistry and physiology of the organisms and without appropriate laboratory studies to provide baseline information we are at a loss to interpret these patterns.

1.5.10. Uncertainty quantifying carbon stable isotopes due to lipids

Often lipids are extracted from samples prior to SIA. The reason for this is to reduce variability due to isotopically lighter lipids which may influence the carbon isotope ratio. During synthesis and accumulation of lipids, $\delta^{13}C$ values are typically more negative than proteins and carbohydrates within an individual organism (DeNiro and Epstein 1977). Lipids can influence $\delta^{13}C$ in two potential ways. First, fractionation of $\delta^{13}C$ during lipid synthesis results in ratios between lipids and other tissues differing by ~6-8‰ (Deniro and Epstein 1977; Post et al. 2007). Second, lipid content is highly variable in animal tissues. For example, lipid content of muscle tissues in fish from north temperate lakes varies from 3 to 34% (Post 2000). Within-individual heterogeneity also exists among tissues which can bias results (Sweeting et al. 2004).

As a result of the uncertainty and variability that lipids influence isotopic composition, researchers use two methods to remove or account for lipids during analyses of samples. First, lipids are often physically removed from samples using a methanol-chloroform solution. This reduces lipid concentrations so it does not significantly affect analysis, however this method is time-consuming and may cause fractionation of $\delta^{15}N$ (Pinnegar and Polunin 1999). Second, a mathematical normalization technique is used to estimate the difference (in $\delta^{13}C$) between lipids and other tissues using C:N to produce normalized (and post-hoc) $\delta^{13}C$ for each sample (McConnaughey and McRoy 1979; Post et al. 2007). This method is advantageous because it accounts for lipid variation using

C:N ratio for a sample, which is typically already measured during SIA analysis (Post et al. 2007). Despite the use of these techniques, there is no consensus as to whether lipids need to be specifically addressed during SIA. While some studies have found lipids to have an effect, many others have not (Post et al. 2007). Post et al. (2007) discussed that lipid extraction or normalization should be used when lipid content among consumers is variable, and when differences in $\delta^{13}C$ between end-members is <10-12‰. Most natural variation occurs under these criteria making lipid-addressing methods important (Post et al. 2007). More rigorous evaluation and effectiveness of the two methods of accounting for lipid variation is necessary.

1.5.11. Uncertainty caused by fasting

In addition to spatial and temporal variables, behavioural attributes also play a role in influencing isotopic composition. Fasting is common in numerous species, often initiated as a result of season, reproduction, nursing, or migration. Like many aspects concerning SIA, the specific influence of fasting on isotopic composition is poorly known. Hobson and Clark (1992) suggested that nutritional stress can influence $\delta^{15}N$ in bird tissues. The authors found more enriched tissues (for $\delta^{15}N$) in American crows (*Corvus brachyrhynchos*) with reduced mass gain (fed grain) compared to crows fed a high protein diet of fish. The difference however may have been caused by differences in the diet items and not nutritional stress. To test this, Hobson et al. (1993) measured $\delta^{15}N$ of several tissues of Ross' geese (*Chen rossii*) before and after egg-laying and incubation periods. The authors found that post-incubating birds had reduced body mass values and increased $\delta^{15}N$ values compared to pre-incubating birds.

Isotopic fractionation of ^{15}N is believed to occur during deamination and transamination of amino acids (Minagawa and Wada 1984). As a result, nitrogenous waste is depleted in ^{15}N relative to diet. Hobson et al. (1993) suggested that when fasting or under nutritional stress, a greater proportion of nitrogenous compounds available for protein synthesis are already enriched which causes a greater enrichment in $\delta^{15}N$. This will lead to all tissues of the animal being enriched at a comparable rate to the metabolic turnover of each tissue. Since fractionation of ^{13}C occurs primarily during respiration, $\delta^{13}C$ is not influenced by fasting or nutritional stress (Hobson et al. 1993).

1.5.12. Applications in the Canadian Arctic - introduction

Stable isotope analysis (SIA) is a complimentary technique to other methods (e.g., diet and fatty acid analysis) as it provides inference to diet through assimilation in tissues. Due to ecosystem-specific variability the use of SIA alone is sometimes insufficient to accurately assess food web relationships (Post 2002). Nevertheless, SIA is increasingly used in the Arctic to study trophic position, food web dynamics, habitat selection, and transfer of contaminants, among others. The application of SIA in the Arctic aquatic environment includes all types of organisms including bacteria, algae, phytoplankton, zooplankton, invertebrates and vertebrates found in fresh, marine, estuarine, and brackish water.

For SIA to effectively delineate feedings patters in organisms, tissue of the study species needs to be examined but also those of prey items. Without organisms to compare from the same ecosystem, it is impossible to accurately understand their role in the food web. As a result, these studies are only capable of comparing individuals of the same species to determine if specific variables affect isotopic composition. Although many simply reference the isotopic composition of prey from other studies (e.g., Hobson 1993), researchers are sampling prey items in the same system with increasing frequency. Of particular interest in the Arctic is the position and role of top predators such as marine mammals and seabirds, as well as ecologically important fish.

1.5.13. Applications in the Canadian Arctic - marine mammals

The use of SIA to determine trophic level and food web interactions of Arctic marine mammals is complicated by several factors. For example, the ability to move long distances seasonally limits the identification of isotopic sources. As a result, reliable comparisons between predator and prey can be difficult. Although isotope values and relative trophic position vary regionally, narwhal (*Monodon monoceros*), beluga (*Delphinapterus leucas*), and ringed seal (*Pusa hispida*) are consistently shown to be feeding near the top of the food web.

Since large-scaled comparisons are difficult, the most informative SIA studies in relation to marine mammals examine variables within that specific system including the influence size, age, and sex has on isotopic composition. For example, in the Beaufort Sea, Loseto et al. (2008) found that both δ^{13}C and δ^{15}N were best described by the length of the whale, and therefore larger beluga feed at higher trophic levels. Similarly, Lesage et al. (2001) found male belugas feeding at a higher trophic level than females in the Gulf of St. Lawrence. In sub-Arctic Hudson Bay adult ringed seals had higher δ^{15}N values compared to juveniles suggesting age-specific foraging behaviour (Young et al. 2010). Further, Dehn et al. (2007) showed that female ringed seals captured in Barrow, Alaska had higher δ^{15}N than males possibly due to spatial segregation or differential use of resources.

Some marine mammal studies have shown possible differences in foraging habitat. For example, belugas harvested from Tuktoyaktuk had less enriched δ^{13}C levels compared to those from Paulatuk suggesting the former fed more pelagically, and the latter fed on terrigenous sources (Loseto et al. 2008).

1.5.14. Applications in the Canadian Arctic - seabirds

Similar to marine mammals, the ability to move long distances can cause uncertainty as to isotopic composition in seabirds. Since seabirds are readily visible researchers have a greater ability to explain spatial habitat and foraging. However, migration and movement in the Canadian Arctic is poorly known, therefore temporal examinations of isotopic composition is necessary. Whereas SIA studies of marine mammals almost exclusively use muscle or skin (and sometimes liver), the study of seabirds has included a greater number of tissues, providing greater temporal variation. For example, Hobson (1993) examined liver, muscle, and bone collagen of seven Arctic seabirds to estimate short-, medium -, and long-term trophic level. The authors suggested that in general the seabirds increased their consumption of lower trophic-level invertebrates during the breeding season. Numerous studies have found that glaucous gulls (*Larus hyperboreus*) are feeding at the highest trophic level among birds, and dovekies (*Alle alle*) and common eiders (*Somateria mollissima*) are feeding at the lowest trophic levels based on δ^{13}N (Hobson 1993; Hobson et al. 2002a; Dahl et al. 2003). This is consistent with foraging observations and stomach content analyses. Several studies also found that many seabirds rely more heavily on invertebrates than fish based on δ^{13}N values. Interestingly, Hobson (1993) and (Hobson et al. 2002a), found that juvenile seabirds were feeding at a higher trophic level than adults, possibly due to a higher fish-based diet fed to juveniles. ^{13}C values also vary among seabirds based on foraging habitat and common prey items. For example, Hobson (1993) found that δ^{13}C of common eiders was more enriched, likely as a result of a diet dominated by benthic invertebrates. Alternatively, northern fulmars (*Fulmarus glacialis*) fed on pelagic prey such as Arctic cod and squid and had the least enriched δ^{13}C values.

1.5.15. Applications in the Canadian Arctic - fish

Arctic cod is one of the most important species of fish in the Arctic. It is abundant and is a dominant prey item of seabirds, seals, and whales. Despite this, little research has been conducted on how life-history, temporal, and spatial traits affect isotopic composition. For the most part, studies have shown that adult cod feed at a higher trophic level than juvenile or larval cod (e.g., Hobson and Welch 1992a; Hobson et al. 2002a). This is not surprising and corroborates stomach content analyses. It does however highlight the need to separate samples of cod based on ontogenetic differences as most studies only sample a small number of cod with limited ranges in size (e.g., Hobson and Welch 1992a). More research is needed to determine the size or age that diet shifts occur and how the isotopic composition changes.

SIA has been used in the Arctic to determine the relative importance of Arctic cod as a prey item. Based on δ^{15}N values, Hobson and Welch (1992a), and Hobson et al. (2002) argued that stomach content analyses over-represented Arctic cod in the diet of seabirds, seals, and whales. These authors suggest that invertebrates make up a large proportion of the diet. By contrast, (Holst et al. 2001) argued that the diet of ringed seals was primarily cod since $\delta^{15}N$ values of ringed seals from Grise Fjord and Qaanaaq were 17.5‰ and 17.0‰, respectively, and a diet of only cod would be approximately 17.8‰.

Little research has been conducted with respect to $\delta^{13}C$ and cod feeding. Holst et al. (2001) suggested that ringed seals from Qaanaaq fed more on Arctic cod than in Grise Fjord (where they fed more on *A. glacialis*) because they were less enriched in $\delta^{13}C$. The authors argued that because Arctic cod associate with ice, and *A. glacialis* occur in demersal habitats, *A. glacialis* are more enriched. However, Arctic cod are known to occur throughout the water column (Gradinger and Bluhm 2004; Benoit et al. 2008) which contradicts this rationale. More research and habitat-specific sampling of Arctic cod is needed to understand how $\delta^{13}C$ changes in the Arctic.

Arctic char (*Salvelinus alpinus*) is an important predator in freshwater and marine food webs. Numerous studies have been conducted using stable isotopes in combination with other techniques to infer trophic relationships. These include, but are not limited to, diet (Vander Zanden et al. 1997; Guiger et al. 2002), growth (Adams et al. 2003), contaminants (Paterson et al. 2006; Guildford et al. 2008), growth and diet (Power et al. 2002, 2005), diet and parasites (Gallagher and Dick 2010), diet and contaminants (Kidd et al. 1998), diet and habitat (Hindar & Jonsson 1982; Amundsen et al. 2008), and energy, contaminants and fatty acids (Haffner 2010). This highlights the strength of using different approaches as complimentary techniques (Guiguer et al. 2002; Dick et al. 2009; Gallagher and Dick 2010) providing a better picture of the flow of energy and structure of food webs. For example, Gallagher and Dick (2010) demonstrated that diet, parasites, and stable isotopes used in complement explained trophic structure better than when applied separately.

Specifically, $\delta^{15}N$ consistently shows a positive relationship with size in char. For example, Hobson and Welch (1995) found a stepwise increase in $\delta^{15}N$ as the diet of char switched from invertebrates to being cannibalistic. Similarly, Guiguer et al. (2002) used stable isotopes to differentiate between morphotypes of char. SIA has also been used to corroborate observed among-lake differences and similarities in species diets (Power et al. 2002).

1.5.16. Critique of food web studies

The most informative and superior SIA studies are those that measure isotopic composition of organisms throughout the food web. This enables more accurate comparisons between organisms and identification of potential sources of isotope signatures. Therefore estimates of trophic level will reflect the organisms in the system as opposed to variability at the base of the food web. This is especially true if a primary consumer is selected as a baseline with consistent isotopic composition. Several studies of this sort have been conducted in the Canadian Arctic and two will be reviewed and discussed.

1.5.17. Critique #1

Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ *and* $\delta^{15}N$ *analysis - Hobson and Welch (1992a)*

The authors measured $\delta^{13}C$ and $\delta^{15}N$ in 322 tissue samples from 43 species in the Barrow Strait and Lancaster Sound Region during July-August, 1988-1990. The species included primary producers, invertebrates (e.g., bivalves, molluscs, copepods, mysids, and amphipods), fish, marine birds, and marine mammals. As hypothesized, there was a step-wise enrichment of $\delta^{15}N$ between predators and prey. This enrichment was +3.8‰ between polar bears (*Ursus maritimus*) and their prey ringed seals. The same enrichment was calculated between *Calanus hyperboreus* and its primary food particulate organic matter (POM). With the exception of seabirds, the authors used this enrichment factor to create a simplified food web model for all the organisms. The model confirmed a food web consisting of five trophic levels (e.g., polar bears – 5.1; POM – 1).

There are limitations to this study. First, although numerous species were examined, for the most part they were very small sample sizes. Therefore it is unclear if any variation in isotopic composition is caused by inherent variability, year of collection, or other variables. Second, the authors assumed a constant enrichment among each predator-prey relationship when this did not necessarily apt. A different enrichment value was applied for birds due to research of captive feeding trials which showed less fractionation in muscle tissue (Hobson and Clark 1992). However this relationship is not necessarily true for the seabirds in question and is a large assumption. Third, the authors conclude that lower level organisms (e.g., invertebrates) were more important to top predators such as seals and whales, and that Arctic cod are not as much of an important link in the food web as previously thought. However this deduction is only accurate if the enrichment factors applied to all trophic levels are also accurate. Again this was a major assumption which ultimately affects the calculated importance of invertebrates and

Arctic cod. Fourth, their analysis also did not take into account if consumers fed at multiple trophic levels which would alter isotopic signatures and position in the food web. A two-ended mixing model could have been useful to account for the proportions some organisms fed on multiple prey. Many of the organisms studied however are known to feed primarily on one or few prey items and therefore the simplicity of the model is a useful starting point for this type of study. The main strength of the study is that organisms throughout the food web were analyzed allowing for relatively accurate comparisons with baseline values. This study was one of the first studies in the Canadian Arctic to examine stable isotopes across the food web and was presented as a preliminary analysis and therefore was instrumental in providing introductory information of the relationships between trophic structure and stable isotopes in this area.

1.5.18. Critique #2

A stable isotope ($\delta^{13}C$, $\delta^{15}N$) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants - Hobson et al. (2002)

The goal of this study was to analyze the movement of energy and contaminants throughout the food web in the North Water Polynya (NOW) using SIA. NOW has high biological activity making it an important feeding ground for organisms, especially larger predators. $\delta^{13}C$ and $\delta^{15}N$ was examined in organisms at all levels of the food web including POM, algae, molluscs, arthropods, echinoderms, fish, seabirds, and marine mammals. The authors assumed *C. hyperboreus* occupied a TL of 2.0 and calculated the TL of other organisms based on this value using an enrichment factor compared to diet (for ^{15}N) of 2.4‰ for seabirds, and 3.8‰ for all other organisms. Values of δ^{13}C had a strong tendency to categorize invertebrates based on feeding habitat (e.g., planktonic, benthic, and epi-benthic). The authors also suggested the importance of lower trophic-level organisms to contribute to the transfer of energy to higher trophic-level predators and that Arctic cod was important but not to the extent commonly proposed. Finally the authors used PCB 153 to examine the bioaccumulation of contaminants in the High Arctic food web using stable isotopes (δ^{15}N) as a biomarker.

The limitations of the study are as follows. First, the authors used the same enrichment factors as Hobson and Welch (1992). While this was a conservative decision and allowed comparison to the previous study, it ignored the isotopic relationships that were calculated (e.g., enrichment between polar bears and ringed seals). Also, since the sampling location was different as well as the structure of the food web, using enrichment values from other locations are likely inaccurate. Second, the authors suggest that lower trophic-level organisms are more important in the diet than Arctic cod. While this is possible, the authors do not examine what proportion of prey items would result in the isotopic compositions calculated. Hence, the use of a mixing model would be very useful to determine the importance of prey items. Third, the use of *Calanus hyperboreus* as a baseline organism may not be appropriate since it is a primary herbivore which tends to be more isotopically variable than carnivores. An alternative organism (i.e. secondary consumer) would provide or more reliable baseline value to base calculations of trophic level (Jardine et al. 2009). Fourth, since many of the predators in this study are migratory, the isotopic compositions calculated do not necessarily reflect the NOW food web. For example, muscle was sampled in whales, seals, and birds, which typically has a turnover time of several weeks or more (Hobson and Clark 1992). Since samples were taken in May and June, isotopic values are actually indicative of feeding habits in wintering areas. Surprisingly, despite multiple tissues being collected from birds and mammals, only muscle was used. A time-integrated view of foraging could have been determined to better identify signatures from that location and time of season. Muscle would also skew the importance of prey items such as Arctic cod that become more abundant and readily available during the later summer (Bain and Sekerak 1978).

More positively, this study had a much larger sample size than Hobson and Welch (1992), especially for top predators. Further, many of the predators are from different locations which provide a larger database to make comparisons with. Unlike Hobson and Welch (1992), the authors do not use POM as a baseline. Due to the amount variation that would be expected at the bottom of the food web, this is a more conservative and appropriate approach. Additionally, the authors completed a considerable examination of δ^{13}C and discussed the importance of habitat and feeding behaviour. Finally, the authors expanded on the report of SIA and trophic interactions by including uptake of contaminants which is intrinsically related to trophic structure. This study was conducted a decade after that of Hobson and Welch (1992), and although newer methods were used, many aspects of the analysis and presentation could be expanded upon.

1.5.19. Summary of uses of stable isotopes

Nitrogen stable isotopes are commonly used to infer food web position as it fractionates approximately 3.4‰ at each trophic level (Cabana and Rasmussen 1994). Additionally, δ^{13}C reflects carbon sources and is often used to determine benthic or pelagic food sources (France 1995). Since there is little fractionation (i.e. 0.4‰), $\delta^{13}C$ can also reflect prey items directly (France 1996). These isotopes are commonly measured in muscle and liver due to a difference in metabolic turnover rates. For example, muscle isotope values reflect a medium-term representation (i.e. weeks-months), while liver values reflect a short-term (i.e. days-weeks) (Hobson and Clark 1992; Tieszen et al. 1983).

1.5.20. Summary of advantages of stable isotopes

Stable isotope analysis provides a quantifiable and relatively simple means of conducting trophic analyses. It is highly advantageous because it examines food web and trophic structure based on assimilated diet and not diet directly. This allows for analysis of diet and habitat based on the metabolic turnover of tissues and as a result can provide a very informative time-line of feeding habits. Alternative diet analyses such as stomach content analysis only provides the researcher with diet items consumed within a very short time-span (i.e., hours) and also can misrepresent retention time based on digestion rates. SIA is even more informative if complimentary analysis techniques are used (e.g., stomach content, fatty acid, and parasite analysis). These can provide additional time-lines of food consumption, confirm diet items that SIA cannot, confirm trophic structure, and uncover new trends.

Since isotopic composition (particularly $\delta^{15}N$) increases with trophic level, SIA is very useful as a biomarker to examine the movement and accumulation of contaminants in the food web. SIA has enabled researchers to link wild animal populations to their diet and contaminant source because the route of exposure to heavy metals, organochlorines, and other persistent contaminants is through the diet (Jardine et al. 2006). For example, Gantner et al. (2009) found that large Arctic char (with more enriched $\delta^{15}N$ values) from Lake Hazen, Nunavut had higher Hg concentrations than char with less enriched signatures. This shows the importance of contaminants such as Hg increasing with trophic position.

Specifically in the Arctic, sampling can be expensive and temporally limited (i.e., due to ice) and since SIA is able to provide a time-integrated view of diet it is much easier to examine trophic structure over a long-term period. Additionally, the food chain in the Arctic is relatively simple compared to other areas (i.e., lower diversity), making SIA less complicated because potential sources of carbon or prey are limited.

1.5.21. Summary of limitations of stable isotopes

The limitations associated with SIA are numerous and a formal understanding is necessary to use SIA to examine food web dynamics with precision. Without accurate selection of baseline isotopic composition a proper estimate of trophic level for all organisms in the food web is impossible. Isotopic variation among tissues, organisms, and diet is also a major concern that can be temporally and spatially heterogeneous. Jardine et al. (2006) suggested assessing and utilizing variation in stable isotope diet-tissue fractionation found in the literature. Other life history or behavioural traits such as ontogeny, growth, migration, and fasting can also affect isotopic composition and should be considered when analyzing results. Additionally, SIA studies without the use of supplementary techniques are very limited in their ability to compare and rationalize results. For example, Young et al. (2010) examined stable isotopes and Hg and liver and muscle tissues of three different types of seals in Hudson Bay area. While they obtained very interesting results, they provided no diet information and could only speculate as to the causes of different isotope signatures.

Specifically in the Arctic, year-round sampling is difficult and expensive leading to low sample sizes of the study species but also potential prey items. The reduced sampling means limited ability to delineate seasonal, regional, and habitat trends**.** Although many limitations exist, the inherent strengths of stable isotopes make it a useful tool to examine food webs and trophic structure.

1.6. Hydroacoustics

1.6.1. Introduction

Hydroacoustics (or fisheries acoustics) is defined as the use of underwater sound to detect, enumerate, and measure the distribution of fish (and other living marine and freshwater resources) and describe their habitat (Sullivan and Rudstam 2009). The study of sound underwater can be dated back to the 15th century when Leonardo da Vinci listened to the sea using a long hollow tube (Urick 1983). Since then, the study of hydroacoustics has made numerous progressions and has developed into an integral field for the economical benefit of commercial fisheries. Additionally, hydroacoustics is used to study the behaviour, life history, and abundance of fish populations for management purposes and to further knowledge of important species. In most cases, the application of hydroacoustics does not directly examine the interactions between predator and prey. However, to understand the cues that encourage foraging or initiate feeding, it is important to examine the distribution, habitat, and movement of prey.

Primarily, the field of hydroacoustics originated during the First World War when it was discovered that Sound Navigation and Ranging (SONAR) could be used to detect submarines by listening for the echo of a sound transmission (Simmonds and MacLennan 2005). The first experiment to validate acoustic detection of fish was reported by Kimura (1929). In a shallow pond, Kimura installed a transmitter that projected a horizontal signal to a receiver. Fish passing through the signal caused a noticeable change in amplitude on an oscilloscope. The application to fisheries was soon recognized and advances such as producing detections on paper were made (i.e., Wood et al. 1935). The Second World War encouraged rapid development of technology and afterwards scientists and fishermen started using echo sounders widely (Simmonds and MacLennan 2005). By the end of the 1950s, SONAR systems were affordable and allowed for greater fishing success. The rise of computers meant that large amounts of data could be stored and analyzed in the field or laboratory (Sullivan and Rudstam 2009). Today, our ability to detect fish, delineate behaviour and determine abundance has greatly improved in the short existence of the field of hydroacoustics in fisheries. New techniques and technologies are continually being realized making it a cost-effective and viable way to study the animals living in fresh and marine waters.

1.6.2. Hydroacoustic system

The primary components of a hydroacoustic system include an echo sounder, one or more transducers, a chart recorder, an oscilloscope, and a computer-based echo processing system (HTI 2011). In practice, a pulse of electrical energy is transmitted by an echo sounder to a transducer. The transducer, which is submerged underwater and typically attached to a moving vessel, converts the electrical signal to sound energy. The pulse of energy travels approximately 1500 ms^{-1} through the water until it encounters a solid object such as the bottom or a fish. Energy is reflected in the form of an echo back to the transducer, translated back to electrical energy, and the signal is amplified by the echo sounder. The oscilloscope measures the signal which can then be processed to a visual device such as a chart recorder (i.e., echogram). In order to separate desired targets (i.e., fish) from undesired targets (i.e., zooplankton), a specific threshold is selected that will reject echoes based on the measured intensity of the signal and therefore its size. If the measured signal does not exceed the threshold value, the echogram recognizes the object. If it does, the object is not counted.

Echo sounders allow for the measurement of time delay between the transmission and reception of echoes, as well as the intensity of the returning echo, also known as echo level (Sullivan and Rudstam 2009). This is not only important for detecting fish and their location but also in determining the abundance of fish in the water column. The echo level however, can be affected by many factors including the intensity of a transmitted sound wave, the loss of intensity of the sound wave as it travels through water, reflectivity and position of the target, and losses from equipment during conversion to electric energy (Sullivan and Rudstam 2009). Since the intensity of an echo decreases the further it moves (i.e. the deeper the target), echosounders are equipped with a time varied gain amplifier (TVG). Depending on the time taken for the signal to return it is amplified by a standardized function. Typically the signal is amplified by 20 log R but also 40 log R when the echo level is expected to be weaker, where R represents the echo range (Johannesson and Mitson 1983).

1.6.3. Acoustic Transducers

A transducer is an electro-mechanical device which translates electrical energy to sound energy producing a hydroacoustic signal. When echoes return, the transducer translates the sound energy back to electrical energy for analysis (HTI 2011). The acoustical signal which is produced varies in intensity at different directions due to interference patterns (Sullivan and Rudstam 2009). This creates a beam pattern where objects can theoretically be detected, although the echo level will be greatest if detected in the main axis. The main lobe is conical-shaped at a manufacturer-specified angle. Since wave fronts of the beam are highly variable until they become parallel, data close to the transducer head (near-field distance) should not be included in the analysis (Sullivan and Rudstam 2009).

1.6.4. Target Strength

As previously mentioned, when a sound wave is transmitted part of the energy is lost to the environment, absorbed by an object, and part of it is reflected (FAO 1981). Target strength (and back scattering cross-section) is a measure of the reflectivity of a target (HTI 2011). It is the acoustic size of an object present in decibels (dB) and therefore reflects the actual size of the object in question. Species-specific standardized equations are used to convert dB readings to estimated sizes. For example, Crawford and Jorgenson (1996) suggested the following equation for Arctic cod (*Boreogadus saida*):

$$TS = 21.8 \log L - 72.7 \text{ dB} \tag{4}$$

where TS is Target strength (dB)

L is fish length (m)

For target strength measurements, the 40 log R TVG function is used to completely compensate for loss of the signal because single targets are required for accurate detection (Cotel 1998). Target Strength (TS) can be highly variable depending on the orientation, behaviour, and depth of the fish (Sullivan and Rudstam 2009). Based on density, each target (i.e. species) has characteristic properties of signal transmission which is reflected in the TS (FAO 1981). Primarily, the TS of fish is affected by swimbladder size and shape, state of maturity, and fat content (Horne 2003). Maximum TS occurs when the swim bladder is aligned perpendicular to the primary axis and can diminish greatly the closer it moves parallel to this axis. TS of fish can vary over 30 dB depending on the extent of tilt and roll of the fish (Reeder et al. 2004). When analyzing densities, the mean TS is often taken to reduce the effect of possible outliers in terms of orientation (Sullivan and Rudstam 2009).

The likelihood of detecting echoes from individuals (detection probability), is strongly dependent on TS parameters (i.e., specified threshold values), as well behaviour of the fish (i.e., orientation) (Sullivan and Rudstam 2009). Further, objects located at the edge of the beam will have less detection probability due to interference patterns away from the primary axis. The margins of the water column (i.e. surface and bottom) also present difficulties in detecting echoes. At the surface, the volume of water above the transducer is not included, nor is the near-field distance (Ona and Mitson 1996). “Deadzones” at the bottom make sampling demersal species difficult because the bottom creates a much stronger echo than any fish.

1.6.5. Frequency

The echo sounder has a suite of parameters that require optimal setting for the specific application intended. The frequency at which the transducer sends the signal can be important based on the characteristics of the expected targets. Transducers typically range from 38 kHz to 420 kHz. Higher frequencies have shorter wavelengths and as a result can detect smaller objects but have limited range due to higher absorption. Therefore lower or moderate frequencies are suggested for deep water studies. The ability to separate individuals that are closely aggregated is integral for studying schooling species. Higher frequencies allow for shorter pulse durations which are able to discriminate individuals to a greater extent (Sullivan and Rudstam 2009). TS becomes more variable with the use of higher frequencies because the effects of orientation on detection are more pronounced. Therefore size-class differentiation will be more difficult and detection thresholds may become variable (Sullivan and Rudstam 2009). Nevertheless there is little evidence that the frequency used will provide different absolute values of TS compared to other frequencies (Johannesson and Mitson 1983).

1.6.6. Beam width

A narrow beam increases the detection probability of individual fish because it increases the horizontal resolution (Sullivan and Rudstam 2009). As a result narrow beams reduce the bottom dead zone. In contrast, wider beams sample a larger area but are less likely to separate individual fish close together. Wider beams become parallel more quickly and therefore decrease the near-field zone, but are sensitive to noisy environments (Sullivan and Rudstam 2009). Therefore larger beam widths may be more practical in shallow, quiet waters and where targets are encountered less frequently. Additionally, in terms of logistics, the higher the frequency and larger the beam width, the smaller the physical size of the transducer.

1.6.7. Transducer Configuration

There are four main types of transducer configurations, each providing more information on the target (i.e. TS) than the last. These include single beam, dual beam, split beam, and multi beam. Single beam provides mainly presence or absence information and depth. The location of the target in the beam is not provided as the angle off the primary axis is unknown. Dual beam uses both a narrow and wide beam at the same frequency to determine the target's depth and distance from the primary axis based on the ratio between the two echo levels. Split beam provides a three dimensional output by comparing phase deviations of the returning signal. Since the split beam transducer is divided into four sections, the specific location of the target is obtained. This allows for increased reliability of directivity, TS, and even swimming speed (Arrhenius et al. 2000). Finally, multi beam uses numerous transducers of same frequency each directed at different angles to provide a larger horizontal range (Gerlotto et al. 1999). With this method, the volume of water sampled can be as much as 14 times larger than two dimensional transducers (Gerlotto et al. 1999).

1.6.8. Transducer deployment

There are two major types of mobile survey transducer deployments including towed and attached. Towed transducers are held by a long rope or cable that trails behind the vessel as it moves. To be optimally functional the transducer head should move parallel to the bottom. The transducer is less affected by wave action since it is not rigidly attached to the vessel. This method is also advantageous for detecting demersal species if the transducer is pulled close enough to the bottom where resolution of targets and bathymetry is increased, and noise is reduced (Sullivan and Rudstam 2009).

Transducers can also be attached to the vessel directly via hull mountings or detachable gunnel arrangements. The major limitation of this deployment is that if the vessel pitches or rolls the acoustic beams may not be directed properly. This can be minimized using sensor data technology (Benoit et al. 2008). It is often a favourable arrangement since deployment and removal are typically more efficient especially when mounted to the hull. Transducers can also be deployed sideways (side beam) to sample a larger volume of the horizontal water column. Transducers can even be placed out of water in compartments in the hull that have specialized rubberized diaphragms and oil that allow sound waves to pass. This setup can be very expensive, does not work well in cold water at high frequencies, and can be complicated to calibrate (Fleisher et al. 2002). Additionally, transducers can be deployed in fixed-locations which is useful for studies of extended periods of time or in locations where presence of fish is known or of interest.

1.6.9. Calibration

Prior to conducting field surveys, calibrations are required for the environment being sampled. Specific calibration guides are provided by the manufacturer. Sullivan and Rudstam (2009) offer many of the conditions required for optimal calibration. These include: calibration should be performed in the same environmental conditions as planned for the study; calibration should occur in water with depths large enough to avoid near-field or other limitations; calibration should occur prior to the survey as well as after to ensure conditions have not altered; and many of the settings for the study must be the same during calibration including pulse duration, power, and bandwidth. To calibrate the hydroacoustic system a calibration sphere of known TS (dependent on water temperature and salinity) is suspended by a monofilament line in the beam range of the echo sounder. The speed of sound and acoustic absorption is calculated and used to adjust for the time signals take to reach an object and then return. The sphere must remain stable to calibrate for on-axis sensitivity. TS is calibrated by noting the TS measured in relation to the known TS of the calibration sphere. Similarly the volume backscattering strength in relation to theoretical values should be noted, as well as the area of beam scattering. Data should be collected for 5-10 minutes.

1.6.10. Design of Survey

It is important prior to beginning sampling to have a clear set of objectives (Pollock et al. 2002). Deciding which species, size-classes, and habitats is necessary to know what characteristics to focus on (i.e. TS) (Sullivan and Rudstam 2009). Time of day or year may have important bearing on the outcome of the survey and is something to be cognisant of. It may also be required to catch fish directly in order to ground-truth the TS versus actual size of fish.

Typically there are two types of survey designs: parallel and zig zag transects. Parallel transects consist of equally (or unequally) spaced lines running parallel to each other. This type of design is simple both in implementation and statistical analysis. It also spreads out sampling effort evenly throughout the study area. Zig zag transects consist of consecutively placed ‘w’ shaped lines. This type of design maximizes sampling amount relative to time. The major limitation is that the end and beginning of each consecutive transect is not independent and may overlap based on the spatial scale used. However, if analyzed properly (i.e., geostatistical approach) this design better characterizes small-scale variation (Sullivan and Rudstam 2009). The layout of designs can be stratified to increase sampling of specific areas (i.e., high density areas), randomly distributed to ensure unbiased sampling, or systematic to cover a uniform area. The choice of what design and layout is dependent on the goals of the study in question.

1.6.11. Quantitative Estimation

One of the major goals of hydroacoustic sampling is to obtain estimates of fish abundance and density. Continuing advances in the past decades have made calibration, TS determination, and calculations of propagation losses more reliable (Foote et al. 1987). This has made analysis more efficient and abundance and density estimates more accurate.

When analyzing data, targets are separated into different bins to account for differences in habitat and depth. The bins are usually separated based on vertical and horizontal intervals. For example, vertical bins can be divided into different layers in the water column (i.e. epilimnion, metalimnion, and hypolimnion), and horizontal bins can be segments of the transect or the entire transect. Again the choice of bin delineation is dependent on the objectives of the study.

A potential source of error during analysis is improperly separating echoes of target species from non-target species or background noise (Sullivan and Rudstam 2009). There are several approaches to avoid this and should be considered prior to calculations of abundance or density. First, fish should be caught directly in the study area to ensure the relationship between TS and fish length is appropriate. Second, the appropriate backscatter threshold should be used based on the expected range of target species. For example, fish with swim bladders will have a greater backscatter signal than non-bladder fish and an appropriate TS threshold should be set. It is important to note that the strength of backscatter changes with depth and needs to be calculated for each bin. Finally, targets can be separated by TS directly however should also be analyzed in vertical bins because the sampling volume increases with depth (Sullivan and Rudstam 2009). If analyzed together, demersal species may be misrepresented.

In order to calculate densities and abundance two main assumptions are employed: target species are appropriately separated from non-target objects and noise, and the backscatter cross-section value is acceptable for the species, group, or depth (Sullivan and Rudstam 2009). Backscatter cross section is calculated as follows:

(5) $\sigma_{bs} = 10^{(TS/10)}$

where σ_{bs} is backscattering cross-section (m^2)

TS is target strength (dB)

The density per unit volume can then be calculated:

(6) $P_v = s_v / \sigma_{bs}$

where P_v is density (m^{-3})

s_v is volume backscattering coefficient ($1\ m^{-1}$)

σ_{bs} is backscattering cross-section (m^2)

The density per area can also be calculated:

(7) $P_a = NASC / 4\pi\sigma_{bs}$

where P_a is areal density (m^{-2})

NASC is nautical area scattering coefficient (nmi^{-2})

σ_{bs} is backscattering cross-section (m^2)

Estimates of abundance can be applied to the entire study area or segments (i.e., transects). For systematic or random parallel transects, the average density (8) and variance (9) can be calculated as follows:

$$\overline{\rho} = \frac{1}{n}\sum_{i=1}^{n} \rho_i \quad (8)$$

where $\bar{\rho}$ is the average density

ρ_i is transect i

n is the number of transects

$$s_\rho^2 = \frac{1}{n-1}\sum_{i=1}^{n}(\rho_i - \overline{\rho})^2 \quad (9)$$

where s^2_p is the variance of the average density

$\overline{\rho}$ is the average density (m^{-2})

ρ_i is transect i

n is the number of transects

If we assume transects are independent and representative of the actual population, we can estimate the abundance by the total area studied:

(10) $N = A \times \bar{\rho}$

where N is an estimate of the total population

A is the area surveyed (m^2)

$\bar{\rho}$ is the average density (m^{-2})

1.6.12. Echo integration

When fish aggregate in dense groups, echoes of individual fish are often difficult to measure accurately because signals overlap and scatter. In general, to overcome this limitation echo integration is used (EI). For example, Crawford and Jorgenson (1993) provided a description of EI analysis from BioSonics Inc. Their survey area was divided into 1m deep intervals and grouped into units that were averaged along each 40m of the transect. Each unit at each depth was then averaged for each transect to estimate fish abundance as follows:

(11) $Q_k = M_k V_k / C_e \bar{\sigma}_{bs}$

where Q_k is fish abundance at k^{th} depth stratum

M_k is mean value of EI output at k^{th} depth stratum

V_k is total volume of water at k^{th} depth stratum

C_e is equipment scaling factor

$\bar{\sigma}_{bs}$ is mean value of fish back-scattering cross section

Total abundance is then calculated by summing Q_k for all depths. The EI measurements also use a TVG function of 20 log R to partially compensate due to multiple echoes returning from different objects (Cotel 1998).

1.6.13. Advantages and limitations

Some of the major advantages of conducting hydroacoustic surveys and using hydroacoustic systems include (HTI 2011; Sullivan and Rudstam 2009):

Cost effective – high sampling power (i.e. nearly all water column sampled) in relation to time

Unobtrusive – does not harm or kill study species and may not affect behaviour

Non-selective – mostly unbiased in detecting size, range, and behaviour

Real-time results – can be analyzed as collected

Collection of large amounts of data – improves statistical analysis

The major disadvantages include (HTI 2011; Sullivan and Rudstam 2009):

Collecton of large amounts of data – exhausting to analyze

Lack of definitive species identification – no ability to directly identify species

Fish detection – variability of TS based on orientation, noise level, etc.

Monitoring fish near boundaries – limitations in dead zones (i.e. near surface and bottom)

Initial investment – high initial costs but equipment has long term applicability

Requires training – large personal investment required to properly learn theory and techniques

A primary bias of hydroacoustic surveys is that movements and noise from the vessel can alter fish behaviour (Handegard et al. 2003). Fish may avoid the vessel by moving horizontally or vertically. If this is a common occurrence, data obtained may not be representative of 'natural' behaviour. Additionally, the reliability of detections is less if fish are descending in the water column due to the angle of orientation and change in swim bladder size. Reactions may also be depth-dependent creating skewed data between upper and lower depths (Vabø et al. 2002).

Another major limitation is that measures of target strength and abundance are based on echo detections of individuals (Soule et al. 1997). This can be problematic when fish school in dense aggregations and individual targets are difficult to differentiate (also see *Echo Integration*). In high density aggregations echoes can scatter off multiple individuals before returning to the transducer and targets may block or shadow other targets.

It is clear that many factors contribute to the accuracy and precision of a study. Errors can occur through calibration, weather conditions, hydrographic conditions, and fish behaviour, among others (Rudstam et al. 2008). As mentioned above, errors associated with behaviour and distribution may be most important. Errors can affect the analysis in additive and multiplicative ways and can even be directional (i.e., overestimations). Uncertainties are commonplace in hydroacoustic sampling (Demer 2004). For example, due to the lack of direct species identification, it is common to include non-target species and exclude target species to an extent during analysis. The main goal should be to optimally set parameters based on the survey area to accurately carry out the objectives of the study.

1.6.14. Hydroacoustics applied to Arctic cod

Hydroacoustic techniques have been used to study various components of the biology and ecology of Arctic cod. These studies focus on movements and behaviour, and determining quantitative estimates of density and abundance. Since Arctic cod are not fished commercially in North America, scientific hydroacoustic surveys provide the most informative accounts of their distribution and are integral to understand temporal changes in behaviour and abundance. In the following sections five Canadian studies that used hydroacoustic technology over the past 30 years to study Arctic cod are summarized. The major advances in technology and techniques used are highlighted as well as major findings of the research.

1.6.15. Case study #1

Analysis of Arctic cod movements in the Beaufort Sea nearshore region, 1978-1979 - Moulton and Tarbox (1987)

The purpose of the study was to investigate the distribution and determine the abundance of Arctic cod in a nearshore area in the Beaufort Sea. Trawl sampling was conducted in addition to hydroacoustic sampling, and salinity and temperature were recorded throughout the study period. The main objective of the study was to compare daily and seasonal changes in environmental parameters with those of Arctic cod distribution.

Hydroacoustic surveys were conducted along four transects, each approximately 4km long, with several replications. A Simrad EY-M echo sounder (70 kHz, 0.6 m s^{-1} pulse rate) was used. The transducer was wide angled with an effective beam angle of approximately 30°. The transducer was attached to a beam of wood and pulled just below the surface, while projecting forwards (to reduce fish avoidance). When not running transects, the transducer was installed for fixed-location sampling (attached to a float just below the surface). Echoes from targets were printed with references to depth and time (i.e., echogram) for analysis. Echo counts and amplitude of detections were viewed via an oscilloscope. The amplitude was used in calculations of TS. The number of fish calculated was determined using a mean TS of -50 dB (~10 cm fish). Any values larger than -60 dB were counted. Densities were calculated by dividing the total number of fish by the volume sampled.

Arctic cod consisted of 98% of trawl catches and based on the size of fish caught, the authors reported they made up the majority of targets in the echograms. Abundance changed seasonally and targets were typically found near the bottom. Based on trawl catches, acoustic sampling, and salinity and temperature profiles, the authors conclude that Arctic cod associate with shallow transition layers (where temperature and salinity form distinct layers) where food is concentrated.

This study was conducted several decades ago and limitations in the analysis are evident. First, the study area is considerably shallow with fish aggregating near the surface and bottom. There is no mention of dead zones (both at the surface and bottom) which will reduce the ability to accurately detect species. Second, although Arctic cod was the primary species caught it is possible that other species are more efficient at escaping trawl nets and were underrepresented in the echograms. Inevitably, many of the targets detected are likely other species than Arctic cod. Third, Rudstam et al. (2008) reported that using echo intensity (as opposed to amplitude) is a more reliable method to calculating TS. Finally, and most importantly, the methods used to calculate density are outdated and not necessarily accurate. With only a single beam transducer configuration, no size information is possible and densities are estimated using a theoretical value of TS averaged across all detections. Nevertheless, some of the methods used were advantageous to the particulars of the study. For example, directing the transducer horizontal and in front of the boat likely reduced fish avoidance and also decreased the volume of dead zones. The wide beam width used is also applicable since detections were relatively sparse, the water was shallow, and the vessel used was small enough as to not create excessive amounts of noise.

1.6.16. Case study #2

Density distribution of fish in the presence of whales at the Admiralty Inlet landfast ice edge - Crawford and Jorgenson (1990)

The purpose of the study was to use hydroacoustic techniques to investigate the affinity between Arctic cod and the undersurface of landfast ice in an area that is commonly used by whales. Since most studies examining this relationship have been limited (i.e., SCUBA), the authors used more thorough methods to explore the distribution of fish, as well as zooplankton under ice.

A fixed 200 kHz system was used with the transducer placed through a whole in ice and either directed vertically into the water column or parallel to the ice undersurface. Digital recording equipment and high resolution graphic chart recorders were used to examine echoes. Several sites were visited and both horizontal and vertical sampling was carried out for 20 and 60 minutes, respectively. Occasionally the threshold of detections was increased to account for zooplankton. A dual beam setup was used in June 1986, while a single beam was used in June 1988.

The authors reported that no detections were made in 1986, while several slow moving fish were detected in four general layers in 1988. Higher densities were recorded just below the ice surface and zooplankton was primarily detected throughout depths less than 100m. The authors conclude that the distribution of fish under sea ice is influenced by the distribution of zooplankton.

Despite the informative description of techniques and analysis, the application of technology was limited, and in reality the study provided limited information and weak conclusions. First, interference caused by the undersurface of ice during horizontal transmissions was unreliable. This caused ranges to be reduced at certain times and limited the ability to compare detections between sampling sites. Some instances the interference was so great that horizontal observations were aborted. Second, depths up to 6m under the ice were likely deadzones and could not theoretically provide accurate detections. Since Arctic cod are commonly reported to be associated directly with ice, this provides considerable restrictions for comparing the link between sea-ice and cod. Third, sampling time was considerably short. This can be a major problem with the study of hydroacoustics because data is time-consuming to analyze. Therefore many studies only sample for a very short time which ultimately reduces the ability to get a time-integrated view of dynamic systems. Fourth, the single beam transducer was the only system that actually detected any fish. Unfortunately, a single beam is considerably limiting and target strength cannot be calculated accurately. Therefore information about the detections is often unreliable. Without TS, the size of fish and confident species identification is almost impossible. This is not as limiting in areas where only one species is expected to be present (i.e., High Arctic), however in regions where several pelagic species are present, species-specific conclusions would be biased. Despite the lack of TS, the authors interpolated densities based on the surface area and volume of the study area. These values are only rough estimates however and should be treated cautiously.

Although clear limitations exist, the authors used thorough methods maximizing the information that could be gained. For example, the authors worked closely with suppliers to correct for volumetric differences with depth. Additionally, the authors crafted a device to lower the transducer to depths which they could not detect from the surface. Innovations such as this, not only allow for novel application of current technologies but lead to improved technologies.

1.6.17. Case study #3

Schooling behaviour of arctic cod, Boreogadus saida, in relation to drifting pack ice - Crawford and Jorgenson (1993)

The objective of the study was to relate Arctic cod schooling behaviour in a small bay during the summer and associate it with the presence of drifting ice. The purpose was to explore the role ice plays as a means of protection from predators.

A dual beam 200 kHz system was used during six days of sampling in which zig zag transects were completed in Resolute Bay, Nunavut. The speed of the vessel was kept constant at approximately 7 km h^{-1} and ice was avoided to reduce the effect of external noise. The authors provide a list of system specifications. A ping pong ball was used to calibrate the system at -41.5 dB and a threshold of -63 dB was set. This threshold ignored targets smaller than 2.8 cm long. Data from TS and backscattering cross section was analyzed using EI to estimate abundance of schools. Biomass was then calculated by multiplying abundance with the mean size of acoustically detected fish. EI-derived contour plots of abundance were superimposed on maps of Resolute which allowed the authors to estimate the surface density (fish m^{-2}) and volume density (fish m^{-3}). The authors also derived the size of fish based on the TS of positive detections of individuals using Equation (4) and scaled appropriately using trawl catch data.

The authors reported that the largest density of fish were found when ice was absent in Resolute Bay. Their hypothesis was that Arctic cod school more tightly as an avoidance reaction, but when ice was present they were less packed because ice provided necessary protection from predators.

Although limitations do exist (i.e., dead zone near surface and small sampling period) the applicability of hydroacoustics for this type of study is clear. It also shows the progression of technology and techniques compared to the previous studies. Extensive calibration, ground-truthing, TS analysis, and EI analysis all add to increase the usefulness of hydroacoustics to study fish populations. The main limitation of the study was that the undersurface of the ice was not directly sampled. Alternatively, a side-mounted beam could have been used however the interference of signals with the undersurface of ice is problematic.

1.6.18. Case study #4

Quantitative studies of Arctic Cod (Boreogadus saida) schools: important energy stores in the Arctic Food Web - Crawford and Jorgenson (1996)

The purpose of this study was to report on large schools of Arctic cod in the Lancaster Sound Region in the Canadian High Arctic using hydroacoustic techniques. Additionally, the occurrence of schools was related to water temperature and the size of schooling and non-schooling cod was examined.

The same system as described by Crawford and Jorgenson et al. (1993) was used and similarly calibrated. The transducer was attached directly to the vessel and towed at approximately 8 km hr^{-1} at a depth of 1.5 m. During sampling, echoes were stored on magnetic tape for future analysis. Both parallel and zig zag transects were followed. Several embayments were studied including Allen Bay, Resolute Bay, Radstock Bay, Erebus Bay, and Gascoyne Inlet. EI was used to determine abundance, density and biomass as previously described. The authors thoroughly examined the relationship between fish size and TS using trawl catches and analyzing echoes from targets detected near the edge of schools.

The authors found very large assemblages of fish in the two years of study. For example two schools were estimated to contain a total of 900 million fish and consisted of a biomass over 30 000 tonnes. Fish detected at the edges of schools were considerably larger than non-schooling fish. Finally, the vertical distribution of fish varied locally. For example, cod around Cornwallis Island were found throughout the water column (>-1.3°C) and cod near Devon Island were only found in shallower (<35 m) and warmer water (>2.0°C).

The authors recognize many of the limitations with the equipment. For example, dense aggregations cause attenuation of the signal and as a result deeper fish reflect less energy. This inconsistency is termed the shadow effect and can occur when densities are as little as 100 fish$\cdot$m^{-2} (Toresen 1991). This can be problematic since the density in the present study was at times >8000 fish m^{-2}. Additionally, the higher frequency used exacerbates the effects of shadowing (Foote 1984). EI analysis is only applicable when fish density and echo intensity have a linear relationship. This does not occur when schools are very dense and as a result densities could be underestimated by as much as 50%. To reduce this bias, EI analysis was only used on individual fish that were detected at the edges of schools. Vessel avoidance may have also altered behaviour among sampling locations and caused errors in estimates due to changes in orientation and tilt (Olsen 1990). Despite these limitations, the values presented were best estimates possible.

1.6.19. Case study #5

From polar night to midnight sun: photoperiod, seal predation, and the diel vertical migrations of polar cod (Boreogadus saida) under landfast ice in the Arctic Ocean - Benoit et al. (2010)

This study examined the vertical migration of Arctic cod during the winter and spring in the Beaufort Sea. The diel movements were compared with water temperatures and the distribution of zooplankton. Much of the data analysed in this study was based from Benoit et al. (2008), which focussed on the abundance and density of Arctic cod in deep (>230m) waters.

A multi-frequency split beam echo sounder was used aboard a large research vessel. All transducers were hull mounted - two were mounted in oil-filled wells (38 and 128 kHz) and one mounted in contact with water (200kHz). The acoustic signal was continuously transmitted at a ping interval of 2 or 3 seconds. This time series was subsampled in pools of 1 hour every two days. Cells for EI analysis were 2 or 3 minutes horizontally, and 3 m deep. TVG was adjusted for each frequency beam and the TS threshold was set to -90 dB. To estimate biomass, a conversion factor was used based on TS and mean weight of fish caught during trawls. Because schools were densely aggregated, *In situ* TS analysis was not used. Instead Equation (4) was used and converted accordingly to obtain fish density.

The authors found large aggregations of cod during the day in the deep inverse thermocline (160-230m; -1.0 to 0°C). During the night, larger cod remained in deep water while smaller cod were detected closer to the surface (i.e., <100 m). The authors suggest that larger cod possess sufficient energetic reserves to stay in colder waters at night and thus avoid seal predation.

The progression of technology over the last decade is clear. Many limitations from previous research were not cause for concern. For example, vessel avoidance was not a factor as the boat was lodged in landfast ice. Special sensors were used to mute interfering sounds that came from the vessel or other equipment. The use of split beam increases information about the location and angle of detections and in combination with multiple frequency beams, the specific requirements of the study were met. For example, during analysis the authors use the 38 kHz transducer because they are studying fish at great depths. The higher frequency transducers would therefore be less reliable because absorption to the environment is greater at depths. Despite these advances, the limitation of analyzing fish in dense schools still remains. The need to use Crawford and Jorgenson's (1993) possibly unreliable size equation provides an indicator of such limitations.

1.6.20. Conclusion

Difficulties and limitations associated with hydroacoustic studies exist and it is important for researchers to be aware of them. Nevertheless, the use of hydroacoustics benefits the study of fish populations, especially Arctic cod. Determining important biological and ecological characteristics of fish including habitat, distribution, density, and abundance are possible. With these discoveries the application of hydroacoustics becomes more comprehensive. The strengths of hydroacoustics allow for a wide range of animal detection increasing the diversity of parameters we are capable of examining. It even allows for the detection of physical properties in the water column, such as temperature transition layers. Compared to conventional sampling (i.e. trawling), hydroacoustics offers increased sampling volume and resolution, among other benefits (MacLennan and Simmonds 1992). Research in the Canadian Arctic has focussed on the behaviour of cod in relation to size, age, depth, density, temperature, salinity, time of day, and presence of ice, prey and predators. By associating schools (e.g., via density or depth) with presence of predators or feeding events, a greater knowledge of foraging behaviour is gained. Additionally, knowing where fish commonly aggregate provides useful information about potential foraging hotspots. It is evident that the applicability of hydroacoustics is wide-ranging.

Table 1.1: Life history parameters of marine mammals in the Arctic

	Beluga **(*Delphinapterus leucas*)**[1]	**Narwhal** **(*Monodon monoceros*)**[1]	**Ringed seal** **(*Pusa hispida*)**[2]
Size Range	Adult males: 3.65-4.25m Adult females: 3.05-3.65m Newborn: ~1.5m	Adult males: ~4.7m Adult females: ~4.0m Newborn: ~1.6m	Adults: ~1.3m Newborn: ~0.65m
Age at maturity	Males: 8 years Females: 5 years	Males: 8 years Females: 6 years	5-7 years
Time of mating	April-May	April-May	April-May
Gestation time	14 months	14 months	10-11 months
Time of birth	June-August	June-August	March-April
Nursing period	18 months	20 months	5-7 weeks

[1]DFO (2011); [2]Smith 1987, McLaren 1993, Marinebio (2011)

Chapter 2: The biology and foraging ecology of Arctic cod in Allen Bay, Canada

Abstract:

Understanding how foraging habitat, prey selection, and energy allocation change seasonally is important for ecologically significant species because they influence food web structure. Arctic cod (*Boreogadus saida*) is a schooling fish that provides a critical link between lower and upper trophic levels in the Arctic. Here, I examined diet and habitat of four Arctic cod size-classes using stomach content analysis, and stable isotope ratios of liver and muscle. Stable isotope analysis compliments stomach content analysis because it indicates prey sources or habitat (i.e., <1‰ δ^{13}C enrichment between predator and prey) and prey items (i.e., ~3.4‰ δ^{15}N enrichment between predator and prey). Further, since the isotopic turnover is influenced by metabolic activity, greater temporal trends can be elucidated using various tissues. Dietary and isotopic niche overlap were calculated using Schoener's index and a Bayesian multivariate approach, respectively. Additionally, the interrelationship among growth, energy storage, and gonadal development was examined to investigate energy allocation associated with foraging. The main findings show that foraging at time of capture reflected sympagic and epi-benthic habitats whereas pelagic prey was more important prior to summer. Further, juveniles separated strongly based on isotopes, while large adults showed the most separation based on diet, suggesting size-related seasonal diet shifts. The combination of numerous empty stomachs and small livers supports speculation that Arctic cod schooling is energetically demanding.

2.1. Introduction

Arctic cod (*Boreogadus* saida) is a critical link structuring energetic pathways throughout the Arctic ecosystem (Bain and Sekerak 1978; Welch et al. 1992). Understanding its role in an ecological context is essential because it is responsible for transferring the majority energy from lower trophic levels to top predators such as seabirds, seals, and whales (Bradstreet et al. 1986; Welch et al. 1992). Arctic cod, as generalist feeders (Walkusz et al. 2011; Renaud et al. 2012), consume a variety of organisms at lower trophic levels and have strong potential to be indicators of the invertebrate community. As prey, Arctic cod distribution affects the movement and distribution of predators (Chapter 5; Gradinger and Bluhm 2008), which directly impacts habitat-use, predator migration patterns, and seasonal concentrations of multi-species predator complexes.

Arctic cod has a Holarctic distribution, occupies demersal, pelagic, and sympagic habitats (Gradinger and Bluhm 2004; Crawford et al. 2012), and often aggregates in abundant and dense shoals (Benoit et al. 2008). The life history of Arctic cod is typified by early maturity, small body size, and short-life span, which is conducive to living in an environment where high mortalities occur (Craig et al. 1982). Like other Arctic fish, fat is stored as triglycerides in the liver for buoyancy and as energy reserves (Hop et al. 1995). Male gonad development for spawning begins in August while female spawning condition is reached by December (Graham and Hop 1995). Spawning occurs in winter between December and March (Bain and Sekerak 1978; Craig et al. 1982). Growth is slow and seasonal, basal metabolism is low, and growth and assimilation efficiencies are high (i.e., efficient energy converters) (Hop et al. 1997b). Information on the general biology of Arctic cod is limited and the interrelationship between growth, energy storage, and gonadal development is not well understood.

Stomach content analysis has been used to describe diets and foraging behaviour of Arctic cod. Prey selection is size-dependent with calanoid copepods and amphipods as the most common food items (Bradstreet and Cross 1982; Walkusz et al. 2011). Prey are typically ice-associated (e.g., gammarid amphipods; Bradstreet and Cross 1982) but during the open water season pelagic crustaceans are also common (e.g., calanoid copepods and hyperiid amphipods; Renaud et al. 2012). Stable isotopes are increasingly used in ecology to study diet and food web interactions as they reflect diet assimilation and are not hindered by biases associated with stomach content analysis (Hobson et al. 1996). Commonly δ^{13}C and δ^{15}N are used because they indicate prey sources (i.e., <1‰ enrichment between predator and prey; Michener and Schell 1994) and prey items (i.e., ~3.4‰ enrichment between predator and prey; Minigawa and Wada 1984), respectively. Further, since the isotopic turnover is influenced by metabolic activity (Tieszen et al. 1983; Kurle and Worthy 2002), temporal trends can be elucidated. For example, the turnover of stable isotope signal is higher in the metabolically active liver and represents more recent food intake compared to muscle due to tissue-specific fractionation (Hobson and Clark 1992). Multiple temporal indicators of diet are important because seasonal availability of resources often leads to diet switching in the Arctic (Sakshaug 2004; Kaufman et al. 2008).

Ontogenetic niche shifts (i.e., changes in resource use with body size or age) are common in animals and affect how different resources are exploited from the same population or habitat (Werner and Hall 1988; Hammerschlag-Peyer et al. 2011). Hobson et al. (2002) cautioned against pooling within species due to ontogenetic changes and suggested more detailed species-specific analyses could greatly improve understanding of the Arctic marine food web. To our knowledge, no study has segregated prey selection of Arctic cod based on size of individuals (and size of prey) to directly explore intra-specific dietary overlap. Similarly, no study has supplemented stomach content data with stable isotopes to provide a timeline of feeding, habitat, and intra-specific isotopic niche overlap.

As the Arctic continues to face significant environmental changes, it is important to compare the current ecological niche and biology of Arctic cod with the past to prepare for future trends. Considering the importance of this species, these types of investigations are essential to further knowledge of local Arctic food webs and the impacts of a changing environment. The purpose of this study was to examine the general biology and feeding habits of Arctic cod in the Canadian High Arctic through the open water period. Specifically, the objectives were to: 1) describe growth and energetic partitioning in tissues (i.e., liver and gonads), 2) determine the dietary overlap between Arctic cod size classes, 3) investigate temporal isotopic differences (i.e., liver and muscle) as reflection of diet and habitat, and 4) compare diet and biology of Arctic cod captured from the same local area over the last three decades (i.e., Bain and Sekerak 1978; Hop et al. 1997a).

2.2. Materials and Methods

Study area

Arctic cod were collected from Allen Bay, Cornwallis Island (74°43'36.78''N 95°09'25.23''W; See Chapter 3, 4, and 5 for maps) between July and August 2010. Allen Bay is a shallow area (rarely >30m deep) located near the community of Resolute Bay and is an important area for subsistence hunting.

Sample collection

Arctic cod were collected using gillnets and seine nets. Gillnets were mostly set near-bottom (28 sets total; 29 Jul – 25 Aug; n=207 cod collected) in water <25m deep and seine nets (29 sets total; 25 – 29 Jul; n=175 cod collected) were deployed along the shore in water <2m deep. Arctic cod aged ≥2+ years were captured by gillnets and all 1+ cod were captured by seine nets. These fish were frozen after collection until further analysis. Additionally, 19 larval cod were collected along the shore by hand and preserved in 5% buffered formalin (with seawater).

General biology

Individuals were thawed, weighed (wet weight, 0.01g) and measured (fork length, mm). Total length of larval cod is presented after correcting for shrinkage due to preservation in formalin (i.e., 4.1% shrinkage; Fox 1996). The relationship between weight and length was fitted with a power regression and further explored using Fulton's condition factor: $CF = (TW \cdot 10^5)/FL^3$, where TW and FL are total weight and fork length, respectively. Liver and gonads were removed and weighed to obtain hepatosomatic (HSI) and gonadosomatic (GSI) indices, respectively using the following: $GSI\ (\text{or } HSI) = GW\ (\text{or } LW)/TW \cdot 100$, where GW and LW represent gonad weight and liver weight. Differences between female and male GSI, HSI, size, and CF were determined by a Student's t-test. Sagittal otoliths were removed, cleaned, dried, weighed, and measured to allow size extrapolations for future studies. Otolith length was defined as the longest dimension between the posterior and anterior edges of the otolith (Hunt 1992). Otoliths were broken to provide a cross section at the nucleus, burned, and annual rings counted (Chilton and Beamish 1982). A von Bertalanffy model was used to describe the age-growth relationship:

$$(12) \quad FL_t = A \cdot 1 - e^{-K(t)}$$

where FL_t represents fork length at age t, A is asymptotic length, and K is the rate of exponential growth decay.

Stomach content analysis

The wet weight (0.001g) of stomach contents was taken and diet items examined immediately or stored in 70% ethanol for later examination. Diet items were measured and divided into 5 groups based on total length (<1mm, 1-3mm, 3-5mm, 5-10mm, 10+mm) to determine prey-size selection. Arctic cod were divided into length size-classes: size class 1 consisted of 1+ individuals (56-93mm, n=50); class 2 (123-159mm, n=13); class 3 (160-184mm, n=13; and class 4 (185-256mm, n=12). The minimum sample size for each size-class was selected based on $n \geq 10$ being adequate to differentiate diet overlap among salmonids (Vinson and Budy 2011). Frequency of occurrence (FO_i), percent composition (N_i), and weight contribution (P_i) of prey were used to examine diet among Arctic cod size classes.

$$(13) \quad FO_i\ (\%) = (S_i/S_t) \times 100$$

where S_i represents the number of Arctic cod with prey type i, and S_t represents the total number of Arctic cod.

(14) $N_i (\%) = (n_i/n_t) \times 100$

where n_i represents the total number of prey type i, and n_t represents the total number of prey. The average weight of individual prey was determined by dividing the weight of stomach contents with only one size range by the number of individuals. The weight contribution (P_i) from each prey size class was then determined by multiplying each average weight by the percent composition of prey. Diet overlap between Arctic cod size classes was calculated using Schoener's index (SI):

(15) $SI = 1 - 0.5 \cdot (\sum |N_{xi} - N_{yi}|)$

where N_{xi} and N_{yi} are the proportions of prey size class i in the stomach of Arctic cod size class x and y, respectively (Schoener 1970). Index values range between 0 (no overlap) and 1 (complete overlap), and values ≥ 0.60 are generally considered to be biologically significant (Zaret and Rand 1971). Using the same approach as the prey-size selection analyses described above, prey items were also examined based on major taxonomic groups.

The presence of internal and external parasites (mainly nematodes and trematodes) was noted during necropsies as an additional tool to assess trophic structure (cf. Gallagher and Dick 2010).

Stable isotope analysis

Between 400 and 600 µg of liver and muscle tissue from individual cod was dried at 70°C for 48 hours and analyzed at the Great Lakes Institute for Environmental Research at the University of Windsor, Canada for stable isotope analysis. Tissues were crushed and grounded using a ball mill grinder (SPEX CertiPrep 8000-D ball milling unit, SPEX CertiPrep, Metuchen, NJ, USA). Lipids were removed using a 5 ml 2:1 chloroform:methanol solvent, and afterwards vortexed for 30 s, left for 24 h, and then decanted for gravimetric determination of lipids (Post et al. 2007). The procedure was repeated and remaining solvents were dried from the tissue by placing samples in a fume hood for an additional 24 hours. Tissue was weighed into tin capsules and carbon and nitrogen stable isotopes were determined using a continuous flow isotope ration mass spectrometer (IRMS, Finnigan MAT Delta^{plus}, Thermo Finnigan, San Jose, CA, USA). The standard reference material was Pee Dee Belemnite carbonate for CO_2 and atmospheric Nitrogen for N_2. Every 12th sample was run in triplicate to assess precision where the standard deviation of $\delta^{13}C$ and $\delta^{15}N$ was generally <0.1‰ and <0.2‰, respectively. Further, lab and National Institute of Standards and Technology (NIST) standards were analyzed every 12 samples for quantification of samples. The analytical precision (standard deviation) for NIST standard 8414 (bovine muscle, n=29) and an internal lab standard (tilapia muscle, n=29) for $\delta^{13}C$ was 0.03 and 0.06, respectively, and for $\delta^{15}N$ was 0.14 and 0.22, respectively. The NIST standards (sucrose and ammonia sulphate, n=3) were within 0.01‰ and 0.07‰ of certified values for $\delta^{15}N$ and $\delta^{13}C$. Stable isotope ratio values are expressed in parts per thousand (‰) using δ notation as calculated using the following equation:

$$(1) \qquad \delta X = [(R_{Sample}/R_{standard})-1] \times 1,000$$

where X is ^{15}N or ^{13}C, R_{sample} is the ratio ($^{15}N/^{14}N$ or $^{13}C/^{12}C$) in the sample, and $R_{standard}$ is the ratio in the standard. Isotope ratios were also determined for the following prey items: *Onisimus* sp. (n=11), *Gammarus* sp. (n=7), *Themisto* sp. (n=1), and copepods (n=2 pooled from >100 harpacticoids and cyclopoids).

The relationship between size, sex, and $\delta^{15}N$ and $\delta^{13}C$ values (for liver and muscle) was investigated using a generalized linear model (GLM). Mean liver and muscle $\delta^{15}N$ and $\delta^{13}C$ values were plotted for each Arctic cod size class. Differences between groups were considered significant if their 95% confidence intervals (CIs) did not overlap (Payton et al. 2003). This method is a conservative approach but provided a simple visual way for detecting differences and exploratory analyses of variance (ANOVAs) produced the same results. Further, we determined isotopic niche overlap using the R package SIAR (Parnell et al. 2010), following Jackson et al. (2011). This Bayesian multivariate approach generates convex hulls encompassing isotope values for all individuals in a group (i.e., size class), as well as standard ellipses which represent 'typical' niche width of members in a population (Jackson et al. 2011, Layman and Allgeier 2012). The area of standard ellipses (SEA_B) (bivariate equivalents to univariate standard deviations) was obtained to calculate niche overlap between size classes. To minimize bias associated with sample sizes among classes, corrected SEA_B values were used (Jackson et al. 2011). Niche overlap is presented as the percentage of the SEA_B of a size class that is encompassed by another size class.

Isotopic discrimination factors ($\Delta^{13}C$ and $\Delta^{15}N$) measure trophic enrichment between predator and prey. Size-specific values were calculated based on equations from Sherwood and Rose (2005) as follows, using $\delta^{15}N$ as an example:

$$(16) \quad \Delta^{15}N = \delta\,^{15}N_{size} - \sum (P_i \cdot \delta\,^{15}N_i)$$

where $\delta\,^{15}N_{size}$ represents the mean $\delta^{15}N$ of an Arctic cod size class, P_i is the weight contribution (as a ratio) of the *i*th prey compared to all prey items, and $\delta\,^{15}N_i$ is the mean $\delta^{15}N$ of prey *i*.

All statistical analyses (except isotopic niche overlap) were run in SAS 9.2 and results were considered significant when $P<0.05$.

2.3. Results

General biology

Arctic cod between the ages of 0+ and 5+ ranged in fork length and wet weight from 10-273mm and 0.1-102.1g, respectively (Table 2). Weight (n=322, $TW=1.72E\text{-}05x^{2.8}$, $R^2=0.96$) and age (n=327, $FL_t = 226.95 \cdot 1 - e^{-0.43t}$, $R^2=0.92$) fit strongly with length (Fig. 1a, b). The age distribution from gillnet catches was mostly 3+ (32%) and 4+ (51%) with similar frequencies of male and females (Fig. 2). A significant linear relationship existed between fork length and otolith length (n=251, FL=24.20x – 4.29, $R^2=0.91$, $P<0.01$), and fork length and otolith weight (n=202, FL=3250.20x + 76.31, $R^2=0.93$, $P<0.01$).

GSI was significantly higher in males (one-tail t-test, df=195, t =-5.47, $P<0.01$), and HSI (one-tail t-test, df=196, t =4.14, $P<0.01$) was higher in females (Table 3). Gonad development throughout the study period did not change for female GSI (n=104, $R^2<0.01$, P=0.42) but male GSI increased (n=93, $R^2=0.23$, $P<0.01$) (Fig. 3a, b). HSI decreased significantly for both females (n=105, $R^2=0.19$, $P<0.01$) and males (n=93, $R^2=0.07$, P=0.01) (Fig. 3c, d). Condition factor was not different between males and females (two tailed t-test, df=197, t=1.25, P=0.21) (Table 3), and showed no significant change over time (female: n=105, R^2=0.02, P=0.20; male: n=94, R^2=0.03, P=0.12). Finally, the size of males and females was not different (two tailed t-test, df=202, t=1.73, P=0.09) (Table 3).

Stomach content analysis

Stomach analysis of Arctic cod ≥2+ found that 42.3% (n=196) had food. Of these, diet items of 38 individuals were analyzed. A total of 50 stomachs from Arctic cod aged 1+ were also examined, 47 containing food. There was a strong size-dependent relationship where smaller Arctic cod consumed smaller prey such as copepods and larger individuals consumed larger prey such as amphipods (Tables 4, 5). Prey <3mm consisted almost exclusively (>95%) of harpacticoid and cyclopoid copepods, and nauplii (barnacle and copepod), while prey >3mm were predominantly hyperiid or gammarid amphipods. Schoener's index based on percent composition of prey sizes showed that the diet of size classes 1, 2, and 3 overlapped but size class 4 did not overlap with any other (Table 6). There was no significant overlap among the cod size classes when prey items were compared (Table 6).

Three groups of parasites were identified. Endohelminthes comprised encysted nematodes within the mesentery and on organs in the body cavity in ~50% of individuals ≥2+. Trematodes were present in the stomach, caecae, or intestinal tract in ~65% of adults and ~80% of juveniles. Finally, parasitic copepods were collected from the gills on 2 occasions (~2% of individuals). We found no significant relationship between trematode infection rate and size of Arctic cod (linear regression, n=115, R^2<0.01, P=0.71).

Stable Isotope Analysis

The GLM analyses showed that size ($F_{1, 100}$=9.84, P<0.01) and sex ($F_{1, 100}$=156.28, P<0.01) were significant predictors of δ^{15}N in liver, but in muscle it was only size ($F_{1, 103}$=8.32, P<0.01). δ^{13}C values in muscle were significantly correlated with cod size ($F_{1, 104}$=6.00, P<0.01). There were no interaction effects in the above analyses. Arctic cod δ^{15}N showed a strong positive relationship with length where muscle tissue (n=149, δ^{15}N =1.5e^{-02}x + 12.6, R^2=0.71, P<0.01) was higher (i.e., enriched) than liver tissue (n= 121, δ^{15}N =1.5e^{-02}x + 11.5, R^2=0.43, P<0.01) (Fig. 4a). By contrast, δ^{13}C values decreased slightly (i.e., became depleted/more negative) as length increased, with muscle (n=149, δ^{13}C =-1.4e^{-03}x – 20.6, R^2<0.01, P=0.48) typically higher than liver (n=121, δ^{13}C =-1.0e^{-03}x – 20.1, R^2=0.02, P=0.14). Variation in liver was high (Fig. 4b).

Examination of liver and muscle showed that juvenile cod (i.e., 1+ year) had significantly lower δ^{15}N than older cod (i.e., non-overlapping CIs; Fig 5.). There was a positive correlation between size classes and δ^{15}N values but it was not always significant (Fig. 5). Liver δ^{13}C values for all size classes were similar (i.e., overlapping CIs) and were typically lower than muscle values (Fig. 5). The isotopic niche overlap analyses revealed that size class 1 shared no overlap with any other size class (Fig. 6). For liver, size class 2 shared 48% and 38% overlap with size class 3 and 4, respectively, and size class 3 had 86% overlap with size class 4 (Fig. 6a). For muscle, size class 2 encompassed 80% and 35% overlap of size class 3 and 4, respectively, and size class 3 shared 51% overlap with size class 4 (Fig. 6b).

Using the isotopic composition of prey items collected from stomachs (Fig. 5) and their contribution to the diet, isotopic discrimination factors were calculated. A summary of δ^{15}N, δ^{13}C, Δ^{15}N, and Δ^{13}C for liver and muscle from each size class are presented in Table 7).

2.4. Discussion

General biology

Arctic cod reached a maximum age of 5 years, and the most abundant age classes were 3+ and 4+ which is consistent with previous work in Allen Bay (Table 8). Arctic cod are reported to reach 7 years old but occurrence of this is rare (Bradstreet et al. 1986). There was appreciable overlap in size among age classes likely because growth is influenced by several factors including feeding (Jensen et al. 1991), season (Craig et al. 1982), temperature (Hop and Graham 1995), and hatching date (Bouchard and Fortier 2011). The length at age was typically higher in our study compared to Bain and Sekerak (1978) and Hop et al. (1997a) however this difference became less pronounced at 4+ and above. The exponent of growth for weight-length relationships, in our case 2.78, supports Bain and Sekerak (1978) that cod follow negative allometric growth during the summer where weight<length^3. Since growth varies regionally (Bradstreet et al. 1986), our otolith regressions provide important reference for future studies in the Canadian High Arctic, particularly those examining predator interactions with cod (e.g., diet reconstruction). The ratio between males and females was similar which differs from most studies (Table 8). For example, Craig et al. (1982) reported that females accounted for 74% of Arctic cod aged 3-6 years from the Beaufort Sea. The difference has been suggested to be due to higher mortality in males throughout the summer (Bain and Sekerak 1978).

GSI showed that male gonads were heavier than females' and were showing spawning condition. This supports previous studies that male gonads begin development in late summer and female gonads develop closer to winter (Hop et al. 1995). The GSI values in this study follow Bain and Sekerak (1978) and Hop et al. (1997a) (Table 8), suggesting that long-term environmental changes (e.g., reduced ice-cover) have not significantly impacted gonadal development at least at its earlier stages. Nahrgang et al. (2010) found an increase in HSI and condition factor from April to September in Svalbard reflecting increased transfer of lipids through the food web. Our sampling period was shorter but showed no change in condition factor and a decrease in HSI. The decrease in liver weight for both males and females suggest that energy is increasingly being mobilized from lipid stores in the liver (Nahrgang et al. 2010). Bain and Sekerak (1978) hypothesized that liver may provide energy for gonadal development and predicted that a decrease in liver weight would coincide with an increase in gonad weight. Hop et al. (1995) found preliminary evidence for this in laboratory-reared Arctic cod, estimating that 40% of energy lost from liver (and muscle to a lesser extent) was incorporated into the gonads in ripe females. Our data supports this relationship for males but was more tenuous for females since gonads remained under-developed. Alternatively, the stomachs of approximately 58% of adult cod in our study were empty, suggesting they were primarily schooling individuals (cf. Hop et al. 1997a) and therefore may be utilizing energy stores in response to low food availability or high competition. HSI values were over two times lower than those calculated by Bain and Sekerak (1978) (Table 8) who found that only ~8% of stomachs were empty, further supporting this hypothesis.

Stomach content analysis

Copepods and amphipods are clearly the major diet items of Arctic cod throughout its distribution (see Table 5 in Renaud et al. 2012). The primary copepods consumed are calanoids which tend to be planktonic/pelagic (Hobson et al. 2002a). Interestingly, in our study, only one calanoid was identified from stomachs despite being present in several zooplankton tows. Harpacticoid and cyclopoid copepods are rarely documented and never to the extent that we observed. Many harpacticoids and cyclopoids possess suitable mouth parts and appendages for grasping and holding prey, and are especially equipped to remove food from surfaces (Grainger 1991). As a result, they are rarely found in the water column, and are mainly epi-benthic and ice-associated (Grainger 1991). Arctic cod feed on ice-adapted organisms (Lønne and Gulliksen 1989) and inhabit demersal layers in both offshore (Geoffroy et al. 2011) and inshore (Chapter 5) waters. Therefore selection of harpacticoids and cyclopoids may be related to habitat preference. Further, other main prey items such as *Onisimus* sp. and *Gammarus* sp. also form strong associations with benthic and ice habitats supporting habitat-specific prey selection. Alternatively, harpacticoid and cyclopoid copepods may have been important due to an absence of calanoids in the water column. Zooplankton tows (Aug 10, 11, and 19) using a Wisconsin plankton net with 153um mesh and 5 inch opening, revealed that calanoids were the primary organisms in the water column however many tows were empty (35/46) and only a few individuals were collected per tow. Further research is needed to validate these hypotheses using more regimented zooplankton sampling from benthic and ice habitats. The variety of prey consumed and lack of dietary overlap (based on prey items) support that cod are generalist feeders and that diet mirrors local heterogeneity (Lønne and Gulliksen 1989).

Size-dependent prey selection was evident among Arctic cod size classes. Size class 1 and 2 primarily consumed prey <3mm (e.g., copepods and nauplii) and as cod reached size class 3 they shifted towards larger prey such as amphipods. The diet of size class 4 did not significantly overlap with any others as prey >5mm made up the majority of the diet. These findings strongly support other studies where prey size was examined. For example, the mean lengths of ingested copepods and amphipods were significantly correlated with the length of offshore and inshore Arctic cod, respectively near Pond Inlet, Nunavut (Bradstreet and Cross 1982). Further, copepods made up 99.8% of the dry weight of inshore one-year-olds while amphipods made up 44.6% in three-year-olds (Bradstreet and Cross 1982).

Parasites provide an additional tool to analyze foraging ecology because many are transmitted in the diet and can be used as temporal indicators depending on the seasonal acquisition and longevity of infection (Gallagher and Dick 2010). Also many parasites are host-specific elucidating dietary pathways. For example, *Mysis* spp. are intermediate hosts for the trematode *Derogenes varicus* but *Themisto libellula* is not (Isinguzo 2009). Our results are similar to Bradstreet et al. (1986) who found that Arctic cod captured in Resolute and Allen Bay had high nematode (*Thynnascaris* sp.) and trematode (*Genolinea* sp. and *D. varicus*) infection rates. We also found larval ascarid nematodes encysted along the viscera and body cavity wall of cod and this intermediate parasitic stage is infective to marine mammal predators. These specimens infect copepods and amphipods as intermediate hosts (Køie 2009) and further identify them as long-term food items of

Arctic cod. The constant rate of infection as cod size increased also suggests that similar prey items are acquired for all size classes.

Stable isotope analysis

Stable isotopes are a major tool to study food web and trophic interactions, and are particularly advantageous because of their predictable nature and high-resolution (Christiansen et al. 2012). Carbon (i.e., $\delta^{13}C$) is useful because it identifies sources of prey in the food web and consequently indicates foraging habitat. For example, benthic habitats are often enriched in $\delta^{13}C$ compared to pelagic habitats because of increased organic deposition (Sherwood and Rose 2005, Wassmann et al. 2006). Nitrogen (i.e., $\delta^{15}N$) is also commonly used because consumers are typically enriched in $\delta^{15}N$ at a consistent rate compared to prey (Vander Zanden and Rasmussen 1999) enabling food web interactions to be explored.

Arctic cod liver and muscle $\delta^{15}N$ values and trophic position (i.e., trophic level=3.4-3.8; calculated from Hobson et al. 2002a) were similar to other studies supporting their role as important intermediaries between lower and upper trophic levels. Interestingly, diet analysis revealed mainly ice-adapted or epi-benthic prey, and stable isotope values from liver and muscle indicated a diet originating from pelagic sources (see Fig. 1 in Hobson et al. 2002a). The highly negative $\delta^{13}C$ values of larval Arctic cod indicate a planktonic diet where movement into Allen Bay was controlled by ocean currents (Sekerak 1982). Our data on cod muscle was slightly lower for $\delta^{15}N$ (-0.3‰) and higher for $\delta^{13}C$ (+1.3‰) compared to Hobson and Welch 1992a. Although temporal variation may affect isotope values at the base of the food web (Tamelander et al. 2009), pelagic prey appeared to be more important twenty years ago. Christiansen et al. (2012)

compared the trophic ecology of sympatric Arctic cod and *A. glacialis*, and suggested spatial segregation between the two species where Arctic cod (mean $\delta^{15}N$=13.64‰, $\delta^{13}C$=-21.25‰) are associated with the pelagic food web to a large extent.

Liver and muscle tissues were analyzed to obtain a time-integrated estimate of diet assimilation to compliment stomach content analysis. Although isotopic turnover is not known for cod, it should reflect the metabolic activity of the tissue examined (Tieszen et al. 1983), suggesting liver will reflect more recent diet assimilation than muscle. For example, Buchheister and Latour (2010) calculated turnover rates of summer flounder (*Paralichthys dentatus*) and found that half-lives of carbon and nitrogen ranged from 10-20 days in liver and 49-107 days in muscle. Growth and metabolic pathways would differ in Arctic species, however our isotopic results may reflect diet from late spring/early summer (liver) and late winter (muscle). Muscle $\delta^{15}N$ and $\delta^{13}C$ values were typically higher than liver (Fig. 4) indicating either a switch in diet items leading up to summer or a shift in nutrient cycling in the environment (e.g., pelagic-benthic coupling during ice melt: Wassmann et al. 2006; Link et al. 2011).

Diet-tissue discrimination factors (i.e., enrichment/depletion of $\delta^{15}N$ and $\delta^{13}C$ ratios between consumer and food) are important because they form the basis of stable isotope analysis in trophic dynamics and feeding ecology (Zhao et al. 2006). Our results were based on prey composition directly, suggesting that liver and muscle isotopes reflected different prey sources since estimated liver and muscle discrimination values differed from expected values (e.g., $\Delta^{15}N$ 3-4‰; Michener and Schell 1994, $\Delta^{13}C$ 0-1‰; Fry and Sherr 1984). The muscle isotopes likely represented diet assimilation when much of the nutrients in the ecosystem were sequestered near the surface with ice. By contrast, our diet findings represent a time when food is available near-bottom and throughout the water column. Further, Arctic cod were captured nearshore where they aggregate during the summer but prior to ice break-up they typically remain offshore in deeper habitats (Benoit et al. 2008). Therefore different prey items (or similar prey with different isotopic signatures) may be more important prior to summer. If cod discrimination factors are consistent with commonly used values, then organisms with more enriched $\delta^{15}N$ (i.e., liver: 10-11‰, muscle: 11-12‰) and more depleted $\delta^{13}C$ (i.e., -20 to -22‰) were excluded from our stomach content analysis. Perhaps larger pelagic crustaceans (e.g., *Mysis* sp. and *Themisto* sp.) were more important prior to summer as Craig et al. (1982) demonstrated. Since Arctic cod are cannibalistic, larvae and juveniles may form a greater proportion of the diet than we observed (i.e., only one occurrence of cannibalism) but based on isotope values (i.e., <2‰ $\delta^{15}N$ difference between size class 1 and 4), it appears unlikely to be a major component. Laboratory-based discrimination studies specifically for Arctic cod are needed to accurately determine prey because discrimination factors vary between species, within species, and within individuals (Zhao et al. 2006).

As cod size increased, $\delta^{15}N$ values increased in liver and muscle supporting size-selective prey consumption. By contrast, $\delta^{13}C$ did not show significant change as length increased except in muscle when separated by size class (i.e., based on GLM and see Fig. 5). This suggests that Arctic cod size affects foraging behaviour to a greater extent in the past (e.g., winter). But the large variation in liver isotopic values suggests considerable variation in diet sources in recent past. Isotopic niche models revealed a greater overlap in liver $\delta^{15}N$ values of size class 3 and 4 than muscle suggesting greater partitioning of diet between the two classes when ice-cover was present. The main difference between our findings in $\delta^{15}N$ values and the stomach content analysis was that size class 1 separated strongly from the other classes based on isotopes (Fig. 5, 6), while size class 4 showed the clearest separation from the other classes based on diet (Table 6). Perhaps during the winter and spring larger cod (i.e., ≥2+) compete for larger pelagic prey, but during the summer as primary production increases size class 2 and 3 switch to smaller, more abundant food sources.

Conclusion

Environmental changes affecting the Arctic marine ecosystem are increasingly a topic of concern (e.g., Cheung et al. 2009). Arctic cod is a vital component of the Arctic marine food web yet still remains sparsely and infrequently studied. It was shown, at a local scale, that the biology of Arctic cod during the summer remained unchanged over the last 30 years. To my knowledge, this is the first study to examine diet of Arctic cod using stomach content analysis and stable isotope analysis of liver and muscle. Furthermore, I was able to use these approaches to discriminate seasonal Arctic cod size patterns. Arctic food sources undergo significant seasonal changes and using multiple indicators we are better suited to obtain a comprehensive view of prey selection and availability. This is an important first step to examine how long-term and seasonal trends influence Arctic cod growth, energy mobilization, diet, and isotopic variation.

Table 2.1: Mean (± S.D.) values and ranges for length and weight of Arctic cod (*Boreogadus saida*) age groups

	Fork length (mm)				**Weight (g)**			
Age	**n**	**Mean**	**S.D.**	**Range**	**n**	**Mean**	**S.D.**	**Range**
0	19	13.8	1.8	10-17	19	0.018	0.006	<0.1
1	100	75.1	7.2	56-93	100	2.3	0.8	1.0-5.3
2	19	149.2	16.7	23-184	19	20.9	7.4	10.3-35.8
3	66	170.5	19.7	125-243	64	29.6	11.0	11.0-85.4
4	106	182.4	16.3	134-234	104	35.1	9.4	17.7-74.0
5	17	207.9	27.2	181-273	16	51.5	21.6	29.5-102.1
Total	327	136.8	58.8	10-273	322	21.7	18.4	0.1-102.1

Table 2.2: Mean (±S.E.) gonadosomatic (GSI) and hepatosomatic (HSI) indices, and condition factor (CF) of male and female Arctic cod (*Boreogadus saida*).

	GSI	**HSI**	**CF**
Male	3.72 ± 0.13	3.66 ± 0.13	0.57 ± 0.01
Female	2.93 ± 0.07	4.47 ± 0.15	0.59 ± 0.01
P-value	<0.01	<0.01	0.21
d.f.	195	196	197

Table 2.3: Frequency of occurrence (% occ.), percent composition (% diet), and percent weight (% weight) of Arctic cod (*Boreogadus saida*) food items based on size ranges of prey and cod.

Prey size	**Size class 1 (56-93mm)**			**Size class 2 (123-159mm)**			**Size class 3 (160-183mm)**			**Size class 4 (185-256mm)**		
	% occ.	% diet	% weight	% occ.	% diet	% weight	% occ.	% diet	% Weight	% occ.	% diet	% weight
<1mm	78.3	64.8	47.5	61.5	94.6	81.8	38.5	60.3	26.3	0	0	0
1-3mm	97.8	34.5	50.3	46.2	3.9	6.7	23.1	21.4	18.6	16.7	3.4	0.8
3-5mm	13	0.6	1.6	0	0	0	7.7	5.3	8.4	8.3	0.7	0.3
5-10mm	8.7	<0.1	0.6	0	0	0	46.2	7.6	26.3	41.7	38.9	37.5
>10mm	0	0	0	7.7	1.5	11.5	23.1	5.3	20.4	58.3	57.0	61.4

Table 2.4: Frequency of occurrence (% occ.) and percent composition (% diet) and percent weight (% weight) of Arctic cod (*Boreogadus saida*) food items based on prey groupings.

Group	**Size class 1 (56-93mm)**			**Size class 2 (123-159mm)**			**Size class 3 (160-184mm)**			**Size class 4 (185-256mm)**		
	% occ.	% diet	% weight	% occ.	% diet	% weight	% occ.	% diet	% weight	% occ.	% diet	% weight
Harpacticoida	97.8	41	39.3	61.5	15.8	13.6	30.8	59.6	27.6	16.7	15.7	2.5
Cyclopoida	67.4	58.3	55.9	30.8	10.9	9.4	23.1	22.1	10.3	8.3	0.3	0.1
Calanoida	0	0	0	7.7	0.2	0.2	0	0	0	0	0	0
Nauplii	0	0	0	30.8	70.6	60.9	0	0	0	8.3	0.6	0.1
Ostracoda	0	0	0	7.7	1	6.1	0	0	0	0	0	0
Onisimus sp.	10.9	0.2	1	7.7	1.5	9.8	53.8	13.7	46.5	58.3	58.7	68.4
Gammarus sp.	6.5	0.5	3.6	0	0	0	15.4	2.3	7.8	41.7	24.1	28.1
Themisto sp.	4.3	<0.1	0.2	0	0	0	7.7	2.3	7.8	8.3	0.3	0.4
Mysida	0	0	0	0	0	0	0	0	0	8.3	0.3	0.4

Note: one Arctic cod otolith was collected from the stomach of a cod (size class 4) and is not included in the analysis above. Nauplii consisted of cirripedian and copepod nauplii.

Table 2.5: Schoener's index (SI) representing dietary overlap between Arctic cod (*Boreogadus saida*) size classes (1: 56-93mm, 2: 123-159mm, 3: 160-184mm, 4: 185-256mm) for stomach content analyses using prey sizes and prey items as variables. SI values ≥0.60 (in bold) are considered biologically significant.

Size class comparisons	**SI (Prey size)**	**SI (Prey item)**
1 vs 2	**0.69**	0.27
1 vs 3	**0.82**	0.34
1 vs 4	0.04	0.10
2 vs 3	**0.66**	0.34
2 vs 4	0.05	0.46
3 vs 4	0.17	0.19

Table 2.6: Sample number (N), mean ± 1 standard error (S.E.) of δ^{15}N (‰) and δ^{13}C (‰), $\Delta\delta^{13}$C (‰) and $\Delta\delta^{15}$N (‰) of Arctic cod (*Boreogadus saida*) in size classes (1: 56-93mm, 2: 123-159mm, 3: 160-184mm, 4: 185-256mm) for liver and muscle tissue.

	Liver					**Muscle**				
Size class	**n**	**δ15N**	**Δ15N**	**δ13C**	**Δ13C**	**n**	**δ15N**	**Δ15N**	**δ13C**	**Δ13C**
Larval (10-17mm)	8	11.78±0.15	NA	-23.38±0.11	NA					
1 (56-93mm)	10	12.41±0.16	3.1	-20.71±0.12	-1.0	35	13.69±0.05	4.4	-20.02±0.06	-0.3
2 (123-159mm)	33	13.77±0.11	4.5	-20.84±0.15	-1.4	33	14.96±0.1	5.7	-20.43±0.06	-1.0
3 (160-184mm)	44	14.28±0.10	5.3	-20.91±0.12	-2.4	44	15.29±0.07	6.3	-20.31±0.04	-1.8
4 (185-256mm)	34	14.35±0.11	5.4	-20.91±0.15	-3.2	36	15.50±0.09	6.6	-20.11±0.05	-2.4
Total	121	14.01±0.07	4.7	-20.88±0.07	-1.2	148	14.89±0.07	5.6	-20.22±0.03	-0.5

Note: Larval Arctic cod liver values represent isotopic analysis of whole body where individuals were pooled into 2 samples. They are not included in the *Total* row. To calculate $\Delta\delta^{13}$C and $\Delta\delta^{15}$N, δ^{15}N and δ^{13}C values from copepods were used for nauplii and ostracods, and values from *Themisto* sp. were used for mysids because isotope values were not available.

Table 2.7: Comparison of biology and diet of Arctic cod (*Boreogadus saida*) sampled from the same locations over the last 30 years.

	Bain and Sekerak (1978)	**Hop et al. (1997a)**	**Present study (2010)**
Location	Allen Bay, Resolute Bay	Allen Bay, Resolute Bay, 3 other locations off Devon Island	Allen Bay
Sampling time	July – September 1976-1977	July – September 1985-1991	July-August 2010
Samples (n)	920	3757	327
Size Range	5-298mm	65-260mm	10-273mm
Age distribution	1-5 3+ (68%) and 4+ (22%)	1-7 3+ and 4+ dominant (mean 3.7)	1-5 3+ (32%) and 4+ (51%)
Sex ratio (male:female)	Range 1:1.6 – 1:4.0	Mean 1:1.18 Range 1:0.81 – 1:1.81	1:1.13
Growth	Exponent of growth = 2.92	NA	Exponent of growth = 2.68
GSI	Males: July=3.51% August=4.15% September=9.71% Females: July=2.66% August=2.73% September=3.84%	Males: 3.8% Females: 2.8%	Males: 3.72% Females: 2.93%
HSI	Males: 8.19% Females: 9.44%	NA	Males: 3.66% Females: 4.47%
Diet	Copepods and amphipods accounted for >90% of food items Cod <100mm consumed mainly copepods while larger cod consumed mainly amphipods Consumed mainly epi-benthic invertebrates (e.g., *Onisimus* sp., calanoid and harpacticoid copepods). *Themisto libellula* was most common zooplankter.	Juveniles from schools (mean=83mm) fed on calanoid copepods while adults (mean=165mm) fed rarely (64% empty) but consumed amphipods and copepods	Harpacticoids and cyclopoids present in >90% of stomachs (with food). Amphipods became more important as size increased.

Figure 2.1: (a) Weight-length and (b) age-length relationship of Arctic cod (*Boreogadus saida*) using a power and von Bertalanffy regression, respectively.

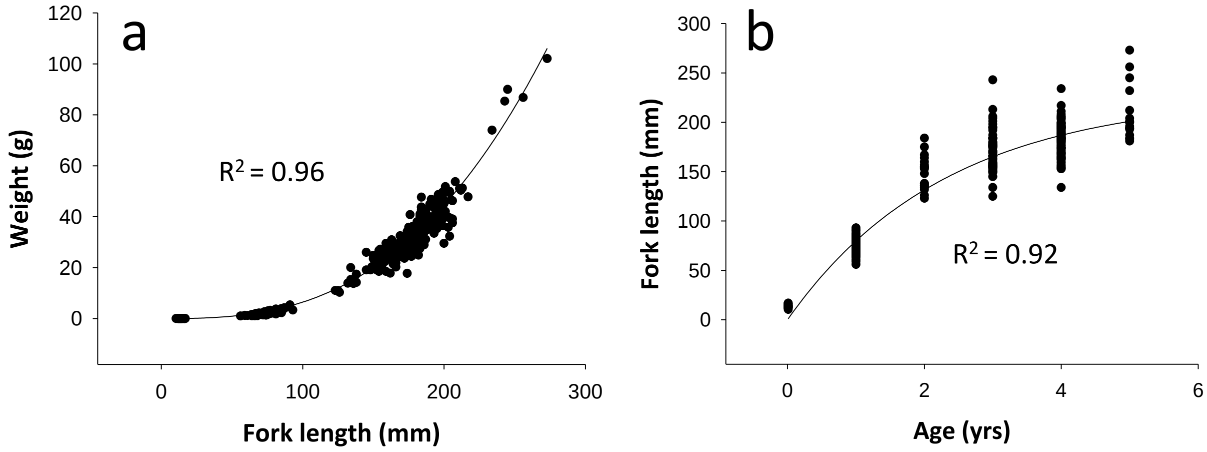


Figure 2.2: Age distribution of male (n=96) and female (n=108) Arctic cod (*Boreogadus saida*) captured from gillnets.

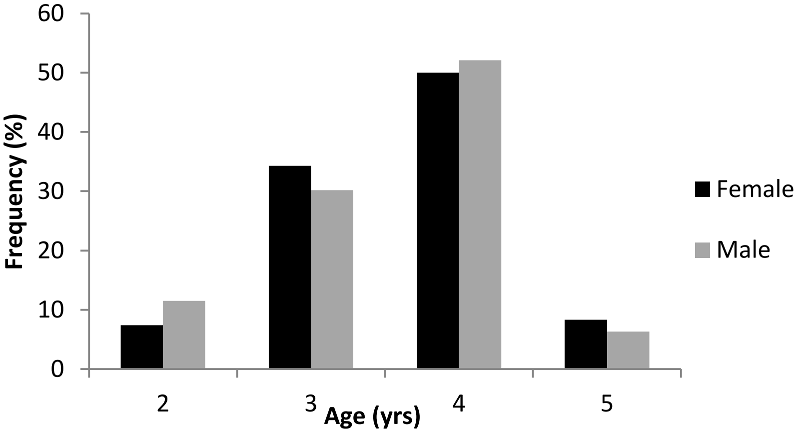


Figure 2.3: Gonadosomatic index (GSI) of (a) female (n=104) and (b) male (n=93) Arctic cod (*Boreogadus saida*), and hepatosomatic index (HSI) of (c) female (n=105) and (d) male (n=93) cod captured from gillnets throughout the study period.

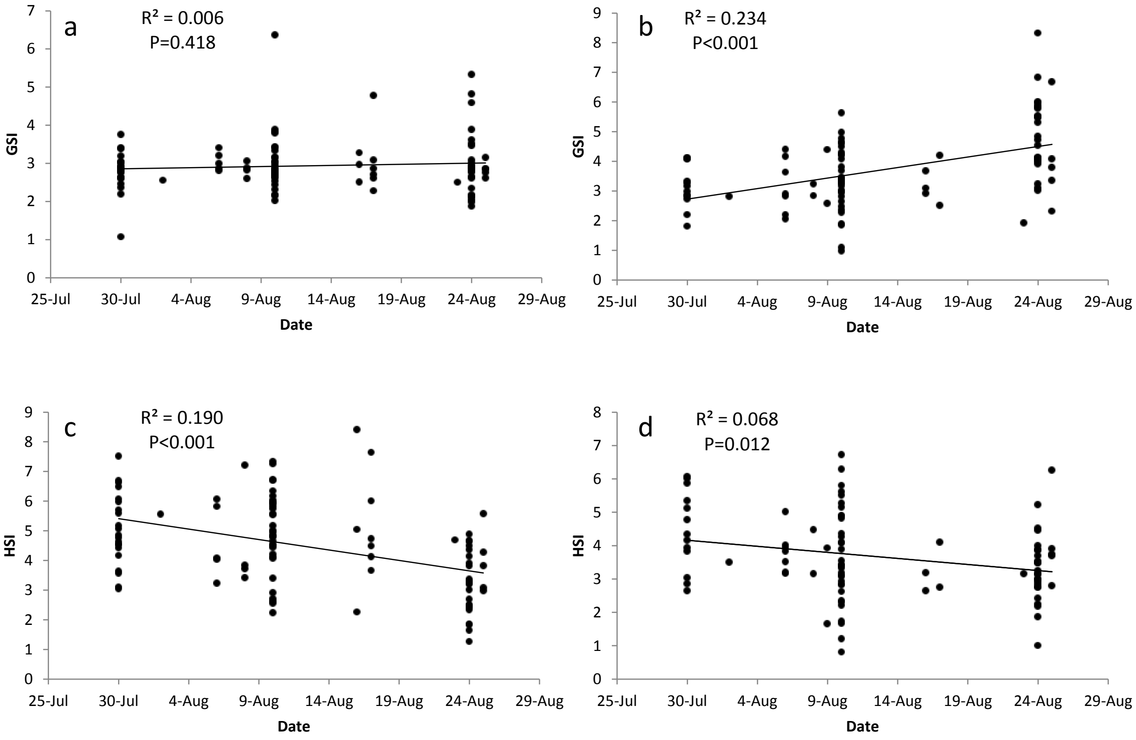


Figure 2.4: Linear regression comparing Arctic cod (*Boreogadus saida*) fork length (mm) with (a) δ^{13}C (‰) and (b) δ^{15}N (‰) for liver (white symbols) and muscle (black symbols). Dotted lines represent 95% confidence intervals.

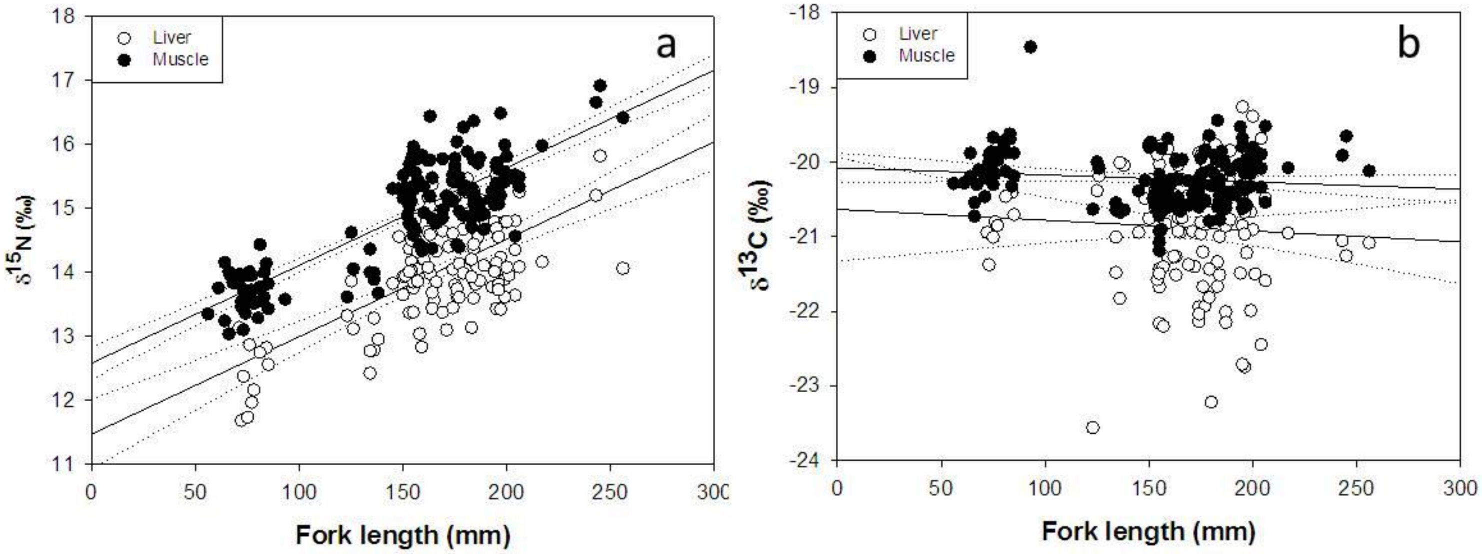


Figure 2.5: Mean ± 95% confidence intervals of liver (white symbols, L) and muscle (black symbols, M) $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) for Arctic cod (*Boreogadus saida*) separated by size classes (Larval cod: 10-17mm; 1L, 1M: 56-93mm; 2L, 2M: 123-159mm; 3L, 3M: 160-184mm; 4L, 4M: 185-256mm) collected from Allen Bay, Nunavut 2010. Common prey species are also plotted.

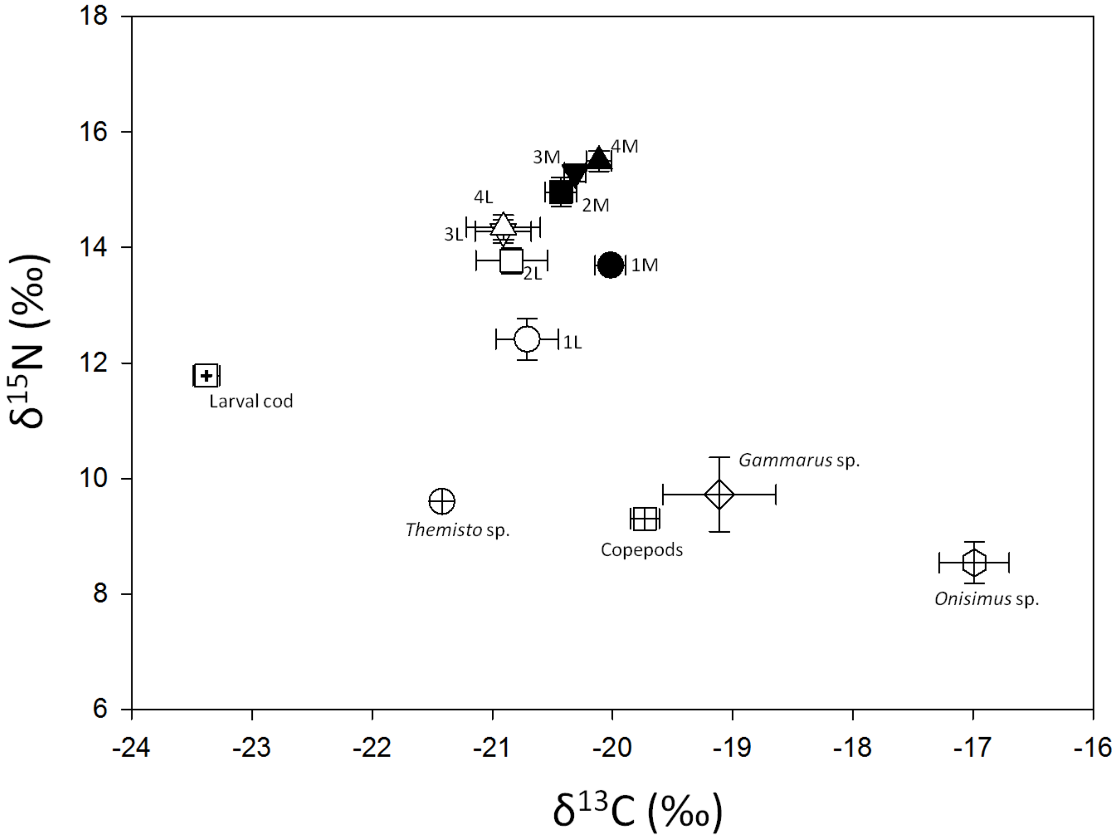
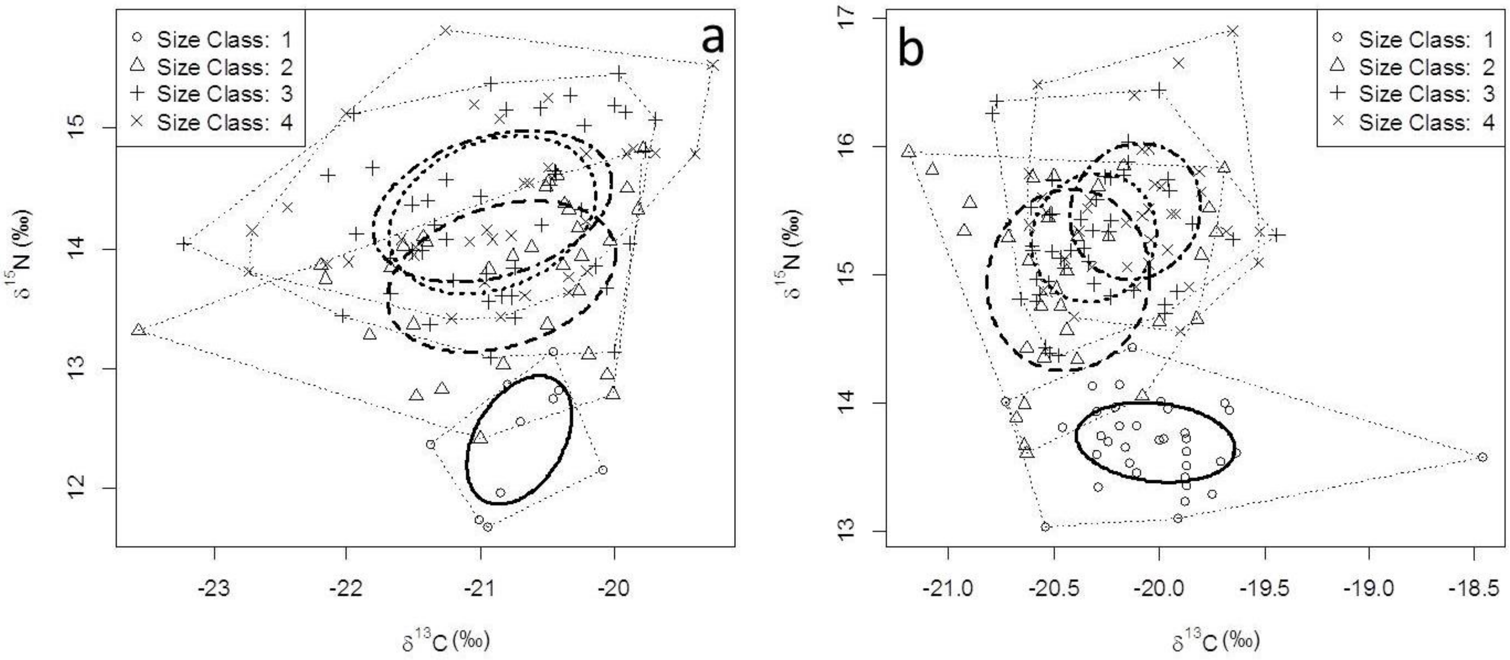


Figure 2.6: Isotopic niche overlap for (a) liver and (b) muscle between Arctic cod (*Boreogadus saida*) size classes (1: 56-93mm, 2: 123-159mm, 3: 160-184mm, 4: 185-256mm). Convex hulls of total niche width are depicted using grey dashed lines. Standard ellipse area (SEA_B) representing isotopic niches are depicted using black lines (size class 1: —— , size class 2: - - - , size class 3: ········ , size class 4: -·-·).



Chapter 3: Seasonal foraging ecology of Arctic marine mammals near Resolute, Canada

Abstract:

Complimentary approaches to study the foraging behaviour of animals can reveal temporal and spatial patterns relating to resource availability and selection. This is particularly important in areas that are difficult to sample repeatedly and with animals that have large ranges. Arctic marine animals pose such challenges, highlighting the need for greater understanding of local and broad scale seasonal foraging decisions. Stomach content and stable isotope analysis (liver and muscle) was used to identify spatial prey selection by ringed seals (*Pusa hispida*), belugas (*Delphinapterus leucas*), and narwhals (*Monodon monoceros*) from late winter to early fall. Arctic cod (*Boreogadus saida*) was the main prey item of all three species of marine mammals around Resolute, Nunavut and diet reconstruction revealed that marine mammal length, age, and sex did not influence the size of Arctic cod consumed. Prey-size selection and observations revealed that ringed seals foraged on non-schooling cod whereas belugas and narwhals exploited schools. Isotope signatures of whales indicated that other prey were also important during migration to summering areas in the Eastern Canadian Arctic. Ringed seal foraging habitat was closely related to the seasonal distribution of Arctic cod based on $\delta^{13}C$ values, and seal length was positively associated with $\delta^{15}N$. Diet-tissue discrimination factors for ringed seals, belugas, and narwhals were also calculated based on local tissue and stomach content sampling, and represent the first attempt to do so for these species.

3.1. Introduction

The foraging behaviour of top Arctic predators provides information about habitat preference, movement, and prey selection, which are increasingly important given the changing Arctic environment. Ringed seals (*Pusa hispida*), belugas (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) are culturally significant animals with integral ecological roles in the Arctic ecosystem as top consumers. In the Canadian High Arctic, Arctic cod is the most important food item (Bradstreet and Cross 1982; Welch et al. 1992). Schools of Arctic cod consisting of millions of individuals that commonly aggregate nearshore during summer are readily available to predators (Crawford and Jorgenson 1996). Welch et al. (1992) estimated that 148,000 tonnes of Arctic cod (>5 billion individuals) are consumed by seabirds, seals, and whales in the Eastern Canadian Arctic annually, representing ~75% of the energy transferred between zooplankton and top consumers. When schools are encountered they provide large energetic gains but distribution and schooling behaviour changes seasonally (e.g., Crawford and Jorgenson 1996; Geoffroy et al. 2011), and predators exhibit different foraging strategies (Bradstreet et al. 1986). Therefore, the importance of schools to predators may be seasonal and species-specific. Life history characteristics also affect prey selection within species. For example the diet of ringed seals is influenced by sex, size, and age (Holst et al. 2001; Dehn et al. 2007) but studies are sparse and findings are variable.

The majority of foraging studies in the Arctic have examined diet using stomach content analysis (SCA). This approach provides direct identification and quantification of prey which is essential to determine important food items and foraging habitat (e.g., Finley and Gibb 1982). Repeat or seasonal sampling is difficult in the Arctic considering the spatial and temporal variability of animals, as well as costs and logistics. Stable isotope analysis (SIA) supplements SCA by increasing the resolution of foraging decisions that can be obtained from an individual. SIA is used to study the Arctic food web because it reflects diet assimilation and can provide temporal and spatial foraging information (Hobson and Welch 1992a). Nitrogen stable isotopes ($\delta^{15}N$) are commonly utilized because there is a relatively consistent enrichment of heavy isotopes from prey to predator (i.e., ~3.4‰; Minigawa and Wada 1984) indicating trophic hierarchy and potential prey items, although variation in this enrichment can be significant (Vander Zanden and Rasmussen 2001). Carbon ($\delta^{13}C$) shows limited enrichment (i.e., <1‰; Michener and Schell 1994) between predator and prey reflecting potential food sources throughout the food web. The turnover of stable isotopes (i.e., the time it takes the isotope to assimilate into consumer's tissue and reflect prey sources) is mainly controlled by an organism's metabolism (Tieszen et al. 1993; Kaufman et al. 2008). Metabolic processes within an individual also vary enabling temporal insight to diet. For example, the turnover of muscle is estimated to be weeks to months, while the turnover of the metabolically more active liver is days to weeks (Hobson and Clark 1992; Tieszen et al. 1993) however this is species- and size-dependent (e.g., Dalerum and Angerbjörn 2005). Multi-source mixing models are increasingly being used to examine the composition of diet based on isotope signatures (Layman et al. 2011). These models estimate the percent contribution of designated prey sources and directly incorporate variability in multiple input parameters (Parnell et al. 2010). Despite the advantages of incorporating SIA, without extensive sampling and knowledge of actual prey items (i.e., via SCA), its application is limited.

Belugas and narwhals migrate to the Canadian Arctic Archipelago during summer mainly from Baffin Bay, Jones Sound, the North Water polynya, and off the western coast of Greenland (Innes et al. 1996) (Fig. 7). They typically migrate along coasts or leads in pack ice to summering areas such as Peel Sound, returning east as the sea ice consolidates (Fig. 7). Examination of diet in wintering areas is limited but squid (e.g., *Gonatus fabricii*) and Greenland halibut (*Reinhardtius hippoglossoides*) supplement Arctic cod (Heide-Jørgensen and Teilmann 1994; Lairdre and Heide-Jørgensen 2005; Gardiner and Dick 2010). We predicted that stomach contents and liver tissue of belugas and narwhals would reflect a recent diet of Arctic cod, while isotopic values in muscle reflect longer term consumption.

The purpose of this study was to investigate foraging behavior of top Arctic marine predators using SCA, SIA, and field observations. Specifically the objectives were to: (1) determine the importance of Arctic cod temporally and spatially using stomach content data, and liver and muscle isotope values; (2) examine sex- and age-class differences in relation to prey size and stable isotope signatures; (3) investigate the importance of schools of Arctic cod as prey sources for mammal predators based on observations and diet reconstruction.

Studies in the Arctic mostly investigate diet using a singular approach (i.e., SCA or SIA), and few incorporate multiple and complimentary techniques. Furthermore, prey data are rarely collected in the same area and at the same time as predator samples making diet reconstruction less reliable. This study investigates local prey selection by whales and seals, which is essential to understand how environmental consequences, such as changing resource availability, may affect the distribution and movement of top predators at a broader scale.

3.2. Materials and Methods

Study area

Resolute Bay and Allen Bay are located by Cornwallis Island, Nunavut near the community of Resolute (74°41′51″N 094°49′56″W; Fig. 7) in the Canadian High Arctic. Belugas and narwhals routinely navigate the shores around Resolute to and from summering grounds, while ringed seals remain year-round. Resolute Bay and Allen Bay are culturally important as the main subsistence hunting locations near Resolute. These bays are also well documented nearshore areas frequented by schools of Arctic cod that return annually during the ice-free period consistently attracting marine mammals to the area. Extensive observations of predator-prey interactions and Arctic cod schools were conducted in Allen Bay throughout July and August, 2010 to supplement sample collection (Chapter 4 and 5).

Sample collection

Ringed seal (n=21, 2010; n=6, 2011), beluga (n=13, 2010), and narwhal (n=3, 2010) samples were collected by hunters in Resolute Bay and Allen Bay during the summer and early fall (Table 9). The following tissues were collected: stomach, liver, muscle, 2nd and 5th lower right teeth (beluga), and lower and upper canines (ringed seal). After collection tissues were frozen and shipped to the University of Manitoba and stored at -20°C until analyses.

Age, maturity, and sex determination

Ringed seals were aged by counting growth layer groups in the teeth (cementum age analysis; Stewart et al. 1996). If age (x, n=4) or length (L, n=2) was not obtained, the following growth model extrapolated values: $L_x = 144.5(1 - e^{-0.099(x+0.61)})^{0.225}$ (McLaren 1993). Individuals were classified as adult, juvenile, and pup if ≥6 years old, 1-5 years old, and <1 years old, respectively (Holst et al. 2001). Beluga and narwhal age was estimated from a thin mounted tooth section by counting growth layer group deposits in the dentine (Stewart 2012) and were classified as adult if ≥12 years old (Stewart 1994; Stewart et al. 2006). The following growth model extrapolated age (x, n=2) and length (L, n=1) of belugas when unavailable: $L_x = 381.5e^{-7.56e^{-0.29x}}$ (female) and $L_x = 432.2e^{-1.16e^{-0.15x}}$ (male) (Luque and Ferguson 2009). The sex of individuals was determined using polymerase chain reaction-based genetic analysis (Shaw et al. 2003).

Stomach content analysis

Stomachs were thawed and contents were filtered through a series of three sieves (4 mm, 1.4mm, and 425 µm) with water. In whales, all parts of the stomach were examined however the forestomach contained the majority of food remains (cf. Finley and Gibb 1982; Laidre and Heide-Jørgensen 2005). The epithelium of the stomach was rinsed with water to remove residual matter. Diet items were identified as close to species as possible and frequency of occurrence (FO_i), percent composition (N_i), and energy contribution (E_i) determined the importance of prey (e.g., Hyslop 1980; Pierce and Boyle 1991):

(13) FO_i (%) = $(S_i/S_t) \times 100$

where S_i represents the number of ringed seals (or belugas or narwhals) with prey type *i*, and S_t represents the total number of ringed seal.

(14) $N_i\ (\%) = (n_i/n_t) \times 100$

where n_i represents the total number of prey type *i*, and n_t represents the total number of prey. Energy contribution (E_i) was calculated by multiplying the average energy content (from Elliott and Gaston 2008) by the percent composition of each prey.

Sagittal otoliths showing little or no degradation from each stomach were measured to extrapolate the length and weight of consumed Arctic cod. If a stomach was full of otoliths, a random subsample of 25 was used. Otolith length was defined as the longest dimension between the posterior and anterior edges of the otolith (Hunt 1992). The relationship between otolith length (OL) and Arctic cod fork length (ACL) from individuals collected in Allen Bay was ACL = 24.20*OL – 4.29 (R^2=0.91, n=251) (Chapter 2). Similarly, ACW = 1.72E-05*$ACL^{2.8}$ (R^2=0.96, n=322) (Chapter 2) was used to determine Arctic cod wet weight (ACW). The average weight of Arctic cod in each stomach was then multiplied by the number of individuals consumed (i.e., 2 otoliths = 1 individual) to estimate energy intake. Amphipods were enumerated by counting whole bodies and disarticulated parts (i.e., eyes and telsons). The average weight of whole amphipods in each respective stomach was multiplied by the total number of individuals to reconstruct diet and obtain energetic content using energy values for *Themisto libellula*. The average weight of squid extrapolated from narwhal stomachs (23g; Laidre and Heide-Jørgensen 2005) was also used.

Stable isotope analysis

Liver and muscle tissue from each seal and whale was dried at 70°C for 48 hours and sent to the Great Lakes Institute for Environmental Research at the University of Windsor, Canada for quantification of stable isotopes. Tissue (400-600 μg) was crushed and grounded, and lipids were removed using a 2:1 chloroform:methanol solvent. A continuous flow isotope ration mass spectrometer (IRMS, Finnigan MAT Delta^{plus}, Thermo Finnigan, San Jose, CA, USA) equipped with a Costech Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA) determined $\delta^{13}C$ and $\delta^{15}N$ using Pee Dee Belemnite carbonate for CO_2 and atmospheric Nitrogen for N_2 as standard reference materials. Stable isotope ratio values are expressed in parts per thousand (‰) using δ notation as calculated using the following equation:

(1) $\delta X = [R_{Sample}/R_{standard})-1] \times 1{,}000$

Where X is ^{15}N or ^{13}C, R_{sample} is the ratio ($^{15}N/^{14}N$ or $^{13}C/^{12}C$) in the sample, and $R_{standard}$ is the ratio in the standard. The standard deviation of samples run in triplicate was generally <0.1‰ ($\delta^{13}C$) and <0.2‰ ($\delta^{15}N$). The analytical precision (standard deviation) for National Institute of Standards and Technology (NIST) standard 8414 (bovine muscle, n = 29) and an internal lab standard (tilapia muscle, n = 29) for $\delta^{13}C$ was 0.03 and 0.06, respectively, and for $\delta^{15}N$ was 0.14 and 0.22, respectively. The NIST standards (sucrose and ammonia sulphate, n=3) were within 0.01‰ and 0.07‰ of certified values for δ15N and δ13C, respectively (run every 12 samples).

Data analysis

To avoid pseudoreplication, the average size of Arctic cod consumed by each individual was calculated as a single experimental unit. To compare the difference in

Arctic cod consumed among ringed seals, belugas, and narwhals a Kruskal-Wallis test was used with a post hoc Bonferroni correction. Similarly, the influence of maturity, length (divided into 3 groups: 90-109cm, 110-129cm, 130-149cm), and sex on size of cod consumed was investigated for ringed seals using this non-parametric approach (each parameter analyzed separately). The stable isotope ratio values followed normal distribution (i.e., Shapiro-Wilk test, $P>0.05$). A multivariate analysis of variance (MANOVA) with Pillai's approximation determined the effect of length (as described above), maturity, and year (with interactions) on ringed seal $\delta^{13}C$ and $\delta^{15}N$ values. Length (divided into 3 groups: <350cm, 350-400cm, >400cm), sex, and maturity (with interactions) were the independent variables used for belugas. Following this, analysis of variance (i.e., three-way ANOVA) was applied to $\delta^{13}C$ and $\delta^{15}N$ separately to explore how life history traits affected each isotope ratio. Mean liver and muscle $\delta^{15}N$ and $\delta^{13}C$ values were plotted for each species and differences between groups were considered significant if their 95% confidence intervals (CIs) did not overlap (Payton et al. 2003).

We investigated trophic enrichment between the marine mammals and prey by calculating isotopic discrimination factors ($\Delta^{13}C$ and $\Delta^{15}N$) based on equations from Sherwood and Rose (2005) as follows, using $\delta^{15}N$ as an example:

$$(16) \quad \Delta^{15}N = \delta\,^{15}N_{predator} - \sum (P_i \cdot \delta\,^{15}N_i)$$

where $\delta\,^{15}N_{predator}$ represents the mean $\delta^{15}N$ of ringed seal, beluga, or narwhal liver or muscle tissue, P_i is the weight contribution (as a ratio) of the *i*th prey compared to all prey items, and $\delta\,^{15}N_i$ is the mean $\delta^{15}N$ of prey *i*.

The seasonal importance of beluga and narwhal prey during migration was investigated, with a Bayesian mixing model using the SIAR package in R (Parnell et al.

2010) and diet-tissue discrimination factors calculated by Hobson et al. (1996) (i.e., muscle: $\Delta^{15}N$=2.4, $\Delta^{13}C$=1.3 ; liver: $\Delta^{15}N$=3.1, $\Delta^{13}C$=0.6). Isotope values of common prey sources were used to calculate trophic enrichment and prey proportion as follows: Arctic cod (liver: $\delta^{15}N$=14.01±0.07 (mean±S.E.), $\delta^{13}C$=-20.88±0.03; muscle: $\delta^{15}N$=14.89±0.07, $\delta^{13}C$=-20.22±0.03; Chapter 2), *T. libellula* ($\delta^{15}N$=9.6±0.02, $\delta^{13}C$=-21.42±0.02; Chapter 2), *G. fabricii* ($\delta^{15}N$=11.98±0.20, $\delta^{13}C$=-21.42±0.09; Gardiner et al. unpubl. ms), and Greenland halibut ($\delta^{15}N$=16±0.21, $\delta^{13}C$=-19.01±0.21; Dennard et al. 2009). Statistical analyses were conducted in the statistical package R and were considered significant when $P \leq 0.05$.

3.3. Results

Stomach content analysis

Arctic cod was the most frequent and numerous food item contributing over 95% of energy intake for all predators (Table 10). Less than half of the beluga stomachs contained food while most ringed seal stomachs (~89%) and all narwhals' were full (Table 10). Amphipods were more prevalent in juvenile ringed seals (Table 10) and comprised *T. libellula, Onisimus* sp., and *Gammarus* sp.. Arctic cod between 160-200mm were the main prey size range for all predators (Fig. 8). The mean length (±S.E.) of Arctic cod consumed by ringed seals (162.1±7.1) was significantly smaller compared to belugas (183.1±2.7), and narwhals (181.4±3.2) (Kruskal-Wallis test, X^2=6.9, df=2, P=0.03). Due to a small sample size, the relationship between life history traits and size of Arctic cod eaten was only examined for ringed seals. No significant differences were found for maturity (Kruskal-Wallis test, X^2=5.6, df=2, P=0.06), length (Kruskal-Wallis test, X^2=1.1, df=2, P=0.59), or sex (Wilcoxon test, W=30, P=0.19).

Stable isotope analysis

Length and year were significant predictors of liver δ^{15}N and δ^{13}C (MANOVA, $F_{2,17}$=3.97 for effect of length, P=0.04; $F_{2,17}$=7.92 for effect of year, P<0.01) in ringed seals. Year was significant for δ^{13}C (ANOVA, $F_{1,18}$=15.92, P<0.01) and length was significant for δ^{15}N (ANOVA, $F_{1,18}$=5.63, P=0.03) when isotope ratios were examined separately. For muscle, δ^{15}N was significantly predicted by length (ANOVA, $F_{1,18}$=4.42, P=0.05). Length, sex, and age did not influence δ^{15}N and δ^{13}C values of belugas (P>0.05). There was considerable overlap between isotope values of ringed seals, belugas, and narwhals (Fig. 9). In 2010, predator δ^{15}N liver values were typically higher (enriched) than respective muscle values, and seal δ^{13}C liver was higher (i.e., less negative) than all other ratios (Fig. 9). Liver δ^{15}N of seals collected in 2011 was significantly lower (depleted) than those collected in 2010. Comparisons between species mainly showed that belugas and narwhals had significantly lower muscle δ^{15}N than ringed seals (Fig. 9).

Diet-tissue isotopic discrimination factors ranged between 1.46-3.45 for δ^{15}N, and 0.63-2.32 for δ^{13}C for both liver and muscle (Table 11). All isotopic discrimination factors were lower in muscle than liver tissue (Table 11). The mixing models showed a greater contribution of Arctic cod in liver tissues compared to other prey. Arctic cod was less important in muscle, where the contribution of Greenland halibut, in particular, increased (Fig. 10).

3.4. Discussion

Stomach content analysis

Frequency of occurrence, percent composition, and energy contribution, all indicated Arctic cod as the main diet item of marine mammal predators from Resolute Bay region during the ice-free period (Table 10). Arctic cod was readily available nearshore during this time aggregating in schools or as dispersed individuals (Chapter 4 and 5). Approximately half the seal stomachs contained amphipods, primarily *Onisimus* sp., but their energetic contribution was minimal (Table 10). Amphipods made up a greater proportion of the diet in juvenile seals indicating ontogenetic prey selection. However, two of the youngest and smallest individuals consumed ~98% of the amphipods signifying that Arctic cod is also important prior to maturity (i.e., 6/8 of juveniles consumed mainly cod). Holst et al. (2001) found a similar trend where immature seals in Grise Fjord, Nunavut fed mainly on the amphipod *T. libellula* in the summer, but Arctic cod and *A. glacialis* dominated the diet of adults. There was no significant relationship between the size of Arctic cod consumed and maturity, length, or sex suggesting that once Arctic cod was selected in the diet, predator size did not strongly affect prey-size selection. These findings corroborate other studies that extrapolated Arctic cod length and compared to age and sex (e.g., Bradstreet et al. 1986; Holst et al. 2001).

Amphipods and squid beaks were collected from belugas and narwhals but Arctic cod dominated (Table 10). More than half the beluga stomachs examined contained no food and all narwhals had recently fed although it was a small sample size (n=3). Bradstreet et al. (1986) hypothesized that belugas migrate to summering grounds to calve and moult, and feed little during July and August but do participate in feeding frenzies as they leave these areas. Lairdre and Heide-Jørgensen (2005) proposed the same pattern in narwhal based on numerous empty stomachs during the summer compared to fall and winter. In this study, feeding intensity was apparently increasing as samples were collected during late summer/early fall when belugas and narwhals began migration back to wintering grounds. However, an empty stomach may not be a reliable indicator of non-feeding. For example, Jobling and Breiby (1986) noted that marine mammals feed intermittently and as a result an empty stomach is common. Further, large whale feeding events occur throughout the open water season (Welch et al. 1993) and both species regularly make deep ‘foraging’ dives mid-summer (Richard et al. 2001; Laidre et al. 2002). Perhaps feeding is not as intense throughout the summer but when schools of Arctic cod are encountered they are exploited, resulting in variable occurrences of empty stomachs.

Welch et al. (1992) suggested that during summer, schools of Arctic cod contain the necessary biomass to support predators but non-schooling cod are not an energetically favourable prey item given low abundance and density. For example, the average standing biomass of non-schooling Arctic cod ($0.062 g\cdot m^{-2}$) was 25 times less than the amount consumed by predators such as seabirds and marine mammals (Welch et al. 1992). During the study (Aug 15, 2010), a pod of belugas were observed feeding on a school of Arctic cod in the nearshore by corralling them to the surface. This event attracted hundreds of seabirds and a dozen harp seals (*Pagophilus groenlandicus*), further supporting the ecological importance of Arctic cod schools. However, ringed seals did not associate with this school and were rarely seen near other schools even when they were more-or-less stationary and at the surface. Bradstreet et al. (1986) reported the same behavior and postulated that the gregarious and mobile nature of belugas and narwhals make schools easier to locate and exploit. By contrast, the predator-avoidance advantages of schooling (Pitcher 1986) prevent ringed seal predation to a greater extent due to their solitary nature. Interestingly, the mean length of Arctic cod captured from schools in Allen Bay was 187.0mm (Crawford and Jorgenson 1996), while non-schooling adults in Resolute Bay were 163.5mm (Hop et al. 1997a). The stomach analysis might further support that ringed seals (mean prey size: 162.1mm) consume non-schooling Arctic cod, and belugas (mean prey size: 183.1mm) and narwhals (mean prey size: 181.4mm) exploit schools. Further research is needed however because prey selection may be size-related.

Stable isotopes

The length of ringed seals was a significant predictor of δ^{15}N in liver and muscle indicating that larger individuals consumed prey at higher trophic level over a longer timeframe. Therefore larger seals may be eating larger cod and invertebrates may be more important to smaller seals. Length is a proxy to foraging ability (e.g., larger ringed seals typically make deeper dives; Born et al. 2004), whereas age is a proxy to foraging experience (Beck et al. 2007), suggesting that physiological or morphometric attributes influence prey selection to a greater extent than skill or knowledge.

There was no difference between life history traits and isotope values (δ^{15}N and δ^{13}C) in whales indicating prey items and prey sources are selected similarly for all individuals. The low diet diversity of belugas in this population may explain why results differed from Lesage et al. (2001) and Loseto et al. (2008) who found length and sex to influence isotope values.

Ringed seal liver $\delta^{13}C$ values were higher in 2010 than 2011 (Fig. 9) indicating more benthic-derived prey sources in 2010. The break-up of sea ice around Resolute occurred much earlier in 2011 (late July in 2010 vs late June in 2011) and schools of Arctic cod were observed less frequently by Inuit in 2011. Therefore, higher liver $\delta^{13}C$ values in 2010 may have reflected nearshore sources while offshore Arctic cod were more important in 2011. Inter-annual carbon flux associated with different sea ice conditions may also account for these findings (Wassmann et al. 2006). In 2011, there was considerable variation in seal muscle (Fig. 9) suggesting that different prey sources contributed to the diet of individual seals. The sample size was too low however to examine intra-specific prey selection.

The higher liver $\delta^{15}N$ values compared to muscle (Fig. 9) indicated that belugas and narwhals were feeding at higher trophic levels more recently. Further, there was a change in the contribution of prey sources between liver and muscle in my mixing models (Fig. 10). Since Arctic cod is more important during the summer (e.g., Finley and Gibb 1982; Lairdre and Heide-Jørgensen 2005), I speculate that muscle ratios represent spring or winter diets when different prey such as Greenland halibut or squid form a greater part of the diet. An alternative explanation for higher liver $\delta^{15}N$ values is due to reduced feeding (or nutritional stress) during the summer, however if this was the case I would expect $\delta^{15}N$ values of belugas and narwhals to be higher than ringed seals. Migration patterns of animals also affect the isotopic signatures due to spatial variability at the base of local food webs. For example, Schell and Saupe (1993) hypothesized that geographic variation affecting zooplankton $\delta^{13}C$ caused different carbon isotope signatures along the length of baleen in Arctic bowhead whales (*Balaena mysticetus*). I found no difference between muscle $\delta^{13}C$ ratios of whales and seals indicating local carbon input in each tissue were similar during migration. Broad scale baseline isotopic sampling is required to further explore carbon variability along migratory routes.

Diet-tissue discrimination factors (i.e., enrichment/depletion of $\delta^{15}N$ and $\delta^{13}C$ ratios between consumer and food) are critical in food web analysis because they determine the relationship between predator and potential prey. For example, the application of mixing models relies heavily on user-defined diet-tissue discrimination factors to select prey sources based on optimal iterations of $\delta^{15}N$ and $\delta^{13}C$ signatures fitting that input (Layman et al. 2011). Without accurate discrimination factors, actual prey sources can be misrepresented. A diet-based discrimination approach using prey contribution directly and isotopic values of prey from the same year and location was utilized. Since Arctic cod was the main diet item during the summer, this analysis predominantly calculates the discrimination between Arctic cod and the different marine mammals. This approach poses potential difficulties when other prey items become more frequent. For example, our muscle discrimination values are calculated based on diet contribution during summer, but this tissue represents long-term assimilation. If the diet consists of different prey during winter as expected, these values would be less reliable and likely explains why muscle discrimination values are different than liver. For this reason and to avoid biasing the mixing models we used discrimination factors calculated by Hobson et al. (1996).

Conclusion

Complimentary approaches to study food web structure and foraging behaviour are increasingly important in locations and for species that are difficult to sample. Obtaining time-integrated indicators of prey and habitat further strengthen our understanding of how top marine predators exploit resources. Here, I used three temporal indicators of diet and habitat to show how prey composition of three iconic marine mammals varied seasonally. Studies exploring turnover in large marine mammals are rare (e.g., Lesage et al. 2002; Caut et al. 2011), and the time-line for each tissue are best estimates available. Similarly, diet-tissue discrimination values based on controlled feeding trials are needed to determine how prey is assimilated into different tissues of different animals. Since there is regional variation in otolith size (Bradstreet et al. 1986) and stable isotope signatures (Dietz et al. 2004), increased local sampling is needed throughout foraging ranges to examine how prey selection varies according to available resources. Similarly, annual sampling is required to determine if emerging climate patterns in the Arctic are affecting foraging. For example, comparisons of $\delta^{13}C$ among local sites over several years as sea-ice regimes change could indicate if carbon linkages vary based on prey items or if nutrient input in the system is different. Although sample size was smaller than other studies (e.g., Bradstreet et al. 1986; Holst et al. 2001; Labansen et al. 2007), the results corroborated findings such as seal life history does not influence the size of Arctic cod consumed, and that immature seals feed more on amphipods. This is the first study to combine stomach content and stable isotope analysis with observations of predator feeding on Arctic cod populations. This approach provided further evidence that seals feed on non-schooling cod, and elucidated seasonal and annual diet shifts associated with migration and changing sea-ice conditions. Another novel finding was the quantification of trophic enrichment values of ringed seals, belugas, and narwhals based on isotopic values and prey items directly. Discrimination factors are critical in isotopic-based food web analysis and the values presented are, in my opinion, the best available especially for liver because Arctic cod was the main diet item during summer. Small bays are important areas for Arctic cod during the summer and consequently are productive foraging grounds for Arctic marine predators. Here, I provided new insight into foraging during the summer locally in Allen Bay and Resolute Bay, as well as provided supplementary evidence of seasonal resource partitioning. As climate trends risk altering the distribution of Arctic species (Cheung et al. 2009), there is increasing need to understand the habitat and prey that are seasonally important to marine mammals. This research is valuable as initial steps to form a baseline for prey selection patterns at a local scale to help understand broad scale foraging.

Table 3.1: Sample collection information of ringed seal (*Pusa hispida*), beluga (*Delphinapterus leucas*), and narwhal (*Monodon monoceros*).

	Ringed seal	**Beluga**	**Narwhal**
Collection Date	Aug 9 – Sep 14 2010	Sep 1 – Sep 16 2010	Sep 16 – Sep 17 2010
Males	17	8	3
Adult	9	6	3
Juvenile	4	2	-
Pup	4	NA	NA
Females	4	5	-
Adult	4	3	-
Juvenile	-	2	-
Pup	-	NA	NA
Total stomachs with contents	17 (2)	5 (7)	3 (0)

Note: Maturity of ringed seal was determined as follows: adult ≥6 years, juvenile 1-5 years, and <1 years. Maturity of beluga and narwhal were determined as follows: adult ≥12 years and juvenile <12 years. The numbers in parentheses represent empty stomachs.

Table 3.2: Number of prey, frequency of occurrence (% occurrence), percent composition (% diet) and energy contribution (% energy) of ringed seal (*Pusa hispida*), beluga (*Delphinapterus leucas*), and narwhal (*Monodon monoceros*) food items.

	Number of prey[a]	**% occurrence**	**% diet**	**% energy**
Ringed seal				
Juvenile[b] (n=8)				
Arctic cod	160	87.5	23.6	>99
Amphipods	519[c]	50	76.4	<1
Adult (n=11)				
Arctic cod	578	100	91.9	>99
Amphipods	51	36.4	8.1	<1
Beluga (n=12)				
Arctic cod	556	41.7	93.6	>95
Amphipods	34	16.7	5.7	<1
Squid	4	25	<1	<1
Narwhal (n=3)				
Arctic cod	257	100	81.6	>95
Amphipods	55	66.7	17.5	<1
Squid	3	66.7	1	<1

[a] Number of Arctic cod calculated by dividing the total number of otoliths by 2 (e.g., 320/2=160 individuals)

[b] Includes pups

[c] Two individuals contributed to ~98% of amphipods collected from juvenile and pups

Table 3.3: Sample number (n), mean ± 1 standard error (S.E.) of liver and muscle $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰), $\Delta\delta^{13}C$ (‰) and $\Delta\delta^{15}N$ (‰) of ringed seal (*Pusa hispida*), beluga (*Delphinapterus leucas*), and narwhal (*Monodon monoceros*) collected near Resolute in 2010 and 2011.

		Liver				**Muscle**			
Species	**n**	**δ15N**	**Δ15N**	**δ13C**	**Δ13C**	**δ15N**	**Δ15N**	**δ13C**	**Δ13C**
Ringed seal	21	17.45±0.18	3.45	-18.56±0.10	2.32	17.21±0.18	2.33	-19.35±0.14	0.87
Beluga	12	17.00±0.12	3.00	-19.14±0.10	1.74	16.33±0.20	1.46	-19.28±0.09	0.96
Narwhal	3	16.97±0.12	2.98	-19.57±0.14	1.31	16.34±0.07	1.48	-19.59±0.11	0.63
Ringed seal (2011)	6	16.50±0.17	NA	-19.37±0.14	NA	16.96±0.43	NA	-19.76±0.23	NA

Note: $\Delta^{13}C$ and $\Delta^{15}N$ values were calculated using the following prey sources: Arctic cod (liver: $\delta^{15}N$=14.01±0.07 (mean±S.E.), $\delta^{13}C$=-20.88±0.03; muscle: $\delta^{15}N$=14.89±0.07, $\delta^{13}C$=-20.22±0.03; Chapter 2), *T. libellula* ($\delta^{15}N$=9.6±0.02, $\delta^{13}C$=-21.42±0.02; Chapter 2), *G. fabricii* ($\delta^{15}N$=11.98±0.20, $\delta^{13}C$=-21.42±0.09; Gardiner et al. unpubl. ms), and Greenland halibut ($\delta^{15}N$=16±0.21, $\delta^{13}C$=-19.01±0.21; Dennard et al. 2009).

Figure 3.1: Eastern Canadian Arctic with names of important whale habitats shown as in text. Inset contains sample location Allen Bay and Resolute Bay off Cornwallis Island.

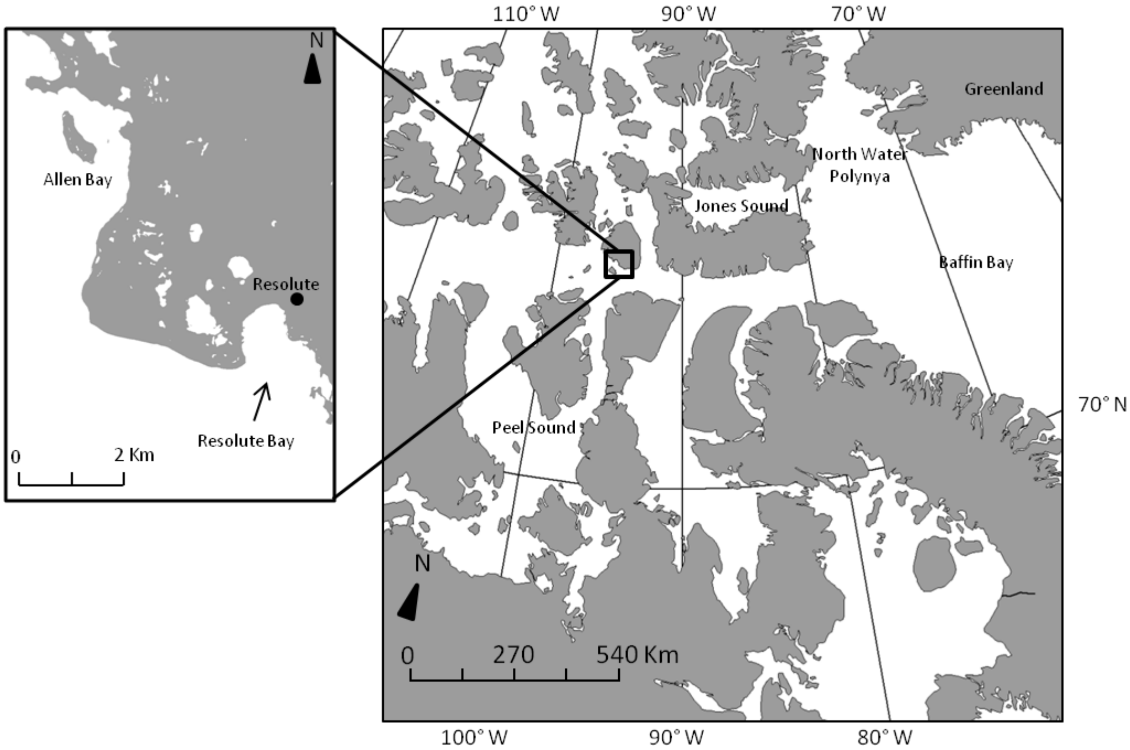


Figure 3.2: Frequency distribution of Arctic cod length (mm) collected from stomachs of ringed seal (*Pusa hispida*), beluga (*Delphinapterus leucas*), and narwhal (*Monodon monoceros*). Fork length was extrapolated from otolith length using ACL = 24.20*OL – 4.29 (Chapter 2).

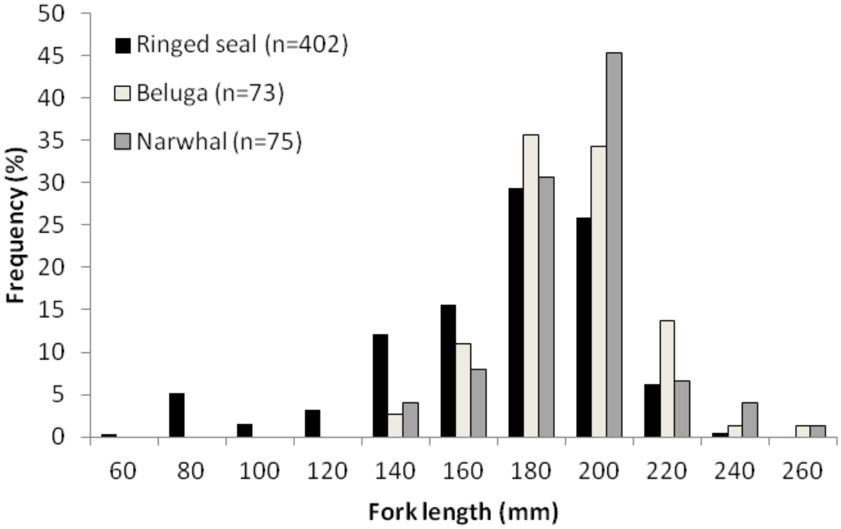


Figure 3.3: Mean ± 95% confidence intervals of liver (black symbols) and muscle (white symbols) $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) for ringed seal (*Pusa hispida*), beluga (*Delphinapterus leucas*), and narwhal (*Monodon monoceros*) collected near Resolute in 2010 and 2011.

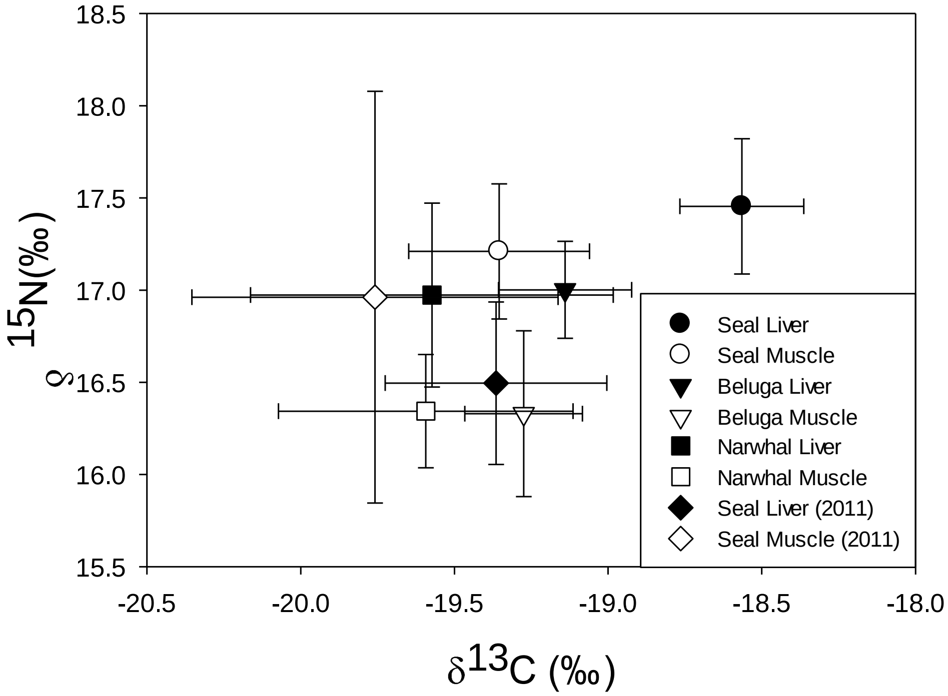
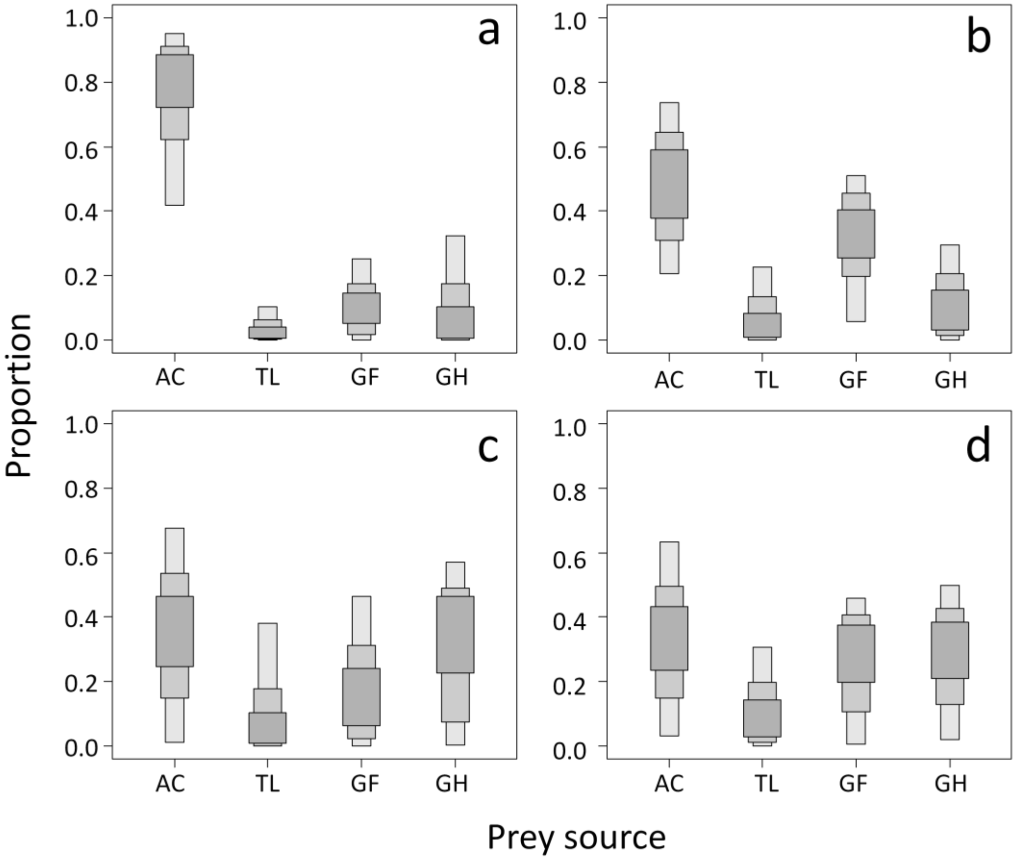


Figure 3.4: Mixing model output for beluga (*Delphinapterus leucas*) (a) liver and (b) muscle, and narwhal (*Monodon monoceros*) (c) liver and (d) muscle. Prey sources used in the model were Arctic cod (*Boreogadus saida*; AC), *Themisto libellula* (TL), *Gonatus fabricii* (GF), and Greenland halibut (*Reinhardtius hippoglossoides*; GH). The boxplots represent probability densities for credibility intervals of 95% (lighter boxes), 75%, and 50% (darker boxes).



Chapter 4: Seabird predation on Arctic cod during summer in the Canadian Arctic

Abstract:

Seabirds feed heavily on Arctic cod (*Boreogadus saida*) during the summer in the Canadian Arctic but little is known of the interactions among birds while foraging and the factors that drive feeding behaviour. The objective was to describe the relationship between seabirds and Arctic cod in a productive feeding area distant from breeding colonies. Transect surveys were completed using standardized count protocols to determine the density of seabirds in Allen Bay, Cornwallis Island, Nunavut. Shore-based observation sites determined seabird foraging behaviour associated with the presence of schools and environmental variables. The density of birds (156 birds km^{-2}) was high compared to other locations in the Canadian Arctic. Several bird species were more active early in the morning and with winds from the South possibly due to an increase in Arctic cod feeding on zooplankton at the surface. Northern fulmar (*Fulmarus glacialis*) and black-legged kittiwake (*Rissa tridactyla*) captured Arctic cod directly from the water however lost nearly 25% of captures to glaucous gull (*Larus hyperboreus*) and parasitic jaeger (*Stercorarius parasiticus*). These kleptoparasitic seabirds benefited the most in Allen Bay obtaining as much as eight times more Arctic cod than species capturing cod directly. Northern fulmars captured three times more Arctic cod from schools and black-legged kittiwakes captured similar proportions of schooling and non-schooling cod. I conclude that non-schooling Arctic cod are as important as schooling cod as an energy source for seabirds in nearshore areas such as Allen Bay, during the summer.

4.1. Introduction

The Canadian Arctic encompasses important marine habitats and productive regions, however ecological interactions within those areas are poorly understood (Niemi et al. 2010). Specifically, information on foraging behaviour of top predators within the Arctic marine environment is lacking (Reeves and Aubin 2001; Elliott et al. 2008). Understanding foraging decisions of top predators, such as seabirds, is key because they have important roles in the food web and are indicators of marine ecosystems (Piatt et al. 2007).

Seabirds use a number of strategies to capture marine prey directly including plunge diving, surface dipping, and pursuit diving underwater. Indirect captures are also important for species that steal food from other individuals. Kleptoparasitism is the act of obtaining food from other individuals through harassment, intimidation, or physical harm. This form of foraging is thought to be an adaptive method to obtain food when resources are limited (Giraldeau and Caraco 2000). Consequently, many species are opportunistic kleptoparasites, while few species rely mainly on kleptoparasitism to obtain food items (Furness 1987a). Kleptoparasitism can be beneficial because often less energy is expended compared to capturing prey directly (Stempniewicz and Iliszko 2010). Nevertheless, little attention has been given to this foraging method in the Canadian High Arctic.

The main prey item for marine seabirds in the Canadian High Arctic is Arctic cod (*Boreogadus saida*) as it is an abundant, ubiquitous, and high energy forage fish (Bradstreet et al. 1986). Consuming 12-32 individuals is energetically equivalent to approximately 34,500 calanoid copepods (Bradstreet and Cross 1982). As such, cod is a keystone species linking lower and higher trophic levels (Welch et al. 1992). Large feeding aggregations including hundreds of whales and seals, and thousands of seabirds have been described in relation to cod schools, with the suggestion that such an event could lead to the consumption of 20 tonnes of cod daily (Welch et al. 1993). However Arctic cod are spatially and temporally unpredictable and non-schooling cod may also be an important component of the Arctic marine food web.

This study describes the relationship between seabirds and Arctic cod in Allen Bay, Cornwallis Island, Nunavut, known for its abundance of cod and predatory interactions during the summer (Welch et al. 1993). The objectives were to: (1) determine the density of seabirds in Allen Bay; (2) examine predator activity and feeding behaviour in relation to environmental variables; (3) describe and quantify predatory interactions; and (4) determine the importance of cod schools as food sources. In addition to increasing the knowledge of the behavioural ecology of Arctic species, this study is important to establish the significance of nearshore marine habitats away from breeding colonies as energy sources during the summer.

4.2. Materials and Methods

Study Area

Allen Bay is located on the south-western end of Cornwallis Island, Nunavut, in the Lancaster Sound Region (74°43’36.78’’N 95°09’25.23’’W). It is a small (~200km^2) and relatively shallow (rarely >30 m) bay located near the hamlet of Resolute Bay. It is an important area for subsistence hunting of whales and seals. Ice break-up varies annually but in 2010 occurred in early August, although drift ice was continually present throughout the summer. The study area consisted of the southern-most section of the bay (approximately 10 km^2) (Fig. 11a). Surveys were conducted between 13-31 August 2010, and included observations of black-legged kittiwakes (*Rissa tridactyla*), northern fulmars (*Fulmarus glacialis*), glaucous gulls (*Larus hyperboreus*), parasitic jaegers (*Stercorarius parasiticus*), and Arctic terns (*Sterna paradisaea*).

Density of Seabirds

Parallel transects provided baseline information of seabird density (Fig. 11b). Boat speed was ~10-12 km hr^{-1} and one observer identified and counted birds. Transect start points were selected randomly. Additional transects were consecutively sampled at 500 m intervals based on a random selection of travel direction (Fig. 11b). The orientation of transects was selected to avoid bias relating to expected sighting gradients and therefore ran perpendicular from a straight line enclosing the bay (Fig. 11b). The pattern of search was a 90° arc from bow to side beam using the strip-width method at 150 m to enumerate seabirds (Fig. 11b). Distance estimates were checked daily with a laser range finder. The survey side (i.e., port or starboard) was selected so that the observer faced the overall direction of travel unless glare from the sun caused sighting difficulty (Fig. 11b). Each transect was divided into 300 m sections (i.e., ~110-sec intervals at 10 km hr^{-1}) in which birds flying within the strip (i.e. 300 m x 150 m) at the start of the section were instantaneous counts (Tasker et al. 1984). To avoid effect of the boat on bird behaviour, birds on the water or ice in each section were counted continuously as far ahead as possible (Gould and Forsell 1989). Birds associating with the boat were not included unless they were seen within the survey section prior to the change in behaviour.

Shore-based observations

Foraging activity and *feeding behaviour* were recorded from elevated positions on shore. Sample periods were divided into 6-hr categories (0:01-6:00; 6:01-12:00; 12:01-18:00; and 18:01-24:00) during 24 hours of daylight. Three locations were randomly sampled for ~ 4 hours in each time category (i.e., total of 16 hours per location). The following environmental variables were collected because little information is available on direct extrinsic influences on foraging behaviour of seabirds in the High Arctic: wind speed (km hr^{-1}), wind direction (deviation from South), tidal state (ebb or flood tide), visibility (km), air temperature (°C), Beaufort scale (an empirical scale to measure wind speed locally using wave action), and presence of ice (estimated percent cover in study area and bay).

Four shore-based observation sites were selected (Fig. 11a) based on visibility, access, and heterogeneity of the local marine environment. Lookout 1 (74°43'46.12"N 95°01'25.79"W) and 3 (74°43'59.83"N 95°02'48.45"W) covered a relatively homogeneous area of the bay with depths >15 m. Lookout 2 (74°44'55.10"N 95°03'07.45"W) covered the area in the vicinity of McMaster River outflow (Fig. 11a). It exhibited the most tidal effects in the study area as small islands were partially or completely submerged at high tide and a shallow shoreline was exposed at low tide. Lookout 4 (74°43'01.88"N 95°03'42.19"W) referred to Dynamite Shoal, a narrow (<100 m) shoal usually <5 m deep extending from Dynamite Beach where build-up of thick ice floes was common.

Foraging Activity

Lookouts 1, 2, and 4 were fixed (Fig. 11a) and sampling plots ~300 m^2 adjacent to the shoreline were established based on initial observations that every individual entering the area was visible to the observer. Foraging behaviour was defined as the search for prey (flying and swimming), direct feeding or attempting to feed, and indirect interaction with prey (e.g., kleptoparasitism). Seabirds passing through the grid were counted with the aid of 10x15 binoculars in 15-min intervals to avoid multiple counts of the same bird and observer fatigue. Seabirds on ice floes, fast ice and water while in the grid were not counted unless they demonstrated foraging behaviour.

Feeding Behaviour

Lookouts 2, 3, and 4 were used as observation sites and sample plots ~1 km^2 were created using landmarks on May Island and the adjacent shoreline. Each plot was divided into three sections to ensure independent sampling (Fig. 11a). A foraging bird was randomly observed for 5 min in a section using a 15-45x 60 mm spotting scope. As glaucous gulls and parasitic jaegers were less abundant, individual observations were omitted if they could not be located after 1 min. Arctic terns were not included in the analysis of feeding behaviour on cod because they only consumed surface invertebrates. Otherwise, for all species, the first foraging individual was chosen for observation. An individual's time flying, on ice, and on water; feeding attempts; agonistic interactions between birds; and presence of cod schools were recorded. Elevated lookout sites enabled identification of cod schools from a distance. Although rare, if confirmation of a school was not possible (e.g., waves), foraging seabird behaviour was used to discriminate between schooling and non-schooling cod. For example, many birds were attracted to an area when a school was present (cf. Hoffman et al. 1981) and dived repeatedly but if individual birds were feeding on non-schooling cod other birds were rarely attracted and repeat dives were rare. If the bird was lost or the distance was too far for accurate identification sampling was terminated. If cod was not seen in the beak when feeding or stealing, the event was considered unsuccessful. Cod was the only fish species captured by seabirds and by gillnetting in Allen Bay during the study, confirming it was the only pelagic fish.

Analysis of Data

Locations were pooled for feeding as there was no difference for both feeding attempts (Kruskal-Wallis test; n=314, P=0.80) and successful captures (Kruskal-Wallis test; n=314, P=0.58). Principal component analysis (PCA) was used to compare environmental variables (correlation matrix – log transformed), seabird activity and feeding (variance-covariance matrix – log transformed). Redundancy analysis (RDA) was used to determine the influence of environmental variables on feeding behaviour and foraging activity (log transformed). To avoid multicollinearity, if several variables were strongly associated in the PCA, only one of them was included in the RDA. Visibility was removed from analyses due to a small range throughout the study period. Exploratory linear regressions were completed for the above scenarios prior to ordination techniques in order to reveal the most important variables. For PCA and RDA plots, variables furthest from the origin have greatest discriminatory ability. Variables plotted closely together show a strong positive association and those plotted directly opposite show a strong negative association. Observations for each daily study period were averaged to ensure independent analysis. If there was an extended break (>4 hours) between study periods or location changed during the same day, observations were grouped separately. Feeding on cod (excluding kleptoparasitism) was assessed with logistic regression (LR) where presence of schools was the dependent variable and feeding success (i.e. from air or water) was the independent variable. The presence of cod schools differed among lookout locations (Kruskal-Wallis test; n=309, P<0.01), however due to a low sample size all locations were pooled. All 5-min sampling periods were analyzed as individual observations (instead of average values) to maximally represent species-specific foraging behaviour and all feeding observations were standardized on a min^{-1} basis. Alpha was set to 0.05. Ordination analyses were completed using SYN-TAX Ordination 2000. All other analyses were completed using SAS 9.1.

4.3. Results

Density of seabirds

Forty four transects (77.6 km) were completed at an average speed of 10.51 km hr^{-1} (Table 12). Northern fulmar and black-legged kittiwake (hereafter referred to as fulmar and kittiwake) were the most abundant seabirds while glaucous gull, parasitic jaeger and Arctic tern had lower densities (Table 12). A total of 1811 birds (five species) were counted with a density of 156 birds km^{-2} (Table 12). Kittiwakes were more likely to be on ice while fulmars preferred the water, and glaucous gulls occurred equally on water or flying (Table 12). Iceland gulls (*Larus glaucoides*) were rare (<5%) in Allen Bay but may have been included in glaucous gull density estimates due to the difficulty deciphering the two species.

Foraging activity

Foraging activity was recorded over 15 sampling periods and 191 replicates (47.75 hrs). Foraging seabirds in the sample grid showed no association with each other (Fig. 12a). Fulmar, kittiwake, and parasitic jaeger were more active in the early morning and with winds from the South (Fig. 12b). Glaucous gull was positively associated with low wind speed, low Beaufort scale, ebb tide, and high ice in the bay (Fig. 12b). By contrast, Arctic tern was not affected by the environmental variables listed (Fig. 12b).

Feeding behaviour

Fulmar (n = 132; 488.5 min total observation time) and glaucous gull (n=55; 196.5 min total observation time) flew and rested on water or ice almost equally (Fig. 13a). Kittiwake (n=100; 381.5 min total observation time) and parasitic jaeger (n=22; 99.5 min total observation time) spent the majority of foraging time in flight (Fig. 13a). Only fulmar fed on prey other than cod, including zooplankton and food scraps from hunters (cf. Mallory et al. 2010).

Fulmar successfully captured cod 24% and 19% of the time when diving from air (21 attempts) and the water surface (32 attempts), respectively (Fig. 13b). The kittiwake's success rate when plunging from air was 49% (49 attempts) and did not attempt to feed from the water surface (Fig. 13b). Glaucous gull successfully fed by plunge diving (50%) and dipping from surface (100%) however direct feeding attempts (i.e., 6) were rare (Fig. 13b). Fulmar, kittiwake, and glaucous gull made 0.10, 0.13, and 0.03 feeding attempts per minute of foraging, respectively. The parasitic jaeger was not observed capturing cod directly.

Fulmar and kittiwake had ~25% of captures stolen but stole few cod (<10% of cod consumed) from other birds (Fig. 13c). Glaucous gull and parasitic jaeger successfully stole cod 44% and 26% of agonistic interactions, respectively (Fig. 13c). Table 13 lists the net average number of fish caught per hour of foraging.

Fulmar was more successful at capturing cod during periods of lower wind speeds and early (0:01-6:00) in the morning (Fig. 14). Later in the day (18:01-24:00) there were less successful captures from dives underwater. Higher wind speeds were associated with less captures from air but higher air temperatures and winds from the South were associated with more captures (Fig. 14). Kittiwake feeding was not strongly correlated with environmental variables based on the RDA (axis_1:20.99%, axis_2:0.34% of total feeding variance).

Fulmar had more feeding attempts (LR; n=132, $X^2 = 4.50$, L = -0.80 + 2.89x, P=0.03) and were more successful (LR; n=132, $X^2 = 4.22$, L = -0.73 + 11.11x, P=0.04) when diving from water (Table 15). Glaucous gull captured significantly more schooling cod than non-schooling cod (LR; n=60, $X^2 = 5.50$, L = -0.79 + 11.59x, P=0.02) (Table 14). Although not statistically significant the following observations are interesting. There were more feeding attempts by all species of birds and greater feeding success when schools of cod were present (Table 14). Also, the mean success rate of capturing schooling and non-schooling cod was similar at 37% and 39%, respectively, for all species of birds. Finally, fulmars captured three times more cod from schools (Table 14). A total of 40 cod were captured directly (50% schooling; 50% non-schooling) during the feeding behaviour study.

4.4. Discussion

Density of seabirds

Seabird population data are lacking in much of the Canadian Arctic (Mallory and Fontaine 2004; Niemi et al. 2010), particularly in locations distant from breeding colonies. Our density estimates of seabirds in Allen Bay were high compared to other studies in the Canadian Arctic using similar techniques. McKinnon et al. (2009) reported a density of 3.6 ± 0.5 birds km^{-2} in early fall in the Northwest Passage (Table 12) and Diemer et al. (2010) reported encounters of 5.5 birds km^{-1} (equivalent to 18.4 birds km^{-2}) in Cumberland Sound during the summer (Table 12). Allen Bay is a smaller more protected area than either the Northwest Passage or Cumberland Sound and has significant concentrations of Arctic cod, fulmars, and kittiwakes during the summer. The nearest breeding colony of fulmars and kittiwakes is >100 km and ~50 km, respectively (Mallory and Fontaine 2004) and does not appear to be factor affecting our density estimates since many of the birds using Allen Bay are likely non-breeding or immature individuals (M. Mallory, pers. comm.). Perhaps scale affected density estimates but until data is collected from larger concentrated feeding areas we can only speculate on its effect.

Foraging Activity

Foraging activity of fulmar, kittiwake, glaucous gull and parasitic jaeger was affected by environmental variables such as time of day, wind, tide, and ice. The strong association of fulmar, kittiwake, and parasitic jaeger activity with wind direction from the South may be attributable to an increase in fish movement into the area. For example, with strong winds (>30km hr^{-1}), zooplankton located within Resolute Passage or the

Barrow Strait may be pushed north into Allen Bay causing upwelling (Lagadeuc et al. 1997; Carmack and Macdonald 2002) and attracting cod. In this study fulmar activity was not positively associated with wind speed but on occasions when winds reached as much as 50 km hr^{-1} fulmars were usually the only species in flight. This behaviour is supported by Furness and Bryant (1996) who suggested fulmars glide during high wind speeds at sea to reduce field metabolic rates.

Glaucous gull and parasitic jaeger foraging activity was independent of the species they stole from (Fig. 12a) suggesting their movements are more readily affected by environmental variables (e.g., Bélisle and Giroux 1995). Both wind speed and Beaufort scale affected glaucous gull activity indicating it is not profitable to forage in strong winds with poor water visibility in Allen Bay. Although cod was stolen from species that showed no strong association with tide (Fig. 12b) the glaucous gull may be foraging during ebb tide to maximize its ability to capture prey directly when the water level is lower and prey may be more exposed (e.g., Moore et al. 2008).

Feeding Behaviour

Two basic feeding strategies by marine birds to capture schooling and non-schooling cod were identified in Allen Bay: direct feeding (diving from air and water, and surface dipping); and indirect feeding (kleptoparasitism). Fulmars are only capable of shallow dives underwater (<2.6m deep) (Garthe and Furness 2001). They had a higher dive success rate from water when a school was present but capture rates were lower compared to the other birds (Table 13). This indicates an inability to pursuit-dive underwater to exploit non-schooling cod. Since fulmars were more likely to successfully feed when the wind speed was low, wave action and visibility at the water surface may reduce their ability to see and capture prey. While the fulmar has adaptations to reduce energetic requirements, such as low basal metabolic rate (Birt-Friesen et al. 1989; Bryant and Furness 1995), and increased lipid metabolism to reduce flight load (Warham 1997), its poor foraging success on cod (e.g., Table 13) likely explains why it was observed consuming organisms other than cod, unlike the other birds. Finally, the higher feeding success by fulmars in the morning (i.e., 0:01-6:00) may reflect the presence of cod near the surface feeding (c.f. Benoit et al. 2010). Since cod feed on amphipods and calanoids that migrate to the surface at night during late spring (Fortier et al. 2001) and summer (Sameoto 1984) this may make them more vulnerable to shallow diving birds.

Kittiwakes relied exclusively on capturing cod directly by plunge diving from the air and spent little time on the ice or on water while foraging (Figure 3a). Daunt et al. (2002) calculated that 47% of time was spent flying during foraging trips (excluding flight from the colony) in the North Sea. My observations, which selectively chose birds exhibiting foraging behaviour, may account for the higher flying time (i.e. 75%). However, kittiwakes use flexible foraging strategies in response to local conditions (Daunt et al. 2002)**.** The high success rates may result in shorter foraging bouts and higher flight time during those bouts. Welcker et al. (2010) reported that kittiwakes did not adjust their metabolic rate in response to environmental variability, suggesting they have little buffering capacity against extrinsic factors and constantly perform close to an energetic ceiling. Perhaps this explains why environmental variables did not strongly influence kittiwake feeding. Even if cod schools were influenced by wind direction and wind speed, kittiwakes were able to forage independently of schools since they feed as efficiently on non-schooling cod. Since schools are patchy and often unpredictable, the ability to exploit non-schooling fish may explain why kittiwakes are typically more piscivorous in other parts of the Arctic compared to fulmars and glaucous gulls (Bradstreet 1976; Hobson 1993). Kittiwakes were the most successful at capturing cod, and it follows that they were also the species most commonly kleptoparasitized. Nevertheless, if we assume a breeding adult requires 215 g cod day^{-1} (Brekke and Gabrielsen 1994) or 6.44 cod day^{-1} based on size measurements from Allen Bay (Welch et al. 1993), foraging for 4 hours per day is sufficient to meet energetic requirements.

Glaucous gulls and parasitic jaegers were responsible for the majority of cod stolen from other birds. The glaucous gull was highly efficient, capturing prey from other birds in almost half its attempts. Glaucous gulls were also successful at capturing cod directly but few attempts were made indicating they rely more on other birds. Optimal foraging theory predicts that predators will forage to maximize the net intake of energy (Stephens and Krebs 1986). Kleptoparastism appears to be more energetically profitable than capturing cod directly. While glaucous gull uses its speed and size to steal food, the parasitic jaeger utilizes its aerial-acrobatics skill to harass other birds thereby optimizing its chance of acquiring food. Furness (1987b) suggested that a successful stealing rate of 10-20% for parasitic jaegers would be sufficient to sustain food stealing as a foraging strategy. Based on the success rate of stealing cod, glaucous gulls and parasitic jaegers are likely able to survive around Allen Bay during the summer without any other foraging method. It is not surprising that fulmars only lost cod to glaucous gulls while kittiwakes lost many captures to both parasitic jaegers and glaucous gulls. Since fulmars usually remain on the water after captures, parasitic jaegers were unable to use their aerial-acrobatic skill to successfully steal cod. By contrast glaucous gulls efficiently stole cod from birds in air and on water using their speed and size. Acquiring Arctic cod from other birds was also observed for common ravens (*Corvus corax*) when they consumed discarded cod along the shore (Appendix). This opportunistic scavenging behaviour further highlights the importance of associating or interacting with other species to gain food.

Conclusion

This study has provided new information on seabird foraging in relation to a keystone species in the Canadian Arctic, but there are some limitations. Initially, non-schooling cod may have been overestimated since schools could have been present but unseen. Further, since observation periods were averaged to ensure independent results, the sample size was reduced. Finally, this was a single-year study and future changes in cod distribution and environmental variables may affect foraging.

To my knowledge, this is the first systematic study to describe and quantify direct observations of feeding interactions distant from breeding colonies in the Canadian High Arctic. Piatt et al. (2007) considered the most important parameters to study seabirds as indicators are associated with foraging grounds (as opposed to breeding colonies) because most responses depend on prey acquisition from the sea.

Seabirds are typically opportunistic generalists but in Allen Bay showed specialized feeding on cod during the summer. Both schooling and non-schooling cod were important sources of energy for seabirds and differs from the hypothesis of Welch et al. (1992) that non-schooling fish provide a limited energy source for predators. Kleptoparasitism was a major component of interspecific interactions in this area of the Arctic during the summer and may be somewhat unique. Kleptoparasitism enabled glaucous gulls and parasitic jaegers to obtain up to eight times more cod compared to direct feeding by fulmars and kittiwakes. Harding et al. (2007) suggested that seabird responses to differing prey availability could be used as indicators of fish distribution. I provided evidence that seabirds are indicators of the marine ecosystem in a nearshore Arctic feeding area.

Table 4.1: Transect survey results for the density (birds km^{-2}) of seabirds in Allen Bay.

	This study	**Diemer et al. 2010**	**McKinnon et al. 2009**
Date	Aug 17-28, 2010	Jul 29-Aug 9, 2008	Sep 16-21, 2005
Transect (n)	44	31	132
Total Distance (km)	77.6	173.1	526.7
Area Covered (km^2)	11.6	51.93	158
Mean Speed ($km\ hr^{-1}$)	10.5	15-17	7.4-35
Total Birds	1809	953	588
Total Density on water	75		2
Total Density flying	45		2
Total Density on ice	36		
Total Density	155	18	4
Total Density of Species			
Northern fulmar	58	<1	1
Black-legged kittiwake	63		<1
Glaucous gull	27	6	<1
Arctic tern	4		
Parasitic jaeger	<1		
Density on water			
Northern fulmar	44		1
Black-legged kittiwake	20		<1
Glaucous gull	10		<1
Arctic tern	1		
Density flying			
Northern fulmar	14		1
Black-legged kittiwake	18		<1
Glaucous gull	10		<1
Arctic tern	3		
Parasitic jaeger	<1		
Density on ice			
Northern fulmar	1		
Black-legged kittiwake	29		
Glaucous gull	7		
Parasitic jaeger	<1		

Note: When McKinnon et al. (2009) and Diemer et al. (2010) presented values as abundances and encounter rates, respectively, density was calculated based on described methods.

Table 4.2: Net amount of Arctic cod (*Boreogadus saida*) consumed by seabird species.

Species	**cod consumed hour of foraging^{-1}**
BLKI	1.73
NOFU	0.61
GLGU	4.89
PAJA	4.82

Note: GLGU = glaucous gull (*Larus hyperboreus*), PAJA = parasitic jaeger (*Stercorarius parasiticus*), NOFU = northern fulmar (*Fulmarus glacialis*), BLKI = black-legged kittiwake (*Rissa tridactyla*). Note: values calculated by dividing the total cod captured directly and lost/gained during antagonistic interactions by the total time observed per species.

Table 4.3: Feeding attempts and success of seabird species in relation to schooling and non-schooling Arctic cod (*Boreogadus saida*). Values are presented as mean ± S.E.

		Non-schooling	**Schooling**	**P-value**
All species n = 309	Feeding Attempts	0.08 ± 0.01	0.11 ± 0.02	0.16
	Successful captures	0.03 ± 0.01	0.04 ± 0.01	0.37
BLKI n = 100	Successful captures	0.08 ± 0.02	0.06 ± 0.02	0.57
NOFU n = 132	Successful captures	0.01 ± 0.01	0.03 ± 0.01	0.07
GLGU n = 60	Successful captures	0.01 ± 0.01	0.07 ± 0.02	**0.02***

Note: GLGU=glaucous gull (*Larus hyperboreus*), NOFU=northern fulmar (*Fulmarus glacialis*), BLKI=black-legged kittiwake (*Rissa tridactyla*).
* denotes significant values.

Table 4.4: Feeding attempts and success of northern fulmar (*Fulmarus glacialis*) (n=132) from plunge dives (from air) and dives underwater from the surface (from water) in relation to schooling and non-schooling Arctic cod (*Boreogadus saida*). Values are presented as mean ± S.E.

		Non-schooling	**Schooling**	**P-value**
Feeding attempts	From air	0.04 ± 0.01	0.05 ± 0.02	0.65
	From water	0.04 ± 0.01	0.10 ± 0.03	**0.03***
Successful dives	From air	0.01 ± 0.01	0.01 ± 0.01	0.98
	From water	<0.01	0.02 ± 0.01	**0.04***

* denotes significant values

Figure 4.1: (a) Study area in Allen Bay, Cornwallis Island, Nunavut including shore-based observation locations. Sample plots for seabird feeding behaviour study are also included. Each location (i.e. Lookout 1 – L1; Lookout 2 – L2; Lookout 4 – L4) was divided into 3 sections (i.e. 1, 2, 3) using visible landmarks and was alternated randomly after each five minute sample period. (b) Example of boat route for the survey to determine the density of seabirds.

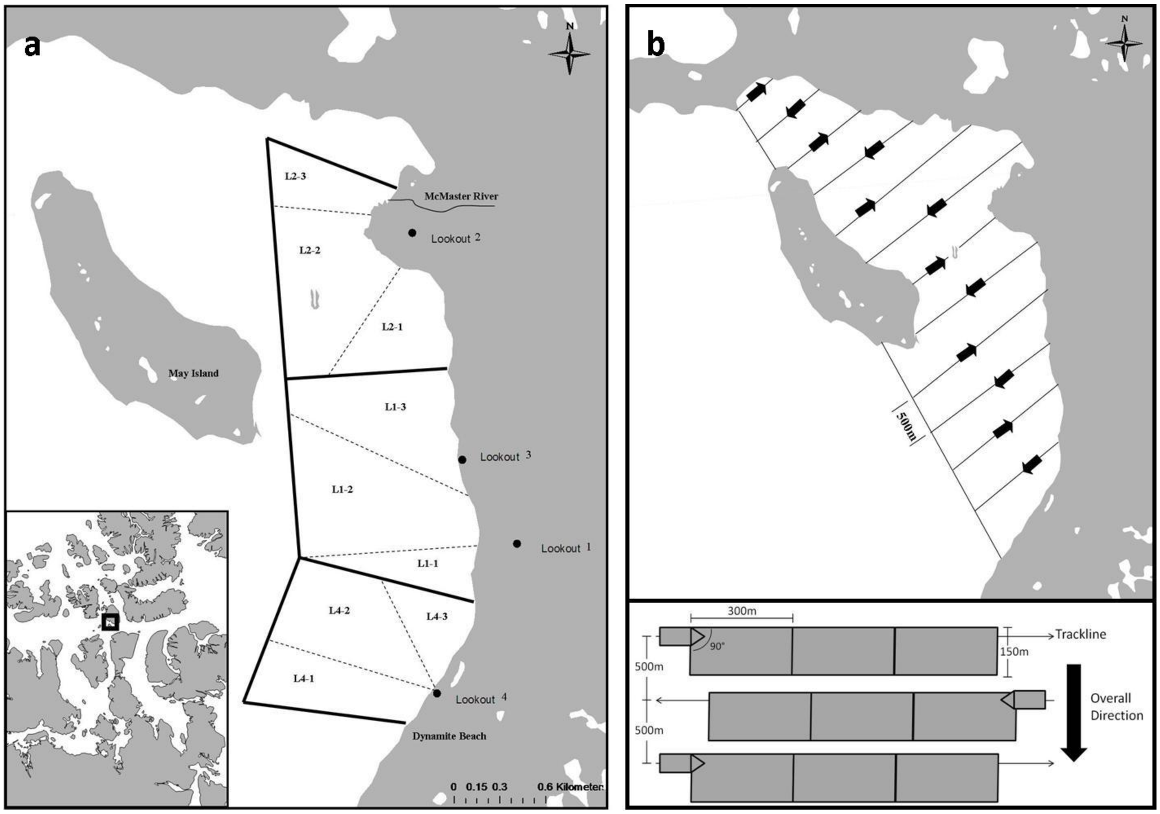


Figure 4.2: (a) Principal component analysis ($axis_1$: 57.46%, $axis_2$: 16.81% of the total variance) and (b) redundancy analysis ($axis_1$:20.66%, $axis_2$:7.94% of total activity variance) of seabird activity. ARTE= Arctic tern (*Sterna paradisaea*), GLGU = glaucous gull (*Larus hyperboreus*), PAJA = parasitic jaeger (*Stercorarius parasiticus*), NOFU = northern fulmar (*Fulmarus glacialis*), BLKI = black-legged kittiwake (*Rissa tridactyla*). Small squares associated with numbers refer to lookout sites. Larger squares and ovals represent associated variables and/or species. Note: Air temperature was positively associated with wind direction in the PCA and was removed to avoid multicollinearity. Similarly, tide and ice (in the bay) were removed as they were associated with wind speed.

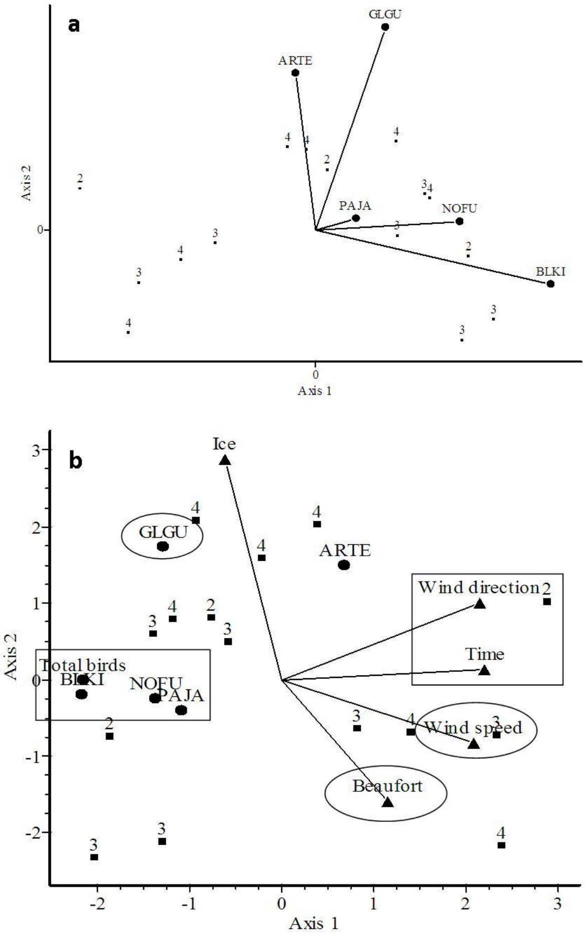


Figure 4.3: (a) Total time (%) spent flying, on water, and on ice/shore during the feeding behaviour study. (b) Total feeding attempts (successful and unsuccessful) from either plunge dives from the air or dives from the water surface (standardized min^{-1} foraging). (c) Total counts of seabird antagonistic interactions (successful and unsuccessful). GLGU = glaucous gull (*Larus hyperboreus*), PAJA = parasitic jaeger (*Stercorarius parasiticus*), NOFU = northern fulmar (*Fulmarus glacialis*), BLKI = black-legged kittiwake (*Rissa tridactyla*).

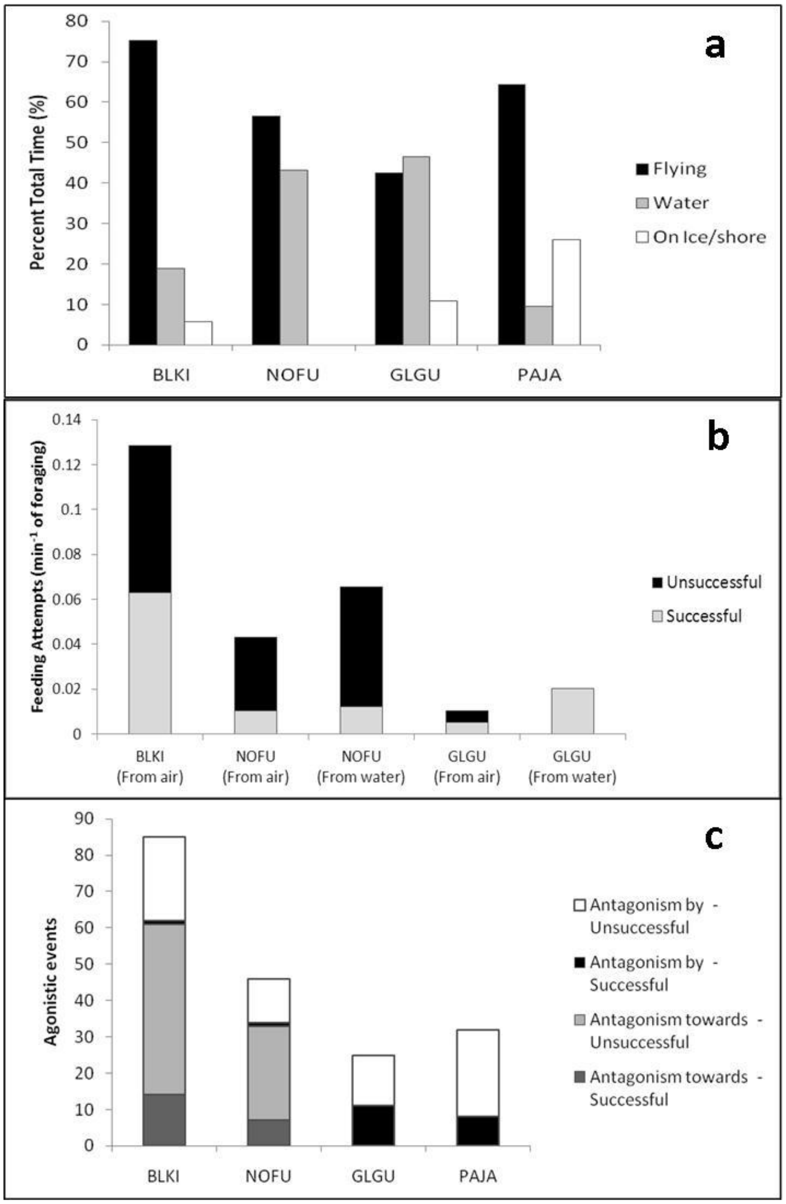
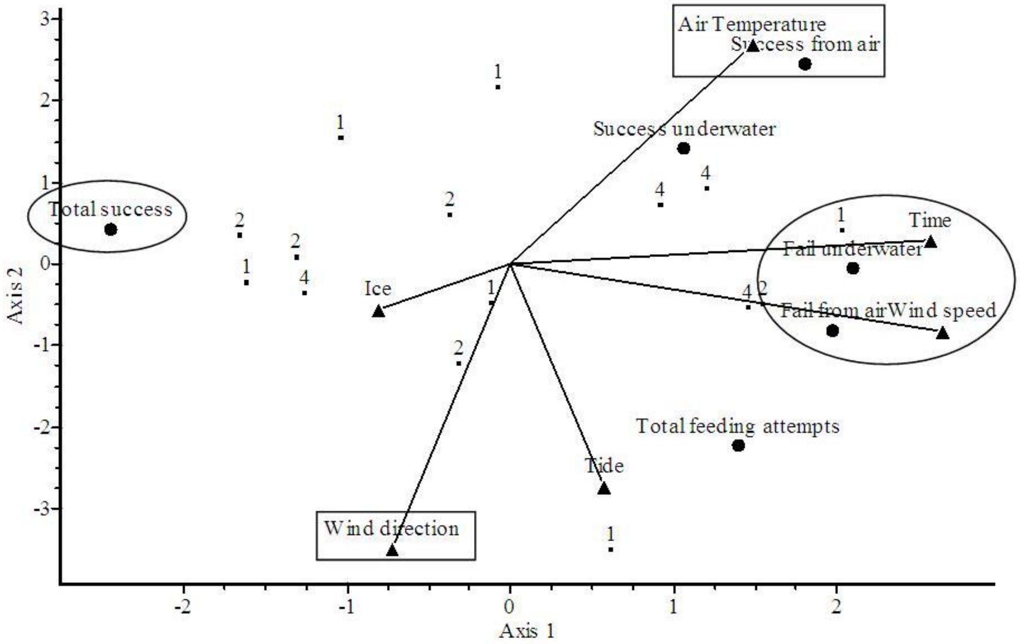


Figure 4.4: Redundancy analysis (RDA) of northern fulmar (*Fulmarus glacialis*) in relation to environmental variables for 15 sampling periods (axis$_1$:16.99%, axis$_2$:11.34% of total feeding variance.   Small squares associated with numbers refer to lookout sites. Larger squares and ovals represent associated variables and/or species. Note: Beaufort scale was removed to reduce multicollinearity with wind speed. Ice represents the percentage ice in the study area.



Chapter 5: The application of hydroacoustics to study the distribution of Arctic cod and behaviour of shallow-diving seabirds in the Canadian Arctic

Abstract:

Productive areas in the Canadian Arctic seasonally provide top predators with accessible and often predictable sources of energy. Arctic cod (*Boreogadus saida*) school in shallow bays during the summer and are exploited by seabirds and marine mammals. Information concerning how prey are presented to predatory seabirds, and the cues seabirds use to optimize foraging potential is limited. Hydroacoustic surveys were completed in Allen Bay, Nunavut to determine the presence, density, abundance, and depth of Arctic cod schools in relation to shallow-diving seabirds. Schools were also documented using standardized protocols to examine the influence of environmental variables (e.g., wind, ice, tide state) and seabird behaviour. The presence of schools was a significant predictor of the distribution of northern fulmars (*Fulmarus glacialis*) but not black-legged kittiwakes (*Rissa tridactyla*). Glaucous gulls (*Larus hyperboreus*) associating with northern fulmars are likely optimizing chances of stealing Arctic cod. The density, size, and depth of schools did not significantly affect the distribution of the seabirds. I speculate that Arctic cod from demersal schools separate to feed at the surface in satellite schools (groups of dispersed fish), thus reducing competition but increasing risk of predation.

5.1. Introduction

High-density aggregations of prey provide efficient transfer of energy through marine food webs by maximizing predator-prey encounter rates and minimizing predator search efforts (Davoren et al. 2003a). The recurrence of these aggregations in predictable locations enables foraging species to utilize productive areas repeatedly (i.e., seasonally) (Irons 1998). These locations are found by memory or by reacting to cues of other animals (Davoren et al. 2003b), and act as vital resources in an environment where high energy prey is often difficult to locate (Irons 1998). How seabirds distribute and locate prey is critical to understand the importance of aggregations and their influence on predator-prey interactions. This is especially significant given the concerns of anthropogenic impacts affecting the Arctic ecosystem. In addition to predator behaviour, determining the conditions that influence the behaviour of prey is important to understand how seabirds associate with prey (Piatt et al. 1989).

Arctic cod (*Boreogadus saida*) is a small circumpolar fish that is an important link between lower and higher trophic levels (Welch et al. 1992). It is the major diet item of top predators in the Arctic and provides more than 2000 times the energy of a single calanoid copepod (Bradstreet & Cross 1982). During the summer, Arctic cod aggregate in shallow bays where they are exposed to seabird predation (Welch et al. 1993). The recurrence of Arctic cod in Allen Bay on the southern coast of Cornwallis Island, Nunavut is an annual source of energy for seabirds. The number of fish per school varies but is estimated to exceed 900 million individuals (Crawford & Jorgensen 1996). Arctic cod also distribute as scattered or dispersed individuals at low densities (Crawford & Jorgenson 1993). The movements of Arctic cod are influenced by ocean conditions (i.e., temperature and salinity), feeding behaviour, and predator avoidance (Benoit et al. 2008; Geoffroy et al. 2011; Crawford et al. 2012).

Most studies, to date, describe the feeding of deep diving seabirds (e.g., murres) and deep schools (>25m) (e.g., Mehlum et al. 1996; Logerwell et al. 1998; Davoren et al. 2003a). By contrast, not much is known about foraging cues for shallow-diving seabirds. Moreover, as seabirds exhibit different foraging patterns in response to prey (Elliott et al. 2008), the extent of association is likely species-specific. Surface feeding seabirds such as northern fulmars (*Fulmarus glacialis*) and black-legged kittiwakes (*Rissa tridactyla*) are important components of the Arctic ecosystem, estimated to consume ~11,000 tonnes of Arctic cod annually in the Lancaster Sound Region (LSR) (Welch et al. 1992). According to Hobson and Welch (1992) and Garthe and Furness (2001) northern fulmars only pose a threat to fishes distributed within the upper 3m of water. Our observations of diving behaviour support this and we estimate black-legged kittiwakes are restricted to the top 1m. Compared to deep-diving birds such as the thick-billed murre (*Uria lomvia*), northern fulmars and black-legged kittiwakes consume more Arctic cod per individual in the Canadian Arctic (see Table 8 in Welch et al. 1992; see Table 18 in Mallory & Fontaine 2004).

Standardized observations and hydroacoustic surveys were used to examine the predator/prey behaviour of shallow-diving seabirds and Arctic cod in a nearshore habitat to identify cues predators use to locate prey. Preliminary observations revealed that northern fulmars primarily fed on schooling Arctic cod while black-legged kittiwakes captured dispersed and schooling Arctic cod equally (Chapter 4). Based on these observations I hypothesized that the presence of schools significantly influenced the distribution of northern fulmars but not black-legged kittiwakes. I predicted that the density of northern fulmars would be highly correlated with schools but the density of black-legged kittiwakes would not. Since schools represent large pools of energy for seabirds, my second hypothesis was that the nature of the schools (areal density, number of individuals, and the minimum depth of schools) are key factors attracting northern fulmars and black-legged kittiwakes to schools and there will be a density-dependent relationship. By contrast, glaucous gulls (*Larus hyperboreus*) acquire food indirectly by stealing Arctic cod from other birds, particularly northern fulmars (Chapter 4). Consequently, my third hypothesis was that the association of glaucous gulls with northern fulmars is more important than the presence or nature of the schools. I predicted that glaucous gulls associate with northern fulmars whether or not schools are present and this association is unrelated to school size, fish density and depth. Specifically, the objectives of this study were to: (1) determine the extent to which seabirds distribute in relation to Arctic cod and their potential as indicators of fish distribution; (2) examine cues that predators react to in order to maximize foraging potential; and (3) describe the importance of schooling for predators.

5.2. Materials and Methods

Study Area

Allen Bay is located in the Canadian Arctic Archipelago (74°43’36.78’’N 95°09’25.23’’W) (Fig. 15). It is a small (~200km^2), shallow (rarely >30m deep) bay located near the community of Resolute on Cornwallis Island. The bay opens on the productive Resolute Passage and LSR (Cota et al. 1987; Welch et al. 1992). The timing of ice break-up varies annually and in 2010, it occurred in early August, although drift ice was continually present throughout the summer. Once ice moves out of the bay, seabirds return to the area annually to feed on schools of Arctic cod. This study focussed on the southeastern part of the bay (approximately 10km^2) (Fig. 15) after an initial survey revealed fish and predation activity were less common in the north. Preliminary observations of seabird and cod behaviour began in early July 2010.

Shore-based survey

The shore-based survey studied the influence of environment variables as predictors of the presence of schools from 13-31 August 2010. Individual foraging seabirds were randomly observed for five minutes from three elevated locations on shore. Sample periods were divided into 6-hr categories (0:01-6:00; 6:01-12:00; 12:01-18:00; and 18:01-24:00) during 24 hrs of daylight. Observation periods at each location were ~4 hrs in each time category (i.e., total of 16 hrs per location) (Fig. 15). Environmental variables and presence (or absence) of Arctic cod schools were recorded. Environmental variables included: wind speed (km hr^{-1}), wind direction (deviation from South), tidal state (ebb or flood tide), air temperature (°C), Beaufort state (0-5) (a measure of wave action), and presence of ice (estimated percent cover in study area and bay) (See Chapter 4 for more detail).

Elevated lookout sites on land enabled visual detection and characterization of schools close to the surface. A number of cues were used to detect schools including dark areas in the water (i.e., evidence of a school), turbulence caused by surface-dwelling fishes, and foraging activity of predators such as seabirds, seals, and whales. Location, size, and shape of schools were recorded. Estimates of school size were based on surface area and then standardized using a qualitative scaling grade of 0-5 ($0 \leq 30m^2 < 1 \leq 200m^2 < 2 \leq 1000m^2 < 3 \leq 6000m^2 < 4 \leq 10{,}000m^2 < 5$). If >100 birds were seen feeding on a single school or in a concentrated area, the species and number of birds, size and location of the school, and associated behaviours of predator and prey were recorded.

Hydroacoustic survey

Fish density and distribution was examined on 29 and 31 August 2010 with a BioSonics DTX hydroacoustic system (200 KHz; split beam; 6^o nominal half-power beam angle; 1 m blanking range) operated from a GPS-equipped 6.6 m skiff at 6.7 km h^{-1} (average). The transducer was mounted on a staff attached to the boat and fixed at the shallowest depth to avoid turbulence from the boat and waves (0.75 m). The system was calibrated with a tungsten-copper standard target (Foote et al. 1987) prior to the survey. Sampling (6 pings s^{-1}) commenced upon leaving the launch site and was conducted in an 'adaptive' zig-zag survey pattern (Fig. 15) to avoid drifting and grounded ice pans. When the northern extent of fish distribution was reached, the remainder of the survey covered the region southward to a shallow flat near Dynamite Beach (Fig. 15) where ice floes lodged in the shallow water restricted boat operations.

Individual target data (echo minimum threshold -65 dB) was extracted from the overall data set and analyzed separately (1 m depth bins). Minimum and maximum depths of each target, as well as ping numbers, local time and position (latitude and longitude) for leading and trailing edges were recorded. All targets were analyzed with target strength (TS) analysis (Visual Analyzer program; BioSonics, Inc.) to measure backscatter cross section and possibly derive acoustic estimates of fish size. Data from schools and groups of scattered fish (satellite schools), were analyzed with echo integration (EI) to derive estimates of area density (fish m^{-2}) and volume density (fish m^{-3}) (Crawford and Jorgenson 1996). Transect abundance (TA) of cod was obtained by multiplying area density times the length of the section of a school traversed during a transect (obtained from converting GPS coordinates marking the leading and trailing edges of the section). Arctic cod was the only fish species seen captured by seabirds, and over 40 days of gillnetting and seining in Allen Bay confirmed that cod was the only common pelagic fish species which is consistent with other studies in the same area (e.g., Crawford and Jorgenson 1993). Trap netting recovered Arctic cod and two benthic sculpin species.

Concurrent with hydroacoustic sampling the observer searched in a 90° arc from bow to side beam using the strip-transect method to enumerate seabirds and identify species. The strip width was 150m where birds on both sides of the boat were counted (i.e., 75m from the port and starboard side of the observer). Birds flying and resting on water and ice were counted instantaneously following Tasker et al. (1984) in ~250m long sections to compare with Arctic cod distribution at a fine-scale. Individual birds were counted only once.

Analysis of data

Akaike information criterion with a small-sample bias adjustment (AIC_c) (Akaike 1974; Burnham & Anderson 2002) was used to select the linear models that best associated environmental variables with the presence of Arctic cod schools during the shore-based survey. Linear regression was used to examine the relationship between size of schools and number of birds for large feeding events (>100 birds) observed from shore. Data from both days were pooled for the hydroacoustic component due to low sample size. Logistic regression was used to determine if density of seabirds (independent variable) was associated with the presence of schools (dependent variable). Each section (150m x 250m) was designated as a sample. The relationship between the number of birds and density of schools was examined by categorizing bird density in each section as being above or below the average density of each species during the survey. Logistic regression was then used to compare the areal density (i.e., fish per unit area or FPUA) of schools (independent variable) with presence of above- and below-average bird densities (dependent variable). Since sample size was low ($n<100$), each data set was also analysed using a Kolmogorov-Smirnov (K-S) test, but no difference was found. The P-values presented for these analyses represent the logistic regression tests. The minimum depth and TA were similarly compared to bird densities.

Spearman rank correlation (using densities) and Phi coefficient of association (using presence or absence) were used to explore the distributional associations between seabird species and schooling, and non-schooling Arctic cod. Fisher exact probability test (two-tailed) was used to determine significance of Phi coefficient. Jaccard's coefficient of similarity was also used but is not presented here as trends were the same as Phi coefficients. Seabirds resting on ice were not included in the analyses. Alpha was set to 0.05 for all analyses.

5.3. Results

Shore-based survey

Based on the optimal linear models applied to environmental variables, the presence of schools was best predicted by the presence of ice (positive association) and air temperature (negative association) (Table 16).

The first school of Arctic cod was observed 1 August 2010 and many were observed throughout the study period. The size, shape, and location of schools varied across the study area (Fig. 16, 3). Arctic cod often swam near the surface and close to shore in waters <10m deep. Moving schools were typically long and narrow while schools aggregating in a particular area were more compact (Fig. 16, 3). On several occasions the three species of seabirds followed a school when visible even if individual fish were too deep to capture.

Eight feeding events resulted in a large number of cod being captured, two of which were larval Arctic cod (Fig. 17). School size was not correlated with seabird abundance (df=5, R^2=0.071, P=0.609). On three occasions (School L, M, and N; Figure 3) schools aggregated near shore in water <2m where in one instance at least 164 Arctic cod were taken by <200 birds in only 10 minutes. These Arctic cod did not attempt to escape into deeper water but it was not clear why because there was no obvious predator pressure from below (e.g., from seals or whales; Welch et al. 1993). These feeding events were brief (<one hour) and resulted in the mortality of most individuals in a school. Other larger feeding events lasted longer (School I and K; Fig. 17). For example, on 15 August a group of nine belugas (*Delphinapterus leucas*) fed on a school close to shore and as a result, one of the largest concentrations of foraging birds during the entire

study period was observed (Fig. 17). When the belugas moved on, approximately half the birds followed, while the rest remained in the area for at least four hours, occasionally capturing dispersed Arctic cod presumably from the original school.

Hydroacoustic survey

Thirty six transects (25.4 km) were completed on 29 and 31 August and revealed that school distribution and shape was highly variable. On average, schools remained at depths >5m with vertical ranges between 6.2 and 18.4 m (Table 17). Maximum volume density (FPCM) ranged up to 614 fish m^{-3}, and the mean FPCM was 9.6 and 25.4 fish m^{-3} on 29 and 31 August, respectively (Table 17). Often small satellite schools were detected close to the surface near larger demersal schools (Fig. 18). This was corroborated by numerous independent observations on the water and also observing seabirds commonly feeding on loosely aggregated individuals at the surface.

On 31 August the northern section of the study area contained several schools and high densities of seabirds compared to the southern section (Fig. 19). Northern fulmars (P=0.007) and glaucous gulls (P=0.036) were significantly associated with the presence of Arctic cod schools but not black-legged kittiwakes (P=0.574) (Fig. 20). Above-average number of all species were present when schools were more dense, more numerous, and closer to the surface but the correlations were not significant (Fig. 21). Glaucous gulls were significantly associated with northern fulmars regardless if schools were present or absent (Table 18).

5.4. Discussion

Behaviour and distribution of Arctic cod

Higher ice cover and lower air temperature were significant predictors of schools of Arctic cod in Allen Bay. Arctic cod associate with sea ice during the spring and summer as they hide within ice cracks to avoid predators (Lønne & Gulliksen 1989; Gradinger & Bluhm 2004). Crawford & Jorgenson (1993) reported that schools occurred in denser aggregations in open water after wind pushed ice out of Resolute Bay (i.e., when ice cover diminished) and suggested this behaviour was related to predator avoidance. Arctic cod also associate with ice to feed on ice-adapted invertebrates (Bradstreet & Cross 1982; Lønne & Gulliksen 1989). The negative relationship between air temperature and presence of schools may relate to air temperature affecting surface salinity by changing freshwater input during ice formation and melting. A positive relationship between Arctic cod abundance and salinity in Beaufort Sea coastal waters reported by Craig et al. (1982) corroborates this explanation. Arctic cod also alter their vertical distribution according to water temperature however they are usually attracted to warmer water (Crawford & Jorgenson 1996; Benoit et al. 2008; Crawford et al. 2012). An upward-looking transducer mounted on an Autonomous Underwater Vehicle (with CTD probes) could be used to evaluate the influence of ice, water temperature, and salinity on Arctic cod distribution during the summer.

Schools of Arctic cod were primarily detected in the lower half of the water column which supports observations by Crawford & Jorgenson (1993 and 1996). Arctic cod schools in our study were more dense than those detected in Resolute Bay (Crawford & Jorgenson 1993) but less dense than larger schools in Allen Bay (Crawford &

Jorgenson 1996). Echograms revealed small schools of Arctic cod near the surface in close proximity to larger demersal schools (Fig. 18). Although the volume of water sampled near the surface is less than in deeper water (Simmonds & MacLennan 2005) and vessel avoidance likely altered the composition of shallow schools (e.g., Crawford & Jorgenson 1993), observations of satellite schools were made on numerous occasions from boats that were either stationary or slow moving. Furthermore, black-legged kittiwakes were observed catching fish just beneath the surface as they flew by but did not dive. Swimming close to the surface in smaller schools or individually placed Arctic cod within the range of birds and reduced the potential benefit of schooling (i.e., protection from predators (Pitcher 1986)). The trade-off may be access to more abundant food or smaller prey items that are scarce in the vicinity of the large school. For example, Longhurst et al. (1984) reported a shallow epiplankton layer in the upper 5m throughout the Canadian Arctic often containing higher abundances of copepods than deeper layers. Additionally, schooling adults have a much higher frequency of empty stomachs than non-schooling adults (Hop et al. 1997a) and zooplankton is often less abundant near schools (Crawford & Jorgenson 1996). Future research could examine the distribution of prey (e.g., zooplankton netting) in conjunction with hydroacoustics to understand their effect on Arctic cod behaviour and the functional role of satellite schools

Target strength (TS) is a function of fish size (e.g., Foote et al. 1987). However, TS based length analyses were not included due to limitations in collecting TS data close to the surface (i.e., near-field distance; Simmonds & MacLennan 2005). Preliminary estimates of Arctic cod size from satellite schools using a TS-length relationship TS = 21.8 log L – 72.7 dB; Crawford & Jorgenson 1996) (mean = 7.57cm on 29 Aug, and

8.16cm on 31 Aug) were smaller than cod captured directly from schools (mean = 16.05cm, N = 51). This is consistent with findings by Crawford & Jorgenson (1993) and Geoffroy et al. (2011). The TS-length relationship for Arctic cod and corresponding length-based distribution patterns warrant further research, especially in the top 3 m**.** Benoit et al. (2010) found that larger Arctic cod remained deeper than smaller Arctic cod in Franklin Bay (Beaufort Sea) and suggested that the greater energetic reserves (i.e., larger livers) of larger Arctic cod reduced the need to feed in shallow waters thus minimizing seal predation. It is unclear if a similar relationship exists in near shore areas as large Arctic cod (>15cm) were captured by seabirds on numerous occasions.

Seabird foraging

Seabirds have adapted a variety of methods to locate prey including the use of memory, foraging in areas used by other individuals, and reacting locally to captures (local enhancement) (Hoffman et al. 1981; Davoren et al. 2003b). It is not surprising, given these adaptations and the association with Arctic cod schools that the few large schools <3m deep were heavily exploited. Local enhancement was one of the major behavioural cues attracting birds to Arctic cod in Allen Bay even when only one bird was feeding. This is not an uncommon occurrence (e.g., Hoffman et al. 1981) and provides insight as to why there was not a significant density-dependent relationship during the shore-based surveys. Kleptoparasitism (food stealing) is also an important foraging method for marine birds (Furness 1987a). The presence of glaucous gulls was significantly correlated with northern fulmar presence likely to increase encounters that supported kleptoparasitism. In addition to using other birds and schools directly as foraging cues, seabirds associate with marine mammals to exploit food sources that are driven towards the surface in nearshore areas (e.g., Welch et al. 1993). These events provide seabirds with high net energetic gains considering the ease to capture prey. Interestingly, on 15 August when the whales ended feeding, ~50% of the seabirds followed them and ~50% remained in the feeding area >4 hrs. The feeding intensity decreased after the whales departed, but many Arctic cod were still captured and a small group of harp seals (*Pagophilus groenlandicus*) were seen lingering in the area. Although large shallow schools provided high short-term benefits for the seabirds these events were infrequent and our observations suggest smaller, less exploited schools were a more reliable food source.

The dynamics of feeding on Arctic cod by the three species of birds differed. There was a strong association between northern fulmars and glaucous gulls and between northern fulmars and Arctic cod. By contrast, the relationships between black-legged kittiwakes and northern fulmars, and black-legged kittiwakes and glaucous gull were more tenuous. Based on our observations there appeared to be a mutual relationship where black-legged kittiwakes and northern fulmars utilized cues of the other to locate and capture Arctic cod. This was evident from the higher association between black-legged kittiwakes and northern fulmars in the presence of Arctic cod schools (Table 18).

Seabirds did not significantly associate with shallow schools during the hydroacoustic survey, contradicting our second hypothesis. However, based on observations, seabirds frequently used depth as a cue, aggregating by schools that were close to the surface or nearshore. There are several possible reasons for the lack of correlation. First, the noise and presence of the survey boat may have caused Arctic cod to move to deeper water (Crawford & Jorgenson 1993). Second, the volume of water sampled near the surface is greatly reduced compared to deeper water because of the cone-shaped detection beam (Simmonds & MacLennan 2005). Third, both predator and prey are highly mobile and this type of survey provided a snapshot in space and time of a highly dynamic system. Fourth, the top 1.75m of the water column could not be sampled due to limitations of the hydroacoustic equipment.

The spatial overlap between high predator-prey areas is dependent on the predators' foraging spatial scale (Craig et al. 1982). We demonstrated that northern fulmars associated with schools of Arctic cod at a fine-scale (<300m^2). This association was also apparent at a larger scale when there was a greater abundance of birds in the northern section of the study area compared to the south on 31 August. By aggregating in areas where schools of Arctic cod were present, northern fulmars maximized efforts allocated to predation and focussed their energetic cost on readily captured Arctic cod. The distribution of black-legged kittiwakes was more independent of schools as they frequently fed on dispersed Arctic cod (Chapter 4). Similarly, Piatt et al. (1989) found that black-legged kittiwake's density was not correlated with Arctic cod density at any depth stratum in coastal and offshore areas in the southeastern Chukchi Sea**.**

Conclusion

Northern fulmars foraged at a fine-scale in areas where Arctic cod were present. By contrast, the distribution of black-legged kittiwakes was not significantly dependent on schools (validating my first hypothesis). The implications of these specialized foraging behaviours were that black-legged kittiwakes spent more time in flight searching for prey compared to northern fulmars however they captured more Arctic cod because they also fed on dispersed individuals (Chapter 4). My second hypothesis was rejected as there was not a significant association by northern fulmars and black-legged kittiwakes with Arctic cod density, abundance, and depth. Finally, glaucous gulls appeared to rely primarily on northern fulmars to feed on Arctic cod (validating my third hypothesis). Using the presence of schools and behaviour of other birds as foraging cues allowed the predators to capture Arctic cod that typically remained >5m deep but occasionally swam to the surface, individually or in small schools. Arctic cod in satellite schools risked predation near the surface but this was likely outweighed by the benefit of reduced competition and perhaps an abundance of more suitably sized smaller prey organisms. Despite the limitation of blanking range the acoustic beam still detected Arctic cod below 1.75 m and within the foraging depths of the surface feeding birds. Further, it allowed determination of how seabirds reacted to the presence of schools.

This study provided new insights about the feeding dynamics of marine predators on Arctic cod, and constitutes a starting point for future research. There are numerous small inshore areas like Allen Bay in the Canadian Arctic Archipelago and the energetic value of these local feeding events may be important in the ecosystem budget. Since there are numerous anecdotal reports of large-scale bird and mammal feeding events on Arctic cod, future studies should also focus on these large schools to further elucidate the relationship among predators and Arctic cod. More importantly, will the findings from Allen Bay hold up at larger scales or is foraging simply opportunistic and random? Further, will the distribution and behaviour of large schools, satellite schools and individual Arctic cod persist regardless of scale? The development of methods and dedicated surveys will help improve our knowledge of these predator-prey interactions at a broader scale.

Table 5.1: Akaike information criterion with small-sample bias adjustment (AIC_c) optimal linear model selection for environmental variables influencing the presence of schools of Arctic cod (*Boreogadus saida*) during shore-based observations (n=15). The best eight models are presented based on the smallest AIC_c differences.

Number of variables in model	**R-square**	**AIC_c**	**SSE**	**Variables in model**	**P value**
2	0.532	-35.507	0.882	air temperature presence of ice^1	*0.004 0.081
2	0.514	-34.941	0.916	air temperature presence of ice^2	*0.004 0.106
1	0.391	-34.237	1.148	air temperature	*0.013
3	0.568	-33.529	0.814	air temperature presence of ice^1 presence of ice^2	*0.003 0.265 0.358
4	0.664	-33.473	0.633	air temperature presence of ice^1 Beaufort state wind speed	*0.002 *0.034 0.119 0.076
3	0.566	-33.462	0.817	air temperature presence of ice^1 wind speed	*0.004 0.075 0.372
3	0.556	-33.122	0.836	air temperature presence of ice^1 time of day	*0.007 0.086 0.455
3	0.556	-33.100	0.837	air temperature presence of ice^1 visibility	*0.004 0.095 0.461

Note: Beaufort state is a measure of wave action. SSE represents the error sum of squares. * indicates significant variables. ^{1} indicates the estimated presence of ice in the study area and ^{2} indicates the estimated presence of ice in Allen Bay.

Table 5.2: Summary results of hydroacoustic survey during 29 August 2010 and 31 August 2010.

		Targets (n)	**FPUA (fish m^{-2})**	**FPCM Max (fish m^{-3})**	**FPCM Average (fish m^{-3})**	**Average TS (dB)**	**Target Depth Upper Limit (m)**	**Target Depth Deepest Limit (m)**
29 Aug 2010	**Average**	118.1	82.0	61.9	9.6	-52.83	7.2	13.1
	Max	497	718	614	92.4	-48.64	11.1	17.0
	Min	7	0.1	0.0	0.0	-55.33	1.8	3.6
	Std Dev	144.8	169.1	145.4	23.0	2.23	2.6	3.4
31 Aug 2010	**Average**	197.0	209.8	93.0	25.4	-53.54	6.2	18.4
	Max	800	521.3	223.6	73.3	-49.64	8.2	24.8
	Min	9	1.4	1.0	0.2	-55.33	2.9	12.0
	Std Dev	223.0	166.6	71.5	21.7	1.90	1.5	4.1

Note: FPUA is fish per unit area (areal density), FPCM is fish per unit area (volume density), and TS is target strength in decibels.

Table 5.3: Association between seabird densities in each 250m long section (n=87) on 29 August 2010 and 31 August 2010 partitioned when schools were present and absent.

	NOFU-BLKI	**NOFU-GLGU**	**BLKI-GLGU**
School present	R^2=0.333	R^2=0.665	R^2=0.313
	P=0.047*	P<0.001*	P=0.063
	Phi=0.265	Phi=0.422	Phi=0.056
	P=0.156	P=0.027*	P=0.999
School absent	R^2=0.263	R^2=0.404	R^2=0.268
	P=0.062	P=0.003*	P=0.058
	Phi=0.129	Phi=0.326	Phi=0.211
	P=0.407	P=0.037*	P=0.221

Note: GLGU = glaucous gull (*Larus hyperboreus*),
NOFU = northern fulmar (*Fulmarus glacialis*),
BLKI = black-legged kittiwake (*Rissa tridactyla*).
R^2 is Spearman rank correlation and Phi is Phi coefficient of association. * indicates significant differences P<0.05.

Figure 5.1: Study area in Allen Bay, Cornwallis Island, Nunavut. Inset: the Canadian Arctic Archipelago. Zigzag illustrate the hydroacoustic transects (29/08/10 and 31/08/10) and shore-based observation locations (circles).

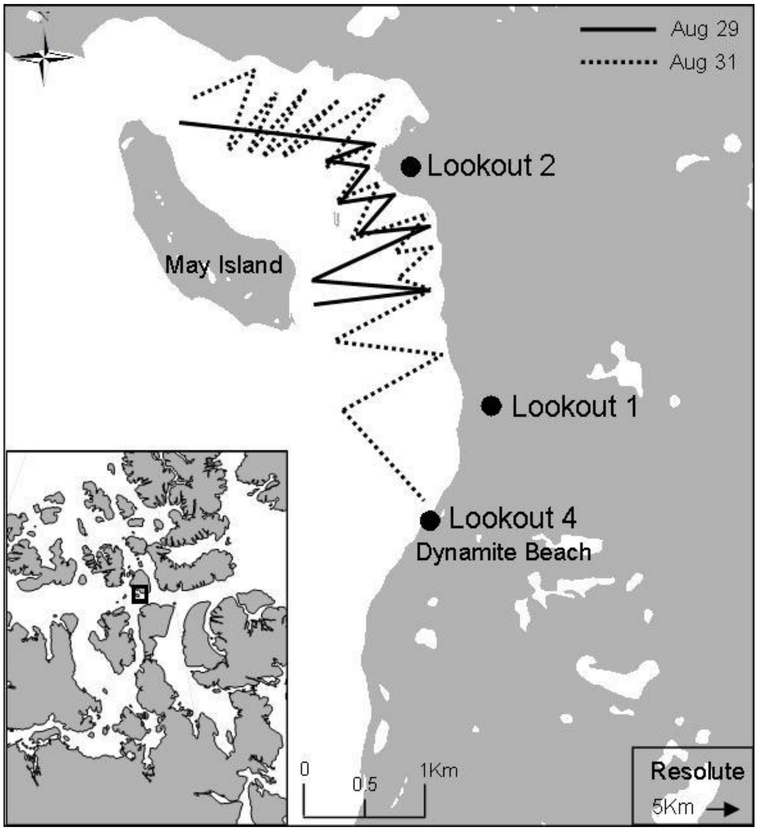
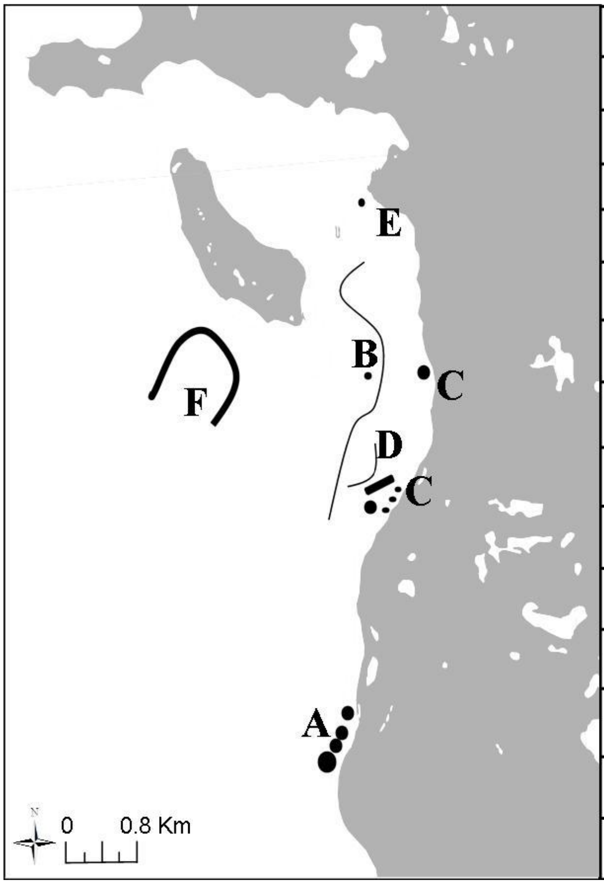
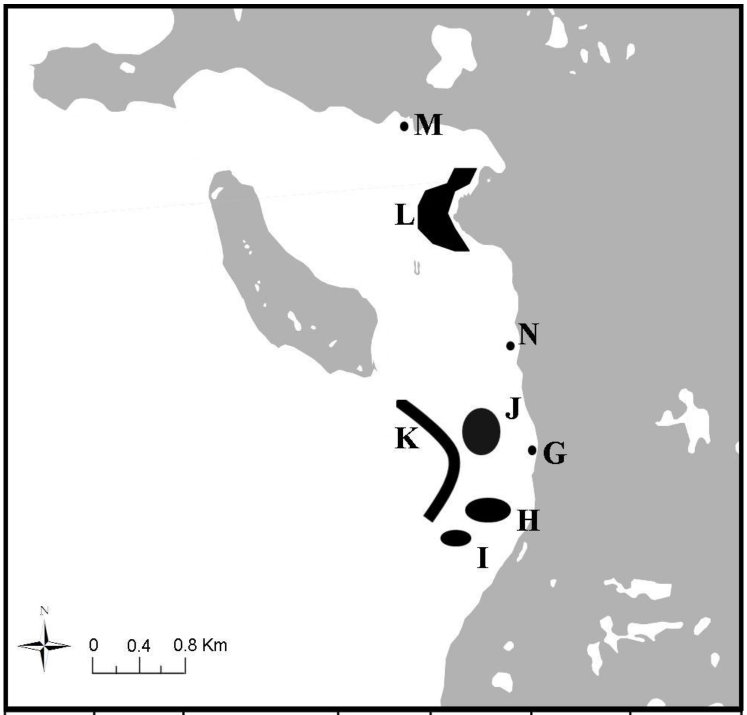


Figure 5.2: Representation of visible schools (A-F) observed from elevated positions during shore-based observations. Inset: Letters correspond to a school which is shown in its approximate size and shape. Size was estimated based on surface area and standardized using a qualitative scaling grade of 0-5 ($0 \leq 30\text{m}^2 < 1 \leq 200\text{m}^2 < 2 \leq 1000\text{m}^2 < 3 \leq 6000\text{m}^2 < 4 \leq 10{,}000\text{m}^2 < 5$).



School	Date	Size (0-5)
A	Aug 17	3
A	Aug 17	2
A	Aug 17	2
A	Aug 17	2
B	Aug 19	4
B	Aug 19	1
C	Aug 21	3
C	Aug 21	0
C	Aug 21	0
C	Aug 21	0
C	Aug 21	3
D	Aug 22	4
E	Aug 23	1
F	Aug 29	5

Figure 5.3: Location and shape and size and duration (inset) of schools (G-N) and number of birds observed during large feeding events (>100 birds). Note school G and H consisted of larval Arctic cod (*Boreogadus saida*) and size was not estimated. School G and H were observed from our boat before surveys commenced. The size of schools was not correlated with the number of birds. GLGU = glaucous gull (*Larus hyperboreus*), NOFU = northern fulmar (*Fulmarus glacialis*), BLKI = black-legged kittiwake (*Rissa tridactyla*).



School	Date	Duration	NOFU	BLKI	GLGU	Size of school
G	Aug 1	16:31-19:15	160	0	0	-
H	Aug 7	10:30-12:30	150	0	0	-
I	Aug 15	16:00-20:00	150	150	55	3
J	Aug 16	5:15-5:40	35	30	5	3
K	Aug 19	20:30-23:45	65	150	30	4
L	Aug 30	10:40-11:30	40	170	240	3
M	Aug 30	14:47-15:13	40	140	20	1
N	Aug 30	16:22-17:00	34	160	12	2

Figure 5.4: Demersal school (black arrow) and nearby shallow 'satellite' schools (white arrows). The dashed area represents the blanking range of ~1.75m. Note this echogram was recorded off-effort of bird survey on 29 August 2010.

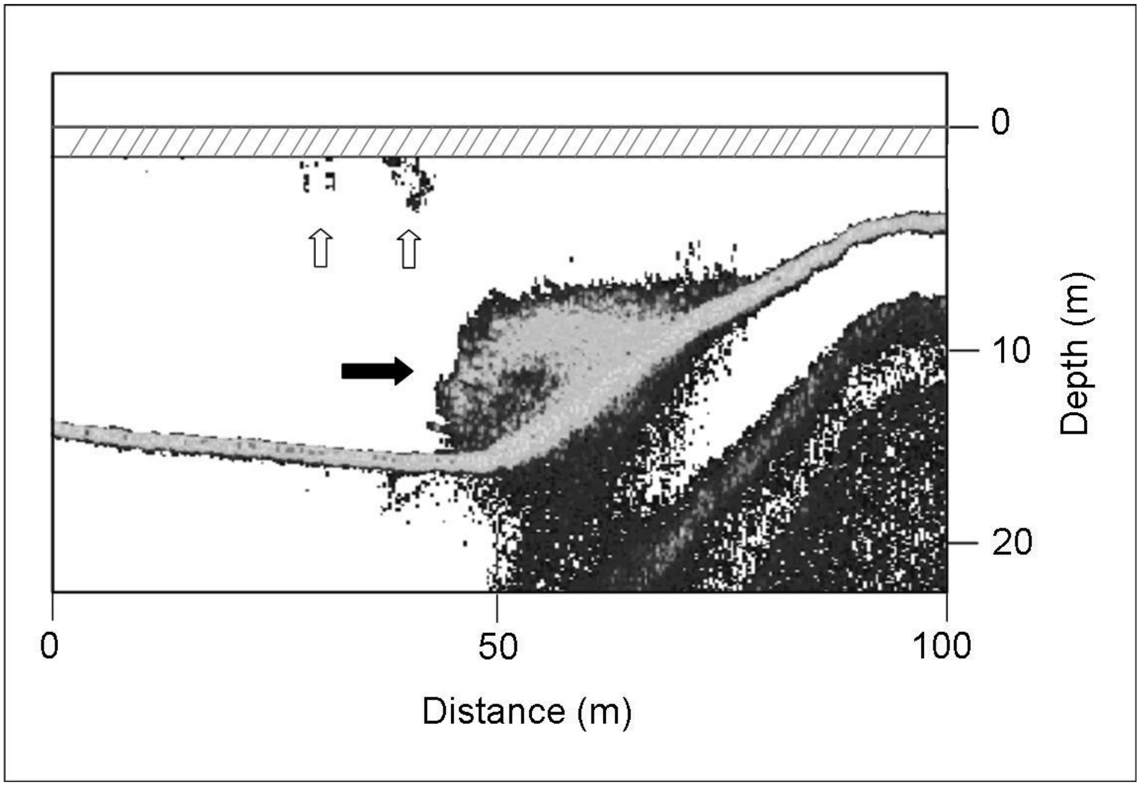


Figure 5.5: (a) The density (birds km^{-2}) of black-legged kittiwakes (*Rissa tridactyla),* northern fulmars (*Fulmarus glacialis*), and glaucous gulls (*Larus hyperboreus*) during 31 August 2010 survey. (b) Schools detected in Allen Bay during August 31st survey. Solid bars represent length of school.

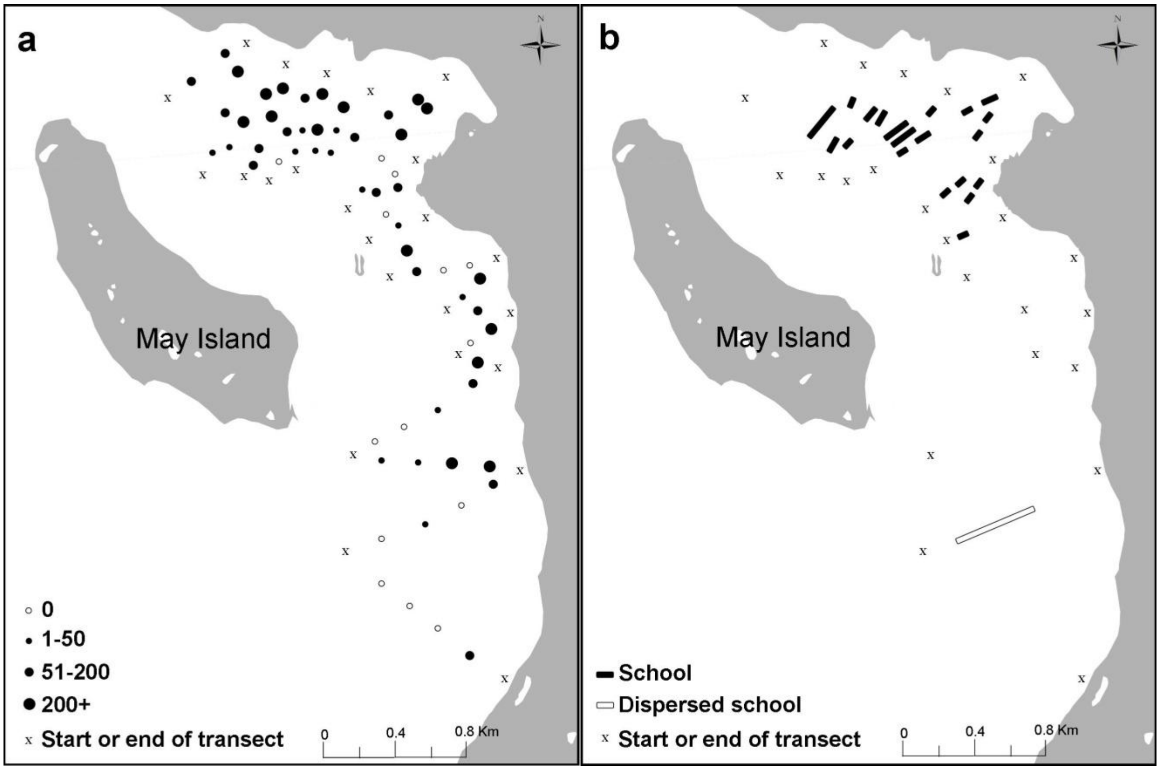


Figure 5.6: Density of seabirds counted in each 250m long section (n=87) on 29 August 2010 and 31 August 2010 partitioned when schools were present and absent. GLGU = glaucous gull (*Larus hyperboreus*), NOFU = northern fulmar (*Fulmarus glacialis*), BLKI = black-legged kittiwake (*Rissa tridactyla*). * indicates significant differences P<0.05.

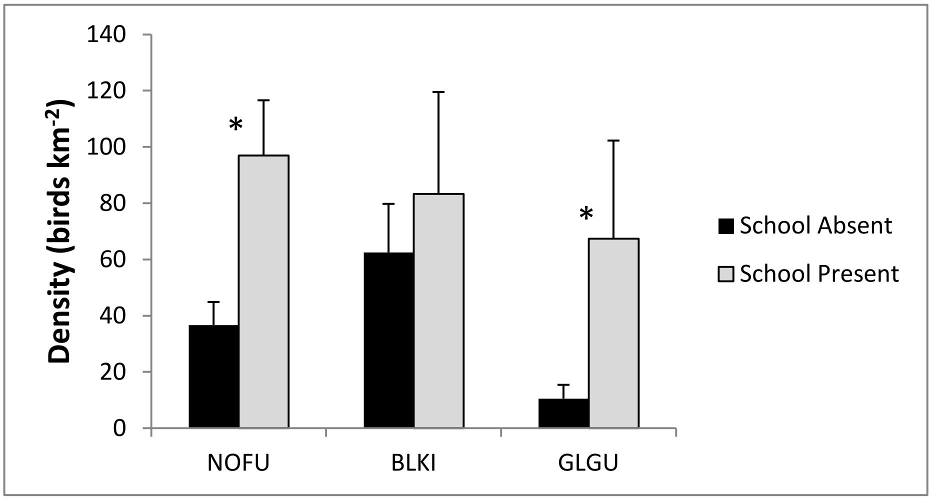
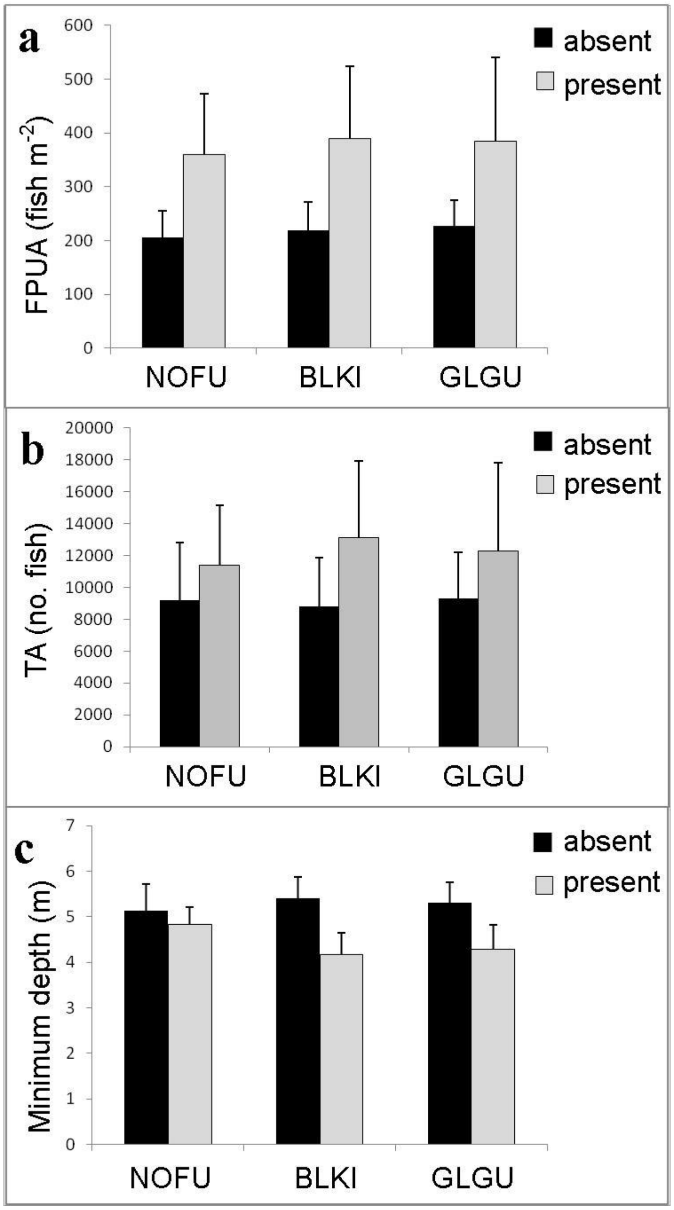


Figure 5.7: (a) Arctic cod per unit area (FPUA; fish m^{-2}), (b) Transect abundance (TA), and (c) minimum depth of Arctic cod (*Boreogadus saida*) schools (n = 35) when below (absent) and above (present) average densities of each seabird species occurred. GLGU = glaucous gull (*Larus hyperboreus*; average density = 34.08 birds km^{-2}), NOFU = northern fulmar (*Fulmarus glacialis*; average density = 61.61 birds km^{-2}), BLKI = black-legged kittiwake (*Rissa tridactyla*; average density = 71.12 birds km^{-2}). P>0.05 for all comparisons.



Thesis Conclusions

This thesis investigated foraging of seabirds, ringed seals, belugas, and narwhals focusing on interactions with Arctic cod during the summer in the Canadian High Arctic. Additionally, the biology and feeding ecology of Arctic cod was examined. I used several methodological approaches including structured observations, surveys, stomach content analysis, and stable isotope analysis. These helped reveal several interesting and novel findings relating to the behaviour of predators and prey in the Arctic.

In Chapter 2, I showed that Arctic cod foraging at time of capture reflected sympagic and epi-benthic habitats whereas pelagic prey were more important prior to summer based on stable isotope analysis of liver and muscle. Further diet shifts were apparent for different size-classes where juveniles separated strongly based on isotopes, while large adults separated based on diet. I also showed that energetically demanding processes or behaviours such as gonad development and schooling cause the mobilization of stored energy from the lipid-rich liver.

In Chapter 3, I corroborated that ringed seals consume non-schooling Arctic cod, while whales exploit schools (Bradstreet et al. 1986). Life history did not affect the size of Arctic cod consumed by seals and whales, however length was an important predictor of trophic level. Chapter 3 also showed seasonal and annual diet shifts associated with migration and changing sea-ice conditions and provided the first isotopic discrimination factors (for liver and muscle) of Arctic marine predators directly from prey.

In Chapter 4, I quantified seabird feeding and showed that black-legged kittiwakes and northern fulmars capture the majority of Arctic cod in Allen Bay, but lose a considerable proportion to parasitic jaegers and glaucous gulls. The kleptoparasitic nature of these species enabled them to obtain substantial energetic gains at limited costs. Also, schools of Arctic cod were commonly exploited by northern fulmars, while dispersed cod were more important to black-legged kittiwakes.

In Chapter 5, I found that the presence of schools significantly influenced seabird distribution independent of the density, depth, and abundance of schools. The presence of schools was a more important predictor of northern fulmar density and glaucous gulls tightly associated with fulmars to optimize chances of stealing Arctic cod. Chapter 5 also showed the presence of ‘satellite schools’ where small groups of Arctic cod separated from schools likely to feed at the surface where competition was reduced but risk of predation was high.

Several themes were apparent in the four research chapters. For example, predators showed species-specific foraging decisions and behaviours to capture prey. Diet analysis revealed that Arctic cod, ringed seals, and whales consumed prey that were readily available in the habitat or environment they were located in. Therefore, the importance of Arctic cod in the diet is a reflection of its availability in the Arctic. This is a major concern as climate change is predicted to alter the distribution of many marine species and affect resource utilization throughout the Arctic. This thesis also showed that contrary to many reports, schooling Arctic cod are not important to several species. Belugas, narwhals, and northern fulmars appear to be quite reliant on schools during the summer however ringed seals and black-legged kittiwakes appear to be better suited to capture dispersed or non-schooling cod. This could have repercussions as changing oceanographic conditions (e.g., changing temperature and salinity) could impact the distribution and depth that Arctic cod occur, making prey capture more difficult. Further, traditional Inuit hunting may be negatively impacted if seal and whale movements transition offshore in response to prey availability. This thesis not only showed the importance of Arctic cod, but determined how predators utilize this significant resource.

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Appendix:

Observation of common raven (*Corvus corax*) scavenging Arctic cod from seabirds in the Canadian High Arctic

Abstract:

The common raven (*Corvus corax*) is one of the most intelligent avian species, known for its ability to scavenge from humans and other animals. This adaptive nature is critical in habitats where food can be scarce. The Arctic is such an environment and optimizing associations with sources of prey is important. Large aggregations of Arctic cod (*Boreogadus saida*) in shallow waters provide a high energetic source for top predators such as seabirds and marine mammals, and consequently potential food sources for ravens. I documented, to my knowledge, the first observations of a raven feeding on Arctic cod discarded by seabirds. This report supplements knowledge of ravens to opportunistically meet dietary requirements and the importance of Arctic cod to avian ecology in the Arctic.

Introduction

The ability to exploit numerous food sources using varied foraging strategies is important for many avian species (Lefebvre et al. 1997) and is especially significant in areas where food is sparse and seasonal. Biodiversity and productivity in the Arctic ecosystem is one of the lowest (Wookey 2007; Niemi et al. 2010). Nevertheless, top consumers persist in the Arctic using physiological, behavioural, and cognitive adaptations. The common raven (*Corvus corax*) is an opportunistic forager and one of the few bird species that remain in the Arctic year-round (Kessel and Cade 1958). Its association with human activity is well established (Restani et al. 2001; Webb et al. 2004; Marzluff and Neatherlin 2006). But it also forages independent of humans, capturing prey directly (e.g., Careau et al. 2007; Powell and Backensto 2009), or scavenging deaths and kills of other animals such as wolves (*Canis lupus*) (Vucetich et al. 2004), Arctic foxes (*Vulpes lagopus*) (Careau et al. 2007), and polar bears (*Ursus maritimus*) (Smith 1980).

Despite the low productivity in the Arctic, large ephemeral packets of energy exist in species like Arctic cod (*Boreogadus saida*). It is a small circumpolar forage fish that schools nearshore during the summer (Bradstreet et al. 1986; Welch et al. 1993). These schools attract marine predators such as whales, seals, and seabirds to coastal areas where over 40 tonnes or half a million Arctic cod are estimated to be consumed daily (Welch et al. 1993). Arctic cod close to the surface are readily captured by seabirds such as northern fulmars (*Fulmarus glacialis*), black-legged kittiwakes (*Rissa tridactyla*), and glaucous gulls (*Larus hyperboreus*) (Chapter 4). I documented a raven scavenging Arctic cod discarded by seabirds during feeding. To my knowledge, this is the first account of ravens scavenging Arctic cod and provides new insight on the interactions among birds and Arctic cod in the Canadian High Arctic.

Methods and Results

The movements of Arctic cod and associated behaviour of predators in Allen Bay, Nunavut (74°43’36.78’’N 95°09’25.23’’W) were studied during the summer of 2010. Allen Bay is located in the Canadian High Arctic near Resolute Bay, a small Inuit community consisting of approximately 230 people. A group of ~30 ravens remains year-round and forages at the local dump.

Large schools of Arctic cod migrate to Allen Bay during the open water season providing food for marine birds and mammals. Seabird and marine mammal foraging was monitored daily between July and September. On August 30th we observed, on two occasions, a group of ~200 seabirds feeding on a small school of Arctic cod inshore in water <5m deep. During the first feeding event, a raven was observed on a nearby ice floe lodged along the shore (Fig. 1). Northern fulmars captured Arctic cod by shallow dives and surface dipping (Fig. 2), black-legged kittiwakes captured Arctic cod by diving from the air, and glaucous gulls grabbed Arctic cod mainly from the shore (Fig. 2). After birds fed to satiation, during the second feeding event, ~100 carcasses of Arctic cod were discarded in the water, on shore and on a small ice floe. I noted that most Arctic cod were eviscerated due to preference of the birds for the lipid-rich liver (Finley et al. 1990) and black-legged kittiwakes placed carcasses into small piles on the ice floe (Fig. 3). A raven began consuming Arctic cod on the shore that had been discarded by glaucous gulls within 1m of the water’s edge (Fig. 2 and Fig. 4a). The raven continued to feed for approximately 5 minutes before departing with an Arctic cod in its beak (Fig. 4b).

Discussion

Scavenging by Arctic ravens is typically associated with terrestrial food sources, especially human waste dumps. Reports of ravens foraging on marine sources mainly refer to scavenging on remains of ringed seals killed by hunters and polar bears (e.g., Stirling 1977; Gilchrist and Robertson 2000; Stirling and Smith 2004). The role and importance of other marine sources during the open water season are not well known.

Did the raven actively react to the cues of feeding seabirds and the presence of cod schools, or was this simply an opportunistic event? Although ravens are opportunistic foragers, encounter rates with prey are increased by remaining in close proximity to predators. For example, Stahler et al. (2002) showed that ravens preferentially associate with wolves in the presence and absence of food in Yellowstone National Park. The close association is thought to be an adaptive foraging strategy to obtain as much as 43kg of food (or 75% of edible biomass) from packs of wolves per day (Kaczensky et al. 2005). Although ravens rarely associated with seabirds in Allen Bay, the raven at the first feeding event was attracted to the area despite no Arctic cod carcasses on shore. This suggests the raven responded to feeding cues in anticipation of food availability. Moreover, ravens are known to horde food (Bugnyar and Kotrschal 2002) and the raven departing with a cod in its beak (Fig. 4b) may be doing so to cache food for future consumption or to feed nestlings, although it was late in the season.

Perhaps this was an opportunistic and rare event since only one raven was observed consuming Arctic cod during the summer. Allen Bay is located only a few kilometres from Resolute where ravens primarily forage at the local dump and Inuit hunters in Resolute never observed ravens feeding on Arctic cod. However, stranded Arctic cod is not an uncommon occurrence and seabirds are not the only potential link to ravens. Seals and whales (Finley et al. 1990; Welch et al. 1993), severe weather conditions (Craig et al. 1982), and tide (Bain and Sekerak 1978) cause the stranding of Arctic cod on shore.

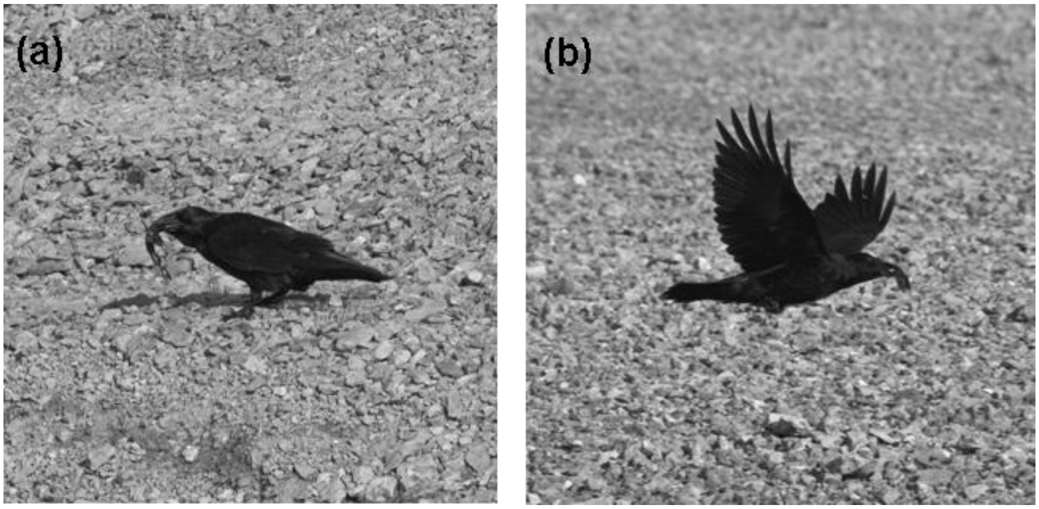
The occurrence of nearshore Arctic cod schools during the summer provides a significant energetic contribution to predators and consequently a potential dietary source for scavengers. Arctic cod may be an important food source for ravens away from human settlements and near seabird breeding colonies where interactions with predators are common (e.g., Montevecchi 1979). Information on movements, habitat, and foraging behaviour of common ravens in the High Arctic is needed, especially to understand the importance of marine food sources, such as Arctic cod during the open water season.

Figure 1: A common raven (*Corvus corax*) associating with black-legged kittiwakes (*Rissa tridactyla*) and northern fulmars (*Fulmarus glacialis*) during the first Arctic cod (*Boreogadus saida*) feeding event (Photo by R.E. Crawford)

Figure 2: Common raven (*Corvus corax*) and glaucous gulls (*Larus hyperboreus*) feeding on Arctic cod (*Boreogadus saida*). Northern fulmars (*Fulmarus glacialis*) are dipping from the water surface (Photo by R.E. Crawford)

Figure 3: Arctic cod (*Boreogadus saida*) carcasses gathered by seabirds and placed in a small pile on an ice floe (Photo by R.E. Crawford)

Figure 4: (a) Common raven (*Corvus corax*) feeding on discarded Arctic cod (*Boreogadus saida*) along the shore and (b) departing with an Arctic cod in its beak (Photo by R.E. Crawford)



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