

**AN ANALYSIS OF
ARCTIC SEABIRD TROPHIC LEVELS AND FORAGING
LOCATIONS USING STABLE ISOTOPES**

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ABSTRACT

Arctic ecosystems are vulnerable to human-induced changes such as increases in contaminant levels and climatic warming. To predict effects of these changes, it is important to understand trophic relationships among Arctic organisms and how they change in response to time and environmental perturbations. Seabird diet can reflect relative availability and abundance of planktivorous fish and zooplankton in remote areas. The measurement of naturally occurring stable isotopes presents an alternative approach to evaluating dietary patterns of seabirds at both an individual level and at a larger, ecosystem level. Relative changes in $\delta^{13}\text{C}$ values provided an indication of changes in consumption of benthic vs. pelagic prey and changes in $\delta^{15}\text{N}$ values provided an indication of changes in trophic level.

I investigated trophic positions of four seabirds (Thick-billed Murres (*Uria lomvia*); Northern Fulmars (*Fulmarus glacialis*); Black-legged Kittiwakes (*Rissa tridactyla*); and Glaucous Gulls (*Larus hyperboreus*)) at Prince Leopold Island, Nunavut, 1988 – 2003, using my own and previously measured stable isotope measurements in blood samples. Trophic level and space use among years differed within and among species and may be related to ice conditions and species-specific foraging strategies. The species with the most flexible foraging methods, Thick-billed Murres, varied their foraging location and trophic level the most. In 2002, fewer chicks than average for all species were fledged and Thick-billed Murre chicks were lighter than in other years; however, only murres showed a concurrent decrease in the proportion of fish in their diet. Adult body condition of murres in 2002 was positively correlated with trophic level.

Breeding season dietary patterns of Thick-billed Murre adults and chicks were examined on Coats Island, Nunavut, Canada, in 2004. Adult trophic level increased slightly through the breeding season and $\delta^{13}\text{C}$ values indicated a switch from benthic to pelagic foraging locations. Chick and adult murre did not differ in either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ values; however, within a family (two parents, one chick), chicks were fed at or slightly below adult trophic level. I found little variation in stable isotope values which suggests adult murre did not preferentially select prey for either themselves or their chicks.

Finally, stable isotope analysis was used to investigate winter foraging ecology of three species of alcids (Thick-billed Murre; Common Murre (*U. aalge*) and Razorbill (*Alca torda*)), off Newfoundland, Canada, 1996 – 2004. Thick-billed Murre fed at a higher trophic level than Common Murre. Razorbill $\delta^{15}\text{N}$ values were highly variable and overlapped those of both murre species. I found no significant differences in $\delta^{13}\text{C}$ values among the three species confirming a common spatial feeding pattern. Both murre species became depleted in ^{13}C during winter suggesting foraging location or prey species shifted from nearshore to offshore. For Common Murre, hatching-year individuals fed at a higher trophic level and foraged farther offshore than after-hatch year birds. For Thick-billed Murre, I contrasted trophic level determined for the breeding colony at Prince Leopold Island with those determined for winter over four years and found considerable inter-annual variation in patterns of seasonal difference in trophic level. However, the proportion of lower trophic level (amphipod) vs. higher trophic level (fish) prey was generally greater in the winter than the summer.

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CHAPTER 1: INTRODUCTION

1.1 GENERAL INTRODUCTION

An animal needs to eat to live but choosing *what* to eat can be a more complicated decision. A number of factors can affect foraging and food choice and include prey availability, risk of predation, competition, habitat structure, hunger, experience, sex and reproductive state, dietary preference, nutrient requirements, sensory limitations, morphological characteristics, and physiological parameters (Perry & Pianka 1997). Some of these factors remain fixed throughout an organism's life while others fluctuate with time and result in changes in an organism's diet. For example, seasonal fluctuations in precipitation or temperature can lead to variable resource availability. Organisms can take advantage of changing conditions and minimize energy expenditure by switching prey items as they become depleted or less common (Norberg 1977). Understanding diet variability can provide insight into an organism's environment and is essential to the study of the ecology of individuals and species.

Although the Arctic marine ecosystem is relatively simple compared with those of temperate regions, it is still relatively poorly understood. A major factor influencing seasonality here is ice cover. Primary production in the Arctic is driven mainly by ice algae and phytoplankton (Welch et al. 1992). Ice algae require ice as a substrate and both require light to grow (Hirche 1991). Many Arctic vertebrates depend on ice, ice edges or adjacent open-water polynyas (Stirling 1997). Ice conditions can vary significantly between and within years (Parkinson 2000) and climate change is expected to further transform the Arctic (Clark & Harris 2003). Already, declines in ice cover

(Parkinson 1999, 2000), and ice thickness (Wadhams & Davis 2000) and an increase in the ice-free season (Parkinson 2000) have been documented in the Arctic. Warming sea temperatures directly affect when phytoplankton bloom, how much is produced and how abundant it is (Smayda et al. 2004) which have indirect effects on the rest of the Arctic marine ecosystem.

Seabirds are top predators in the marine Arctic ecosystem, and their diet and behaviour can reflect changes in prey abundance (Furness & Camphuysen 1997). Arctic seabirds are closely linked with ice due to foraging opportunities provided at ice edges and polynyas (Bradstreet 1980; Stirling 1997). As a result, ice cover and timing of ice break-up are important environmental factors influencing reproduction. Early ice break-up in the Canadian high Arctic can lead to improved body condition and chick growth in Thick-billed Murres (*Uria lomvia*; Gaston et al. 2005) while heavy ice years can lead to breeding failure (Nettleship et al. 1984). Poor chick growth and poor body condition suggest that ice conditions affect reproductive success through diet but directly linking these factors has been difficult using traditional methods of dietary analysis.

Traditional approaches of dietary analysis include the direct examination of stomach contents (e.g., Gaston & Noble 1985; Elliot et al. 1990), monitoring foraging behaviour (e.g., Davoren et al. 2003; Weimerskirch et al. 2005) and chick feedings (e.g., Gaston et al. 2003), and analysis of pellets, feces and regurgitations at colonies (e.g., Ludynia et al. 2005). All of these approaches have their limitations. Stomach content analysis indicates short-term prey intake, often within 24 hours or less (Uspenski 1956 (in Furness et al. 1984)), and is affected by differential digestion rate of prey items (Duffy & Jackson 1986). Soft-bodied prey such as zooplankton are digested more quickly than hard prey items or parts of prey such as fish otoliths or squid beaks which

can lead to an overestimation of the importance of upper trophic-level prey (Hobson 1993; Hobson et al. 1994). Monitoring at-sea foraging behaviour can be logistically difficult and transmitters can have significant behavioural impacts (Ackerman et al. 2004; Paredes et al. 2005). Because chicks and adults may feed on different prey (Baird 1991; Hobson 1993; Davoren & Burger 1999; Wilson et al. 2004), one cannot extrapolate adult diet from at-colony observations of chick feeds. More recently, stable isotope analysis (SIA) has been used for seabird dietary analysis and applied to seabird paleodiet (Hobson & Montevecchi 1991), prey regime shifts over both short (Ainley et al. 2003) and long time frames (Thompson et al. 1995; Hobson et al. 2004; Ainley et al. 2005), toxicological and contaminant studies (Jarman et al. 1996; Campbell et al. 2005; Braune et al. 2006), conspecific competition (Cherel et al. 2002) and seabird ecosystem relationships (Forrero et al. 2004).

Isotopes of elements differ in the number of neutrons in the nucleus. For example, the common form of carbon, ^{12}C , has two heavier isotopes: ^{14}C , which is a radioactive isotope and decays into nitrogen; and ^{13}C which is stable and does not decay. Stable isotopes occur naturally, often at low levels in the environment (Ehleringer & Rundel 1989) and are distributed according to specific biological, geological, and chemical processes. The two most important stable isotopes in marine ecological research have been ^{13}C and ^{15}N . Nitrogen-15 is discriminated against during excretion so organisms are enriched in ^{15}N compared to their diet. This enrichment occurs consistently enough that ^{15}N values can be used to estimate trophic level. For example, in the Arctic, marine organisms show about a 3.8‰ enrichment with trophic level (Hobson & Welch 1992). In marine environments ^{13}C in phytoplankton varies for several reasons including temperature, the dissolved inorganic carbon pools, metabolic

process and growth rates (Michener & Schell 1994). Generally, pelagic primary producers are depleted in ^{13}C compared with benthic or nearshore organisms. Stable isotopes are expressed in δ (delta) notation, in ‰ (parts per thousand):

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000 \quad [1.1]$$

where X is the heavy isotope in question (^{13}C , ^{15}N), R is the ratio of the heavy to the lighter isotope of the element ($^{15}\text{N}/^{14}\text{N}$, $^{13}\text{C}/^{12}\text{C}$), R_{sample} and R_{standard} are the isotopic ratios of the sample and standard (^{15}N – AIR), ^{13}C - PDB (PeeDee belemnite)), respectively.

Stable isotope values in prey differ from consumer tissues according to tissue-specific fractionation values which must be considered before drawing conclusions about diet composition. For example, prey and seabird feather tissue differ in $\delta^{13}\text{C}$ values by +2.3‰ (Bearhop et al. 1999) whereas prey and seabird blood differ by +4.3‰ (Bearhop et al. 2002); therefore, a feather would have a $\delta^{13}\text{C}$ value 2.0‰ greater than that of blood within the same individual. I assume fractionation values are constant among the seabird species used in my thesis. One of the advantages of SIA over stomach-content analysis is that prey items in stomachs provide a snapshot of diet, whereas stable isotopes reflect average diet over a longer time. Half-life, the time it takes for half the isotopes in tissues to reflect stable isotope ratios in the diet, varies depending on the metabolic rate of the tissue (Hobson & Clark 1992b). Stable carbon isotopes in plasma have a half-life of 2.8 days and therefore reflect average diet during the previous week (Hobson & Clark 1992a), although this time frame can differ with species (Hobson & Bairlein 2003). Bone collagen, on the other hand, has a long half-life and reflects average diet over the lifetime of the individual (Hobson & Clark 1992a). By

appropriate tissue selection, one can address both long-term and short-term dietary variation, and it is possible to look at diet variation within an individual.

To provide broader insight into seabirds breeding at northern latitudes, it has been suggested that events which occur during the non-breeding season may be connected to breeding success and survival. This effect, referred to as ‘seasonal interaction’, has been found in a range of migrating species (e.g., Hobson 2005; Norris 2005) and is theorized to occur in Thick-billed Murres in the Canadian Arctic. High and low Arctic murre colonies exhibited similar population trends suggesting population limiting effects during winter when they use the same habitat (Gaston 2003). Definitely making a link between breeding and non-breeding seasons has been hampered by the lack of information about winter murre diet.

The comparatively limited variety of prey choices available to seabirds in an Arctic ecosystem allows for relatively simple models of diet to be constructed. Investigations into diet variation of several seabird species, in both adults and chicks in association with climate variables and wintering behaviour, has allowed me to describe seabird diet variation over different time scales. I focused on two breeding locations at different latitudes in the Arctic to examine variation within the breeding range. These two colonies also provided two different seabird communities – one with several different species, and one with a single seabird species and a wider range of prey species. Finally, because one bird species at both of these colonies share a common wintering area off Newfoundland, I was able to look at this species’ diet through the year.

1.1.1 Study areas

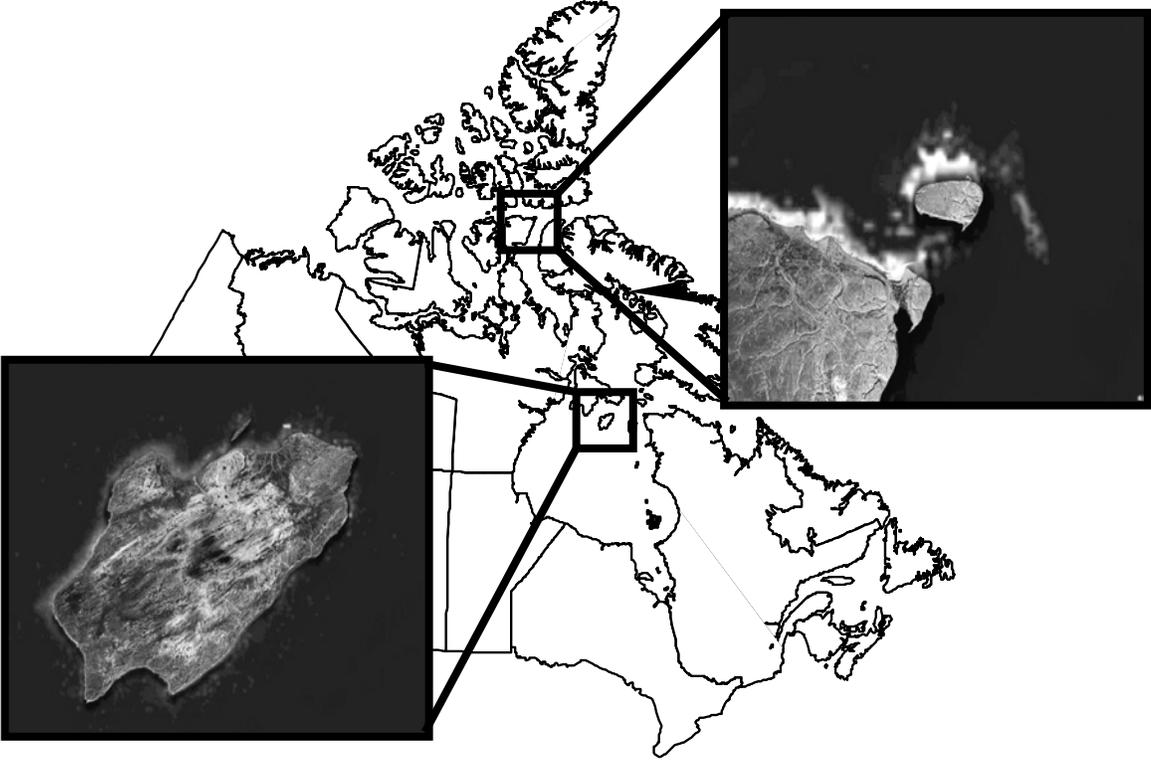
To examine diet variation at a range of scales, birds were sampled during breeding and non-breeding seasons and at breeding colonies in the high and low Arctic. Breeding birds were sampled on Prince Leopold Island, Nunavut, (2000-2003), in the high Arctic, and Coats Island, Nunavut, (2004), in the low Arctic (Fig. 1.1).

Prince Leopold Island (PLI) has one of the most diverse seabird colonies in the eastern Canadian Arctic with a total of five species breeding on or near its cliffs (Gaston & Nettleship 1981). This island was the site of long-term monitoring of seabird breeding biology including one of the first studies of seabird diet using stable isotopes (Hobson & Welch 1992) which allowed me to look at inter-year diet variation from a period in the late 1980s to 2003 and to relate diet to breeding success and body condition. By combining information from four seabird species with different foraging strategies, I was better able to estimate prey availability with time (Montevecchi 1993). I have assumed that the baseline stable isotope values of the ecosystem around PLI remain constant among years.

Coats Island, the location of a more southern Thick-billed Murre breeding colony, has a more diverse prey community than PLI (Gaston & Bradstreet 1993) and known murre dietary specialists (Woo 2002). I used this breeding colony to investigate inter-individual diet variation in murres including diet specialization and compared parent and chick diets within family groups.

Wintering birds were sampled off Newfoundland (NL) where they were taken as part of the legal 'turr' hunt. Thick-billed Murres that breed in the eastern Arctic, including those of PLI and Coats Island, winter off Newfoundland and Labrador (Gaston et al. 1994) allowing comparisons of winter and breeding season diet of the same population. Although Thick-billed Murres are the primary target of the hunt, accidental

Figure 1.1: Locations of study sites in Nunavut, Canada. Right – Prince Leopold Island ($74^{\circ}1'59''\text{N}$ $90^{\circ}4'59''\text{W}$); left – Coats Island ($62^{\circ}30'0''\text{N}$ $83^{\circ}0'0''\text{W}$).



harvest of Common Murres (*U. aalge*) and Razorbills (*Alca torda*) allowed investigation of winter diet differences between species. The sample of birds may be biased towards hatch-year birds (Gaston et al. 1983) but I address this potential bias during data analysis.

1.1.2 Study species

For my thesis, I used a variety of seabird species: Thick-billed Murres (PLI, Coats, NL); Northern Fulmars *Fulmarus glacialis* (PLI), Black-legged Kittiwakes *Rissa tridactyla* (PLI), and Glaucous Gulls *Larus hyperboreus* (PLI); Common Murres (NL), and Razorbills (NL). All of these species breed colonially, are relatively long lived and have low annual reproductive rates (Lack 1968).

Thick-billed Murre

The Thick-billed Murre, my main study species, is one of the most numerous and well studied marine birds in North America (Gaston & Hipfner 2000). These auks weigh slightly less than 1 kg and can be distinguished from Common Murres by their thicker bill, marked with a white line along the tomium during the breeding season. PLI and Coats Island have major colonies of 172,000 and 60,000 breeding birds, respectively (Gaston & Hipfner 2000). Murres are pursuit divers and forage at depths from 10-180 m where they ‘fly’ underwater in pursuit of prey (Gaston & Hipfner 2000). Foraging range from colonies can be up to 170 km (Gaston & Hipfner 2000) but is generally shorter (Benvenuti et al. 1998; Woo 2002). In the high Arctic, Thick-billed Murres’ main prey is zooplankton (amphipods and euphausiids) and Arctic cod (*Boreogadus saida*; Gaston & Nettleship 1981); while in the low Eastern Arctic they also fed on capelin (*Mallotus villosus*), sandlance (*Ammodytes* spp.) and benthic fish such as sculpins (Cottidae) and zoarcoids (eelpouts; Zoarcoidei) (Gaston & Bradstreet 1993; Woo 2002; Gaston et al.

2003). Thick-billed Murre winter diet also consists of amphipods, euphausiids, Arctic cod, capelin and squid (Teuthida) (Elliot et al. 1990; Rowe et al. 2000). Band returns show that Thick-billed murre breeding in the Eastern Canadian Arctic winter off Newfoundland (Gaston 1980).

Common Murre

Common Murres are very similar in appearance to Thick-billed Murres but breed in more southerly locations. Common Murres also winter in the same areas as Thick-billed Murres, that is, offshore Newfoundland, but tend to migrate ahead of Thick-billed Murres (Elliot 1991). They are also pursuit divers, preying on fish and zooplankton all year (Bradstreet & Brown 1985), and may forage up to 120 km from breeding colonies (Ainley et al. 2002).

Razorbill

Razorbills, closely related to murres, are also large auks and have a distinctive laterally compressed bill. These birds breed from the low Arctic to Maine and winter mainly in the Bay of Fundy and Gulf of Maine (Hipfner & Chapdelaine 2002). Like murres, razorbills are pursuit divers and feed on schooling fish such as sandlance and capelin but polychaetes and crustaceans are also important in their diet (Thompson et al. 1999; Hipfner & Chapdelaine 2002).

Northern Fulmar

The Northern Fulmar, a medium-sized petrel, breeds throughout the Arctic and, during winter is found off the coast of Newfoundland and Labrador and south to Georges Bank. Fulmar diet ranges from zooplankton to squid to fish to scavenged marine mammal remains (Hatch & Nettleship 1998). Fulmars forage up to 300 km from breeding colonies but rarely dive deeper than 3m (Hatch & Nettleship 1998).

Black-legged Kittiwake

Black-legged Kittiwakes in the Western Atlantic nest on cliffs from the Arctic to the Maritimes (Birkhead & Nettleship 1988), and eastern populations winter offshore from Newfoundland to Florida (Baird 1994). Kittiwakes are surface-plungers or – dippers, foraging within 1 m of the surface. They feed mainly on fish as well as some invertebrates and feed within 50 km of breeding colonies (Baird 1994).

Glaucous Gull

Glaucous Gulls can feed on fish and invertebrates but are also one of the main predators at seabird colonies in the Canadian Arctic, eating eggs and chicks of other seabird species (Gilchrist 2001). This species is a large gull which breeds throughout the circumpolar region and winters in both marine and freshwater environments.

1.2 THESIS OUTLINE

Diet is a fundamental component of the ecology of an organism, and knowledge of diet is necessary to address questions relating to the evolution of species' traits, individual behaviour, and the role individuals and species play in communities and food webs. Because the Arctic marine environment varies in both space and time, upper trophic level species such as seabirds, may change their diet to take advantage of more abundant prey, or to respond to changes in their energy requirements. Understanding seabird diet through time can thus provide important insights into seabird foraging ecology and the interaction between diet and other life history traits. Importantly, diet or trophic position, may be the method by which linkages can be made between different periods of the life cycle of seabirds. The objective of my thesis was to describe how seabird trophic level and foraging location changes at various temporal scales (within breeding season, between breeding seasons, and between breeding and wintering

periods), and potentially, in response to changes in ambient conditions such as ice cover. I concentrated on Thick-billed Murres but also considered several other species both within a high Arctic seabird community, and on the wintering grounds. I used a stable isotope approach in order to avoid numerous limitations of conventional approaches to evaluating seabird diets, especially outside the breeding season.

Chapter 2 examines inter-annual diet variation among a community of seabirds on PLI, Nunavut, with different feeding behaviours. Specifically, I hypothesized that (1) variable prey availability due to ice cover would produce different dietary responses in each species; and (2) in a year of poor food availability, birds with lower body condition would feed at a lower trophic level than those with better body condition.

My third chapter looks at diet variation within a breeding season and between individual Thick-billed Murres and their chicks. Energy requirements change during egg laying and chick-rearing and diet variation may allow adults to adjust to increased energy demands during this time. I also examined variation in dietary relationships within families, between adults and chicks. Parents have to transport prey from foraging grounds to chicks which may result in different prey being eaten by chicks and adults who feed themselves at the foraging grounds. I predicted that (1) chicks would feed at a higher trophic level than their parents; (2) adults would reduce the proportion of invertebrates in their diet through the breeding season; and (3) if specialists exist there would be a large range in stable isotope values.

Finally, Chapter 4 examines diet variation between seabird species during winter and between seasons. Stable isotope analysis combined with simple season- and tissue-specific isotope models allowed direct comparison between winter and breeding season diet. I predicted (1) species would show significant dietary overlap; (2) diet would

remain constant through the non-breeding season; and (3) non-breeding and breeding season diet would differ.

Together, these chapters describe annual diet variation in Thick-billed Murre diet though much of its range as well as examining seabird communities in the high and low Arctic and the northern temperate regions.

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CHAPTER 2: HIGH-ARCTIC SEABIRD TROPHIC RESPONSE TO AN ANOMALOUS YEAR REVEALED THROUGH LONG-TERM ISOTOPIC MONITORING

2.1 INTRODUCTION

It is now generally realized that large-scale environmental changes in polar regions can be linked to global climate change (Morison et al. 2000; Corell 2006; Steffen 2006). In Arctic marine regions such changes include reduced sea-ice extent and thickness, and longer ice-free seasons (Parkinson 2000). During spring and summer, ice edges serve as important foraging areas for many species ranging from zooplankton to seabirds and marine mammals (Stirling 1997). Sea-ice conditions during the breeding season of high-Arctic seabirds influence clutch initiation dates, and rates of chick growth and survival (Nettleship et al. 1984; Gaston & Hipfner 1998; Gaston et al. 2005a and b). More directly, high-Arctic seabird diet may be affected by ice conditions and related changes to marine food webs, but this has been difficult to quantify since these birds nest in remote areas and conventional seabird dietary analysis has significant limitations (Duffy & Jackson 1986; Gaston & Noble 1985). The development of stable isotope approaches to study trophic interactions in high-latitude regions provides a complementary approach to the long-term monitoring of seabird diet in particular, and the structure of Arctic marine food webs in general (Hobson et al. 1994, Hobson et al. 2004). For seabirds, this approach has been used to evaluate seabird trophic relationships (e.g. Hobson 1993; Cherel et al. 2002; Forero et al. 2005), and their role in the bioaccumulation of contaminants (Jarman et al. 1996; Buckman et al. 2004). The

isotopic analysis of archived museum materials has also revealed seabird paleodiets (Hobson & Montevecchi 1991), and long-term changes in diet associated with changes in marine predators through commercial fisheries (Thompson et al. 1995) or oceanic regime shifts (Hobson et al. 2004; Ainley et al. 2003, 2005; Becker & Bessinger 2006).

The ratios of heavier to lighter isotopes of nitrogen ($^{15}\text{N}/^{14}\text{N}$, measured as $\delta^{15}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$, $\delta^{13}\text{C}$) have been particularly useful in previous seabird dietary studies. Stable-nitrogen isotope values typically show a progressive enrichment with trophic level (Hobson & Welch 1992, Kelly 2000) whereas $\delta^{13}\text{C}$ values are less influenced by trophic position but can be used to indicate relative use by seabirds of pelagic vs. benthically linked food webs (Hobson & Welch 1992; Hobson et al. 1994). The time period over which isotope measurements integrate trophic position or foraging area depends on the metabolic rate of the tissue considered (Hobson & Clark 1992, Hobson 1993). Blood cellular fractions or muscle tissue are expected to represent diet over about a 6 week period for most medium-sized Arctic seabirds. The combined use of both isotopes measured on such tissues can thus provide a convenient means of assessing seabird diet averaged over much of the short, high-latitude breeding season.

Seabirds are important indicators of prey availability and the health of marine environments (Furness & Camphuysen 1997). Analysis of several seabird species in a single location can provide a more complete understanding of how marine food webs respond to environmental changes (Montevecchi 1993). Surface-feeding and pursuit-divers feed at different depths and together reflect prey abundance through the water column. I investigated the seabird community on Prince Leopold Island (PLI), Nunavut, Canada, to assess inter-annual dietary variation in seabirds representing different foraging methods. I sampled Thick-billed Murres (*Uria lomvia*), Northern Fulmars

(*Fulmarus glacialis*), Black-legged Kittiwakes (*Rissa tridactyla*) and Glaucous Gulls (*Larus hyperboreus*). Thick-billed Murres are pursuit divers of fish and amphipods and can reach depths of over 100 m (Gaston & Hipfner 2000). In this region, Black-legged Kittiwakes generally consume more marine invertebrates than murres (Hobson 1993) and are restricted to foraging within 1 m of the surface (Baird 1994). Northern Fulmars consume a varied diet ranging from zooplankton to scavenged marine mammal carcasses and typically forage farther offshore than either murres or kittiwakes (Hatch & Nettleship 1998). Glaucous Gulls are one of the major avian predators on PLI (Gaston & Nettleship 1981) and consume eggs and chicks of other species during their chick-rearing period (Gilchrist 2001). This diversity of foraging techniques and prey items makes PLI an ideal community in which to examine dietary variation in response to environmental change using stable isotopes. Moreover, isotopic measurements were made on seabirds at this colony in the late 1980's (Hobson 1993) thus providing a useful benchmark for our more recent measurements.

I also compared indices of individual seabird body condition with seabird tissue stable isotope values. Trade-offs between self-maintenance and chick provisioning may only be apparent in years with limited food availability (Stearns 1992). I anticipated that birds in poorer body condition, in a year with poor food availability, would be more constrained with respect to prey choice and thus be forced to exploit slower low trophic-level prey compared to birds in better body condition.

2.2 MATERIALS & METHODS

2.2.1 Field methods

Seabird tissue samples were collected at PLI (74°02'N, 90° 00'W), Nunavut, during chick-rearing (mid-July to late August), 2000 to 2003. Adult Thick-billed Murres, Northern Fulmars and Black-legged Kittiwakes were captured from cliffs and Glaucous Gull chicks from nesting areas above cliffs. Birds were weighed, and measured (flattened wing length, tarsus, culmen, and bill depth (Thick-billed Murres, Black-legged Kittiwakes), or depth at gonys and nostril (Northern Fulmars)). Blood samples (~0.5 ml) were taken from the brachial vein using a syringe and stored in equal volumes of 70% ethanol until laboratory processing (Hobson et al. 2002). Sample size varied with species and year (Table 2.1). In 2002, as part of another study (S. Jacobs & A.J. Gaston, unpubl.), 26 adult Northern Fulmars, 28 adult Black-legged Kittiwake, and 31 adult Thick-billed Murres were collected for analyses of body condition and tissues from these birds were made available to us. These birds were frozen in the field and later dissected at the University of Ottawa, Ottawa, Ontario. Muscle samples were taken for stable isotope analysis (SIA) and frozen until processing.

2.2.2 Stable isotope analysis and trophic-level calculations

Lipids tend to be depleted in ^{13}C compared with other tissues (Hobson & Clark 1992) and lipid content in seabird tissues can vary among individuals. To reduce inter-individual variation in $\delta^{13}\text{C}$ values due to differential lipid content, lipids were removed from muscle samples using 2:1 chloroform:methanol soak and rinse. Following drying, all samples were analysed in a Europa 20:20 continuous flow isotope ratio mass spectrometer (CFIRMS) interfaced with a Robo-Prep elemental analyzer at the Department of Soil Science, University of Saskatchewan. Laboratory standards, Bowhead whale (*Balaena mysticetus*) baleen and egg albumen, were placed between

every five unknowns. Measurement error has been estimated to be $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.3\text{‰}$ for $\delta^{15}\text{N}$ measurements. Stable isotope values are presented in δ (delta) notation in parts per thousand (‰) as described previously (Hobson 1993).

To evaluate long-term changes in stable isotope values of birds at PLI, muscle $\delta^{15}\text{N}$ values from Hobson (1993) were used. I converted muscle $\delta^{15}\text{N}$ values to the equivalent value in blood using the following formula:

$$D_b = (D_m - \Delta_m) + \Delta_b \quad [2.1]$$

where D_b is the equivalent $\delta^{15}\text{N}$ value of blood, D_m the measured $\delta^{15}\text{N}$ value of muscle, Δ_m = discrimination value between seabird diet and muscle (+3.4‰; Hobson et al. 1994) and Δ_b = discrimination value between seabird diet and blood (+3.1‰; Hobson & Clark 1992).

2.2.3 Body condition analyses

Several estimates of individual body condition were used to compare with individual stable isotope values in 2002: mass, mass-corrected-for structural size (Thick-billed Murres and Northern Fulmars only), carcass lipid mass and carcass lipid mass-corrected-for structural size. Body-condition indices of Glaucous Gull chicks were not calculated because I could not correct for age differences among the sample of growing birds. Morphometric data were used in Principal Component Analyses (PCA) and the first principal component (PC1) was used as an indicator of size (Jakob et al. 1996). PC1 was regressed against mass and un-standardized residuals of the regression were used as indicators of body condition as body mass corrected for structural size. Birds with positive residuals in these regressions were considered in better condition than those with negative residuals. Not all birds sampled for SIA were measured so sample sizes

for morphometric analysis were lower than the total number of individuals sampled for stable isotope values.

Carcasses collected in 2002 had lipid mass of skin, pectoral muscle, liver, and organs measured and these data were combined using PCA as described above. Here, the first principal component (PC1-lipid) was used as another estimate of body condition. PC1-lipid was regressed against PC1-size to obtain body lipid mass corrected for body size using residuals. Birds sampled for blood and muscle were considered two separate groups and PCAs performed separately for each group. For each species, average mass was compared between years.

2.2.4 Ice-cover analysis

Digital ice-cover data corresponding to a 150 km radius of PLI (Gaston & Hipfner 1998) were obtained from the Canadian Ice Archive (<http://ice-glaces.ec.gc.ca>). One week summaries were taken to represent pre-lay (May 15), laying (June 22-28) and hatching (July 20-26), 1998-2003. Ice conditions 2 years prior to 2000 were also examined for potential time-lag effects. Ice cover was estimated using ArcView Geographic Information System (GIS), Version 3.2.

2.2.5 Statistical analyses

Analysis of Variance (ANOVA) was used to examine effects of species, year and interaction between these variables on stable isotope values (Zar 1999). Where results from ANOVA were significant, Tukey's post-hoc tests were used to determine where significant differences existed among or between groups. Pearson's correlations were used to determine relationship between stable isotope values and body condition indices. Because $\delta^{13}\text{C}$ values can be correlated with $\delta^{15}\text{N}$ values, I ran Pearson's correlations to compare these values. Statistical analyses were performed using SPSS, version 12.0.

Statistical significance was arbitrarily set at 0.05. To compare 2000-2003 data with previously published stable isotope values from 1988-90, I used multiple t tests with a Bonferroni correction applied to the alpha value where necessary. Within each species, I had four comparisons of blood stable isotope values, so I used a corrected alpha value of 0.0125. Exact two-tailed p-values were calculated using the VassarStats website (<http://faculty.vassar.edu/lowry/tabs.html?#t>).

2.3 RESULTS

I excluded seven Thick-billed Murre and eight Northern Fulmars blood samples from 2002 because their stable isotope values were below invertebrate (*Parathemisto* spp.) values from the local marine food web ($9.7\text{‰} \pm 0.1\text{‰} \delta^{15}\text{N}$ and $-20.4\text{‰} \pm 0.1\text{‰} \delta^{13}\text{C}$; Hobson et al. 2002). I also excluded Glaucous Gull blood samples in 2002 because their stable isotope values were below those of Arctic cod ($14.0\text{‰} \pm 0.2\text{‰} \delta^{15}\text{N}$ and $-19.3\text{‰} \pm 0.1\text{‰} \delta^{13}\text{C}$; Hobson et al. 2002). Since these anomalous values were repeatable when the samples were reanalysed, I concluded they had been contaminated in some way. The C:N ratio of these samples were also abnormal as the carbon content tended to be higher than other blood samples, supporting the idea these samples were contaminated. Regardless, they could not be used since they fell outside the viable food web model for this location (Hobson and Welch 1992, Hobson 1993).

When all species in all years were pooled, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were correlated ($r^2 = 0.517$, $p < 0.001$, $n = 399$); however, these correlations varied with species and year. Thick-billed Murre $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were correlated when years were pooled ($r^2 = 0.609$, $p < 0.001$, $n = 140$), in 2002 ($r^2 = 0.792$, $p < 0.001$, $n = 33$), and in 2003 ($r^2 = 0.452$, $p = 0.021$, $n = 26$), but not in 2000 ($r^2 = 0.110$, $p = 0.72$, $n = 13$) or 2001 ($r^2 = 0.078$, $p = 0.53$, $n = 13$). When all years were pooled, fulmar $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were

correlated ($r^2 = 0.282$, $p = 0.002$, $n = 122$). Fulmars stable isotope values were negatively correlated in 2001 ($r^2 = -0.368$, $p = 0.038$, $n = 32$) and 2003 ($r^2 = -0.584$, $p < 0.001$, $n = 34$), and positively correlated in 2000 ($r^2 = 0.446$, $p = 0.022$, $n = 26$) and 2002 ($r^2 = 0.851$, $p < 0.001$, $n = 30$). Kittiwake $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were consistently correlated whether all years were pooled ($r^2 = 0.583$, $p < 0.001$, $n = 109$) or if each year was considered separately (2000: $r^2 = 0.731$, $p = 0.004$, $n = 13$; 2001: $r^2 = 0.502$, $p < 0.001$, $n = 47$; 2002: $r^2 = 0.884$, $p < 0.001$, $n = 20$; 2003: $r^2 = 0.854$, $p < 0.001$, $n = 29$). Glaucous gulls showed no correlation when all years were pooled ($r^2 = 0.238$, $p = 0.22$, $n = 28$) or within any year (2000: $r^2 = 0.145$, $p = 0.76$, $n = 7$; 2001: $r^2 = 0.355$, $p = 0.20$, $n = 15$; 2003: $r^2 = 0.397$, $p = 0.44$, $n = 6$).

2.3.1 Trophic level variation

Stable isotope values of seabird blood were influenced by species ($\delta^{15}\text{N}$: $F_{3, 386} = 78.14$, $p < 0.001$; $\delta^{13}\text{C}$: $F_{3, 386} = 56.64$, $p < 0.001$) and year ($F_{3, 386} = 15.80$, $p < 0.001$; $\delta^{13}\text{C}$: $F_{3, 386} = 53.76$, $p < 0.001$) and there was an interaction between these two variables ($\delta^{15}\text{N}$: $F_{9, 386} = 13.72$, $p < 0.001$; $\delta^{13}\text{C}$: $F_{9, 386} = 12.26$, $p < 0.001$).

Overall, blood $\delta^{15}\text{N}$ values increased in the order Northern Fulmar < Black-legged Kittiwake < Thick-billed Murre < Glaucous Gull (Tables 2.1 and 2.2; Figure 2.1). Fulmars and murrees differed in all years (all $p < 0.001$) and Glaucous Gulls were enriched in ^{15}N compared with all species in all years (2000: all $p < 0.001$; 2001: all $p < 0.001$; 2003: all $p \leq 0.003$). Black-legged Kittiwake $\delta^{15}\text{N}$ values did not differ from those of Northern Fulmars in 2000 ($p = 0.94$) or Thick-billed Murre values in 2002 ($p = 0.78$) or 2003 ($p = 0.74$).

Table 2.1: Mean (\pm S.E.) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for Black-legged Kittiwakes (BLKI), Glaucous Gulls (GLGU), Northern Fulmars (NOFU), and Thick-billed Murres (TBMU) blood and muscle samples, Prince Leopold Island, Nunavut. Data from 1998-90 from Hobson (1993).

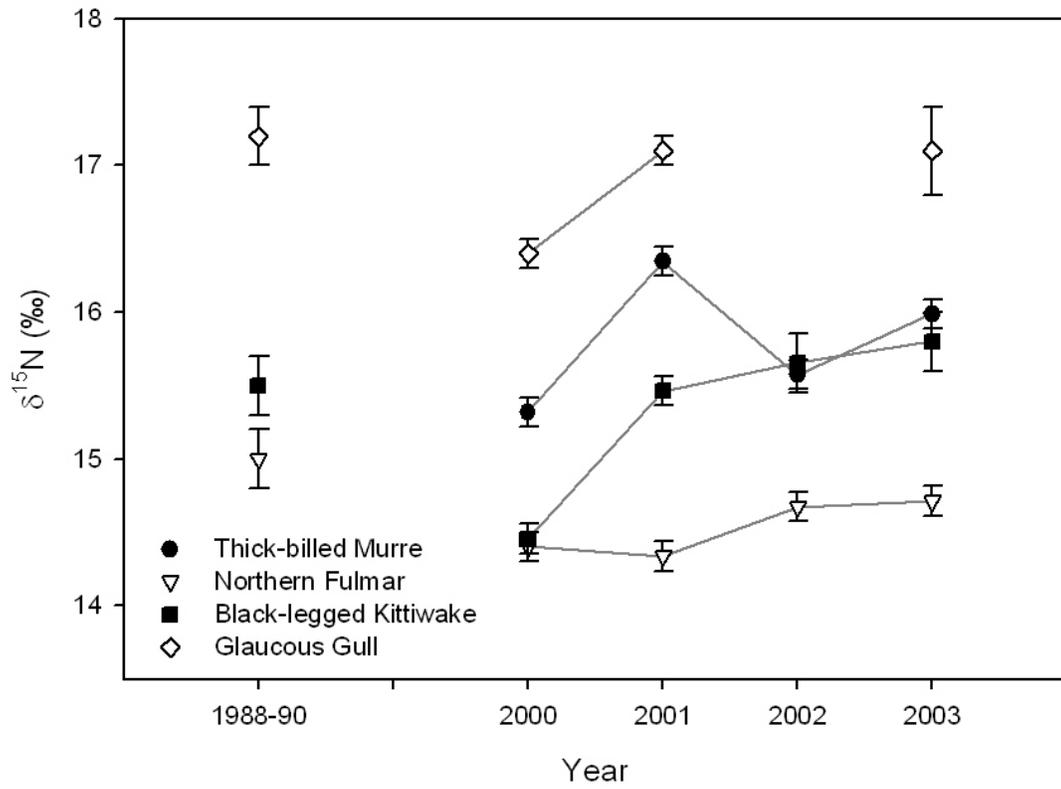
Species	Tissue	Year	<i>n</i>	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)
BLKI	blood	1988-90	20	15.0 ± 0.2	
		2000	13	14.5 ± 0.1	-21.2 ± 0.1
		2001	47	15.5 ± 0.1	-20.3 ± 0.1
		2002	20	15.7 ± 0.2	-21.1 ± 0.2
		2003	29	15.8 ± 0.2	-20.9 ± 0.1
	muscle	1988-90	20	15.3 ± 0.2	
		2002	28	14.5 ± 0.2	-19.9 ± 0.1
GLGU	blood	1988-90	22	17.2 ± 0.2	
		2000	7	16.4 ± 0.1	-19.0 ± 0.1
		2001	15	17.1 ± 0.1	-18.8 ± 0.1
		2003	6	17.1 ± 0.2	-19.3 ± 0.3
	muscle	1988-90	22	17.5 ± 0.7	
NOFU	blood	1988-90	25	15.0 ± 0.2	
		2000	26	14.4 ± 0.1	-20.4 ± 0.1
		2001	32	14.3 ± 0.1	-19.7 ± 0.1
		2002	29	14.7 ± 0.1	-20.0 ± 0.1
		2003	34	14.7 ± 0.1	-20.0 ± 0.1
	muscle	1988-90	25	15.3 ± 0.2	
		2002	26	13.4 ± 0.3	-19.5 ± 0.1
TBMU	blood	1988-90	36	15.5 ± 0.2	
		2000	13	15.3 ± 0.1	-19.1 ± 0.1
		2001	68	16.4 ± 0.1	-19.0 ± 0.1
		2002	32	15.8 ± 0.1	-19.7 ± 0.2
		2003	26	16.0 ± 0.1	-19.5 ± 0.1
	muscle	1988-90	36	15.8 ± 0.2	
		2002	31	14.9 ± 0.1	-18.5 ± 0.1

Table 2.2: Probability values, from Tukey’s multiple comparison tests, for inter-year comparisons of seabird blood samples, Prince Leopold Island, Nunavut, 2000-2003.

Species	Isotope	Years	<i>p</i>
Black-legged Kittiwake	$\delta^{15}\text{N}$	2000-2001	< 0.001
		2000-2002	< 0.001
		2000-2003	< 0.001
		2001-2002	0.79
		2001-2003	0.26
		2002-2003	0.92
	$\delta^{13}\text{C}$	2000-2001	< 0.001
		2000-2002	0.88
		2000-2003	0.35
		2001-2002	0.001
		2001-2003	0.008
		2002-2003	0.76
Glaucous Gull	$\delta^{15}\text{N}$	2000-2001	0.70
		2000-2003	0.74
		2001-2003	0.04
	$\delta^{13}\text{C}$	2000-2001	0.54
		2000-2003	0.47
		2001-2003	0.06
Northern Fulmar	$\delta^{15}\text{N}$	2000-2001	0.98
		2000-2002	0.37
		2000-2003	0.22
		2001-2002	0.15
		2001-2003	0.07
		2002-2003	0.99

Northern Fulmar	$\delta^{13}\text{C}$	2000-2001	< 0.001
		2000-2002	0.05
		2000-2003	0.07
		2001-2002	0.22
		2001-2003	0.11
		2002-2003	0.99
Thick-billed Murre	$\delta^{15}\text{N}$	2000-2001	< 0.001
		2000-2002	0.01
		2000-2003	< 0.001
		2001-2002	< 0.001
		2001-2003	< 0.001
		2002-2003	0.19
	$\delta^{13}\text{C}$	2000-2001	0.87
		2000-2002	0.002
		2000-2003	0.04
		2001-2002	< 0.001
		2001-2003	< 0.001
		2002-2003	0.74

Figure 2.1: Inter-annual variation in derived (1989-90) or measured (2000-2003) $\delta^{15}\text{N}$ (mean \pm S.E.) of seabird blood, Prince Leopold Island, Nunavut, 1988-2003.

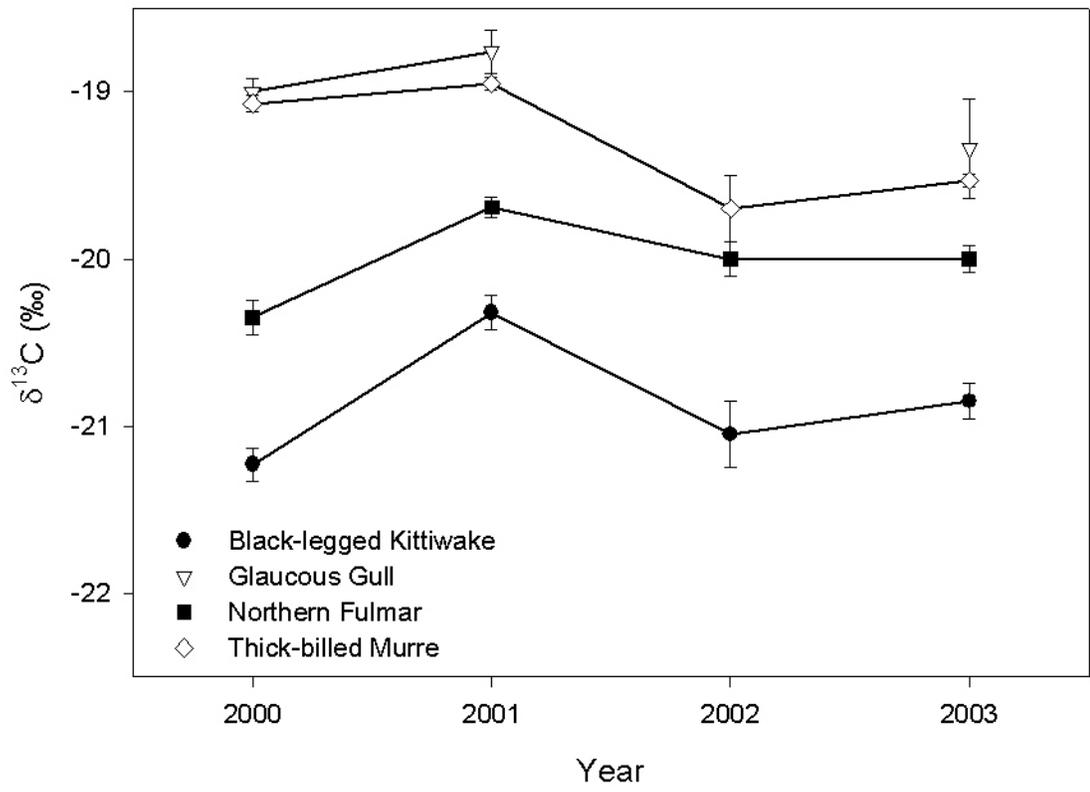


Black-legged Kittiwakes were depleted in ^{13}C compared with the other species in all years (all comparisons $p < 0.001$; Tables 2.1 and 2.2; Figure 2.2). Northern Fulmars were enriched compared with kittiwakes but depleted compared with the other species (all comparisons $p \leq 0.012$) except in 2002, when they were not significantly different than murre (p = 0.405). There were no significant differences in $\delta^{13}\text{C}$ values between Thick-billed Murres and Glaucous Gulls ($p \geq 0.510$).

Blood stable isotope values showed species-specific patterns of enrichment with year (Tables 2.1 and 2.2; Figures 2.1 and 2.2). Northern Fulmars showed no difference in $\delta^{15}\text{N}$ values among years (2000-2001: $p = 0.979$; 2000-2002: $p = 0.366$; 2000-2003: $p = 0.225$; 2001-2002: $p = 0.153$; 2001-2003: $p = 0.073$; 2002-2003: 0.995). Kittiwakes were depleted in ^{15}N in 2000 compared with other years ($p < 0.001$ for all comparisons) and there were no differences among $\delta^{15}\text{N}$ values in 2000, 2002 and 2003 (2001-2002: $p = 0.789$; 2001-2003: $p = 0.260$; 2002-2003: $p = 0.918$). Thick-billed Murres' $\delta^{15}\text{N}$ values were lowest in 2000 (2000-2001: $p < 0.001$; 2000-2002: $p = 0.014$; 2000-2003: $p < 0.001$) and highest in 2001 (2000-2001: $p < 0.001$; 2001-2002: $p < 0.001$; 2001-2003: $p < 0.001$). There was no difference in murre $\delta^{15}\text{N}$ values between 2002 and 2003 ($p = 0.193$). Glaucous Gull $\delta^{15}\text{N}$ values in 2000 did not differ from those in 2001 ($p = 0.703$) or 2003 ($p = 0.742$), but 2001 values were lower than those in 2003 ($p = 0.039$).

In 2002, species differed in their muscle $\delta^{13}\text{C}$ ($F_{2, 91} = 155.0$, $p < 0.001$) and $\delta^{15}\text{N}$ ($F_{2, 91} = 20.0$, $p < 0.001$) values (Table 2.1). Thick-billed Murre and Northern Fulmar muscle $\delta^{15}\text{N}$ values did not differ ($p = 0.136$) and were higher than those of Black-legged Kittiwake values ($p < 0.001$ for both comparisons). Murres were enriched in ^{13}C compared with both fulmars ($p < 0.001$) and kittiwakes ($p < 0.001$) and fulmars were enriched compared with kittiwakes ($p < 0.001$).

Figure 2.2: Inter-annual $\delta^{13}\text{C}$ (mean \pm S.E.) variation of seabird blood, Prince Leopold Island, Nunavut, 2000-2003.



Northern Fulmar blood was depleted in ^{15}N compared to 1988-90, in 2000 (Table 2.3; $t = 2.6833$, d.f. = 49, $p = 0.010$), and 2001 ($t = 3.1305$, d.f. = 55, $p = 0.003$), but not in 2002 ($t = 1.3416$, d.f. = 52, $p = 0.186$) or 2003 ($t = 1.3416$, d.f. = 57, $p = 0.185$). Black-legged Kittiwakes in 2003 ($t = 2.8284$, d.f. = 47, $p = 0.007$) and Thick-billed Murres in 2001 ($t = 4.0249$, d.f. = 102, $p < 0.001$) were enriched in ^{15}N compared with the older stable isotope values but other years did not differ from historic values (Table 2.3). Glaucous Gull chicks were depleted in ^{15}N in 2000 ($t = 3.5777$, d.f. = 27, $p = 0.001$) compared with 1988-90 but 2001 ($t = 0.4472$, d.f. = 35, $p = 0.658$) and 2003 ($t = 0.3536$, d.f. = 26, $p = 0.726$), values did not differ. Muscle $\delta^{15}\text{N}$ values were significantly lower in 2002 compared with 1988-90 in all species (TBMU: $t = 2.8284$, d.f. = 46, $p = 0.007$; NOFU: $t = 5.2697$, d.f. = 49, $p < 0.001$; BLKI: $t = 4.0249$, d.f. = 65, $p < 0.001$).

2.3.2 Body condition

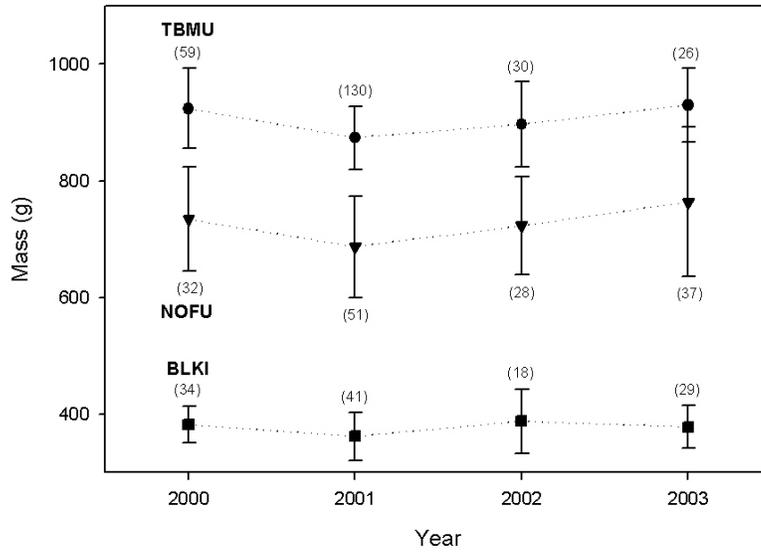
Mass of Thick-billed Murres differed among years (Figure 2.3; $F_{3, 241} = 12.6$, $p < 0.001$) with average mass lower in 2001 than in 2000 ($p < 0.001$) and 2003 ($p < 0.001$). Average mass in 2002 did not differ from the other years (2000: $p = 0.204$; 2001: $p = 0.224$; 2003: $p = 0.185$). Mass of Northern Fulmars also differed among years ($F_{3, 144} = 4.56$, $p = 0.004$) with lowest values in 2001 and highest in 2003. No mass changes were found among years for Black-legged Kittiwakes ($F_{3, 118} = 2.51$, $p = 0.062$).

Regressions between body size (as indicated by PC1 scores; Appendix 1) and mass were significant for Northern Fulmars ($r^2 = 0.292$, $p < 0.001$, $n = 24$) but not for Black-legged Kittiwakes ($r^2 = 0.119$, $p = 0.072$, $n = 16$) or Thick-billed Murres ($r^2 = 0.054$, $p = 0.099$, $n = 29$). Therefore, I only used mass corrected for size as an index of body condition for fulmars. Regressions of PC1-lipid mass corrected for PC1-size were not significant for any species and therefore were not used as a body condition indicator.

Table 2.3: Probability values from multiple t tests for inter-year comparisons of blood $\delta^{15}\text{N}$ values of seabirds, Prince Leopold Island, Nunavut, 1988/90-2003. 1988/90 data from Hobson (1993). Significant differences, at a corrected alpha value of 0.0125, indicated with *.

Species	Years	<i>p</i>
Black-legged Kittiwake	1988/90-2000	0.03
	1988/90-2001	0.03
	1988/90-2002	0.02
	1988/90-2003	0.007*
Glaucous Gull	1988/90-2000	0.001*
	1988/90-2001	0.66
	1988/90-2003	0.73
Northern Fulmar	1988/90-2000	0.010*
	1988/90-2001	0.003*
	1988/90-2002	0.19
	1988/90-2003	0.18
Thick-billed Murre	1988/90-2000	0.38
	1988/90-2001	< 0.001*
	1988/90-2002	0.18
	1988/90-2003	0.03

Figure 2.3: Mass (mean \pm S.D.) of Thick-billed Murres (TBMU), Northern Fulmars (NOFU), and Black-legged Kittiwakes (BLKI), Prince Leopold Island, Nunavut, 2000 – 2003. Sample size is indicated in parentheses.



Mass was correlated with blood $\delta^{15}\text{N}$ values in Thick-billed Murres (Figure 2.4; $r^2 = 0.140$, $n = 28$ $p = 0.046$) and with muscle $\delta^{15}\text{N}$ values in Black-legged Kittiwakes (Figure 2.5; $r^2 = 0.143$, $n = 27$ $p = 0.047$). For all species, there was no correlation between body condition indices and blood $\delta^{13}\text{C}$ values ($p > 0.28$ for all comparisons).

2.3.3 Ice cover

Heavy ice remained in the area of PLI in June 1998, 2001 and 2002, and into July in 2001. This was unlike in 1999, 2000 and 2003 when ice break-up was underway before laying began (Figure 2.6). Ice cover in May 2000 was much lower than other years.

2.4 DISCUSSION

The four species of seabirds examined on PLI had different patterns of blood stable isotope values which were likely linked to differences in foraging behaviours influenced by ice conditions. Thick-billed Murres and Black-legged Kittiwakes both showed a significant increase in trophic level from 2000 to 2001. Ice cover in 2000 was light, and ice break-up was earlier that year than in any of the other 7 years I compared; in contrast, ice cover in 2001 was heavy and remained so until late in the season. Distant, ill-defined ice edges in 2000 may have prevented murres and kittiwakes from taking fish. Glaucous Gull chicks also showed a trend of increased trophic levels from 2000 to 2001, likely a reflection of the increased trophic levels of kittiwakes and murres; adult gulls are the major predator at seabird colonies and feed their chicks a similar diet (Gilchrist 2001). Because fulmars normally forage at a greater distance from the colony and/or on different prey items, they may not have been affected by the distant ice edge.

Offshore foragers, such as Northern Fulmars, and pursuit divers, such as Thick-billed Murres, presumably have greater options for finding prey than nearshore, surface

Figure 2.4: Mass correlated with blood $\delta^{15}\text{N}$ values, Thick-billed Murres, Prince Leopold Island, Nunavut, 2002. $n = 28$ $p = 0.046$.

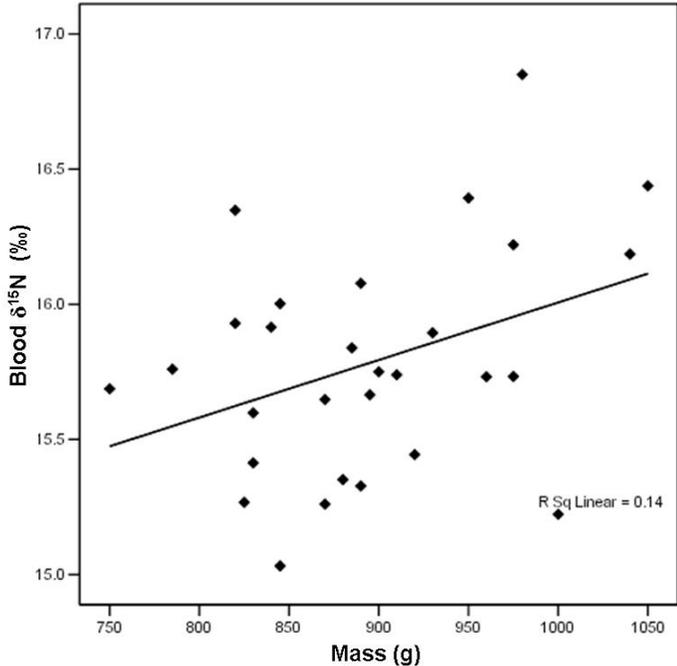


Figure 2.5: Mass correlated with muscle $\delta^{15}\text{N}$ values, Black-legged Kittiwakes, Prince Leopold Island, Nunavut, 2002. $n = 27$ $p = 0.047$.

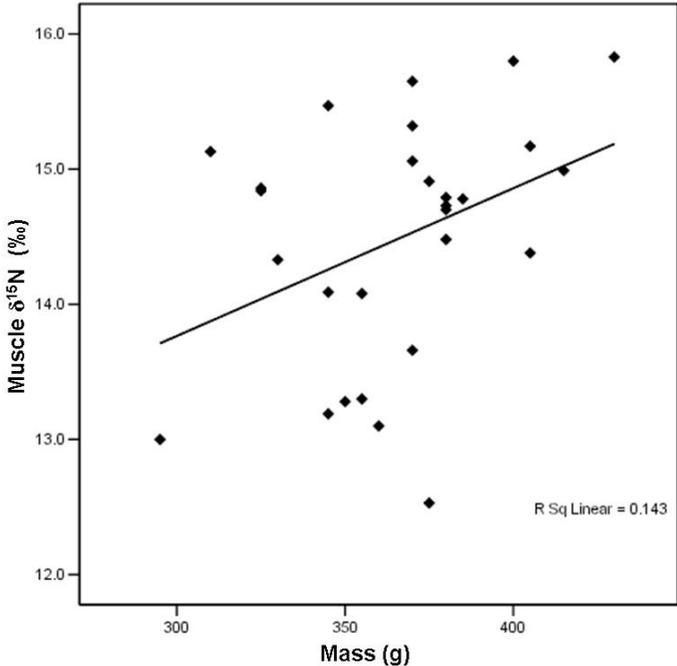
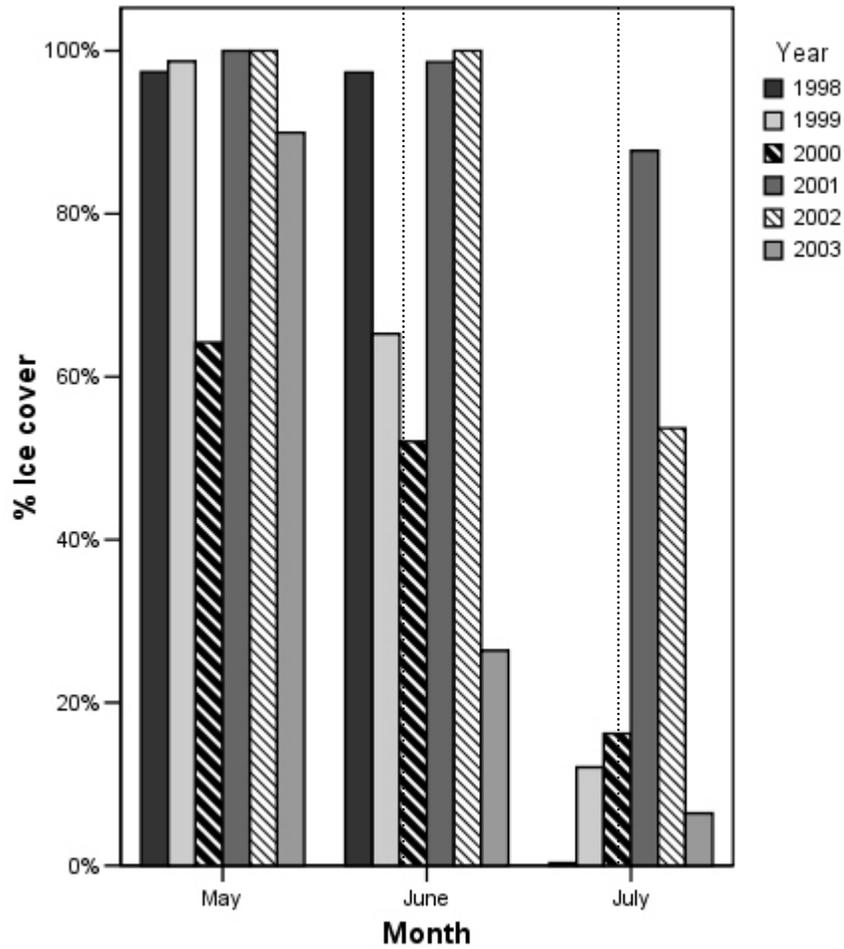


Figure 2.6: Ice cover within 150 km radius of Prince Leopold Island, Nunavut, 1998 – 2003, showing highly variable ice conditions. Summarized from the Canadian Ice Archive (<http://ice-glaces.ec.gc.ca>).



foragers like kittiwakes, making them less sensitive to fluctuations in prey availability (Montevecchi 1993). However, Thick-billed Murres on PLI showed the most variation in stable isotope values among years. Most data gathered on murre diet in the Arctic come from observations of chick feeding, and parents may not have the ability to vary chick diet as much as their own. Adult diet, according to stomach content analysis, is more variable and includes lower trophic-level items such as euphausiids and amphipods (Gaston & Nettleship 1981). Prey items brought to chicks tend to be large and energy-rich fish such as capelin and Arctic cod, and the proportion of low trophic level items is consistently small (Gaston & Nettleship 1981; Woo 2002). For instance, this pattern is found in Barents Sea Thick-billed Murres which brought fish for their chicks while feeding themselves on euphausiids (Mehlum et al. 1998).

Heavy ice conditions in 2002 around PLI reduced breeding success of most species (Gaston et al. 2005), and our isotopic analyses indicated Thick-billed Murres had the lowest trophic level in 2002. Clearly, seabirds that year had difficulty obtaining enough food for successful breeding but this difficulty was only reflected in diet of adult murres. Both 2002 and 2001 had heavy ice and late ice break-up and low adult mass (also see Gaston et al. 2005) but murre trophic level and foraging locations were affected only in 2002. A lag between climatic conditions and seabird diet has been reported previously for Atlantic Puffins (*Fratercula arctica*) in Norway. Breeding birds preferred first-year herring, and abundance of this age class was affected by sea surface temperatures early in the season, before puffins bred (Durant et al 2003). Thick-billed Murres prefer 1- to 2-year old Arctic cod (Gaston & Noble 1985; Woo 2002), and ice effects on Arctic cod recruitment may result in a lag of 1 to 2 years before seabird prey is influenced. Ice cover in 2000 was low in May which may have negatively affected

Arctic cod hatched that year resulting in poor Arctic cod availability 2 years later in 2002. Alternatively, two successive heavy ice years, 2001 and 2002, may have resulted in cumulative effects on breeding seabirds at PLI. Adults may have been able to buffer poor prey availability in 2001 by working harder to maintain normal chick growth at the cost of their own body mass as was observed by Gaston et al. (2005) and adult diet *per se* may not have been affected. In the second heavy ice year, 2002, adults clearly switched to lower trophic-level prey which may have enabled them to maintain their body condition (as indicated by body mass) but at the cost of reproductive success, as chick mass or number of chicks fledged declined. Seabirds, like other long-lived species, should maximize life-time reproductive success and therefore, accept lower risk while breeding compared to short-lived species (Ricklefs 1990). Conditions in 2002 may have been bad enough for parents to trade off chick growth for long-term survival.

Overall, seabird stable isotope values have remained relatively constant since 1988 with the exception of Northern Fulmars, which have declined in trophic level. Northern Fulmars feed on a wider variety of prey items than the other seabirds on PLI and changes in the availability of prey items other than euphausiids and Arctic cod may be responsible for the observed $\delta^{15}\text{N}$ decline. Northern Fulmars on PLI are known to include various other crustaceans (e.g. *Calanus hyperboreus* and *Onisimus* spp.) and squid in their diet (D.N. Nettleship unpubl. in Hatch & Nettleship 1998), all of which are lower in trophic level than Arctic cod. Northern Fulmars may have increased their intake of these prey items since 1988-1990, and therefore decreased in trophic level. SIA of eggs, in association with contaminant analysis, also showed that female pre-laying Northern Fulmars fed at a lower trophic level compared to Thick-billed Murres and Black-legged Kittiwakes averaged over 1975 to 1998 (Braun et al. 2001).

In 2002, when Thick-billed Murres decreased in blood $\delta^{13}\text{C}$ values and trophic level, Black-legged Kittiwake and Northern Fulmar values were unchanged. However, 2002 was a year of poor reproductive success, and especially low chick growth rates for all species, suggested reduced prey availability for all species not just murres. Only in extremely poor food years do pursuit divers suffer from reduced reproductive success (Montevecchi 1993).

I was particularly interested in knowing if individuals of different body condition responded differently to the anomalous situation in 2002. For murres and kittiwakes, body condition was weakly correlated with trophic level but not foraging location. Birds in better condition tended to feed at a higher trophic level. This suggests that obtaining higher trophic-level prey such as Arctic cod may require more effort and hence favour birds in better body condition. Alternatively, the consumption of higher trophic-level prey may result in birds increasing or maintaining their body condition compared to birds feeding on lower trophic-level prey. Although euphausiids have a higher lipid percentage than Arctic cod (Bradstreet & Brown 1985; Percy & Fife 1981; Falk-Petersen et al. 2000), their small size may make it more energy efficient for murres to focus on larger cod, which suggests feeding on high trophic-level prey results in better body condition.

Both ^{13}C and ^{15}N can show trophic enrichment (Michener & Schnell 1994) although this is not always the case with ^{13}C (Hobson et al. 1994). Our results show the strength and direction of this correlation can vary with species and year. Decoupling may be related to how stable isotopes are routed from the diet to the birds' tissues. Nitrogen generally comes from dietary protein or, if an animal is nutritionally stressed, can come from recycling of its own body protein (Hobson et al. 1993). Carbon in a

consumer can come from a number of dietary sources including lipids, carbohydrates and glycogenic amino acids (Focken & Becker 1998). Lipids and carbohydrates may also be used as energy sources, bypassing integration into consumer tissues (Gannes et al. 1997). The decoupling of ^{13}C and ^{15}N that I observed may have happened because carbon and nitrogen came from different dietary sources. Thick-billed Murres had a decoupling of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in 2000 and 2001, when they had, the lowest and highest $\delta^{15}\text{N}$ values, respectively. Lipids are significantly depleted in ^{13}C compared with other macromolecules (Hobson & Clark 1992) and particularly lipid-rich high trophic level prey in 2001 may explain the decoupling of ^{13}C and ^{15}N in that year. In 2000, prey items were likely of low trophic level and relatively low in lipids.

My study has revealed the potential for using stable isotope analyses for long-term monitoring of seabird diets and understanding the ways in which seabirds may respond to changes in environmental conditions and putative shifts in prey availability. At remote high Arctic locations, the relatively simple sampling of blood is more feasible logistically than conventional dietary analyses which can only typically provide information on chick and not adult diets. Here, I was able to show that not all individuals within a colony respond in the same way to such changes in prey availability. Moreover, I have provided evidence that in two species, foraging strategy was partially explained by body condition. Current climate change models for the high Arctic predict less ice cover and greater periods of open water. As discussed by Gaston et al. (2005), such conditions may well favour seabirds by opening up more foraging area. However, without an understanding of how prey availability may be influenced by such conditions, especially the abundance of specific age classes of high trophic-level prey like Arctic cod, such predictions may prove erroneous. Future models of Thick-billed Murre

response to climate change should incorporate adult diet information in addition to demographic and breeding success information.

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CHAPTER 3: LOSS OF DIETARY SPECIALIZATION AMONG BREEDING THICK-BILLED MURRES (*URIA LOMVIA*) AT A LOW ARCTIC COLONY: A CONSEQUENCE OF CHANGES IN PREY COMPOSITION?

3.1 INTRODUCTION

Chick rearing is one of the most energetically costly periods for adult birds because they must forage for both themselves and their offspring (Drent & Daan 1980). Pursuit-diving seabirds, which often breed in colonies and located far from their foraging grounds (Lack 1968), have increased flight costs due to high wing loading and therefore expend considerable energy during chick-rearing (Pennycuick 1987). Norberg (1981) suggested that chick-rearing birds may adaptively reduce their body mass to reduce wing loading. However, to maintain chick development, parents must increase foraging effort with chick age (Croll et al. 1991) and adjust to increased energy demands without further weight loss. Niizuma et al. (2002) proposed several mechanisms whereby adult birds may increase available energy without mass loss including increasing the size of energy-supplying organs (e.g. Karasov 1996), increasing digestive efficiency (Afik & Karasov 1995; Dykstra & Karasov 1992), a cellular change in muscle fibers (Driedzic et al. 1993) and diet change from low- to high-quality prey.

On Coats Island, Nunavut, Canada, previous studies reported adaptive mass loss in Thick-billed Murres (*Uria lomvia*; Croll et al. 1991; Gaston & Perin 1993), whereby adults lost mass at hatching and mass remained low for the duration of chick-rearing; parents with chicks flew more than incubating birds and their lower mass saved energy.

In the late 1990s, Woo (2002) found specialist murrelets on Coats Island which fed their chicks from a more limited range of prey than consumed by the colony generally. Specialists' chick diets consisted of proportionally more benthic zoarcids and sculpins (Cottidae) than pelagic Arctic cod (*Boreogadus saida*) and capelin (*Mallotus villosus*). Since then, the forage fish composition around Coats Island has shifted as southern species, such as capelin and sandlance (*Ammodytes* spp.), have replaced more northern species, like Arctic cod, sculpins and zoarcids, in the diets of chicks (Gaston et al. 2003). My objectives were to determine if breeding murrelets at Coats Island changed diet as the season progressed in order, presumably, to compensate for increased energy demands of chick rearing, and to determine how diets of individuals were related to the diets provided to chicks in parent-offspring pairs. Adult diet information was missing from Woo's (2002) study because these diets could not be determined by conventional means. I used stable isotope methods that allowed me to monitor both adult and chick trophic patterns throughout the breeding period. Measurements of stable isotopes of nitrogen ($^{15}\text{N}/^{14}\text{N}$, referred to as $\delta^{15}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$, or $\delta^{13}\text{C}$) are often used in studies of seabird foraging ecology (e.g. Ainley et al. 2003; Cherel et al. 2002, Forero et al. 2004; Hodum & Hobson 2000; Hobson et al. 2002) because they offer several advantages, especially when combined with traditional methods of dietary analysis. Although there can be trophic enrichment in $\delta^{13}\text{C}$ (Hobson et al. 1994), seabirds that forage on benthic species tend to be enriched in ^{13}C compared with pelagic foragers (Hobson & Welch 1992). In Arctic ecosystems, $\delta^{15}\text{N}$ values in consumers increase by about 3.8‰ per trophic level (Hobson & Welch 1992) which allows estimation of consumer trophic position. An advantage to applying stable isotope methods in high Arctic systems is that food webs tend to be relatively simple and dietary options limited.

Recently, SIA has been used to investigate individual diet specialization in generalist predator species (Bolnick et al. 2003; Inger et al. 2006). A generalist predator population may be composed of many individuals that each eat a varied diet, so the stable isotopic variance of this population would be relatively low. Alternatively, the generalist population may be composed of a number of distinct sub-groups that tend to prefer one prey type. The range of stable isotope values of the population would then reflect the stable isotope differences in the prey species and could be comparatively large. Stable isotopic differences between benthic zoarcoids and sculpins, and pelagic capelin and Arctic cod (Hobson & Welch 1992), allows dietary insights using stable isotope methodology and may be able to determine to what extent specialists may still exist in the Coats Island population following the shift in prey availability and composition in recent years. At the population level, high variance in stable isotope values of seabird tissues would suggest higher levels of dietary specialization among individuals compared with low levels of variance.

Based on prior research into murre chick diets in the Arctic (Hobson 1993), I predicted that chicks would be fed at a higher trophic level than their parents and that adults would reduce the proportion of invertebrates in their diet through the breeding season. If specialists remain in this murre population, I expected to see a large range in stable isotope values, $>2\text{‰}$ (Bolnick et al. 2003; Podlesak et al. 2005).

3.2 MATERIALS & METHODS

3.2.1 Field methods

Twelve adult breeding Thick-billed Murres were sampled for blood three times through the breeding season (Table 3.1) on Coats Island, Nunavut, 2004. Sampling periods corresponded with incubation (June 27-29), and early (July 19-22) and late (August 8-9)

chick rearing. Blood samples (~0.5 ml adults; ~0.3 ml chicks) were taken from the brachial vein using a syringe and stored in equal volumes of 70% ethanol until laboratory processing (Hobson et al. 2002). Fourteen family groups, each consisting of two parents and their one chick, and not including serially sampled individuals, were also sampled during late chick rearing (August 2-3 – 6 families, August 7 – 8 families). I divided parents into two groups based on time of capture because females incubate mainly at night and males during the day (Gaston & Hipfner 2000). However, most birds were caught within an hour of their mate so it was unlikely that groups were exclusively male or female.

3.2.2 Prey base

No stable isotope analysis has been conducted on the prey species of Coats Island murre; however, SIA in Newfoundland and in the high Arctic allowed us to estimate relative trophic levels of the major prey species. Capelin, the most common prey item brought to chicks on Coats Island (Gaston et al. 2003), fed at a lower trophic level than Arctic cod in Newfoundland and all fish were enriched in ^{15}N compared with invertebrates (amphipods, euphausiids, and mysids; Sherwood & Rose 2005). In the high Arctic, young-of-the-year (YOY) Arctic cod and euphausiids fed at similar trophic levels, lower than adult Arctic cod or other fish (Hobson & Welch 1992).

3.2.3 Stable isotope analysis

Blood samples were freeze-dried and analysed in a Europa 20:20 continuous flow isotope ratio mass spectrometer (CFIRMS) interfaced with a Robo-Prep elemental analyzer at the Department of Soil Science, University of Saskatchewan. Laboratory standards, Bowhead Whale (*Balaena mysticetus*) baleen and egg albumen, were placed between every five unknowns. Measurement error was estimated to

Table 3.1: Average (\pm S.E.) mass and blood stable isotope values of Thick-billed Murres, Coats Island, Nunavut, 2004.

DATE	GROUP	<i>n</i>	MASS	$\delta^{13}\text{C}$ (\pm S.E.)	$\delta^{15}\text{N}$ (\pm S.E.)
June 27-29	Adult		1039g \pm 16g	-18.8‰ \pm 0.03‰*	15.3‰ \pm 0.07‰*
July 19-22	Adult	12	1082g \pm 13g	-19.2‰ \pm 0.03‰*	15.7‰ \pm 0.07‰*
August 8-9	Adult		945g \pm 12g*	-19.6‰ \pm 0.04‰*	16.1‰ \pm 0.06‰*
August 2-7	Chick	14		-19.3‰ \pm 0.09‰	16.0‰ \pm 0.14‰
	Parent	28		-19.5‰ \pm 0.04‰	16.0‰ \pm 0.04‰

* significantly different from other sampling periods, $p < 0.001$

be $\pm 0.1\%$ for $\delta^{13}\text{C}$ and $\pm 0.3\%$ for $\delta^{15}\text{N}$ measurements. Stable isotope values are presented in δ (delta) notation in parts per thousand (‰) relative to the Vienna PeeDee Belemnite (VPDB) and atmospheric AIR for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values as described previously (Hobson 1993).

3.2.4 Statistical analyses

Repeated-measures Analysis of Variance (ANOVA) was used to compare stable isotope and mass changes in serially sampled individuals. Difference between sampling times were assessed using paired-sample t tests (Zar 1999). Adult and chick values were pooled to enable comparison with previous research. One-way ANOVAs were used to assess differences between pooled adult and chick stable isotope values. Nested ANOVAs were used to determine the effect of age on stable isotope values within families. Homogeneity between chick and adult variance was compared using the Levene statistic, and F ratios were used to compare published variances of adult and chick Common Tern (*Sterna hirundo*) stable isotope values (Nisbet et al. 2002) with my chick variances (Zar 1999). Pearson correlations were used to compare individual parent and chick stable isotopes. Statistics were analyzed using SPSS, Version 12.0. Statistical significance was arbitrarily set at 0.05.

3.3 RESULTS

3.3.1 Serially sampled individuals

Serially sampled adult murrelets showed significant differences in stable isotope values among sampling periods (Table 3.1; $\delta^{15}\text{N}$: $F_{2,22} = 60.5$, $p < 0.001$; $\delta^{13}\text{C}$: $F_{2,22} = 169.2$, $p < 0.001$; paired t tests all $p < 0.001$). Birds became enriched in ^{15}N (Figure 3.1; $r^2 = 0.702$, $p < 0.001$) and depleted in ^{13}C (Figure 3.1; $r^2 = 0.875$, $p < 0.001$) through the

season. As expected, body mass of adults was lowest during late chick rearing (Figure 3.2; $F_{2,22} = 35.1$, $p < 0.001$; paired t tests $p < 0.007$).

3.3.2 Family patterns

Stable isotope values of adults and chicks did not differ when families were pooled ($\delta^{15}\text{N}$: $F_{1,40} = 0.010$, $p = 0.92$; $\delta^{13}\text{C}$: $F_{1,40} = 2.331$, $p = 0.14$) nor were there differences between families ($\delta^{15}\text{N}$: $F_{13,14} = 1.5$, $p = 0.23$; $\delta^{13}\text{C}$: $F_{13,14} = 1.67$, $p = 0.18$). However, within families, chick $\delta^{15}\text{N}$ values were lower than those of adults (Figure 3.3; $F_{14,14} = 2.47$, $p = 0.05$) but $\delta^{13}\text{C}$ values did not differ between parents and chicks (Figure 3.4; $F_{14,14} = 1.61$, $p = 0.19$). Adult variance in $\delta^{15}\text{N}$ values was less than that for chicks (Appendix 2; Levene statistic $_{1,40} = 11.101$, $p = 0.002$), but adult and chick $\delta^{13}\text{C}$ variances did not differ (Levene statistic $_{1,40} = 1.974$, $p = 0.17$). Parent $\delta^{15}\text{N}$ values showed no correlation with chick $\delta^{15}\text{N}$ values (Parent A: $r^2 = -0.004$, $p = 0.99$, $n = 14$; Parent B: $r^2 = 0.049$, $p = 0.87$, $n = 14$) or $\delta^{13}\text{C}$ values (Parent A: $r^2 = 0.232$, $p = 0.42$, $n = 14$; Parent B: $r^2 = 0.085$, $p = 0.77$, $n = 14$). Our chick blood $\delta^{15}\text{N}$ variance was lower than chick and adult feather $\delta^{15}\text{N}$ variance published for Common Terns (Nisbet et al. 2002) (COTE chick variance-TBMU chick variance: $F_{15,13} = 4.44$, $p = 0.004$; COTE adult variance-TBMU chick variance: $F_{19,13} = 5.71$, $p < 0.001$).

3.4 DISCUSSION

3.4.1 Adult trophic level

During the breeding season, adult Thick-billed Murres increased their dietary trophic level and consumed a higher proportion of pelagic prey. Adult body mass was lowest during late chick-rearing, suggesting murres may alter their trophic level and behaviour in addition to adjusting their mass to compensate for the increased energy demands of chick-rearing (Croll et al. 1991).

Figure 3.1: Blood stable isotope values (mean \pm SE) of serially sampled adult Thick-billed Murres, Coats Island, 2004. $n = 12$. Dates represent sampling period.

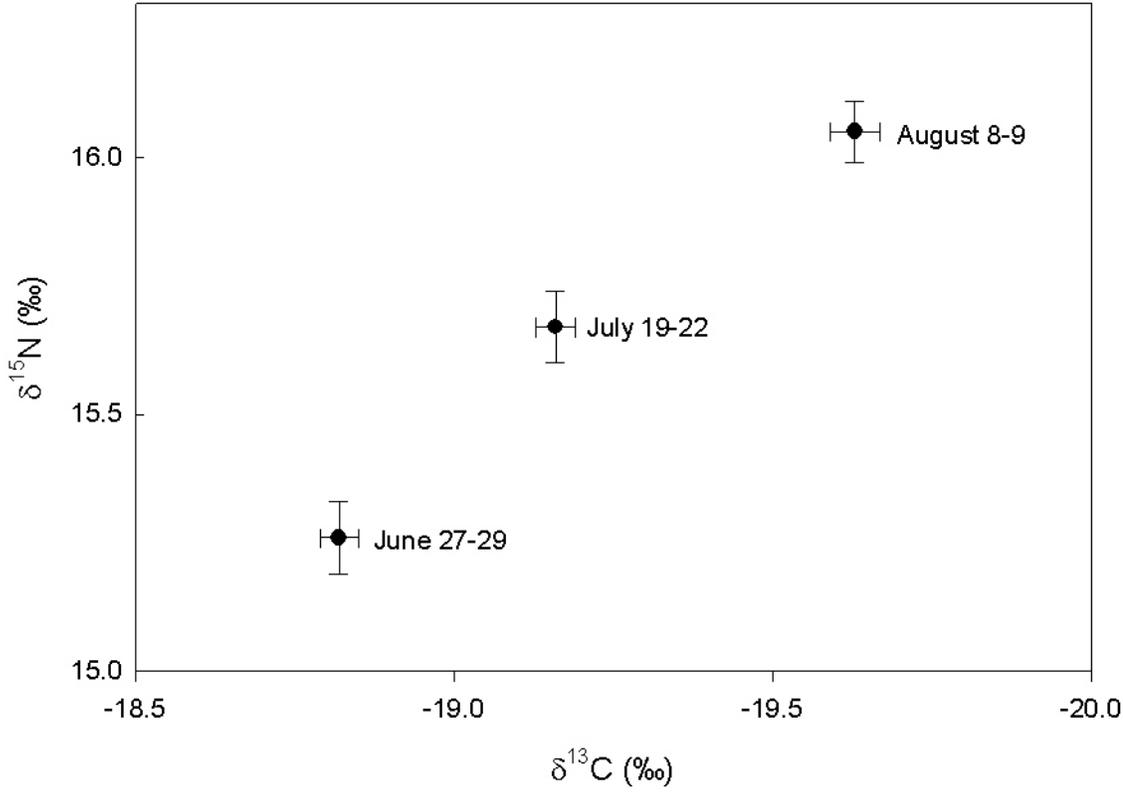


Figure 3.2: Average mass (\pm S.D.) of serially sampled adult Thick-billed Murres, June 27 through August 9, Coats Island, Nunavut, 2004. $n = 12$.

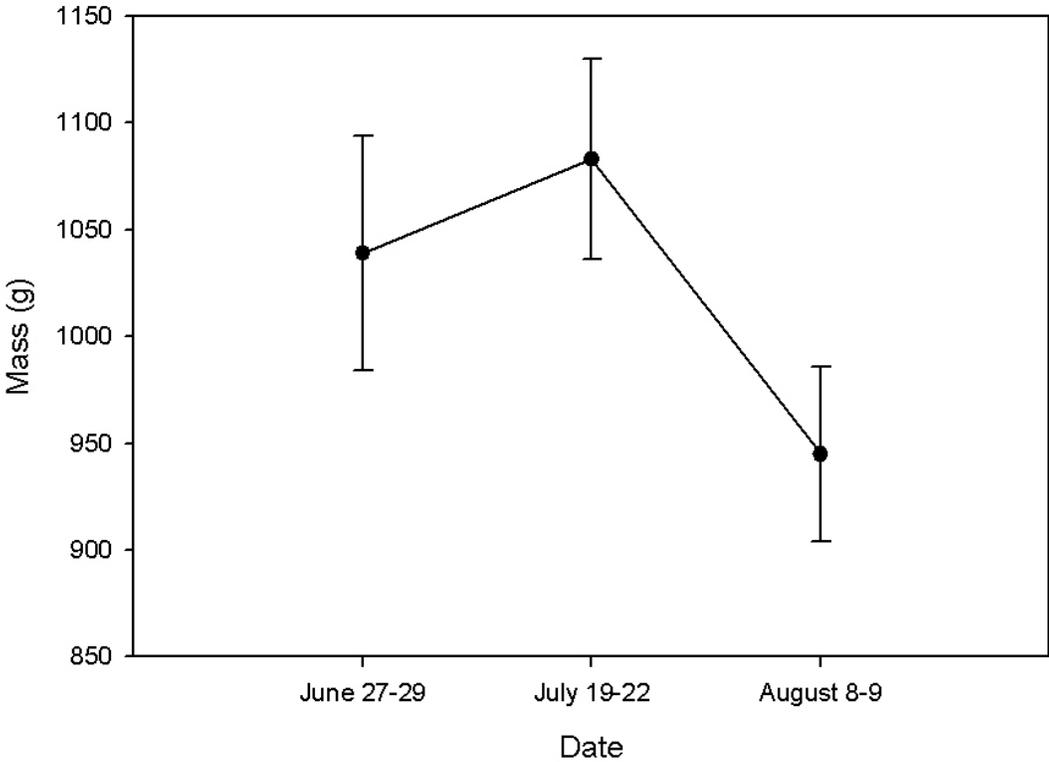


Figure 3.3: Blood $\delta^{15}\text{N}$ values of Thick-billed Murre parents and chicks, Coats Island, Nunavut, 2004; $n = 14$ chicks, 28 adults. Horizontal line is mean $\delta^{15}\text{N}$ chick and adult values, $16.0\text{‰} \pm 0.14\text{‰}$ and $16.0\text{‰} \pm 0.04\text{‰}$, respectively. Black - Parent A; Light Grey - Parent B; Medium Grey - Chick.

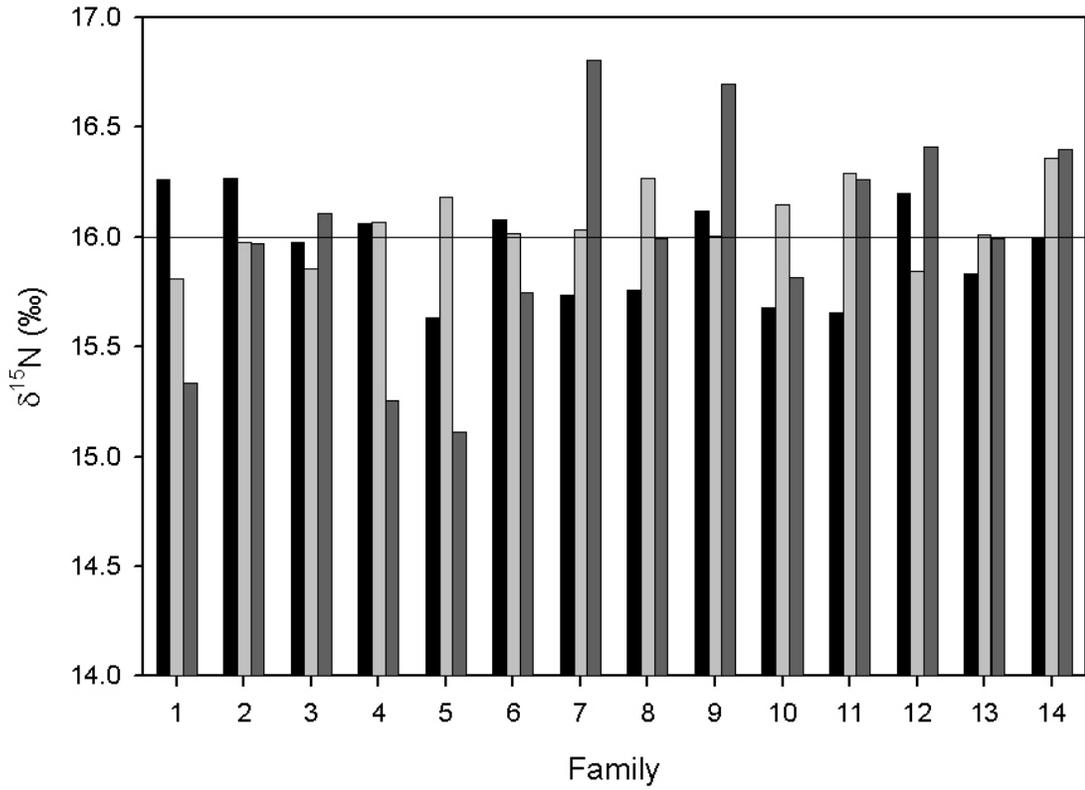
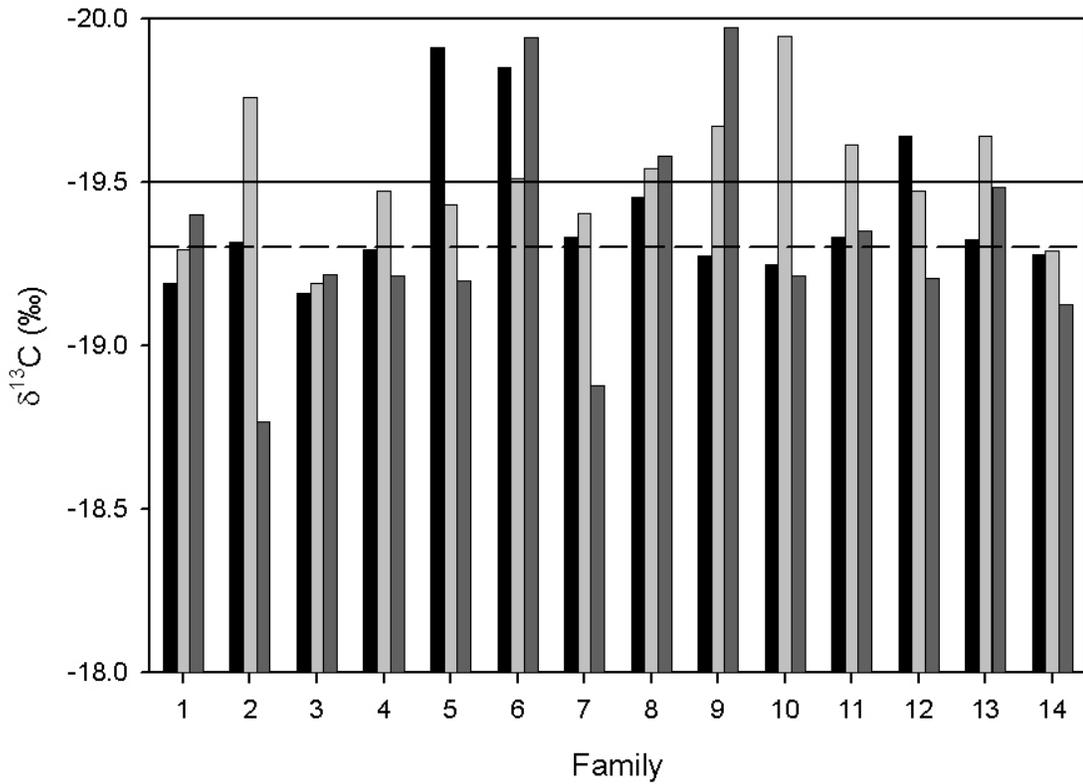


Figure 3.4: Blood $\delta^{13}\text{C}$ values of Thick-billed Murre parents and chicks, Coats Island, 2004; $n = 14$ chicks, 28 adults. Dashed horizontal line is average $\delta^{13}\text{C}$ chick value, $-19.3\text{‰} \pm 0.09\text{‰}$, and solid horizontal line is average adult value, $-19.5\text{‰} \pm 0.04\text{‰}$. Black - Parent A; Light Grey - Parent B; Medium Grey - Chick.



Trophic level increase during the summer may result from adults changing their diet in a number of ways: consuming less invertebrate prey, less YOY Arctic cod, or murre switching from capelin to adult Arctic cod as the summer progresses. The combination of trophic level (i.e. ^{15}N) enrichment together with ^{13}C depletion suggests that murre do not switch from invertebrate prey to more vertebrates since invertebrates, like amphipods and euphausiids, are generally low in both isotopes compared with vertebrates (Hobson et al. 2002; Sherwood & Rose 2005). Capelin have become more abundant in chick diet since the 1990s (Gaston et al. 2003) but they are at a lower trophic level than Arctic cod (Sherwood & Rose 2005). We know little about fish abundance around Coats Island and capelin may become less available to murre as the season progresses. The combination of the changes in the two isotopes suggests that murre likely switch to higher trophic-level, pelagic prey.

The change in adult $\delta^{15}\text{N}$ values within the breeding season, while significant, represented only about one fifth of a trophic level (Hobson & Welch 1992) making it impossible to infer a trophic level switch *per se*. This change may instead reflect minor changes in prey stable isotope values. Little information is available about within-season stable isotope changes in the marine Arctic ecosystem; however, some temporal variation between seasons has been found in Newfoundland cod (Sherwood & Rose 2005) and among zooplankton in the Gulf of Alaska (Kline 1999). Without concurrent sampling of prey with consumer tissues, I cannot make the assumption that stable isotope values in consumers are solely a result of consumers' food choices.

Fasting and nutritional stress has also been linked with increased ^{15}N in breeding birds (Hobson et al. 1993). Like murre, Ross' Geese (*Chen rossii*) lose mass during incubation and it is thought that muscle catabolism enriches tissues with ^{15}N . But, Ross'

Geese are capital breeders and undergo much more extreme mass loss (over 50%; Hobson et al. 1993) compared to murre, and Hobson et al. (1993) did not find a simultaneous change in $\delta^{13}\text{C}$ in goose tissues during fasting. Although the break-down of muscle may contribute to the increased $\delta^{15}\text{N}$ values during the breeding season, it is not likely that it is a significant factor.

Large isotopic variance has been linked to inter-individual trophic level differences in largemouth bass (*Micropterus salmoides*; Post 2003), White-throated Sparrows (*Zonotrichia albicollis*; Podlesak et al. 2005) and Common Terns (Nisbet et al. 2002). At the population level, I found little variance in stable isotope values of adults providing little evidence for specialization in adult trophic level (Bolnick et al. 2003). Stable isotope values of adult blood ranged from 15.6‰ to 16.4‰ for ^{15}N and from -19.2‰ to -19.9‰ for ^{13}C , both isotopic ranges were well below the 2‰ Podlesak et al. (2005) suggested indicated individual warbler specialization in bayberries (*Myrica pensylvanica*).

3.4.2. Chick diet

Both traditional dietary analysis and SIA have shown that seabird chicks generally feed at a higher trophic level than adults (Forero et al. 2005; Nisbet 2002; Baird 1991) including Thick-billed Murre chicks on Prince Leopold Island and Coburg Island, which have two major colonies in the Canadian high Arctic (Hobson 1993, Hobson et al. 2002). In contrast, our SIA indicated that parents fed at a slightly higher trophic level than their own chicks but this difference disappeared when all adults and chicks were pooled, as they were for the Prince Leopold Island analysis.

Chick $\delta^{15}\text{N}$ values were more variable than those of adults possibly due to some specialization by adults in chick provisioning. Chick $\delta^{15}\text{N}$ blood values differed by

1.7‰, somewhat lower than the 2‰ limit used by Podlesak et al. (2005). However, chick $\delta^{15}\text{N}$ variability was still low (e.g. S.D. $\pm 0.14\text{‰}$) and there was no difference in variance between chick and adult $\delta^{13}\text{C}$ values. Common Tern chicks had less variable $\delta^{15}\text{N}$ values than did adults, which exhibited individual specialization (Nisbet et al. 2002). Thick-billed Murre chicks were less variable than either chick or adult Common Terns. Although Woo (2002) found adult Thick-billed Murre specialists who brought more benthic prey to their chicks than average parents, our results suggest that specialization by adult murrens may have declined since the 1990s. At the colony, the proportion of benthic prey in Thick-billed Murre chick diets has generally declined between the 1980s and 1999-2002, being replaced by capelin and sandlance (Gaston et al. 2003). This is consistent with the idea that changes in the marine environment allowed southern species to move into the area around Coats Island while decreasing the abundance of benthic prey. Therefore the apparent difference in specialization between studies may reflect a recent decrease in benthic prey available to parents.

The difference in relative chick and adult trophic levels among Thick-billed Murre colonies may be due to differences in prey abundance and distance to foraging grounds. On Prince Leopold Island, murre chicks fed at a higher trophic level than adults (Hobson 1993); however, chicks on Coats Island tend to fledge heavier than those on Prince Leopold Island (Gaston & Hipfner 2000) which suggests more food is available at Coats Island and/or that the costs of foraging are lower. The foraging grounds of the Coats Island colony are also much closer than those of Prince Leopold Island (Gaston & Nettleship 1981; Woo 2002). However, in another inter-colony comparison, murre chicks on Coburg Island, a colony on the Western side of the North Water Polynya, were fed at a higher trophic level than adults fed themselves (Hobson et al. 2002) but Hakluyt

Island murre chicks, from the Greenland side of the North Water Polynya, were fed at a lower trophic level than adults (Hobson et al. 2002). This difference between colonies was linked to a decreased abundance of Arctic cod in the vicinity of Hakluyt Island, and lower foraging costs at Coburg Island due to higher prey abundance (Falk et al. 2002). This contrast between the North Water Polynya colonies and the Lancaster Sound/Hudson Bay colonies, in terms of relative chick and adult trophic levels, suggests that more information is needed about prey abundance and foraging costs at the different colonies. It may be that foraging effort on Prince Leopold Island and Coburg Island is more similar than effort between Coburg Island and Coats Island.

This chapter had three significant findings relating to individual specialization, inter-season adult trophic level and foraging location changes, and chick diet relative to adult diet. I found no evidence of individual dietary specialization, as shown by the range of stable isotope values, in either chick or adult murre diet. Specialization may have declined since the 1990s (Woo 2002) because of a shift in the prey regime surrounding Coats Island (Gaston et al. 2003). During the breeding season, I did find that adult murre increase in trophic level and move to more offshore foraging locations. This is the first description of a breeding season trophic level change for this murre population. Finally, I showed that adult murre and their chicks fed on similar diets. This contrasts with comparable work at some other murre colonies in the Arctic (Hobson et al. 2002; Hobson 1993) and shows that chick trophic level relative to adults may be more variable than accepted.

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CHAPTER 4: ALCID WINTER DIET IN THE NORTHWEST ATLANTIC DETERMINED BY STABLE ISOTOPE ANALYSIS

4.1 INTRODUCTION

It is becoming increasingly clear that migratory birds are influenced by factors occurring at broad temporal and spatial scales and so the establishment of connectivity between breeding, wintering, and stopover sites for specific populations has been emphasized (Webster et al. 2002; Hobson 2005; Norris 2005). For example, events on wintering grounds, such as reduced resources or climatic conditions, can affect breeding season timing (Saino et al. 2004), reproductive success (Marra et al. 1998, Norris et al. 2004), and/or adult survival (Jones et al. 2002; Barbraud & Weimerskirch 2003). For seabirds, linking events between breeding and wintering grounds is complicated because although many species breed colonially, they disperse over large areas of open ocean during winter. For example, Thick-billed Murres (*Uria lomvia*) wintering off Eastern Canada breed colonially in high Arctic colonies where their behaviour, diet, and breeding parameters are reasonably well known (e.g., Gaston & Nettleship 1981). Gaston (2003) recently suggested that food available to murres during winter or spring migration may affect spring body condition, and subsequent colony attendance and breeding propensity. But, because winter diet is so poorly understood, such connections remain speculative.

Previously, murre winter diet was reconstructed using stomach content analysis of birds collected during the Newfoundland ‘turr’ hunt (Tuck 1961; Gaston

et al. 1983; Elliot et al. 1990; Rowe et al. 2000). The hunt primarily takes Thick-billed Murres but also includes small numbers of Common Murres (*U. aalge*) and Razorbills (*Alca torda*) (Gaston et al. 1983). These three alcids are similar in size, occupy similar foraging locations in winter (Gaston & Hipfner 2000; Ainley et al. 2002; Hipfner & Chapdelaine 2002) and tend to have similar diets in other regions when they occur together (Erikstad & Vader 1989; Ogi & Shiomi 1991). We made use of stable isotope analysis (SIA) of murre tissues obtained opportunistically from the hunt to infer trophic level and source of winter feeding (inshore vs. offshore) in murres occurring off Newfoundland.

Studies of seabird diet, especially for non-breeding individuals, have been hampered by conventional approaches. For example, stomach content analysis tends to overestimate the importance of prey with hard body parts, e.g. squid beaks and fish otoliths, because of differential digestion rates (Duffy & Jackson 1986). Most stomach contents are digested within 24 hours (Uspenski 1956), but hard prey items may remain for several weeks (Bradstreet 1980). This also means that stomach content analysis provides a ‘snap-shot’ of what was ingested in the previous 24 hours but provides little indication of diet over a longer time period. In addition, significant proportions of murres may have empty stomachs (up to 44% in Rowe et al. 2000; up to 15% in Elliot et al. 1990) and therefore provide no information on diet.

The measurement of naturally occurring abundance of ^{15}N and ^{13}C in consumers’ tissues has become an established means to investigate seabird trophic level and foraging location (e.g., Hobson et al. 1994; Hodum & Hobson 2000;

Cherel et al. 2002, Ainley et al. 2003; Forero et al. 2004). Consumer $\delta^{15}\text{N}$ values are often used to estimate trophic level because marine systems can show systematic enrichment in ^{15}N with trophic level (Hobson & Welch 1992; Hobson 1993; Michener & Schell 1994). Stable-carbon isotope abundance shows slight enrichment with trophic level, but it is more commonly used to approximate the relative importance of benthic vs. pelagic sources of carbon (Hobson & Welch 1992, Hobson et al. 1994). Individuals that forage nearshore tend to be enriched in ^{13}C compared with those that forage offshore (Hobson 1993). Stable isotope values are not affected by differential digestion rates of prey items and provide information on assimilated, not just ingested, diet. Unlike stomach content analysis, SIA does not provide information on prey frequency at the species level; however, it does allow estimation of trophic level or proportion of fish vs. lower trophic level prey such as invertebrates (Hobson 1993, Hobson et al. 2004)

Because of differences in turnover of elements among tissues results in SIA providing average diet over a period of time ranging from several days in liver and blood plasma to years in bone collagen (Hobson & Clark 1992). Muscle tissue, readily available from hunted murre, has an intermediate elemental half life of about 12 days and therefore provides average diet over the previous month (i.e., 2-3 half lives; Hobson & Clark 1992).

I used SIA to quantify relative trophic level among three species of sympatric wintering alcids and to examine evidence for dietary and/or foraging location changes over the course of their non-breeding period off Newfoundland. Based on previous dietary analysis (Elliot et al. 1990), I predicted that the alcid

species would show significant dietary overlap. I also expected trophic level to remain constant through the non-breeding season (Rowe et al. 2000).

4.2 MATERIALS & METHODS

4.2.1 Field methods

Wintering bird samples were collected from October to March, 1998 to 2004, from various areas off eastern Newfoundland, Canada (Figure 4.1). Most winter samples were salvaged from birds legally shot by hunters during the annual hunt. The remainder (36 Thick-billed Murres and 25 Common Murres), taken from St. Mary's Bay in 2004, were collected under scientific permit by Canadian Wildlife Service personnel. Birds were sexed by examination of gonads following dissection and aged to hatch-year (HY; 1st winter) or after hatch-year (AHY; 2nd or later winter) using differences in greater covert feather wear (S. Wilhelm, unpubl. data). Muscle samples were taken from the breast or wing of birds and frozen until prepared for SIA. Birds taken in 2004 were dissected in Newfoundland and whole stomachs (proventriculus and gizzard) were examined for contents.

Totals of 89 Thick-billed Murres, 45 Common Murres and 7 Razorbills were collected from 1996 to 2004 (Table 4.1). Most Common and Thick-billed Murres were taken in February, 2004. AHY Thick-billed Murres were taken in November (1), January (1), February (27) and March (7). HY Thick-billed Murres were taken in November (12), February (25) and March (4). HY Common Murres were collected in November (3), December (3), February (26) and March (1). AHY Common Murres were collected in November (6) and January (2). Razorbills were

Figure 4.1: Map of Newfoundland showing sample locations of Thick-billed Murres, Common Murres, and Razorbills, 1996 – 2004.

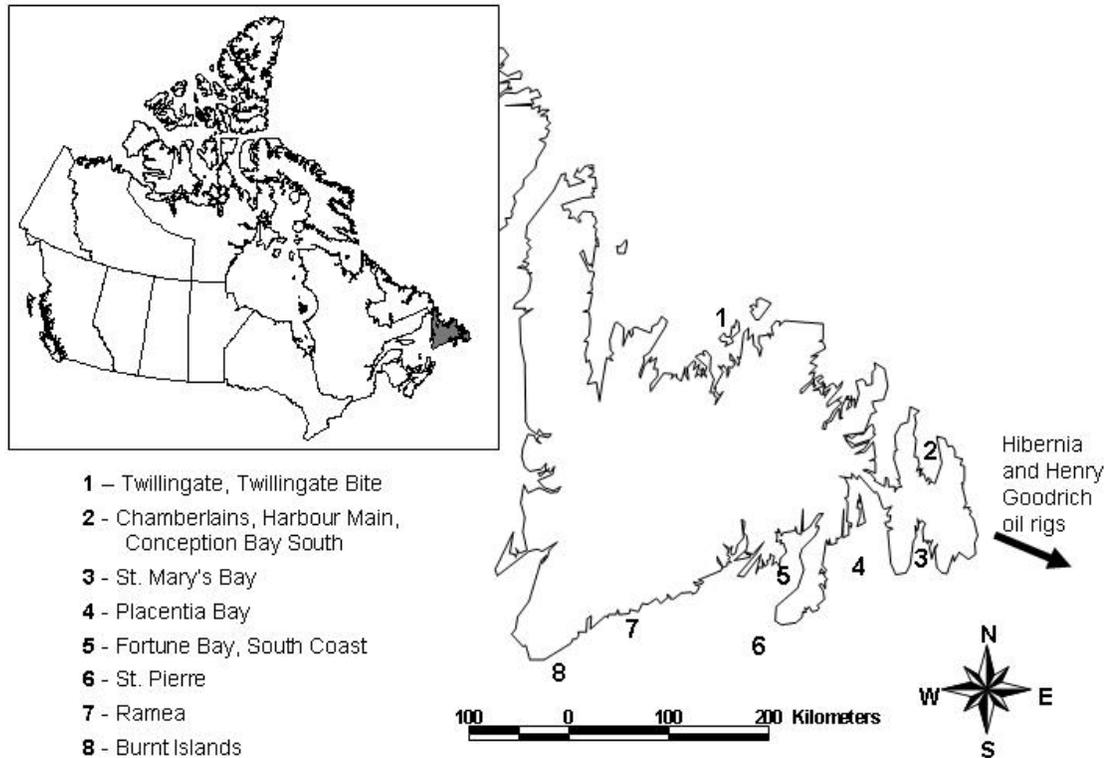


Table 4.1: Date, location, latitude and longitude of Thick-billed Murre (TBMU), Common Murre (COMU) and Razorbill (RAZO) samples collected for stable isotope analysis, Newfoundland, Canada.

Species	Year	<i>n</i>	Location	Latitude & Longitude
TBMU	1996	1	St. Mary's Bay	46°49'N 53°45'W
	1998	1	Hibernia	
		1	St. Pierre	46°50'N 56°20'W
	2000	2	Twillingate Bite	49°40'N 54°46'W
	2001	1	unknown	
		13	St. Mary's Bay	46°49'N 53°45'W
	2002	1	Chamberlains	47°31'N 52°57'W
		1	Placentia Bay	47°00'N 54°30'W
		1	St. Pierre	46°50'N 56°20'W
		2	South Coast	
		1	St. Mary's Bay	46°49'N 53°45'W
		15	Twillingate	49°40'N 54°46'W
	2004	13	Burnt Islands	47°36'N 58°52'W
		1	Henry Goodrich Oil Rig	
36		St. Mary's Bay	46°49'N 53°45'W	
Total	89			
COMU	2000	1	Harbour Main	47°25'N 53°10'W
	2001	1	Ramea	47°31'N 57°22'W
		1	St. Mary's Bay	46°49'N 53°45'W
	2002	3	Conception Bay South	47°30'N 53°00'W
		1	St. Mary's Bay	46°49'N 53°45'W
		12	Twillingate	49°40'N 54°46'W
	2004	25	St. Mary's Bay	46°49'N 53°45'W
	unknown	1	Fortune Bay	47°15'N 55°30'W
Total	45			
RAZO	2000	2	Twillingate	49°40'N 54°46'W
	2001	2	Twillingate	49°40'N 54°46'W
	2002	1	Twillingate	49°40'N 54°46'W
	2003	1	Twillingate	49°40'N 54°46'W
	unknown	1	unknown	
	Total	7		

taken in November from Twillingate, 2000 to 2003, except for one of unknown date and location.

As part of another study, blood samples were collected from breeding Thick-billed Murres on Prince Leopold Island (PLI; 74°02', 90°00'), Nunavut, June to August, 2000, 2001 and 2003. Birds in Summer 2002 had anomalously low stable isotope values and reproductive success and are the topic of Chapter 2. Band returns show that the population of Thick-billed Murres breeding on PLI winter off Newfoundland and Greenland (Gaston 1980). Sample sizes of breeding murres varied with year: 2000 (13); 2001 (68); 2003 (23).

4.2.2 Stable isotope analysis

Lipids tend to be depleted in ^{13}C compared with other tissues (Hobson & Clark 1992) and so to avoid complications in interpretation arising from differential lipid content among individuals, I removed lipids from muscle samples using a 2:1 chloroform:methanol soak and rinse (Hobson et al. 2002). Carbonates were removed from crustacean samples using HCl (Hobson & Welch 1992). Blood, muscle and prey samples were analysed in a Europa 20:20 continuous flow isotope ratio mass spectrometer (CFIRMS) interfaced with a Robo-Prep elemental analyzer at the Department of Soil Science, University of Saskatchewan. Laboratory standards, Bowhead whale (*Balaena mysticetus*) baleen and egg albumen standards were placed between every five unknowns. Measurement error has been estimated to be $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.3\text{‰}$ for $\delta^{15}\text{N}$ measurements.

Stable isotope values are presented in δ (delta) notation in parts per thousand (‰) as:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] * 1000 \quad [4.1]$$

where R is the ratio of the heavy to the light isotope of element X. Standards for this equation were the stable isotope values for PeeDee Belemnite (PDB) for $\delta^{13}\text{C}$ and atmospheric nitrogen (AIR) for $\delta^{15}\text{N}$.

4.2.3 Dietary models & statistical analysis

When comparing stable isotope values of consumer tissues among locations in order to infer dietary or trophic differences, it is important to consider that food webs can differ in their baseline isotopic values (Michener & Schell 1994, Schell et al. 1998). To ensure that dietary models are comparable among areas, stable isotope values of potential prey items in each system must be compared. I adopted this approach by estimating TL based on prey available on the breeding and wintering grounds.

In a two prey system, where each prey item differs isotopically, prey proportions can be determined using the following equation:

$$P_A = (D_t - D_B)/(D_B - D_A) \quad [4.2]$$

where P_A is the proportion of the diet of prey type A, D_t is the isotopic value of the consumer's tissue, D_B , and D_A are the resulting consumer tissue isotope values if only prey B and A are eaten, respectively (Hobson 1993). Stable isotopic value of tissue with a diet of 100% prey type A can be calculated using the following equation:

$$D_A = D_P + \Delta_t \quad [4.3]$$

where D_A is the stable isotope value of the consumer's tissue, D_P is the stable isotope value of prey species A, and Δ_t is the isotopic discrimination factor between diet and murre tissue (3.4‰ muscle, Hobson et al. 1994; 3.1‰ blood, Hobson & Clark 1992). By combining equations 4.2 and 4.3, and incorporating the mean isotopic values I measured for dietary fish and invertebrate samples and murre tissues, the relative importance of vertebrate (fish) vs. invertebrates (amphipods) was determined within each season/location. Prey stable isotope values for the winter were taken from whole prey items in murre stomachs. Breeding season stable isotope values from PLI were obtained from Hobson et al. (2002).

Not all birds were identified by age or sex so sample sizes were lower than the total number of individuals for some categories. Effects of age, sex, and year were not determined for Razorbills because of small sample size. I used analysis of variance (ANOVA) to examine effects of species, age, sex and year on stable isotope signatures (Zar 1999). To address potential sampling bias due to collection methods, interaction terms were examined where sample size permitted. When results from ANOVA were significant, Tukey's post-hoc tests were used to determine where significant differences existed among or between groups. Pearson's correlations were used to investigate how stable isotope values of murre may have changed during the course of the winter. Statistics were analyzed using SPSS, version 12.0. Statistical significance was set at 0.05.

4.3 RESULTS

4.3.1 Species differences

The three alcid species showed significant differences in muscle $\delta^{15}\text{N}$ values (Table 4.2; $F_{1,132} = 4.9$, $p = 0.009$) but not in $\delta^{13}\text{C}$ values (Table 4.2; $F_{2,137} = 2.1$, $p = 0.13$) during the wintering period. Thick-billed Murres were enriched in ^{15}N compared with Common Murres (Tukey's post-hoc, $p = 0.008$). Razorbill $\delta^{15}\text{N}$ values were not different from those of either Thick-billed Murres ($p = 0.42$) or Common Murres ($p = 0.99$).

4.3.2 Temporal patterns

Thick-billed Murre $\delta^{13}\text{C}$ values were significantly affected by month (month: $F_{3,78} = 5.4$, $p = 0.002$) and approached significance for year ($F_{3,78} = 2.6$, $p = 0.06$), but there was no month*year interaction ($F_{1,78} = 0.33$, $p = 0.57$). For $\delta^{15}\text{N}$ values, neither year nor month affected this species' values (month: $F_{3,78} = 1.2$, $p = 0.33$, year: $F_{3,78} = 1.9$, $p = 0.13$) but the month*year interaction was almost significant ($F_{1,78} = 3.7$, $p = 0.057$). In 2004, murre ^{13}C was significantly depleted compared to 2002 (Tukey's post-hoc, $p < 0.001$) but there was no significant difference in $\delta^{13}\text{C}$ values between other years (Tukey's post-hoc, $p > 0.06$). Thick-billed Murres became generally more depleted in ^{13}C from November to March ($r = -0.557$, $p < 0.001$).

Sample size of Common Murres was too low to allow statistical analysis of monthly and annual variation together. When months were pooled, $\delta^{13}\text{C}$ values showed significant differences between years ($F_{2,40} = 7.2$, $p = 0.002$). However, $\delta^{15}\text{N}$ values were not significantly different among years ($F_{2,40} = 3.0$, $p = 0.063$).

Table 4.2: Mean (\pm S.E.) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ muscle values for Thick-billed Murre, Common Murre and Razorbill samples, Newfoundland, 1996-2004.

Species	<i>n</i>	$\delta^{15}\text{N}$ (\pm S.E.)	$\delta^{13}\text{C}$ (\pm S.E.)
Common Murre	45	14.6‰ \pm 0.1‰	-19.9‰ \pm 0.1‰
Thick-billed Murre	89	14.8‰ \pm 0.1‰	-19.8‰ \pm 0.1‰
Razorbill	6	14.6‰ \pm 0.3‰	-19.6‰ \pm 0.2‰

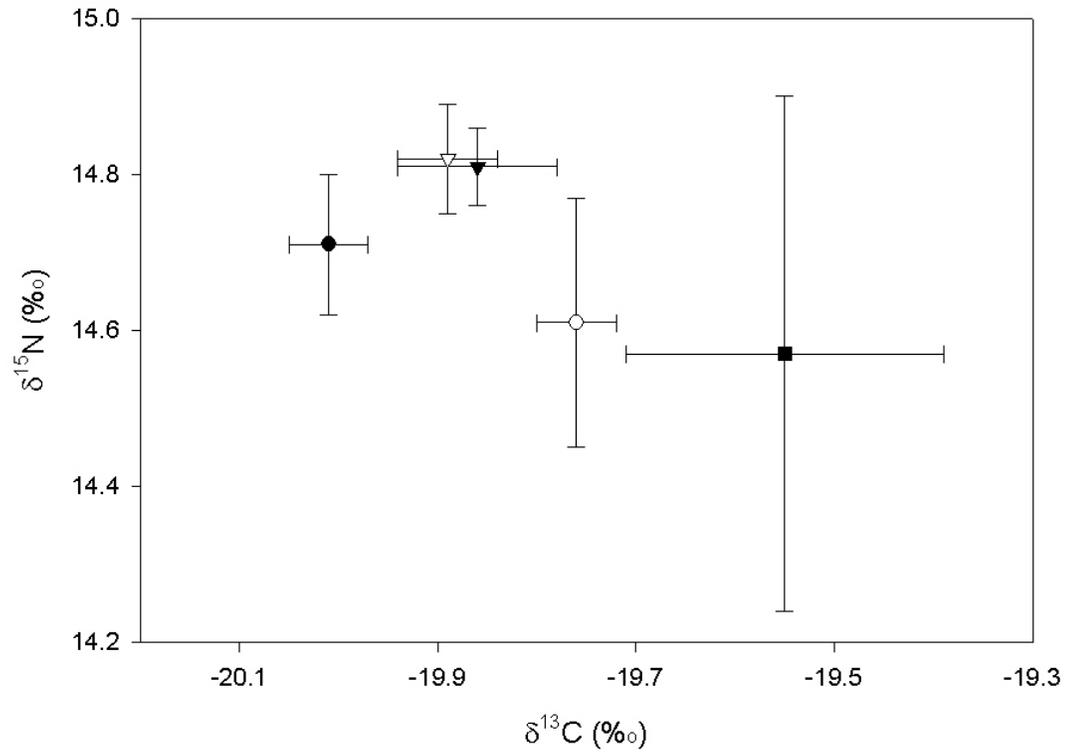
Similar to those of Thick-billed Murres, in 2004 Common Murre $\delta^{13}\text{C}$ values were significantly depleted compared to 2002 ($p = 0.001$) but not to 2001 (Tukey's post-hoc, $p = 0.698$), and 2001 was not significantly different from 2002 (Tukey's post-hoc, $p = 0.692$). After pooling years, Common Murre $\delta^{15}\text{N}$ values did not vary significantly between months ($F_{5,39} = 1.7$, $p = 0.148$), but $\delta^{13}\text{C}$ values did ($F_{5,39} = 7.7$, $p < 0.001$). Like Thick-billed Murres, Common Murres also became more depleted in ^{13}C during the winter ($r = -0.655$, $p < 0.001$, $n = 45$).

There was no difference in stable isotope values between male and female Common or Thick-billed Murres (COMU: $\delta^{15}\text{N}$ $F_{1,9} = 1.6$, $p = 0.24$; $\delta^{13}\text{C}$ $F_{1,9} = 0.02$, $p = 0.89$; TBMU: $\delta^{15}\text{N}$ $F_{1,4} = 0.06$, $p = 0.81$, $\delta^{13}\text{C}$ $F_{1,4} = 0.12$, $p = 0.75$). HY and AHY murres have different migration phenology to the wintering grounds (Gaston & Hipfner 2000) so I considered the effects of age and month. Thick-billed Murres showed no effect of age or month on $\delta^{15}\text{N}$ values (age: $F_{1,70} = 0.02$, $p = 0.88$, month: $F_{3,70} = 1.0$, $p = 0.40$) but there was an age*month interaction ($F_{2,70} = 3.7$, $p = 0.031$) as expected. For $\delta^{13}\text{C}$ values, this species showed no effect of age ($F_{1,70} = 1.4$, $p = 0.23$) but month was important ($F_{3,70} = 7.9$, $p < 0.001$). HY Common Murres were significantly enriched in ^{15}N ($F_{1,39} = 8.3$, $p = 0.006$) and depleted in ^{13}C ($F_{1,39} = 8.9$, $p = 0.005$) compared with AHY Common Murres (Figure 4.2). AHY Thick-billed and Common Murres were significantly different in $\delta^{15}\text{N}$ ($F_{1,42} = 16.1$, $p < 0.001$) but not $\delta^{13}\text{C}$ values ($F_{1,42} = 1.3$, $p = 0.27$). There were no significant differences between HY and AHY Thick-billed murres in $\delta^{15}\text{N}$ ($F_{1,72} = 0.89$, $p = 0.35$) or $\delta^{13}\text{C}$ values ($F_{1,72} = 2.6$, $p = 0.11$).

Five Thick-billed Murres and four Common Murres collected in 2004 had identifiable prey items in their stomachs. Two types of prey tissue were identified: fish, which could not be identified to species, and amphipods. Fish ($n = 4$) had mean (\pm S.E.) $\delta^{15}\text{N}$ values of $13.2\text{‰} \pm 0.3\text{‰}$ and mean $\delta^{13}\text{C}$ values of $-19.7\text{‰} \pm 0.1\text{‰}$. All of the identified amphipods were *Parathemisto libellula* (J.M. Gagnon, Canadian Museum of Nature, Ottawa, ON, pers. comm.). Based on five samples, each consisting of six or seven individuals, these amphipods had mean (\pm S.E.) $\delta^{15}\text{N}$ values of $7.3\text{‰} \pm 0.7\text{‰}$ and mean $\delta^{13}\text{C}$ values of $-22.2\text{‰} \pm 0.2\text{‰}$. The two prey types were significantly different in $\delta^{15}\text{N}$ ($F_{1,8} = 62.6$, $p < 0.001$) and $\delta^{13}\text{C}$ values ($F_{1,8} = 128.0$, $p < 0.001$). Breeding season *P. libellula* from Lancaster Sound, Nunavut, had a mean $\delta^{15}\text{N}$ value of $9.7\text{‰} \pm 0.1\text{‰}$ (Hobson et al. 2002) and Arctic cod, the main prey item of Thick-billed Murres on PLI (Gaston & Nettleship 1981), had a mean $\delta^{15}\text{N}$ value of $14.0\text{‰} \pm 0.2\text{‰}$ (Hobson et al. 2002).

Thick-billed Murres breeding on PLI, were enriched in ^{15}N ($F_{1,226} = 11.0$, $p = 0.001$) and ^{13}C ($F_{1,167} = 236.1$, $p < 0.001$) compared to winter samples. The proportion of fish vs. *P. libellula* eaten by Thick-billed Murres was estimated for winter and breeding season, 2000 to 2004. Winter samples were those taken from October to March of the following year. Using Equation 4.3, I determined winter $\delta^{15}\text{N}$ endpoints of Thick-billed Murre muscle were 10.7‰ , corresponding to a 100% amphipod diet, and 16.6‰ , corresponding to a 100% fish diet. Breeding season $\delta^{15}\text{N}$ endpoints for Thick-billed Murre blood were 12.8‰ , corresponding to a 100% amphipod diet, and 17.1‰ , corresponding to a 100% Arctic cod diet. Dietary proportions calculated using Equation 4.2 varied with season

Figure 4.2: Stable isotope values (mean \pm S.E.) of Razorbills (RAZO), hatch-year (HY) and after-hatch-year (AHY) Thick-billed Murres (TBMU) and Common Murres (COMU), Newfoundland, 1996-2004.



($F_{1,184} = 316.7$, $p < 0.001$) (Figure 4.3). Mean amphipod proportion was $22.8\% \pm 1.2\%$ in summer and $30.1\% \pm 0.8\%$ in winter.

4.4 DISCUSSION

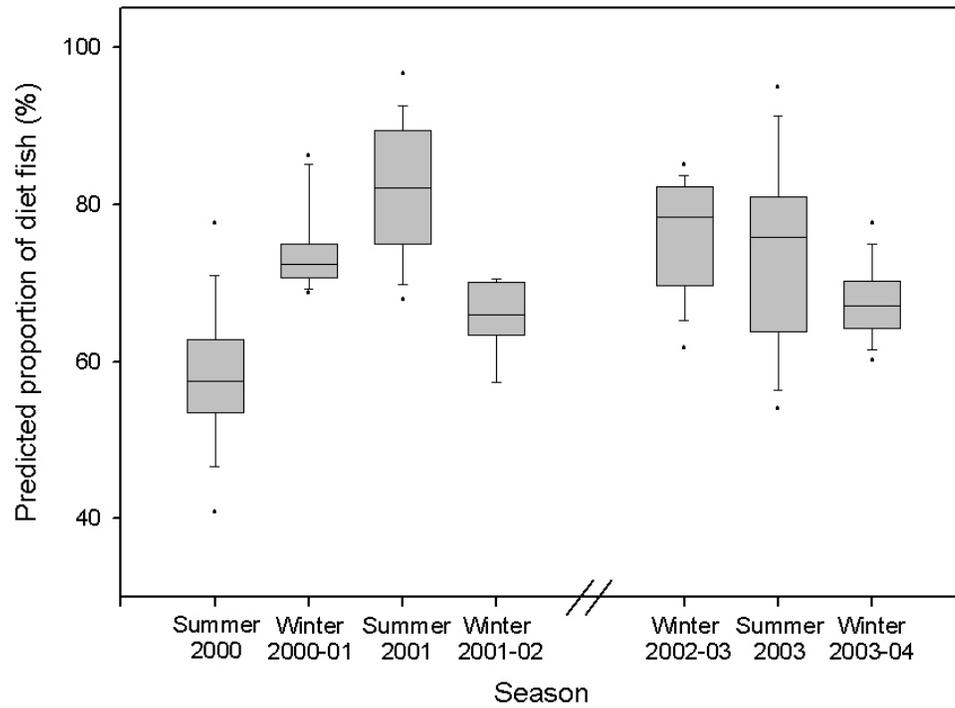
4.4.1 Murre trophic level

In the 1950's, the diet of Thick-billed and Common Murres wintering off Newfoundland was believed to consist entirely of capelin and other fish (Tuck 1961). Later studies of Newfoundland murres found capelin, along with Arctic cod and squid, were important in early winter diet with a subsequent switch to lower trophic level prey (euphausiids and amphipods) in January – March (Gaston et al. 1983; Elliot et al. 1990). Most recently, Rowe et al. (2000) found that Thick-billed Murres off Newfoundland had diets similar to those in the 1980's and 1970's, consisting of a mixture of fish and lower trophic level organisms; however, trophic level no longer decreased in late winter. Our SIA also suggested that murres off Newfoundland fed on a high proportion of invertebrate prey and that trophic level did not decrease late in winter as murre $\delta^{15}\text{N}$ values remained constant through the season.

4.4.2 Murre foraging location

In contrast to $\delta^{15}\text{N}$ values, $\delta^{13}\text{C}$ values in both Common and Thick-billed Murres became more depleted over winter, indicating a possible foraging location shift from nearshore to offshore (Hobson 1993). There are many possible explanations for this trend. Individuals may switch from nearshore to offshore areas due to ice conditions as winter progresses. Both murre species are known to follow the ice edge in pursuit of prey in winter (Elliot et al. 1990) and as ice advances

Figure 4.3: Predicted proportion of Thick-billed Murre diet composed of fish (summer - Arctic cod (*Boreogadus saida*); winter - unknown fish sp.), Summer 2000 to Winter 2003-2004, showing inter-annual variation. Boxes represent 25th-75th percentile around the median (solid line). Dots represent 5th and 95th percentile.



through the winter, birds could shift to offshore foraging grounds. Alternatively, ^{13}C depletion could result from migration of birds wintering in different areas. As winter progressed, and birds began to migrate north to breeding grounds, birds wintering nearshore would give way to birds that had wintered offshore Newfoundland, with expected more depleted ^{13}C values. Alternatively, offshore and nearshore $\delta^{13}\text{C}$ values of murre tissue may reflect the foraging location of their prey rather than that of the birds themselves. During spring, capelin migrate into coastal waters from pelagic areas (Winters 1970; Nakashima 1992); therefore, declining $\delta^{13}\text{C}$ values may reflect different foraging locations of either consumer or prey populations, rather than solely murre switching from one foraging location to another. Also, foodweb food web stable isotope values can vary greatly over relatively small scales. In the Bering-Chukchi-Beaufort Sea, $\delta^{13}\text{C}$ values of euphausiids varied significantly over the area (Schell et al. 1998) and adjacent fjords in southeastern Newfoundland (Fortune Bay and Bay d'Espoir) also differed in $\delta^{13}\text{C}$ values of common species. In both cases, this variation has been linked to differences in water movement, temperature and rates of primary production between areas.

4.4.3 Common vs. Thick-billed Murres

During the breeding season, Thick-billed Murres tend to feed on a wider variety of prey including more benthic species than Common Murres (Bradstreet & Brown 1985) but few studies have examined Common and Thick-billed Murre winter diets when these species occur together. In northern Japan, both Common and Thick-billed Murres fed on sandlance (Ogi & Shiomi 1991) and in Norway,

both fed on capelin although Common Murres tended to feed on smaller, more energy-rich capelin when in mixed flocks (Erikstad & Vader 1989). In the western Atlantic, Bradstreet & Brown (1985) reported wintering Thick-billed Murres consumed more invertebrate prey than Common Murres and Spring (1971) supported this conclusion with anatomical comparisons. Elliot et al. (1990) found the two murres fed on similar diets off Newfoundland during winter but that study suffered from low sample sizes. In contrast, SIA demonstrated AHY Thick-billed Murres fed at a higher trophic level and ate fewer invertebrates than AHY Common Murres. AHY Common Murres tended to be taken early in the season because they migrate earlier (Elliot 1991) and since $\delta^{15}\text{N}$ values did not vary through the season, species $\delta^{15}\text{N}$ value differences represented trophic level differences rather than being an artefact of sampling time.

The difference in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between HY and AHY Common Murres but not between the two ages of Thick-billed Murres was unexpected. In Norway, Lorentsen & Anker-Nilssen (1999) found that immature Common Murres tended to feed on less gadids, and therefore at a lower trophic level (Ruus et al. 2002) than adult birds, in contrast to our results. On the breeding grounds in the Canadian Arctic, Thick-billed Murre chicks fed at a higher trophic level than adults (Hobson 1993) and Arctic cod remained important in chick diet immediately after leaving the colony (Bradstreet 1979). Muscle tissue represents average diet over the previous month (Hobson & Clark 1992); therefore, trophic level differences would be apparent from September to November given males may continue to feed chicks at sea for 1-2 months (Harris & Birkhead 1985). I expected the difference between

HY and AHY $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values to be greatest early in the winter and reduce as the season progressed but this was not the case.

I found no difference in stable isotope values between sexes in Common or Thick-billed Murres wintering off Newfoundland. This result is similar to that found in breeding Thick-billed Murres by both conventional (Bradstreet 1979) and SIA approaches (Hobson 1993). Sex differences in diet during winter have not been described in the Western Atlantic (Rowe et al. 2000; Elliot et al. 1990; Gaston et al. 1983), but female Norwegian Common Murres fed at lower trophic levels than males (Lorentsen & Anker-Nilssen 1999). Sex differences in diet may be expected due to different roles in parental care after the breeding season. Male murres take care of chicks at sea for 1-2 months, continuing to provide chicks with food (Harris & Birkhead 1985). Females are not known to participate in at-sea chick care and so there is a potential mechanism for differences between the sexes in energy requirement, feeding behaviour, and trophic level.

4.4.4 Razorbill trophic level

Razorbill winter diet in the Northwest Atlantic is mainly known from birds collected in the Bay of Fundy. These birds' stomachs contained mainly krill and other pelagic crustaceans in addition to fish and polychaetes (Huettmann et al. unpubl.). The Bay of Fundy is further south than our study site but the results of these stomach analyses agree with those of Tuck (1961), who found that wintering Razorbills off Newfoundland fed mainly on crustaceans. However, our SIA suggests that in winter Razorbills may not feed at a different trophic level compared

with Common and Thick-billed Murres and so may consume more fish than previously thought.

4.4.5 Dietary modelling

The unidentified fish species found in the murres' stomachs had $\delta^{15}\text{N}$ values similar to those found for fish in previous studies but $\delta^{13}\text{C}$ values were lower (Table 4.3). Amphipods were similar in $\delta^{13}\text{C}$ values but differed in $\delta^{15}\text{N}$ values compared with previous work in Newfoundland (Table 4.3).

In our two-endpoint, one-isotope ($\delta^{15}\text{N}$) dietary model, I used fish and amphipods as two isotopically distinct prey types. This is not to suggest that birds did not feed on other prey types (e.g., euphausiids and squid were found in Common and Thick-billed Murre diet (Gaston et al. 1983; Elliot et al. 1990); and polychaetes in Razorbill diet (Huettmann et al. unpubl.)). However, in the late 1990s, amphipods (*Parathemisto* spp.) appear to have replaced euphausiids (*Thysanoessa* spp.) as the primary crustacean in Thick-billed Murre diet off Newfoundland (Rowe et al. 2000). Our estimate of the proportion of diet made up of invertebrates can therefore be considered conservative if euphausiids are a diet component of the alcid species I examined. I did not expect squid to contribute significantly to diet due to the absence of squid beaks in stomachs. Polychaetes were found in Razorbill diet (Huettmann et al. unpubl.) but only in very low numbers in Thick-billed Murre diet (0.4% of stomachs, Elliot et al. 1990). Like squid, polychaetes were enriched in ^{13}C , with $\delta^{15}\text{N}$ values between those of fish and amphipods (Fry 1988).

Variation in Thick-billed Murre winter trophic level between successive years has not been reported but long-term changes in their diet have been described

Table 4.3: Mean (\pm S.E.) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ muscle values for prey species, Newfoundland, except where noted. Adapted from Lawson & Hobson (2000).

Species	Location	Year	<i>n</i>	$\delta^{15}\text{N}$ (\pm S.E.)	$\delta^{13}\text{C}$ (\pm S.E.)	Source
Amphipods (<i>Parathemisto gaudichaudii</i>)	Fortune Bay	1984-85	4	10.2‰ \pm 0.1‰	-22.3‰ \pm 0.1‰	Dickson 1986
	Bay d'Espoir	1984-85	5	10.7‰ \pm 0.1‰	-22.2‰ \pm 0.2‰	Dickson 1986
Amphipods (<i>P. libellula</i>)	nearshore	2004	5 ^a	7.3‰ \pm 0.7‰	-22.2‰ \pm 0.2‰	This study
	nearshore Lancaster Sound, NU	1998	106 ^a	9.7‰ \pm 0.1‰	-20.4‰ \pm 0.1‰	Hobson et al. 2002
Amphipods spp.	offshore	2002	4	9.7‰ \pm 0.86‰	-20.9‰ \pm 0.85‰	Sherwood & Rose 2005
Fish spp.	nearshore	2004	4	13.2‰ \pm 0.3‰	-19.7‰ \pm 0.1‰	This study
Capelin (<i>Mallotus villosus</i>)	Fortune Bay	1984-85	4	13.1‰ \pm 0.2‰	-21.5‰ \pm 0.4‰	Dickson 1986
	nearshore	1990	4	13.0‰ \pm 0.3‰	–	Hobson & Montevecchi 1991
	nearshore	1986-90	11	12.2‰ \pm 0.2‰	-21.4‰ \pm 0.2‰	Ostrom et al. 1993
	offshore	2002	21	12.2‰ \pm 0.09‰	-21.0‰ \pm 0.10‰	Sherwood & Rose 2005
Arctic cod (<i>Boreogadus saida</i>)	offshore	1995	10	13.7‰ \pm 0.1‰	-18.8‰ \pm 0.1‰	Lawson & Hobson 2000

	nearshore Lancaster Sound, NU	1998	8	14.0 ‰ ± 0.2‰	-19.3‰ ± 0.1‰	Hobson et al. 2002
	offshore	2002	10	13.5‰ ± 0.34‰	-19.9‰ ± 0.13‰	Sherwood & Rose 2005
Atlantic cod (<i>Gadus morhua</i>)			1	12.6‰	–	Fry 1988
	nearshore	1990	2	15.1‰ ± 0.1‰	–	Hobson & Montevecchi 1991
	nearshore	1995	10	13.9‰ ± 0.2‰	-19.0‰ ± 0.1‰	Lawson & Hobson 2000
	offshore	2002	155	14.3‰ ± 0.05‰	-19.0‰ ± 0.04‰	Sherwood & Rose 2005
Arctic Squid (<i>Gonatus fabricii</i>)	offshore Labrador	1996	10	8.5‰ ± 0.6‰	-18.5‰ ± 0.1‰	Lawson & Hobson 2000
Sandlance (<i>Ammodytes dubius</i>)	offshore	1996	10	12.0‰ ± 0.1‰	-19.6‰ ± 0.1‰	Lawson & Hobson 2000

^a *n* refers to grouped samples consisting of a number of individuals

(Elliot et al. 1990; Rowe et al. 2000). Inter-annual stable isotope variation has been found in breeding Thick-billed Murres (Chapter 2), and in wintering murres. Common and Thick-billed Murres both differed in $\delta^{13}\text{C}$ values between 2004 and 2002, which suggests possible changes in foraging location. No difference in $\delta^{15}\text{N}$ values between years suggests trophic level was fairly stable in terms of the proportion of vertebrates vs. invertebrates in winter. However, I recognize that temporal and spatial dynamics of stable isotope signatures of marine foodwebfood webs off Newfoundland are poorly understood (e.g., Dickson 1986; Schell et al. 1998).

As expected, food webs associated with murres wintering in Newfoundland and breeding in the high Arctic differed isotopically. By using endpoints specific to site, season and tissue, I could control for this difference and determine there was a seasonal difference in trophic level. During the breeding season, energy requirements may be higher due to egg production, fasting during incubation shifts, and chick provisioning which would require lipid-rich, high trophic-level prey. Alternatively, differences between seasons may reflect food availability with fish being less available during winter (Rowe et al. 2000).

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CHAPTER 5: GENERAL CONCLUSION

Seabirds live in a highly temporally and spatially variable marine environment and show changes in diet both within a season (Cherel et al. 2006; Knoff et al. 2002; Hatch & Nettleship 1998; Gaston & Nettleship 1981) and between breeding and wintering grounds (Hedd & Montevecchi 2006; Inger et al. 2006; Bradstreet & Brown 1985). I used stable isotope analysis to quantify some of these changes in arctic seabirds to better understand what temporal and environmental factors may influence diet.

In the first chapter, I examined inter-annual trophic level and foraging location variation in a seabird community in relation to ecological factors on Prince Leopold Island, Nunavut. Although ice has been linked to seabird reproductive success on Prince Leopold Island (Gaston et al. 2005), neither trophic level nor foraging location was correlated with ice conditions in this study. However, seabird species with different foraging methods responded differently to changes in prey availability: Northern Fulmars had the least varied trophic levels and foraging location; Black-legged Kittiwakes fed at a lower trophic level when ice cover was low early in the breeding season; Glaucous Gulls reflected changes in their prey species, kittiwakes and murre; and Thick-billed Murres showed the most variation in both trophic level and foraging location. In 2002, a year with poor reproductive success in all species, Thick-billed Murres decreased the proportion of fish in their diet and their trophic level was correlated with body condition. The species level differences among years were subtle and detectable only through multi-year sampling. The simplicity and inexpensiveness of stable isotope analysis of seabird blood makes it ideal for long-term monitoring;

however, monitoring species with flexible foraging methods and flexible diets, such as Thick-billed Murres, may be better at indicating prey availability than species that are more restricted in either their diet or their foraging behaviour.

Chapter Two suggested that neither Thick-billed Murre chicks nor adults had specialized diets; however, murres did adjust their diet in response to energy requirements or prey availability. This loss of specialization may have been caused by a change in the forage fish regime surrounding Coats Island, making specialty species, such as benthic sculpins, less attractive to parents looking to feed their chicks. This type of generalized diet may allow seabirds to better take advantage of temporally and spatially patchy prey (Gaston & Nettleship 1981; Sydeman et al. 1997). The difference in $\delta^{15}\text{N}$ between adults and chicks was significant but small, representing only a fraction of a trophic level (Hobson 1993), suggesting that adults and chicks ate similar foods. However, further research into chick-adult diets should consider a combination of SIA and traditional dietary analysis, such as chick-feed observation, adult stomach content analysis, to ensure that this similarity is real.

In my final data chapter, Chapter Three, I used stable isotopes to describe differences in trophic level among alcid species in winter. Winter diet of alcids is largely unknown, although events during this time likely have significant effects on breeding success and survival (Gaston 2003). Thick-billed Murres fed at a higher trophic level than Common Murres, and Razorbill trophic level was not different than the trophic levels of either murre species. Both murre species became depleted in ^{13}C during winter suggesting foraging location or prey species shifted from nearshore to offshore. For Common Murres, hatch-year individuals fed at a higher trophic level and foraged farther offshore than after-hatch year birds. I also applied a site- and tissue-specific model to

compare winter and breeding season trophic level. This model showed that Thick-billed Murres increased the proportion of fish in their diet during the breeding season on Prince Leopold Island. This model also showed that prey and consumers can differ between locations, emphasizing the inadvisability of making direct comparisons between tissues from different locations. Analysis of hunter-killed birds provided an effective method of determining diet during the non-breeding season. This work could be expanded to cover more years by asking hunters to submit parts of each bird taken, similar to the Wing Bee for waterfowl. These wings or heads could then provide tissue for stable isotope analysis, and combined with climate data and demographic information, the information could better model murre survival.

My results show that seabirds undergo stable isotope value changes over several time scales but without having concurrently sampled prey, it was possible that the birds were reflecting stable isotopic changes in their prey. The next step with this work should be to do a similar stable isotope study at different time scales on prey species. Analysis of fish such as Arctic cod and capelin would present the same problems as seabirds – whether stable isotope changes reflect their own diet or the diets of their prey.

Unfortunately, sampling phyto- and zooplankton in the Arctic seems logistically difficult because of the lack of marine surveys. Plankton in Newfoundland could be easier to sample, and is associated with well sampled and well studied predatory fish populations. Also, Newfoundland has several major seabird colonies, making this system well suited to an intensive stable isotope study.

Stable isotope analysis also shows promise for being incorporated with climate modelling. My thesis used ice cover data with seabird diet, but there are many other climate databases which could be used with multi-year stable isotope data. Stable

isotope analysis combined with weather or climate databases could connect events such as El Niño or the Arctic Oscillation with trophic level fluctuation or with survival models. The combination of stable isotope analysis and oceanic and/or temperature data has great potential importance in modeling seabird response to climate change, and may prove more sensitive than models based only on demographic data.

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APPENDIX 1: PRINCIPAL COMPONENT ANALYSIS OF MORPHOMETRIC (2000-2003) AND LIPID MASS (2002) DATA FOR THICK-BILLED MURRES, NORTHERN FULMARS AND BLACK-LEGGED KITTIWAKES ON PRINCE LEOPOLD ISLAND, NUNAVUT.

2000

Thick-billed Murre

Communalities

	Initial	Extraction
wing	1.000	.379
culmen	1.000	.807
depth	1.000	.163
nostril	1.000	.834

Extraction Method: Principal Component Analysis.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	2.184	54.588	54.588	2.184	54.588	54.588
2	.913	22.822	77.410			
3	.750	18.757	96.167			
4	.153	3.833	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix^a

	Component
	1
wing	.616
culmen	.898
depth	.404
nostril	.913

Extraction Method: Principal Component Analysis.

^a 1 components extracted.

Northern Fulmar

Communalities

	Initial	Extraction
culmen	1.000	.777
depth	1.000	.846
nostril	1.000	.862
tarsus	1.000	.760

Extraction Method: Principal Component Analysis.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	1.830	45.746	45.746	1.830	45.746	45.746

2	1.415	35.373	81.118	1.415	35.373	81.118
3	.416	10.390	91.509			
4	.340	8.491	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix^a

	Component	
	1	2
culmen	.878	.079
depth	.552	-.736
nostril	.185	.910
tarsus	.849	.198

Extraction Method: Principal Component Analysis.

^a 2 components extracted.

Black-legged Kittiwake

Communalities

	Initial	Extraction
culmen	1.000	.686
depth	1.000	.557
tarsus	1.000	.674

Extraction Method: Principal Component Analysis.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	1.917	63.903	63.903	1.917	63.903	63.903
2	.625	20.827	84.730			
3	.458	15.270	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix^a

	Component
	1
culmen	.828
depth	.746
tarsus	.821

Extraction Method: Principal Component Analysis.

^a 1 components extracted.

2001

Thick-billed Murre

Communalities

	Initial	Extraction
tarsus	1.000	.366
wing	1.000	.938

culmen	1.000	.758
nostril	1.000	.687
depth at nostril	1.000	.336

Extraction Method: Principal Component Analysis.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	2.084	41.677	41.677	2.084	41.677	41.677
2	1.002	20.037	61.714	1.002	20.037	61.714
3	.926	18.525	80.239			
4	.720	14.391	94.630			
5	.268	5.370	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix^a

	Component	
	1	2
tarsus	.599	.082
wing	.203	.947
culmen	.860	-.134
nostril	.829	.020
depth at nostril	.506	-.283

Extraction Method: Principal Component Analysis.

^a 2 components extracted.

Northern Fulmar

Communalities

	Initial	Extraction
tarsus	1.000	.571
wing	1.000	.648
culmen	1.000	.599
depth at nostril	1.000	.609
depth at gonys	1.000	.373

Extraction Method: Principal Component Analysis.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	2.800	55.996	55.996	2.800	55.996	55.996
2	.917	18.331	74.328			
3	.492	9.847	84.175			
4	.412	8.244	92.419			
5	.379	7.581	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix^a

Component

	1
tarsus	.755
wing	.805
culmen	.774
depth at nostril	.780
depth at gonys	.611

Extraction Method: Principal Component Analysis.
^a 1 components extracted.

Black-legged Kittiwake

Communalities

	Initial	Extraction
tarsus	1.000	.172
wing	1.000	.556
culmen	1.000	.643
depth at nostril	1.000	.679

Extraction Method: Principal Component Analysis.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	2.050	51.247	51.247	2.050	51.247	51.247
2	.931	23.282	74.529			
3	.543	13.569	88.098			
4	.476	11.902	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix^a

	Component
	1
tarsus	.415
wing	.746
culmen	.802
depth at nostril	.824

Extraction Method: Principal Component Analysis.

^a 1 components extracted.

2002

Thick-billed Murre

Communalities

	Initial	Extraction
tarsus	1.000	.625
wing cord	1.000	.688
depth	1.000	.494

Extraction Method: Principal Component Analysis.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	1.806	60.215	60.215	1.806	60.215	60.215
2	.707	23.556	83.771			
3	.487	16.229	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix^a

	Component
	1
tarsus	.790
wing cord	.829
depth	.703

Extraction Method: Principal Component Analysis.

^a 1 components extracted.

Northern Fulmar

Communalities

	Initial	Extraction
tarsus	1.000	.956
length	1.000	.799
wing cord	1.000	.637
depth at nostril	1.000	.711
depth at gonys	1.000	.757

Extraction Method: Principal Component Analysis.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	2.848	56.958	56.958	2.848	56.958	56.958
2	1.012	20.246	77.204	1.012	20.246	77.204
3	.607	12.140	89.344			
4	.308	6.156	95.500			
5	.225	4.500	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix^a

	Component	
	1	2
tarsus	.276	.938
length	.892	.065
wing cord	.719	-.347
depth at nostril	.838	-.092
depth at gonys	.870	.011

Extraction Method: Principal Component Analysis.

^a 2 components extracted.

Black-legged Kittiwake

Communalities

	Initial	Extraction
tarsus	1.000	.378
length	1.000	.642
depth	1.000	.565
wing cord	1.000	.432

Extraction Method: Principal Component Analysis.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	2.018	50.449	50.449	2.018	50.449	50.449
2	.869	21.717	72.167			
3	.601	15.036	87.202			
4	.512	12.798	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix^a

	Component
	1
tarsus	.615
length	.801
depth	.752
wing cord	.658

Extraction Method: Principal Component Analysis.

^a 1 components extracted.**Thick-billed Murre**

Communalities

	Initial	Extraction
skin lipid	1.000	.832
breast muscle lipid	1.000	.945
liver lipid	1.000	.829
organ lipid	1.000	.794
carcass lipid	1.000	.781

Extraction Method: Principal Component Analysis.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	3.017	60.332	60.332	3.017	60.332	60.332
2	1.165	23.304	83.636	1.165	23.304	83.636
3	.402	8.043	91.679			
4	.230	4.608	96.287			
5	.186	3.713	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix^a

	Component	
	1	2
skin lipid	.908	-.083
breast muscle lipid	-.016	.972
liver lipid	.854	-.317
organ lipid	.884	.115
carcass lipid	.825	.316

Extraction Method: Principal Component Analysis.

^a 2 components extracted.

Northern Fulmar

Communalities

	Initial	Extraction
skin lipid	1.000	.721
breast muscle lipid	1.000	.752
liver lipid	1.000	.973
organ lipid	1.000	.672
carcass lipid	1.000	.819

Extraction Method: Principal Component Analysis.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	2.934	58.687	58.687	2.934	58.687	58.687
2	1.002	20.046	78.733	1.002	20.046	78.733
3	.536	10.722	89.455			
4	.394	7.889	97.344			
5	.133	2.656	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix^a

	Component	
	1	2
skin lipid	.849	-.001
breast muscle lipid	.864	.075
liver lipid	.338	.927
organ lipid	.814	-.097
carcass lipid	.831	-.359

Extraction Method: Principal Component Analysis.

^a 2 components extracted.

Black-legged Kittiwake

Communalities

	Initial	Extraction
skin lipid	1.000	.726

breast muscle lipid	1.000	.715
liver lipid	1.000	.348
organ lipid	1.000	.551
carcass lipid	1.000	.781

Extraction Method: Principal Component Analysis.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	2.075	41.497	41.497	2.075	41.497	41.497
2	1.046	20.926	62.423	1.046	20.926	62.423
3	.945	18.904	81.327			
4	.649	12.979	94.306			
5	.285	5.694	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix^a

	Component	
	1	2
skin lipid	.850	.052
breast muscle lipid	.534	-.655
liver lipid	.364	.465
organ lipid	.414	.616
carcass lipid	.874	-.136

Extraction Method: Principal Component Analysis.

^a 2 components extracted.

2003

Thick-billed Murre

Communalities

	Initial	Extraction
tarsus	1.000	.784
length	1.000	.757
depth	1.000	.865
wing cord	1.000	.771

Extraction Method: Principal Component Analysis.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	1.933	48.317	48.317	1.933	48.317	48.317
2	1.243	31.078	79.395	1.243	31.078	79.395
3	.441	11.015	90.410			
4	.384	9.590	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix^a

	Component	
	1	2
tarsus	.781	.416
length	.756	-.430
depth	.335	.867
wing cord	.799	-.364

Extraction Method: Principal Component Analysis.
^a 2 components extracted.

Northern Fulmar

Communalities

	Initial	Extraction
tarsus	1.000	.628
wing cord	1.000	.383
depth at nostril	1.000	.649
depth at gonys	1.000	.773

Extraction Method: Principal Component Analysis.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	2.433	60.818	60.818	2.433	60.818	60.818
2	.757	18.915	79.733			
3	.480	12.003	91.737			
4	.331	8.263	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix^a

	Component
	1
tarsus	.793
wing cord	.619
depth at nostril	.806
depth at gonys	.879

Extraction Method: Principal Component Analysis.

^a 1 components extracted.

Black-legged Kittiwake

Communalities

	Initial	Extraction
tarsus	1.000	.094
wing cord	1.000	.689
length	1.000	.714
depth at gonys	1.000	.741

Extraction Method: Principal Component Analysis.

Total Variance Explained

Component	Initial Eigenvalues	Extraction Sums of Squared Loadings
-----------	---------------------	-------------------------------------

	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	2.238	55.954	55.954	2.238	55.954	55.954
2	.984	24.591	80.545			
3	.411	10.280	90.824			
4	.367	9.176	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix^a

	Component
	1
tarsus	.306
wing cord	.830
length	.845
depth at gonys	.861

Extraction Method: Principal Component Analysis.

^a 1 components extracted.

APPENDIX 3: BLACK-LEGGED KITTIWAKE (BLKI), GLAUCOUS GULL (GLGU), THICK-BILLED MURRE (TBMU), COMMON MURRE (COMU), NORTHERN FULMAR (NOFU), AND RAZORBILL (RAZO) STABLE ISOTOPE VALUES USED IN THIS THESIS, VARIOUS LOCATIONS, 1996-2004.

Species	Location	Year	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Band no.
BLKI	Prince Leopold Island	2000	14.53	-21.20	
			15.12	-21.20	
			14.07	-21.16	
			13.64	-21.67	
			13.99	-21.32	
			14.30	-21.20	
			14.47	-21.10	
			14.44	-21.41	
			13.99	-21.60	
			14.93	-21.34	
			14.29	-21.14	
			15.55	-20.23	
			14.59	-21.41	
		2001	15.51	-20.79	
			14.84	-20.04	
			16.79	-19.89	
			15.70	-20.10	
			15.48	-20.48	
			15.32	-20.45	
			14.97	-21.22	
			14.75	-20.79	
			14.60	-21.20	
			14.22	-21.05	
			14.46	-21.12	
			14.75	-19.93	
			14.97	-20.32	
			15.49	-19.50	
14.09	-22.02				
14.90	-19.76				
14.77	-21.17				
14.30	-20.87				
15.04	-20.31				
15.87	-20.01				
14.51	-21.42				
15.88	-20.04				
15.62	-20.12				
14.93	-20.71				
15.66	-20.15				
15.65	-19.57				
15.38	-20.13				
14.51	-21.28				
14.04	-21.09				
15.44	-19.79				
14.76	-20.70				
17.02	-19.83				
14.58	-17.64				
16.90	-19.98				
15.82	-20.20				

BLKI	Prince Leopold Island	2001	15.80	-20.27
			16.63	-19.86
			16.02	-20.50
			16.78	-19.60
			16.10	-19.93
			16.52	-19.58
			16.77	-19.80
			16.58	-19.90
			15.45	-20.85
			16.45	-20.07
			15.59	-20.93
			16.53	-20.07
			2002	16.74
		16.80		-20.27
		14.11		-23.62
		15.50		-20.84
		16.18		-20.84
		16.23		-20.36
		14.90		-21.79
		16.21		-20.42
		15.77		-20.66
		16.57		-20.25
		14.87		-21.22
		15.37		-21.06
		15.15		-21.15
		15.57		-21.35
		15.36		-21.09
		15.58		-21.60
		15.37		-21.06
		14.99	-22.26	
		16.19	-20.72	
		15.64	-21.05	
		2003	15.03	-20.56
14.92	-21.53			
15.39	-21.35			
14.90	-21.64			
14.45	-21.20			
15.33	-20.52			
14.88	-21.23			
14.67	-21.47			
15.64	-20.82			
15.15	-21.43			
15.73	-20.87			
15.08	-21.40			
16.20	-20.73			
16.07	-20.97			
15.15	-21.62			
16.43	-20.49			
15.71	-20.83			
16.20	-20.89			
16.10	-20.88			
17.29	-19.58			
15.54	-21.42			
16.89	-20.08			
17.29	-19.49			
16.38	-20.12			

BLKI	Prince Leopold Island	2003	15.79	-21.28			
			16.53	-20.30			
			17.09	-20.19			
			17.06	-20.17			
			15.28	-21.59			
chick GLGU	Prince Leopold Island	2000	16.22	-18.73			
			16.35	-19.02			
			16.45	-18.99			
			16.35	-19.26			
			16.47	-18.76			
			16.09	-19.20			
			16.60	-19.07			
		2001	17.14	-18.86			
			17.10	-18.34			
			16.88	-18.46			
			17.22	-17.98			
			17.54	-19.25			
			17.11	-19.49			
			17.47	-18.36			
			17.27	-18.48			
			17.27	-18.23			
			17.40	-18.78			
			17.41	-18.75			
			16.52	-19.83			
2003	16.39	-18.94					
	16.48	-18.98					
	16.72	-19.03					
	17.17	-19.49					
	16.91	-20.79					
chick TBMU	Coats Island	2004	17.30	-18.96			
			17.19	-18.82			
			17.33	-18.95			
			15.34	-19.40	966-89301		
			15.97	-18.77	966-89302		
			16.10	-19.22	966-89305		
			15.25	-19.21	966-89308		
			15.11	-19.20	966-89307		
			15.74	-19.94	966-89313		
			16.80	-18.88	966-89447		
			15.99	-19.58	966-89448		
			16.70	-19.97	966-89996		
			15.81	-19.22	966-89450		
			16.26	-19.35	966-89994		
16.41	-19.21	966-89991					
15.99	-19.48	966-89989					
16.40	-19.13	966-89986					
COMU	Conception Bay South	2002	14.51	-19.54			
			14.57	-20.17			
			14.50	-20.02			
			Fortune Bay		14.75	-19.05	
			Harbour Main	2000	13.63	-19.97	
			Ramea	2001	14.95	-19.75	
			St. Mary's Bay	2002	14.97	-20.26	
		2001		14.34	-20.02		
		2004		13.58	-19.90		
			14.43	-20.30			

COMU	St. Mary's Bay	2004	14.46	-20.43
			14.21	-19.95
			13.91	-20.07
			13.80	-20.05
			14.96	-19.63
			13.89	-19.87
			15.35	-20.04
			14.72	-19.99
			15.02	-20.37
			15.43	-20.00
			15.01	-20.10
			15.33	-20.02
			14.82	-19.97
			14.58	-20.40
			15.17	-20.15
			14.68	-19.96
			15.38	-19.85
			15.25	-19.88
			14.86	-20.23
			14.29	-19.65
14.88	-19.85			
14.70	-20.10			
15.55	-20.13			
	Twillingate	2002	14.16	-19.71
			14.66	-19.92
			13.36	-18.89
			13.54	-19.60
			13.85	-19.49
			14.13	-19.78
			14.42	-19.71
			14.44	-19.61
			15.23	-19.54
			14.43	-19.70
			13.98	-19.88
			14.44	-19.85
NOFU	Prince Leopold Island	2000	14.00	-20.27
			14.92	-19.87
			13.86	-19.96
			13.73	-22.09
			14.44	-21.03
			14.30	-20.96
			14.57	-21.25
			15.12	-20.05
			14.56	-20.33
			14.48	-19.98
			14.19	-19.89
			15.54	-19.63
			14.10	-20.29
			14.14	-20.30
			14.25	-19.98
			14.35	-20.07
			14.22	-20.63
			14.64	-20.33
			13.65	-20.58
			14.36	-20.27

NOFU	Prince Leopold Island	2000	14.88	-20.41
			15.05	-19.83
			14.36	-20.27
			13.78	-20.66
			14.08	-20.10
			14.85	-20.07
		2001	13.95	-19.51
			13.81	-19.55
			13.74	-19.86
			13.51	-19.51
			13.83	-20.11
			14.05	-18.96
			13.69	-19.39
			13.36	-19.26
			14.02	-19.37
			13.15	-19.81
			13.67	-19.53
			13.71	-19.85
			14.33	-19.78
			13.81	-19.85
13.80	-19.96			
14.40	-19.49			
14.13	-19.79			
14.15	-19.35			
14.41	-19.90			
14.27	-19.69			
14.51	-18.90			
14.29	-19.03			
15.53	-20.14			
15.34	-20.03			
14.64	-19.61			
15.91	-19.63			
15.24	-19.65			
14.73	-19.82			
15.43	-20.07			
15.24	-20.15			
14.90	-20.28			
15.21	-20.20			
2002	14.14	-20.74		
	13.63	-21.92		
	14.48	-20.71		
	15.08	-20.66		
	14.15	-20.51		
	14.52	-20.40		
	14.02	-20.68		
	14.34	-21.14		
	14.06	-20.61		
	14.59	-20.65		
	14.06	-20.54		
	14.61	-19.37		
	15.58	-19.25		
	15.10	-18.99		
14.43	-19.11			
14.67	-18.93			
14.50	-19.53			

NOFU	Prince Leopold Island	2002	14.62	-19.56		
			14.76	-19.43		
			15.61	-19.65		
			14.72	-19.22		
			15.07	-19.12		
			14.26	-19.63		
			15.41	-19.08		
			15.35	-19.47		
			14.67	-19.53		
			14.58	-21.28		
			15.76	-19.48		
			14.81	-19.74		
			2003	14.18	-19.35	
				14.20	-19.62	
			13.92	-19.52		
			14.29	-19.51		
			14.71	-20.06		
			14.05	-19.70		
			14.05	-19.72		
			14.30	-19.37		
			13.96	-19.74		
			14.07	-19.50		
			14.32	-19.43		
			14.27	-20.43		
			15.05	-20.57		
			14.17	-20.32		
			14.87	-19.34		
	14.52	-20.51				
	14.57	-19.46				
	14.24	-19.75				
	14.37	-20.03				
	14.31	-19.46				
	14.45	-20.25				
	14.27	-19.82				
	14.78	-20.26				
	14.09	-20.45				
	14.48	-19.93				
	15.17	-20.64				
	15.46	-20.76				
	15.27	-20.39				
	15.51	-20.26				
	15.84	-20.25				
	16.83	-20.57				
	15.62	-20.44				
	16.01	-20.13				
	15.99	-20.40				
RAZO	unknown		15.25	-19.56		
	Twillingate	2001	14.93	-19.06		
			14.85	-19.55		
		2003	13.28	-20.26		
		2000	15.39	-19.36		
			13.91	-19.59		
		2002	15.05	-19.45		
TBMU	Coats Island	2004	16.26	-19.19	966-89032	
			16.26	-19.32	966-61056	

TBMU	Coats Island	2004	15.97	-19.16	966-89034
			16.06	-19.30	966-89038
			15.63	-19.91	966-89040
			16.08	-19.85	966-89042
			15.73	-19.33	966-89093
			15.76	-19.45	966-61456
			16.12	-19.27	966-62553
			15.68	-19.25	966-89091
			15.66	-19.33	966-89045
			16.20	-19.64	966-55969
			15.83	-19.32	966-69179
			15.99	-19.28	966-61458
			15.81	-19.30	966-89039
			15.98	-19.76	966-89041
			15.86	-19.19	966-53500
			16.07	-19.47	966-89035
			16.18	-19.43	966-89036
			16.02	-19.51	966-89043
			16.03	-19.41	966-89044
			16.27	-19.54	966-51329
			16.00	-19.67	966-89092
			16.15	-19.94	966-89047
			16.29	-19.61	785-42862
			15.84	-19.47	966-71552
			16.01	-19.64	966-89048
			16.36	-19.29	966-71554
			15.41	-18.82	996-87028
			15.54	-18.81	996-53772
			15.40	-18.66	996-71520
			14.86	-18.80	996-87030
			15.10	-18.85	996-63203
			15.10	-18.74	996-87027
			14.88	-18.92	996-53663
			15.60	-18.78	996-63567
			15.35	-18.87	996-64627
			15.45	-18.98	996-89006
			15.45	-18.93	996-06504
			15.06	-18.67	996-56774
			15.41	-18.98	996-87028
			15.57	-19.06	996-53772
			15.86	-19.21	996-71520
			15.20	-18.93	996-87030
			15.56	-19.13	996-63203
			15.67	-19.35	996-87027
			15.67	-19.24	996-53663
			15.87	-19.14	996-63567
			15.88	-19.24	996-64627
			15.57	-19.26	996-89006
			15.91	-19.22	996-06504
			15.91	-19.16	996-56774
			15.76	-19.83	996-87028
			15.97	-19.66	996-53772
			16.25	-19.60	996-71520
			15.81	-19.37	996-87030
			15.98	-19.79	996-63203

TBMU	Coats Island	2004	16.26	-19.58	996-87027
			15.92	-19.86	996-53663
			16.05	-19.45	996-63567
			16.31	-19.61	996-64627
			15.82	-19.74	996-89006
			16.27	-19.56	996-06504
			16.24	-19.55	996-56774
	Burnt Islands	2004	14.41	-20.06	
			14.65	-20.01	
			14.81	-19.96	
			14.78	-20.01	
			14.46	-19.83	
			14.60	-20.11	
			14.33	-19.92	
			14.13	-20.13	
			14.73	-20.11	
			14.89	-20.15	
	Chamberlains	2002	14.59	-19.42	
	Henry Goodrich Oil Rig	2004	13.68	-20.23	
Hibernia	1998	14.48	-19.27		
Newfoundland	2001	13.42	-19.14		
Placentia Bay	2002	14.86	-20.42		
Saint-Pierre	2002	15.46	-19.06		
	1998	15.53	-19.48		
South Coast	2002	14.08	-20.06		
		14.56	-20.30		
St. Mary's Bay	2002	14.83	-19.89		
		1996	15.39	-18.72	
	2001	14.75	-20.12		
		15.13	-19.81		
		15.01	-20.24		
		15.69	-19.78		
		14.86	-19.96		
		14.93	-19.73		
		161.01	37.75		
		14.95	-19.70		
		15.79	-19.67		
		14.87	-19.20		
		15.02	-20.57		
		14.80	-19.90		
		15.14	-19.66		
		2004	14.49	-19.97	
			14.66	-20.00	
14.47	-20.19				
14.89	-20.01				
14.50	-19.85				
14.32	-20.52				
14.29	-19.86				
15.51	-20.06				
14.65	-20.42				
14.49	-20.08				
14.57	-19.37				

TBMU	St. Mary's Bay	2004	15.57	-19.45
			14.55	-20.07
			14.80	-19.48
			14.60	-19.74
			15.28	-19.80
			14.95	-19.93
			14.70	-20.02
			14.82	-19.94
			14.81	-19.95
			15.02	-20.18
			14.62	-20.33
			14.85	-20.42
			15.16	-19.67
			14.61	-20.30
			15.08	-19.75
			14.72	-20.24
			14.83	-20.14
			14.38	-20.09
			15.18	-19.82
			15.08	-19.92
			14.46	-20.25
			14.66	-20.69
			14.25	-20.08
			14.78	-20.00
			14.58	-20.14
Twillingate		2002	14.90	-19.59
			15.24	-19.51
			14.79	-18.73
			15.41	-19.42
			14.59	-18.52
			14.87	-20.04
			15.64	-19.61
			14.55	-19.72
			15.60	-19.53
			15.34	-19.97
			15.32	-19.41
			15.59	-19.43
			15.42	-18.37
			14.27	-19.31
			15.74	-19.13
Twillingate Bite		2000	15.10	-19.70
			14.90	-19.42
Prince Leopold Island		2000	15.12	-19.24
			16.20	-19.02
			15.27	-18.90
			14.50	-19.34
			15.18	-18.71
			15.25	-19.18
			15.65	-19.19
			14.88	-18.92
			15.45	-19.18
			15.41	-19.09
			15.04	-19.08
			15.45	-18.79
			15.76	-19.21
		2001	16.06	-18.97

TBMU	Prince Leopold Island	2001	15.59	-19.09
			16.61	-18.96
			16.08	-18.98
			15.93	-19.01
			16.41	-18.85
			16.44	-18.65
			16.74	-18.71
			16.27	-18.65
			15.81	-19.41
			16.09	-18.47
			16.35	-19.06
			16.36	-18.82
			16.48	-18.60
			15.92	-19.08
			16.29	-18.65
			15.99	-19.02
			16.65	-18.24
			16.25	-18.64
			16.41	-18.82
			16.17	-19.31
			16.64	-18.65
			16.34	-19.24
			16.60	-18.84
			17.02	-19.09
			15.92	-18.61
			16.70	-19.25
			16.79	-19.33
			16.40	-19.38
			16.43	-19.39
			16.71	-19.12
			16.35	-19.01
			15.98	-19.14
			15.86	-19.36
			15.82	-19.70
			16.16	-19.27
			16.32	-19.44
			16.21	-19.27
			16.25	-19.06
			16.65	-19.02
			15.70	-19.54
			16.22	-19.05
			16.45	-18.82
			16.38	-19.40
			15.74	-18.25
			15.92	-18.68
			15.98	-18.68
			15.72	-18.83
			15.80	-18.48
			16.83	-19.11
			15.76	-19.02
			16.76	-19.17
			16.30	-18.56
			16.30	-18.95
			16.30	-18.43
			16.75	-19.24
			16.75	-18.90

TBMU	Prince Leopold Island	2001	16.55	-18.90	
			16.57	-18.71	
			16.22	-18.59	
			17.22	-18.66	
			15.59	-18.68	
			17.35	-18.77	
			16.95	-18.89	
			17.06	-18.94	
			17.46	-18.74	
			16.68	-19.02	
			16.22	-19.14	
			2002	16.19	-19.29
				15.33	-19.67
		15.84		-19.40	
		15.60		-19.49	
		15.44		-19.17	
		15.73		-19.34	
		15.93		-19.23	
		15.41		-18.84	
		15.22		-19.18	
		16.35		-18.48	
		15.26		-18.40	
		16.08		-18.79	
		16.85		-19.05	
		15.75		-18.63	
		15.92		-18.21	
		15.69		-18.79	
		15.35		-19.18	
		16.39		-18.15	
		15.89		-20.71	
		15.74		-20.32	
		15.27	-20.52		
		15.76	-20.88		
16.22	-20.73				
15.67	-21.26				
15.73	-20.62				
16.44	-20.25				
16.00	-19.55				
15.03	-21.24				
14.99	-20.88				
15.85	-19.91				
15.66	-21.38				
15.65	-19.89				
2003	16.11	-19.51			
	16.40	-19.49			
	15.24	-19.62			
	15.38	-19.26			
	16.06	-19.41			
	16.30	-19.49			
	15.82	-19.29			
	15.80	-19.78			
	15.03	-19.84			
	16.09	-19.84			
15.77	-19.42				
16.09	-19.57				

TBMU	Prince Leopold Island	2003	15.61	-19.79
			16.70	-19.32
			16.83	-19.63
			16.46	-19.52
			16.15	-19.68
			16.00	-19.45
			16.22	-19.67
			15.17	-19.60
			15.52	-19.67
			15.49	-19.50
			16.97	-19.16
			16.13	-19.36
			16.93	-19.26
			15.44	-19.70