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Foraging ecology of the Thick-billed Murre: patterns of prey location and selection

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Abstract

Patterns of foraging behaviour of Thick-billed Murres (*Uria lomvia*) feeding nestlings at Coats Island, Nunavut in northern Hudson Bay were studied. Small, electronic data recorders attached to adult birds were used to quantify dive behaviour and flight activity while provisioning for nestlings. Observations of individuals returning to the colony were conducted to identify the types and sizes of prey items birds were delivering to chicks. Deployment of data recorders in 1999 indicated that birds were diving to average depths of 25 – 43m, with no differences attributable to sex, but significant variation between self-feeding dives (shallow) and those dives associated with the capture of prey for nestlings (deeper). There were also significant differences in dive depths associated with specific prey types. Estimates of foraging ranges indicated that all trips were within 100km of the colony. Trips resulting in the delivery of sandlance (*Ammodytes* spp.) and Arctic cod (*Boreogadus saida*) tended to be longer, while items such as capelin (*Mallotus villosus*) and crustaceans tended to be shorter. Relation of prey types to foraging ranges provided an indication of prey distribution in the vicinity of the colony. There was a significant positive correlation with the mass of prey items delivered and length of distances travelled, supporting general theories of foraging behaviour in central-place foragers. Trends in species composition of nestling diets were examined from 1994 to 2000. Arctic cod and capelin were the most abundant items, together accounting for over 50% of deliveries in all years. Items such as crustaceans and zoarcoids occurred in lower numbers, with higher variability among years. The proportion of Arctic cod in the diet declined over the study period from 32% to 15%, while capelin increased from 31% to 50%. Sandlance also increased (<1 - 24%). Identification of uniquely marked individuals allowed me to investigate patterns of prey specialisation within the population. Specialisations were most evident on prey items that occurred less frequently in the diet such as sculpins and zoarcoids. Some individuals exhibited distinct preferences for especially rare types of zoarcoids. In some cases, individual specialisations persisted over several years. Differences in the ecology and composition of delivery items in birds exhibiting specialisation and the persistence of some specialisations over time suggest that behavioural mechanisms play a role in the observed patterns. Information obtained on foraging behaviour are discussed in relation to general predictions of central place foraging theory, as well as in relation to the ecology of prey species in the vicinity of the colony. The implications of my results for the value of information gathered from seabirds, as indicators of their local marine environments, is addressed.

Résumé

Le comportement d'approvisionnement des guillemots de Brünnich (*Uria lomvia*) nourrissant leurs oisillons à l'île Coats, Nunavut, au nord de la Baie d'Hudson a été étudié. Des petits dispositifs d'enregistrement de données électroniques ont été attachés aux oiseaux adultes afin de quantifier les comportements de plongée et l'activité de vol lors de l'approvisionnement des oisillons. Des observations d'individus retournant à la colonie ont été entreprises afin d'identifier les types et la grosseur des proies que ces derniers apportent à leurs poussins. Les données enregistrées par ces dispositifs en 1999 ont indiqué que les oiseaux plongent à des profondeurs moyennes de 25 à 43m et qu'il n'y a pas de différence entre les sexes. Parcontre, une différence significative existe entre les plongées pour se nourrir eux-même (peu profondes) et celles pour nourrir leurs oisillons (plus profondes). On retrouve aussi des différences significatives dans les profondeurs de plongées associées aux types de proies attrapées. La distance parcourue en quête de nourriture se limite au plus à 100km de la colonie. Les excursions résultant à la capture de lançon (*Ammodytes* ssp.) et de la morue arctique (*Boreogadus saida*) étaient plus longues que celles résultant à la capture de capelan (*Mallotus villosus*) et de crustacés. La relation entre les types de proies et la distance parcourue pour se la procurer fournie une indication de la distribution des proies à proximité de la colonie. Il y avait une corrélation positive et significative entre la masse des proies livrées et la distance parcourue, ce qui appuie les théories générales du comportement d'approvisionnement chez des chasseurs à partir d'un point central. Les tendances de la composition d'espèces dans la diète d'oisillons ont été examinées de 1994 à 2000. La morue arctique et le capelan étaient les plus abondants, comprenant ensemble plus de 50% des proies livrées à chaque année. Des proies telles les crustacés et les zoarcoïdes représentaient une plus petite proportion du total et comportaient beaucoup de variabilité entre les années. La proportion de morue arctique dans les diètes a décliné de 32 à 15% durant la période d'étude, tandis que la proportion de capelan a augmenté de 31 à 50% et la proportion de lançon a aussi augmenté (<1 à 24%). L'identification d'individus marqués a permis d'observer le degré de spécialisation envers les proies dans la population. Les spécialisations étaient plus évidentes en ce qui concerne les proies qui étaient retrouvées moins fréquemment dans la diète, tels les chabots et les zoarcoïdes. Certains individus démontraient des préférences distinctes pour certains zoarcoïdes rares. Dans certains cas, cette spécialisation individuelle a persisté pendant plusieurs années. Des différences d'écologie et de composition de proies livrées chez des groupes montrant des spécialisations et la persistance de ces mêmes spécialisations avec le temps suggèrent que certains mécanismes de comportement jouent un rôle important dans ce qui a été observé. L'information obtenue sur le comportement d'approvisionnement est discutée par rapport aux prédictions générales du comportement d'approvisionnement chez les chasseurs à partir d'un point central et également par rapport à l'écologie des espèces proies à proximité de la colonie. Les implications de mes résultats quant à la valeur de l'information amassée sur les oiseaux marins en terme d'indicateur de l'environnement marin local sont aussi adressées.

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1. General Introduction

Foraging ecology is a branch of behavioural ecology that deals with the patterns, mechanisms and decisions animals employ when supplying themselves and their offspring with energy for growth, survival and reproduction. As such, the study of how animals acquire these resources is key to understanding life-histories as well as interactions with their environments. Descriptions and models of foraging behaviour are most often addressed in terms of energy expenditure and acquisition. Individuals must expend resources in the process of accumulating them. This requires an animal to locate, capture and process suitable resources. Application of optimality theory to foraging behaviour makes predictions by which observed patterns of behaviour should be governed in an attempt to maximize net energy gains. For avian species, that are highly mobile (able to cover large foraging areas) and often are constrained to a nest or colony during the breeding season, foraging involves extra costs of travelling to and from this fixed location. This type of situation is called central place foraging and was described by Orians and Pearson (1979), who developed predictions of prey selection relative to travel distance.

The application of ecological theory to foraging behaviour can provide rationale to explain observed behavioural patterns and processes of decision making by individuals. Knowledge of how individuals gather resources from their environments is important when drawing conclusions from observations of diet items and behaviour. Many marine birds occupy high positions in their respective marine food webs, sometimes preying on fish species that are also of human economic value. As a result, the study of seabird diets and foraging behaviour may be a useful tool in assessing and monitoring aspects of the marine environments that they inhabit (Monaghan 1996). It is within this framework that I present data on the foraging behaviour and prey selection of the Thick-billed Murre (*Uria lomvia*).

The Thick-billed Murre is one of the larger members of the Auk family. Strong and rugged, it is a bird adapted to cold northern climates, with a circumpolar distribution. It is one of the most abundant seabirds breeding in the Canadian Arctic during the summer, estimated at c. 3 million breeding birds (Gaston and Hipfner 2000). They nest on steep, rocky cliffs, laying a single egg and raising their chicks on often narrow and precarious ledges. During the breeding season they associate in large numbers at a small number of large colonies, the largest of which supports over 1 million birds. Such dense aggregations have the potential to exert large impacts on the marine environments in the vicinity of their colonies where they forage. While foraging, they are capable of travelling large distances (Benvenuti et al. 1998).

Thick-billed Murres are pursuit diving birds, using their wings to propel themselves underwater while chasing and capturing prey. All prey are taken below the surface. Primary diet items include small fish and invertebrates (Gaston 1991). Diets of adult birds have been determined mostly through analysis of stomach contents (Bryant et al. 1999). The range of prey items taken by adults is characterised by a variety of both benthic and pelagic fish species, in addition to several types of zooplankton. Composition of diets varies by season as well as by geographic location (cod in Arctic Canada, capelin off Greenland and squid in the western Pacific) but the occurrence of prey types within populations is similar. Diets of Thick-billed Murre nestlings have been examined largely through observations of adult birds delivering prey items to chicks at the colony (Birkhead and Nettleship 1987). Small fish are the most dominant feature of chick diets throughout their range. When provisioning for nestlings, adult birds capture prey and deliver them whole to the nestling. Due to the fact that birds use their bills to both capture and hold prey, Thick-billed Murres are rarely capable of carrying more than a single diet item at a time. The handling of one item precludes the capture of a second. During transport, prey items are held lengthwise in the bill. This is advantageous to observers, as it allows for identification and estimation of size of prey items when they are delivered to chicks at the colony.

Although diving is an important component of their foraging behaviour, this behaviour has been relatively difficult to describe and quantify. In some cases, dive behaviour has been described as part of overall activity budgets based on the proportion of time individuals spend below the surface of the water (Wanless et al. 1985; Cairns et al. 1987). Development of devices that can measure aspects of birds' behaviour while at sea have allowed for more detailed analysis of foraging behaviour related to diving in recent years. Widespread use of capillary tube depth gauges, adapted for use on diving animals, by Burger and Wilson (1988) provided information on maximum dive depths of several bird species such as penguins (Bost et al. 1994), albatross (*Diomedea* spp.) (Hedd et al. 1997; Huin and Prince 1997), cormorants (*Phalacrocorax* spp.) (Wanless et al. 1997), tropicbirds (*Phaethon* spp.) and boobies (Le Corre 1997) as well as Thick-billed Murres (Croll et al. 1992).

Recent advances in the miniaturisation of electronic data storage devices for attachment to birds the size of Thick-billed Murres have allowed for more detailed analyses of their dive behaviour. Croll et *al.* (1992) were the first to deploy such gauges on murres. Falk et *al.* (2000) provided description of dive patterns, dive depths and duration of Thick-billed Murres at a colony in Greenland. Most recently, similar devices were used to provide details of Razorbill (*Alca torda*) dive behaviour in Iceland (Dall'Antonia et al. 2001).

The object of the studies included in this thesis was to quantify patterns of Thick-billed Murre foraging behaviour and nestling diet and to use these data to develop hypotheses concerning the way in which murres set about locating and catching food. The results are also examined in relation to the ecology of prey species in the vicinity of the colony, as far as these are known. All research was conducted at a colony of approximately 30,000 breeding pairs of birds at Coats Island, Nunavut (62°57' N, 82°00' W). This colony is located in northern Hudson Bay, in an area where little is known about the ecology of the prey species on which the birds feed. Information gathered from observations of birds at the colony is related to patterns of abundance and distribution of these prey species.

The first chapter investigates the behaviour and foraging patterns of birds away from the colony. With the use of recently developed electronic data loggers I was able to describe behaviour which until now, has been difficult to quantify. I report on patterns of dive behaviour and flight activity of individual birds provisioning for their chicks over the course of a single breeding season. Information on these parameters are related to observations of prey species the birds deliver to chicks at the colony. Trends in prey species composition of nestling diet are presented. Combinations of these factors are analysed in relation to predictions of central place foraging theory and interpreted with respect to the distribution and abundance of prey species in the vicinity of the colony.

The second chapter investigates long term patterns in the composition of prey species in nestling diets from 1994 to 2000. Through the use of uniquely marked birds I was able to examine individual patterns of prey choices between years. Trends in individual patterns of prey delivery allowed identification of prey specialists within the population. The implications of these results are discussed in relation to the interpretation of general population trends in diet composition, ecology of prey species and the use of seabirds as monitors of their local environments.

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1.2. Co-Authorship Statement

My contributions to the research and results presented in this thesis were: (1) I provided input into the development of questions and areas of research addressed under the direction of my primary supervisor, Anthony J. Gaston; (2) I was primarily responsible for the design and implementation of field protocols used to address these questions; (3) I organised and analysed all of the data; (4) I wrote all of the chapters/manuscripts.

Co-Authorship of the results presented in chapter 2, primarily reflect the use of equipment developed by L. Dall'Antonia, Istituto di Elaborazione dell'Informazione, C.N.R., Pisa, Italy and S. Benvenuti, Dipartimento di Etologia, Ecologia ed Evoluzione, University of Pisa employed to address my research questions.

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Woo, K.J., Gaston, A.J., Dall'Antonia, L., and Benvenuti, S. Foraging ecology and dive behaviour of chick-rearing Thick-billed Murres (*Uria lomvia*) in relation to prey types.

2. Foraging ecology and dive behaviour of chick-rearing Thick-billed Murres (*Uria lomvia*) in relation to prey types

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Foraging ecology and dive behaviour of chick-rearing Thick-billed Murres (*Uria lomvia*) in relation to prey types

K. WOO, A. J. GASTON, L. DALL'ANTONIA AND S. BENVENUTI

2.1. Abstract

We investigated the dive behaviour and foraging ecology of breeding Thick-billed Murres at Coats Island, Nunavut during the chick rearing period in 1999. Electronic depth and activity recorders were used to quantify the behaviour of birds foraging for their nestlings. The size and identity of food items obtained was observed as birds returned to the colony. Dive depths averaged between 24.9 – 42.9m, with no difference between males and females. Those that resulted in the delivery of crustaceans averaged deeper than those for fish. Dives for self-feeding were shallower than those to obtain food for nestlings. All foraging trips were within 100km of the colony. Foraging trips associated with the delivery of capelin (*Mallotus villosus*) and crustaceans tended to be short, while sandlance (*Ammodytes* spp.) and cod were associated with more distant trips, usually >25km from the colony. The size of items delivered indicated mostly 0 – 1 yr. capelin and 2 yr. and older Arctic cod (*Boreogadus saida*) being taken. Mass of prey items showed a significant increasing trend with increasing distance travelled. The absence of Arctic cod among items caught close to the colony suggests local depletion of prey around the colony.

2.2 Introduction

The Thick-billed Murre (*Uria lomvia*) is the most abundant seabird species breeding in Canadian Arctic waters (Gaston and Hipfner 2000). They breed in several dense colonies from low arctic areas of northern Hudson Bay, south to Newfoundland and the Gulf of St. Lawrence, and north to the high arctic at Coburg Island, Nunavut. The large breeding concentrations of these birds in the summer months are an important component of local marine ecosystems. However, information relating to the distribution and biology of the organisms that inhabit these marine environments is sparse and not heavily studied, especially in northern Hudson Bay.

The breeding behaviour and reproductive success of Thick-billed Murres has been widely studied at the colony (Gaston and Nettleship 1981; Birkhead and Nettleship 1987; Gaston et al. 1993; de Forest and Gaston 1996; Hipfner 1997; Gaston and Hipfner 1998; Bryant et al. 1999), but information on foraging activity has been less thoroughly documented. Information on adult and chick diets have been collected based largely on colony observations and at sea sampling of individuals (Gaston 1985; Gaston and Noble 1985; Gaston and Bradstreet 1993; Bryant et al. 1999).

Until recently, it has been difficult to assess the foraging behaviour of these birds away from the colony. The development and miniaturisation of electronic data loggers in the past several years has allowed for their use on small seabirds, such as Thick-billed Murres. Recent studies where these devices were utilised provide new information describing dive characteristics and flight patterns of individual birds (Bost et al. 1994; Bethge et al. 1997; Wilson et al. 1997; Benvenuti et al. 1998; Charrassin et al. 1998; Cherel et al. 1999; Falk et al. 2000).

The ability to associate information on seabird foraging patterns and diet has been proposed as a useful technique in assessing the distribution and abundance of marine prey stocks where these birds are found (Montevecchi 1993; Monaghan 1996). To obtain information on foraging and diving in relation to prey type for Thick-billed Murres, we were able to implement the use of electronic data loggers, similar to those used in other studies, which provide data on dive depths and flight activity (see Benvenuti et al. in press) in conjunction with colony observations where we identified the prey items birds were delivering to their chicks. We present information on the trends in the types and numbers of prey items observed in the diet of chicks over the course of the 1999 breeding period. Differences in the patterns of dive depths and behaviour are examined in relation to self feeding and chick provisioning. Combining data collected on prey items delivered with that on dive depth and foraging range (estimated from flight activity measurements), we present information on the distribution and abundance of marine prey species in the vicinity of a Thick-billed Murre colony in northern Hudson Bay. The implications of these findings are discussed in relation to the possible effects of prey depletion within the local marine community as a result of the large numbers of birds foraging in the area. In addition, as the travel and pursuit involved in foraging is energetically costly for murres, we examine the relationships between prey items and foraging range in relation to predictions of central place foraging theory.

2.3 Materials and Methods

Collection of data was carried out at Coats Island, Nunavut (62°57' N, 82°00'W), during the 1999 breeding season. This colony of Thick-billed Murres supports a population of approximately 30,000 breeding pairs and has been the subject of a Canadian Wildlife Service monitoring program since 1984. Detailed descriptions of the study site have been reported previously (de Forest and Gaston 1996; Gaston 1991; Gaston et al. 1994). Electronic data recorders were deployed on adult birds rearing chicks at two different study plots within the colony (plot Q and plot Jb). Past observations indicate variation in the timing of breeding at different areas within the colony (Hipfner et al. 1997). Hence, we used two different study areas in order to include individuals with chicks of similar ages throughout the observation period (chicks reared on plot Jb hatched approximately one week behind those on plot Q).

Devices were deployed on three separate occasions, spread over the chick rearing period, covering the dates: July 28 – 30, August 7 – 9, and August 12 – 14. A total of 22 individuals were sampled; 13 females and 9 males (birds were sexed using observational and molecular genetic techniques). In conjunction with deployment of the electronic data recorders, 72 hr. continuous observational watches were also carried out. All observations were made from blinds situated on the study plots, within 6m of the birds. During these observation sessions (FW1, FW2, FW3 – corresponding respectively to the three periods specified above), information on prey items delivered to the colony for chick meals was collected. A total of 156 individuals (including gauge equipped birds) were observed over the course of the study period. Upon delivery, prey items were identified to species whenever possible. Estimates of lengths of prey were also made, by comparison with the adult birds' bill length.

2.3.1. Data recorders

Two different types of electronic data recorders were used in our study. A total of 10 devices were used to collect all data. Two of the gauges were manufactured by Star-Oddi, of Reykjavik, Iceland (Vatnagardar 14, IS-104 Reykjavik). We purchased the data storage tag 200 model (DST-200). The DST-200 is constructed out of polycarbonate and is cylindrical in shape (48mm length, 18mm diameter), rounded at the front to reduce drag. Our gauges were equipped with a timer and a pressure sensor that was sensitive to depths in excess of 200m. The sampling interval was set to log a measurement every 6 seconds for 10 minute intervals with a 20 minute pause between them. There was also a delay of 6 hours from the time of magnet removal (attachment to bird) to the first measurement. DST-200's weighed 12g with a cross sectional area of 2.5cm^2, corresponding to 1% of Thick-billed Murre body mass and 4.4% of frontal cross sectional area respectively. The casing had to be unsealed in order to recover data and thus these gauges could be used only once.

The second type of electronic data recorders we used were developed and provided by researchers in Pisa, Italy (see Dall'Antonia et al. 1995, Benvenuti et al. 1998). These devices are identical to those used on Thick-billed Murres at Hakluyt Island in Greenland by Falk et al. (2000). The Italian depth recorders (TDRs) consist of a hydrodynamically designed carbon fibre casing rounded at the front and with a more flattened profile than the DST-200's. The TDRs were 80mm in length, with a width varying from 23mm (tip) to 30mm (base) and a depth of 13 – 18.5mm. The casing houses a pressure sensor and two motion recorders. The pressure sensor is able to record depths up to a maximum of 76m, while the motion recorders allow us to distinguish between such behavioural patterns as flying, swimming and resting. Our TDRs were programmed to log a depth measurement every 4 seconds and to record activity at 8 second intervals. The gauges were activated just prior to attachment and began recording information immediately. These devices weighed 29g with a cross sectional area of 4.5cm^2, corresponding to 3% of bird body mass and 7.8% of frontal cross sectional area respectively. The data memory of the TDRs could be erased after recovery, allowing deployment of these gauges on multiple occasions.

Individual birds brooding chicks were captured from study plots using a 4.8m pole with a wire noose on the end. Electronic gauges were activated and attached to the backs of the birds. Devices were fastened to feathers in the middle of the lower back using 2 – 3 plastic cable ties. Upon release, birds usually returned to their nest sites within 5 min (Wilson & Gaston in press) and resumed normal brooding behaviour. Gauges were retrieved 1 to 5 days after deployment, at which time birds for which the sex was unknown were bled for DNA sexing. Data from the gauges were downloaded to a notebook computer in the field.

2.3.2. Statistical Analyses

The variety of prey items recorded from observations were grouped into six main categories: capelin (*Mallotus villosus*), Arctic cod (*Boreogadus saida*), sculpins (*Triglops* spp., *Myoxocephalus* spp., *Gymnocanthus tricuspis*), sandlance (*Ammodytes* spp.), zoarcoids (*Eumesogrammus praecisus*, *Stichaeus punctatus*, *Leptoclinus maculatus*, *Gymnelus viridis*), invertebrates (squid, shrimp, amphipods). Estimated lengths of prey items were converted to units of mass in order to provide a better measure of chick meal size, using species specific formulae developed for prey items at Coats Island over the past 15 years (Gaston 1987 and unpubl.). A summary of the models used to make these calculations is provided in Table 1.1. The formula for *Triglops* spp. was used to calculate masses for all species of sculpins included in this study due to the small samples of *Myoxocephalus* and *Gymnocanthus* observed . Masses of deliveries containing Crustacea were estimated at 0.5g per amphipod and 5g per shrimp.

Estimates of flying time for delivery of food to the chicks were calculated from the duration of last flight before arrival at the nest site (recorded ± 1 min.). Arrival times, as measured by the gauges, were matched with observed arrival times recorded on feeding watches.

Estimates of foraging ranges were calculated from travel times based on an average flying speed of 65km/hr and assuming a direct return trip, as described by Benvenuti et al. (1998). Due to the measurement limitations of the Italian TDRs, and in order that depth data from both types of gauges could be combined, all dives greater than 76m were grouped together for the purposes of analysis. All analyses involving associations of prey items with depths were based only on data from the last dives before returning to the colony. Last dives were assumed to be associated with delivery items based on predictions made by Orians and Pearson (1979) related to the foraging behaviour of animals, such as Thick-billed Murres, which are constrained to delivering single prey items at a time. The results presented on seasonal prey trends are based on all birds observed on all watches, while all results relating depths and travel distances are based on gauge-equipped birds only.

Variation in dive depths and travel distances were determined by analysis of variance (ANOVA). Linear regression was used to correlate travel distances with mass of prey items on log transformed data. Where data could not be normalised with standard transformations, an appropriate non-parametric test statistic was used. All analyses of data were done using the SYSTAT 8.0 software package.

2.4. Results

2.4.1. Prey size and composition

Numbers of prey items identified from deliveries over the study period totalled 284 on FW1, 289 on FW2 and 196 on FW3. Arctic cod (28.5%) and capelin (37.4%) comprised the largest proportion of prey over all observations. Zoarcoids (10.5%), sculpins (9.9%) and sandlance (8.6%) aggregated approximately 30% of items, with Crustacea and others accounting for the rest (5.1%). Changes in seasonal proportions of prey were evident over the course of the chick rearing period (Figure 1.1.). Percentage of Arctic cod deliveries declined between watches from 35.9% (FW1: Jul. 28–30), to 21.4% (FW3: Aug. 12–14). The amount of Crustacea in the diet exhibited a large increase later in chick rearing from 0.7% in FW1 to 9.1% in FW3. There was also indication of an increase in the proportion of sandlance, rising from 3.9% in FW1, to 11% in subsequent watches. The proportion of capelin in the diet remained similar over the three watches at approximately 37%.

Size estimates of observed prey items delivered to chicks ranged from less than 5cm to greater than 15cm in length. Frequency distribution of the lengths of prey items exhibited differences in average sizes observed among species. Of the two most commonly observed prey types, capelin (n=286, Figure 1.2a.) was represented primarily by smaller size fish in the 6 – 8cm length range, while Arctic cod (n=213, Figure 1.2c.) showed a much wider size range with an increased frequency between 9cm and 13cm. Most sandlance (n=63, Figure 1.2e.) were in the 7cm length category, with the majority of observations falling between 8 and 11cm. Sizes of sculpins (n=73, Figure 1.2g.) approximated a normal distribution with lengths peaking between 8 and 10cm. Breakdown of zoarcoids by species revealed a large range in size of *Leptoclinus* (n=45, Figure 1.2b.) covering most of the length categories, but commonly observed between 8 and 10cm, while *Eumesogrammus* (n=13, Figure 1.2d.) occurred mainly between 10 – 12cm. *Gymnelus* showed a bimodal distribution (n=17, Figure 1.2h.), with most falling either above or below 11cm. Another zoarcoid, *Stichaeus* was less common in the chick diet (n=4, Figure 1.2f.) but all recorded observations were from 8 – 9cm. Sizes of the categories of prey items which included crustaceans and other invertebrates were estimated from number per delivery rather than lengths. Most specimens of the most common genus involved, the amphipod *Parathemisto*, were approximately 2cm long.

2.4.2. Foraging range

In general, return flights from foraging areas tended to be rather short in 1999, with no trips exceeding 100km (n=81). Distribution of return flights reflect a peak in the 30 – 50km range (Figure 1.3.). There was a significant difference among feeding watches in the average distances birds travelled (ANOVA: $F_{2,77}=18.34$ $p < 0.001$, Table 1.2.). In early and mid chick rearing, foraging ranges averaged 35 – 50km, with the longest trips occurring on feeding watch 2 (Aug. 7-9). There was a marked trend for shorter trips later in the season with return flights averaging less than 20km on feeding watch 3 (Aug. 12-14).

2.4.3. Dive depths

The average depth of all dives was 24.9m (n = 10,391). When dives less than 5m, usually brief and some possibly associated with social behaviour, rather than foraging, are excluded, average dive depth increases to 32.7m (n = 7,604). The average depth of last dives before the return flight to the colony (last dive is assumed to be the dive used to capture chick feeds) was 42.9m (n = 88). Kruskal-Wallis one-way analysis of variance indicated a highly significant difference between average depths of all dives and average depths of last dives (Mann-Whitney U=262780 $p < 0.001$, Table 1.3.). When dives of less than 5m were excluded, the difference between groups remained significant (Mann-Whitney U=250495 $p < 0.001$).

Distribution of dives also indicated a difference between categories of all dives and last dives (Figure 1.4.); 27% of all dives were less than 5m, while 76% were less than 40m, and only

5% greater than 76m. In comparison, only 10% of last dives were less than 5m, with 48% deeper than 40m and 22% reached depths greater than 76m.

There were no significant differences in average depth of last dives among feeding watches (Kruskal-Wallis test statistic=0.393 p=0.822, Table 1.4.), so these were grouped together for further analyses. Dives were also pooled over sex, as no differences between males and females were detected (Mann-Whitney U=891.5 p=0.872, Table 1.4.). Mean and median values for last dives were also very similar, indicating that the 76m depth limit used for the TDRs had little effect on analyses.

2.4.4. Prey and dive depth

We looked at the distribution of prey types over four depth ranges (Figure 1.5.). Cod was represented most at shallow (0-20m) to medium (21-40m) depth ranges (43.8% and 38.5% respectively). Capelin was most abundant at depths between 41-60m (47%), but also well represented in all other depth categories. Zoarcoids compose a higher proportion of prey at depths greater than 40m (22 – 26%) while sandlance were mainly taken at depths of less than 40m (13 - 19%). The highest proportion of Crustacea were found with dives of greater than 60m (18.5%). Although some of the sample sizes are small and variability is high, analysis of variance indicates a significant difference in the average depths associated with each prey class ($F_{5,82}$=2.834 R^2=0.142 p=0.021; Figure 1.6.). Mid-water, schooling fish such as cod and capelin were taken at similar depths, averaging 35m and 44m respectively, while sandlance were found at the shallowest depths (27m). Benthic prey items like zoarcoids and sculpins were associated with medium to deeper depths (53m and 49m respectively). At an average of 62m, Crustacea delivered to the chicks appear to have been obtained at the greatest depths.

2.4.5. Distribution of prey

In order to get an indication of prey distribution within the foraging range we analysed the spectrum of prey delivered in relation to distance of return trip, using three categories: 0-25km, 26-50km and >50km away from the colony. The distribution of prey types among these three distance categories was highly non-random, despite small sample sizes ($\chi^2 = 31.82$ $df = 10$ $p < 0.001$, Figure 1.7.). All of the Crustacea were brought back from within 25km of the colony (25% of prey types). Capelin made up 50% of prey within 25km of the colony, falling to half that amount at greater distances. In contrast, cod was found in low proportions (8%) close to the colony but comprised approximately 40% of prey at distances greater than 25km. Zoarcoids were most common at distances greater than 50km from the colony (29%), while sculpins were in their highest proportions in the 26-50km range and were not delivered at all from greater distances. No sandlance were brought in from less than 26km from the colony and most (12%) were caught at distances greater than 50km.

Results of a one-way ANOVA indicate a significant effect of average distances from foraging areas on prey type ($F_{5,75}=6.565$ $R^2=0.304$ $p<0.001$). Similar to the breakdown of prey distribution by distance, cod and sandlance were associated with the greatest average distances at c. 45km followed closely by zoarcoids at 42km (Figure 1.8.). Capelin and sculpins both averaged about 30km. Crustacea averaged the shortest distances, at 8.1km, significantly different from all other prey types (Tukey's $p < 0.05$).

2.4.6. Travel distances in relation to prey

We found no significant correlation between dive depths and distance of return trips (R^2=0.03, p=0.117). There were also no detectable relationships between dive depth and mass of prey items caught (R^2=0.007, p=0.458). Regression analysis did provide a positive relationship between travel distance and mass of prey items (masses were log transformed for analyses). As travel distance increased, mass of prey items also tended to increase (Figure 1.9.). When all six categories of prey types were included, the resulting relationship explained 15% of the variation (R^2=0.155 $F_{13.9}$ p<0.001). When only cod and capelin were included (which occur in the highest numbers and account for the majority of prey deliveries, >55%), the relationship was similar (R^2=0.174 $F_{9.9}$ p=0.003).

2.5. Discussion

2.5.1. Prey composition

There is relatively little information available on the marine ecology in the area of Hudson Bay surrounding Coats Island, especially in relation to Arctic fish species. The variety of prey species observed delivered to chicks at Coats Island in the current study were consistent with genera previously reported by Gaston (1985). Arctic cod and capelin were the most prominent items in the chick diet, accounting for the largest proportion of deliveries (over 50%). These results were similar to studies carried out in earlier years (Gaston and Bradstreet 1993), and support the idea that these are the preferred species for chick meals (Gaston and Hipfner 1998). Fish such as Arctic cod provide a high mass to length ratio and usually represent a substantial meal for chicks (Cairns 1987; Cairns et al. 1990). Trends in cod revealed a decline during the three week observational period, which may have been related to an overall decline in availability as the season progresses. The seasonal decline in cod observed in 1999 was consistent with yearly trends we have observed since 1997 (unpubl.). The representation of capelin did not show a similar trend, remaining relatively stable throughout the season. Coupled with a decline in cod, there was an increase in smaller prey items, such as crustaceans (largely amphipods) and sandlance later in the season. These smaller items may be less profitable energetically, as previous studies have reported a positive relationship between body size and lipid mass in fish (Cargnelli and Gross 1997; Van Pelt et al. 1997; Robards et al. 1999a).

Size distributions of the most common prey items based on our delivery observations indicate differences in the general age classes of cod and capelin being taken by birds. There were very few small cod recorded, with a large proportion of this species estimated to lengths of 9 - 13cm, suggesting that these fish are mostly second year age class or older (Moskalenko 1964; Lowry and Frost 1981). In contrast, distribution of capelin was highly skewed to lengths of less than 9cm. These smaller size capelin represent mostly 0 – 1yr age classes (Grégoire 1999). The patterns in the sizes of these prey species suggest that there may be differences in the distribution or availability of younger age class cod and older aged capelin in the area of the colony. Size distribution of sandlance did not exceed 13cm, with a strong peak at the 7cm range. Sandlance within this size range are generally associated with 0 – 1yr age classes (Van Pelt et al. 1997; Robards et al. 1999b), suggesting that older aged sandlance may also be absent or unavailable in the area.

Due to the relatively short time that Thick-billed murre chicks remain on the colony before fledging (c. 21-24 days; Gaston and Jones 1998) and the period over which observations were conducted, these trends most likely reflect changes in relative availability of prey items to foraging adults as the season progresses rather than to changes in selection of prey species. Bias due to individual preference must be kept in mind when using seabirds as sampling devices of marine environments (Cairns 1992). Changes in proportions of diet items may be confounded by individual preferences for particular prey, foraging strategies, or foraging areas. There are currently no other independent means of sampling these parameters in the vicinity of this colony. Nonetheless, we believe patterns in prey species composition provide some indication of local conditions and provide a background to which other aspects of Thick-billed Murre foraging behaviour can be compared.

2.5.2. Foraging range

Estimates of distances to foraging areas were based on the time spent flying during the flight period directly preceding a return to the colony, relying on assumptions regarding feeding behaviour of single-prey loaders developed by Orians and Pearson (1979). We also assumed that the return back to the colony was direct, as documented by Benvenuti et al. (1998) and Falk et al. (2000). A bird such as the Thick-billed Murre, with its high wing loading required for flight (Greenwalt 1962), would be expected to minimize energetic costs by exploiting feeding patches close to the colony whenever possible (Kacelnik and Cuthill 1990; Orians and Pearson 1979; Wanless et *al.*1992) . Average distance to foraging areas was less than 100 km in our study, suggesting that adequate food resources were available within relatively short distances from the colony. Distances travelled by birds at Coats Island were similar to those found in Greenland by Falk et al. (2000) at a colony of similar size, but shorter than those reported by Gaston et al. (1985) or Benvenuti et al. (1998) at much larger colonies. The seasonal trend observed at our study site was for a reduction in travel distances towards the end of the chick rearing period. This change in foraging pattern may reflect seasonal changes and movement in the birds' prey base. The reduction in travel distances corresponds to a change in recorded species composition (less Arctic cod, more Crustacea) in late chick rearing. Also, accompanying these changes, was an overall increase in feeding rates, indicating that although individuals may not have been travelling as far to foraging areas later in the season, they may have been working as hard or harder for less energetically profitable prey items. Though we believe these trends are real, they must be regarded in light of reduced sample sizes in the latter portion of the study period, allowing the behaviour or preferences of individual birds to impose greater effects on the results. It is possible that shorter travel distances and increase in the number of deliveries of Crustacea may have been exaggerated by a few selective individuals.

2.5.3. Dive depths and distribution

Dive patterns recorded in our study were similar to those described in other recent studies of Thick-billed murre diving behaviour using similar data loggers to ours. Average dive depths related to foraging ranged from 40 – 45m, closely matching depths reported by Falk et al. (2000). Although some of our data loggers were limited in resolving dives greater than 76m in depth, less than 25% of dives were beyond this threshold, suggesting that the deeper dives were not excessively underestimated. Comparison of the distribution of all dives conducted on foraging trips against those dives taken immediately preceding the return trip to the colony reveals the latter group highly skewed towards deeper depths. This difference in depth distribution suggests that individuals are adopting different dive patterns when self-feeding in comparison to foraging for chick meals. It appears that birds conduct a higher proportion of shallower dives when foraging to fulfil their own energy requirements (assumed to be most of the dives on a foraging trip), as opposed to deeper dives when capturing prey items to feed to chicks just prior to returning to the colony. This change in diving behaviour lends support to earlier reports which found differences in the diet of adults and chicks (Gaston and Nettleship 1981), where chicks were fed predominantly fish while adults had a higher proportion of Crustacea in their stomachs.

Differences in dive patterns between self-feeding and chick prey can also be interpreted in relation to optimal foraging theory with respect to central place foragers (Orians and Pearson 1979). As diving is an energetically costly activity (Croll et al. 1992), adopting a pattern of more frequent, shallower dives within a feeding patch might provide a more efficient energy return to cover individual foraging costs. In contrast, a prolonged, deeper dive initiated for capturing chick prey immediately prior to colony return may increase the chances of encountering larger diet items needed to support chick development. Alternatively, fish of a suitable size for delivery to chicks may be much more common at depths below those typically used for self-feeding. Hence, the bird may be forced to dive deeper in order to obtain a suitable 'package' for delivery to its chick.

Variation in dive depths may also be influenced by time of day effects (Croll et al. 1992; Bost et al. 1994; Robinson and Hindell 1996; Bethge et al. 1997; Wilson et al. 1997; Charrassin et al. 1998; Cherel et al. 1999), where individuals have been shown to dive deeper during the middle of the day, than at night. Differences in depths attributable to time of day were evident when we analysed all dives carried out on foraging trips, but differences due to these effects were not detected when we considered only dives for chick food. This suggests that the behavioural pattern adopted when provisioning chicks was largely independent of time of day, perhaps because the small forage fishes typically delivered do not undertake any significant diurnal change in depth. Thus, for dives analysed here, data were pooled over time of day.

2.5.4. Dive depths in relation to prey types

Distribution of depths in relation to prey species indicate that birds generally dive deeper for benthic prey items such as zoarcoids, while locating mid-water schooling species such as Arctic cod and capelin at intermediate depths. The bathymetry around the colony is characterised by a narrow shelf that extends to distances of 5 to 10km around the island. Depths over the shelf range around 20 –30 m, but drop off sharply beyond this shelf to depths of over 200m. Though not considered benthic organisms, we found Crustacea to be found at the deepest average depths, which may reflect vertical migration patterns within the water column (Wilson et al. 1993) rather than association with physical oceanographic features. Alternatively, it is possible that the deep dives associated with the delivery of Crustacea were unsuccessful attempts to find fish, during which the bird resorted to gathering Crustacea on the return journey to the surface. The depths may not represent those at which Crustacea were actually captured. In contrast, sandlance, known to inhabit sandy sea floors (Robards et al. 1999b), were found at the shallowest depths, suggesting they may be located largely inshore along the shelf. As there is little information available on the behaviour and biology of the prey species in the area of Hudson Bay around our study site, in the absence of commercial fisheries or other independent sampling measures, the data gathered from the birds provide us with some of the best methods of assessing distribution of these species in the vicinity of the colony.

Examination of dive – prey relationships over the entire depth range of our data loggers, provides a picture of relative vertical distribution of prey. Capelin and cod occur widely throughout the depth range, reflecting the ephemeral nature of these mobile, schooling fish species. Sandlance is distributed almost exclusively at depths of less than 40m, further indication they may be located largely on the shelf areas close to shore. Distribution of zoarcoids is concentrated at depths in excess of 40m, suggesting that these territorial, bottom-dwelling prey are further offshore than sandlance. The lack of zoarcoids at shallower depths close to shore suggests that these species densities may have been reduced in these areas as a result of colony feeding pressure.

2.5.5. Foraging range in relation to prey types

Location of prey in relation to bird foraging ranges showed a non-random distribution around the colony. Total foraging range averaged less than 100 km from the colony over our study period. Birds were observed arriving and departing almost exclusively in a westerly direction of the colony. Both land- and ocean-based visual surveys indicated that birds followed flight patterns to and from the colony tracking along the North coast of the island. Average distances associated with prey (Figure 1.8.) indicated that birds feeding close to the colony were more likely to deliver small prey items, like Crustacea, while those foraging further away were more likely to deliver larger, higher energy items such as cod and zoarcoids. Distribution of prey species in relation to foraging range (Figure 1.7.) indicated detectable separation of forage items with distance. Prey species within close range of the colony were dominated by capelin and Crustacea, with sandlance completely absent from within 25 km. Substantial amounts of cod and zoarcoids were brought in from distances greater than 25 km.

The observed differences in distribution of prey species composition provide evidence for local depletion effects in the vicinity of the colony. In his hypothesis for the regulation of seabird populations, Ashmole (1963) suggested that the foraging of large numbers of individuals around a centrally located, densely populated colony could create areas of prey depletion. This theory was supported by observations carried out by Birt et al. (1987), who sampled the density of fish distributions around cormorant (*Phalacrocorax* spp.) colonies in Atlantic Canada. We believe that results from the current study with regards to prey species composition and foraging range provide some evidence that the foraging activity of individuals from the colony at Coats Island may be exerting similar effects on the local community of prey species.

2.5.6. Central Place Foraging Theory

Foraging theory is most often interpreted in terms of energy efficiency and maximization (Stephens and Krebs 1986, Houston 1987). Many avian studies have investigated the principles of central place foraging theory as described by Orians and Pearson (1979), (Andersson 1981; Hegner 1982; see also Ydenberg 1994), but none has dealt specifically with Thick-billed Murres. We are able to address some aspects of murre foraging behaviour within the framework of central place foraging theory by relating size of prey items with individual travelling distances. In contrast to other auk species, such as puffins (*Fratercula* spp.) and razorbills (*Alca torda*) which use their bills to both capture and carry food items and are able to handle several items at a time, Thick-billed murres fall into a category of foraging theory classified as 'single prey loaders' owing to the fact that the capture of one item for transport precludes capture of any additional items. This physical constraint limits an individual's ability to transport prey items back to the colony. Thick-billed murres are rarely observed delivering more than a single prey item to their chicks. Based on this limitation, we assume that individuals use their last dive before returning to the colony to capture prey for chicks. Predictions made by Orians and Pearson (1979) suggest that load size should increase with increasing distance from the central place. A corollary of this theory is that the parents should feed themselves on smaller prey items than those they choose to deliver to the nestling. Examination of length and mass relationships of prey items with respect to foraging range resulted in a significant positive correlation between mass and travel distance, both when all items were considered, and when only the most common species (capelin and cod) were included. In addition, the shallow dives exhibited when birds were feeding themselves were consistent with the idea that they were feeding on small prey, unsuitable for delivery to their offspring. These results are consistent with the general predictions made by Orians and Pearson (1979). This suggests that individual Thick-billed Murres make behavioural decisions about the size of prey items that they should carry back to the colony , based on an assessment of distance or time away from the colony. This pattern is also evident from several anecdotal observations of individuals that made very brief trips away from the colony (<30 min.) after which they often returned with very small prey items, such as amphipods. As the timing of these trips was very short, we assume that the entire trip was used for chick provisioning. Amphipods are generally very small in size and of little mass further supporting the mass – distance prey relationship.

2.5.7. Conclusions

Information collected with the use of small, electronic data loggers coupled with traditional observational protocols has proved to be an effective means of addressing questions relating to prey distribution and ecology and of providing evidence of foraging ecology in relation to behavioural theory. This approach has allowed us to examine new aspects of Thick-billed Murre foraging patterns and to identify some previously inaccessible aspects of the local marine environment. Information on the behaviour and ecology of the organisms on which the birds' prey on is sparsely documented, thus parameters on distribution and depth profiles of these prey species can only add to our understanding of this Arctic marine community.

As predicted by current foraging models, longer travel distances translated into the delivery of larger prey items. However, the distribution of foraging range with prey species also can be interpreted as evidence for local depletions of some species in the vicinity of the seabird colony. Hence, in light of the distributional patterns observed, birds may be forced to travel further and work harder because of their colonial aggregation to maximize energy returns to the colony.

Additional work needs to continue into the investigation of seabird foraging behaviour in relation to its prey, especially in this area of Hudson Bay. Independent methods of sampling around the colony would greatly add to the information presented here in providing a better picture of the local environment. In this way, the implications and impacts of seabird – prey interactions can be assessed in greater detail.

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Table 1.1. Summary of formulae used to calculate mass of prey items from observed estimated lengths. *(from Gaston 1987).*

Species	Formula	Mass of 100mm fish (g)
Capelin (*Mallotus villosus*)	$\text{mass} = (0.103\text{x}10^{-6}) \times \text{length}^{3.794}$	3.99
Arctic Cod (*Boreogadus saida*)	$\text{mass} = (9.250\text{x}10^{-6}) \times \text{length}^{2.929}$	6.67
Sandlance (*Ammodytes* spp.)	$\text{mass} = (5.283\text{x}10^{-6}) \times \text{length}^{2.828}$	2.39
Sculpins (*Triglops* spp.)	$\text{mass} = (1.819\text{x}10^{-6}) \times \text{length}^{3.268}$	6.25
Zoarcoids		
Fish doctor (*Gymnelus viridis*)	$\text{mass} = (0.492\text{x}10^{-6}) \times \text{length}^{3.407}$	3.21
Fourline snake blenny (*Eumesogrammus praecisus*)	$\text{mass} = (2.445\text{x}10^{-6}) \times \text{length}^{3.208}$	6.37
Daubed shanny (*Leptoclinus maculatus*)	$\text{mass} = (986\text{x}10^{-6}) \times \text{length}^{1.767}$	3.37
Arctic shanny (*Stichaeus punctatus*)	$\text{mass} = (1.485\text{x}10^{-6}) \times \text{length}^{3.271}$	5.18

formula: $\text{mass (g)} = \text{A x length (mm)}^{\text{B}}$

Table 1.2. Average distances travelled by birds on return trips from foraging grounds, based on timing of last dive before arrival at the colony. ANOVA: $F_{2,77}=18.34$ $p < 0.001$

feeding watch	*mean (km)*	*sd*	*range (km)*	*n*
FW1: Jul. 27-30	36.4	13.1	9.4 – 58.4	34
FW2: Aug. 7-9	46.6	16.0	17.0 – 74.2	28
FW3: Aug. 12-14	17.3	20.6	3.5 – 85.7	18

Table 1.3. Summary of descriptive statistics for categories all dives and last dives with results of Mann-Whitney U test.

	mean (m)	*sd*	*median*	*n*	*Mann-Whitney 'U'*	*p*
All dives	24.9	22.6	18.0	10391	262780.5	< 0.001
Last dives	42.9	23.9	42.0	88		

Table 1.4. Summary statistics for depths of last dives before colony return grouped by observational watch and sex with results of non-parametric tests for differences between groups.

	mean	*sd*	*median*	*n*	*df*	*Kruskal-Wallis statistic*	*p*
FW1 (Jul. 27-30)	44.3	20.5	43.0	34	2	0.393	0.822
FW2 (Aug. 7-9)	40.3	24.1	40.5	28			
FW3 (Aug. 12-14)	44.6	28.4	46.0	25			
						Mann-Whitney 'U'	*p*
Males	43.5	23.7	46.0	35		891.5	0.872
Females	42.8	24.4	42.0	52			

Figure 1.1. Proportion of prey species delivered by adult Thick-billed Murres to nestlings in 1999, over three 72hr continuous feeding watches.

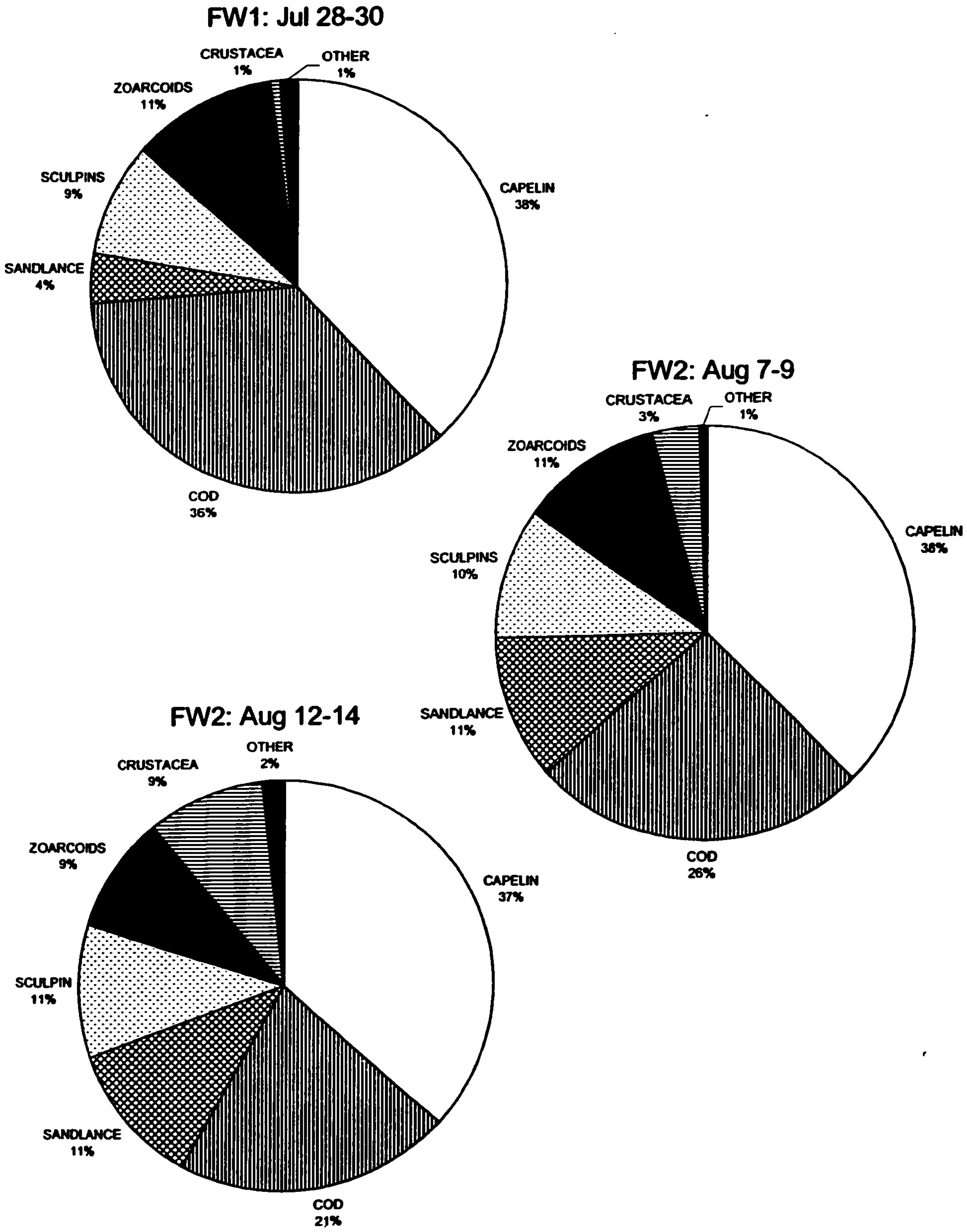

FW1: Jul 28-30
CRUSTACEA 1%
OTHER 1%
ZOARCOIDS 11%
SCULPINS 9%
CAPELIN 38%
SANDLANCE 4%
COD 36%
FW2: Aug 7-9
CRUSTACEA 3%
OTHER 1%
ZOARCOIDS 11%
CAPELIN 38%
SCULPINS 10%
SANDLANCE 11%
COD 26%
FW2: Aug 12-14
OTHER 2%
CRUSTACEA 9%
ZOARCOIDS 9%
CAPELIN 37%
SCULPIN 11%
SANDLANCE 11%
COD 21%

Figure 1.2. Frequency distributions of lengths prey items delivered to chicks grouped by species.

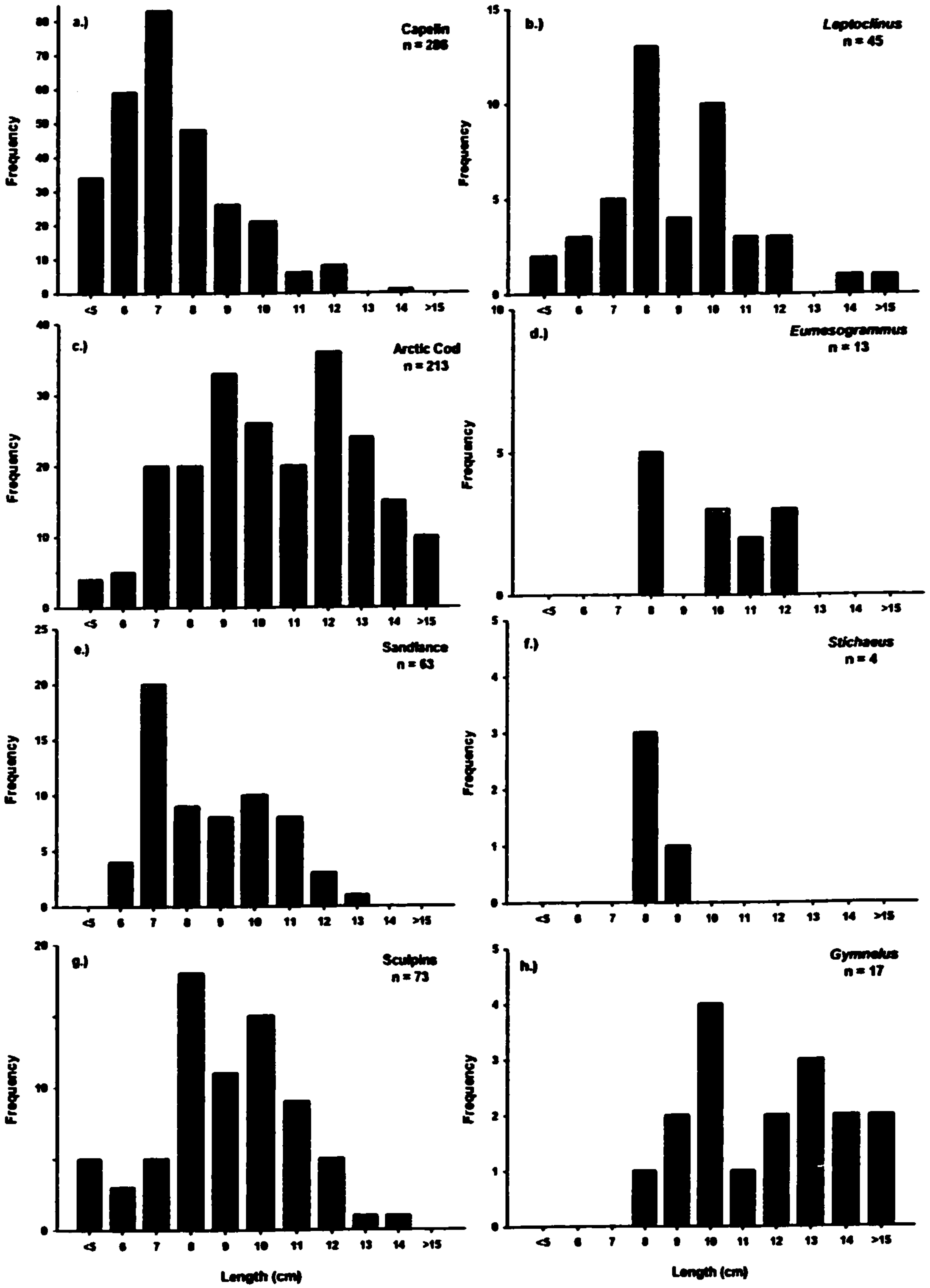
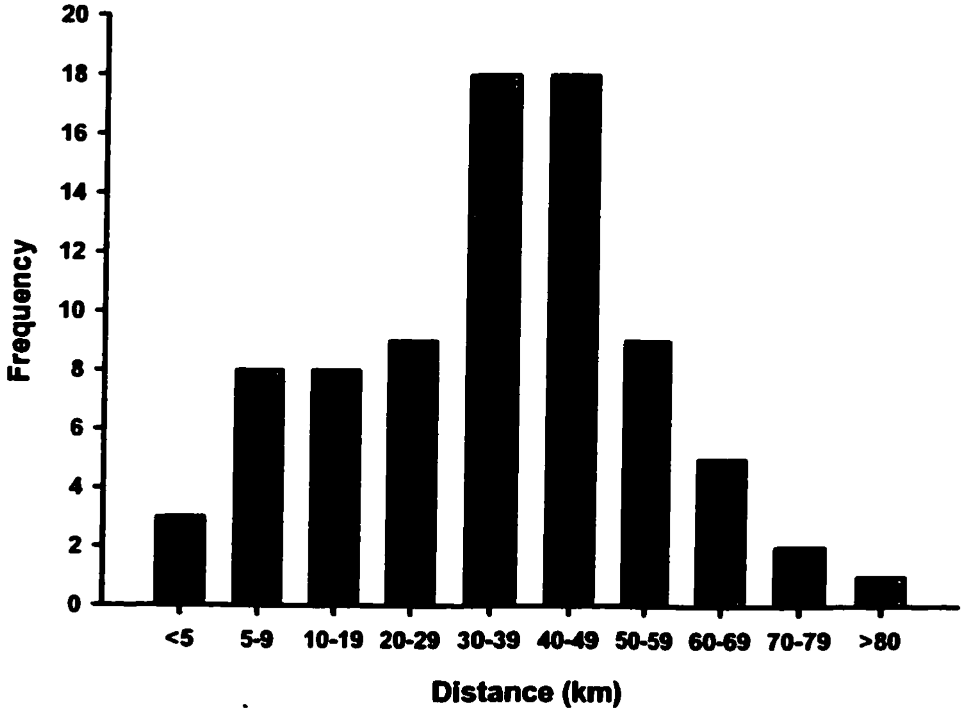

a.)
Capelin
n = 286
b.)
Leptoclinus
n = 45
c.)
Arctic Cod
n = 213
d.)
Eumesogrammus
n = 13
e.)
Sandlance
n = 63
f.)
Stichaeus
n = 4
g.)
Sculpins
n = 73
h.)
Gymnelus
n = 17
Frequency
<5
6
7
8
9
10
11
12
13
14
>15
Length (cm)

Figure 1.3. Frequency distribution of adult Thick-billed Murre flights returning to the colony from foraging areas (n=81).



Frequency
20
18
16
14
12
10
8
6
4
2
0
<5
5-9
10-19
20-29
30-39
40-49
50-59
60-69
70-79
>80
Distance (km)

Figure 1.4. Distribution of dive depths of foraging adults during chick rearing. Open bars represent all dives (n = 10391), shaded bars represent only last dives before returning to the colony (n = 88).

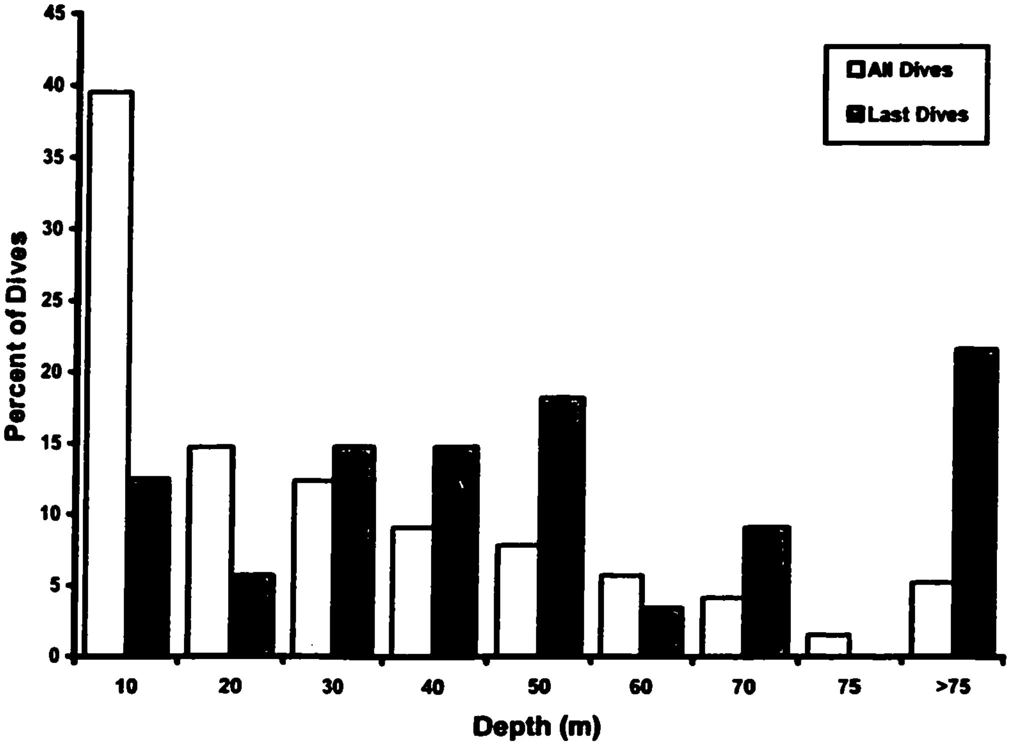
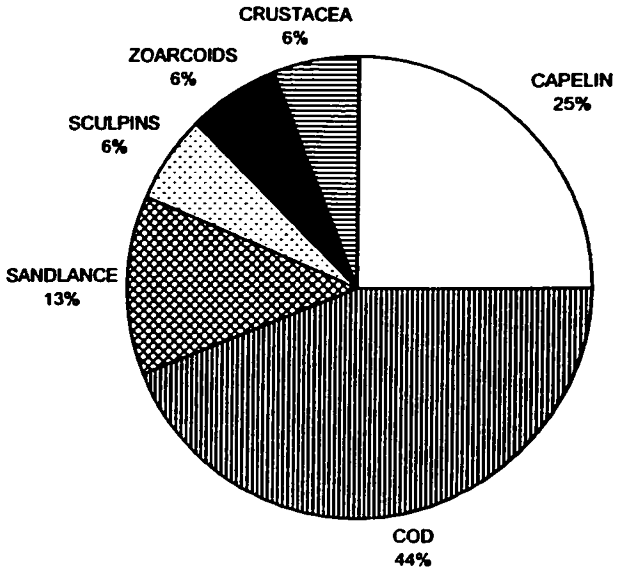
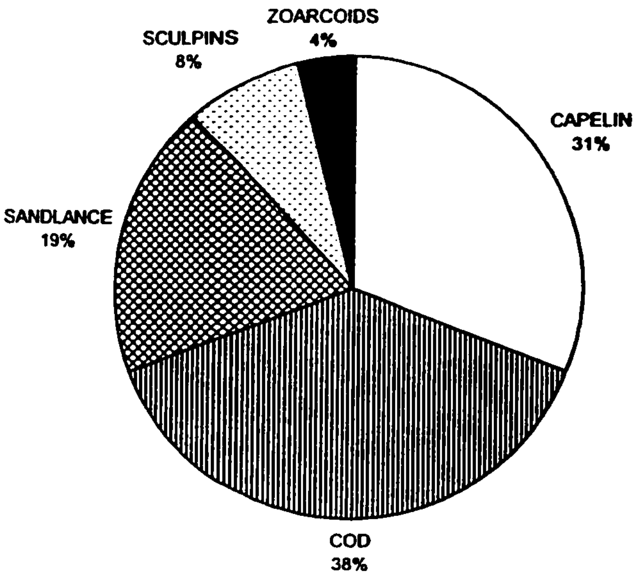
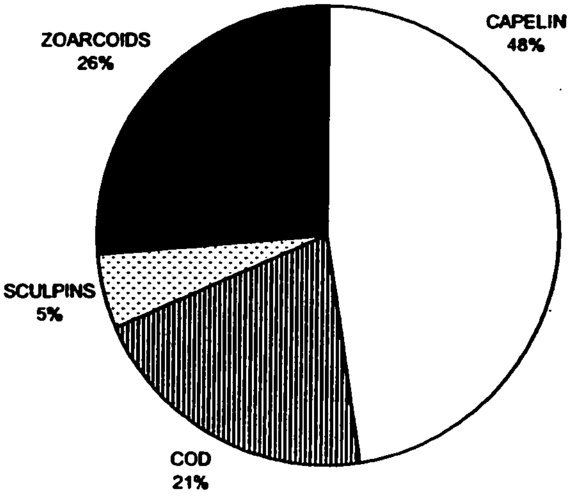

45
40
35
30
25
20
15
10
5
0
Percent of Dives
☐ All Dives
■ Last Dives
10
20
30
40
50
60
70
75
>75
Depth (m)

Figure 1.5. Distribution of prey species delivered to chicks in relation to depth of last dive before a return trip to the colony.


Depth 0-20m n=16


Depth 21-40m n=26


Depth 41-60m n=19

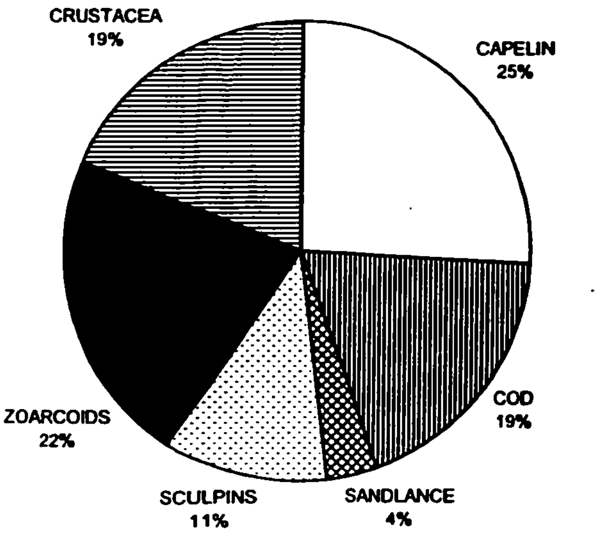

Depth >60m n=27

Figure 1.6. Average depths of last dives associated with prey species. Boxes represent mean ± std. error. Error bars represent std. deviations. There were significant differences between prey classes. ANOVA: $F_{5,82}=2.834$ $R^2=0.142$ $p=0.021$

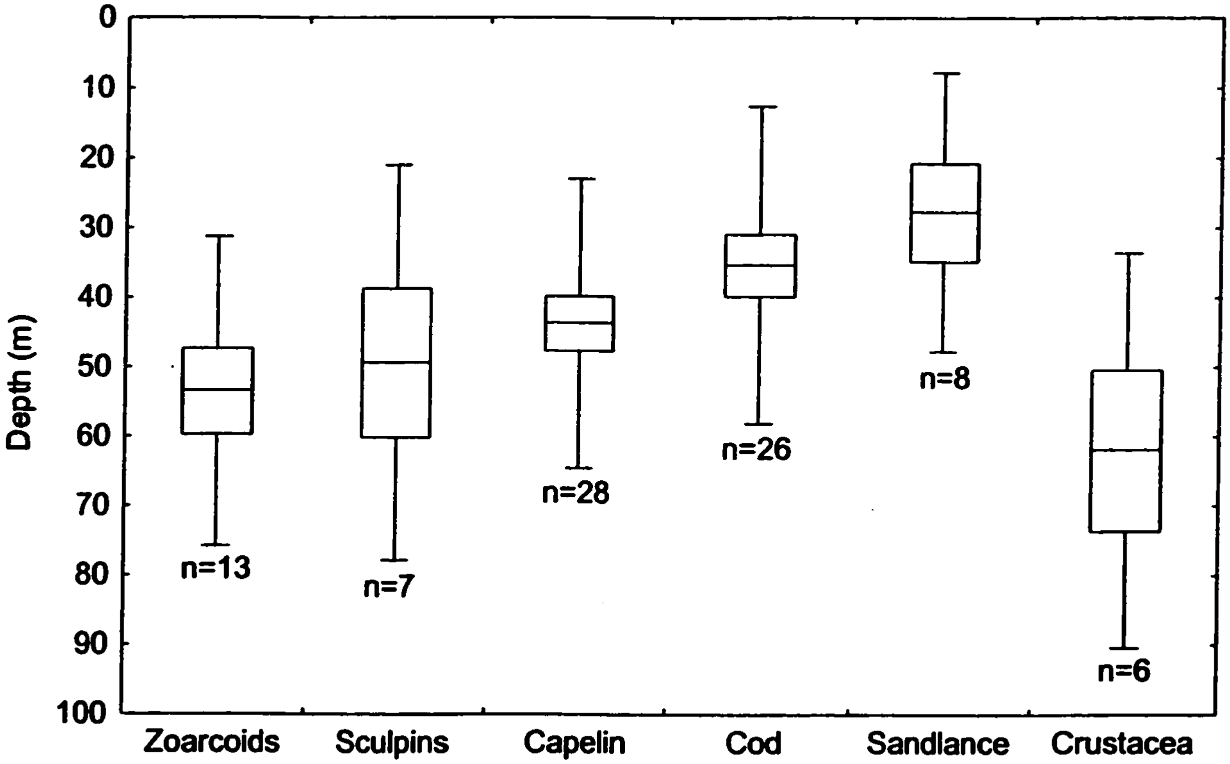

Depth (m)
0
10
20
30
40
50
60
70
80
90
100
n=13
n=7
n=28
n=26
n=8
n=6
Zoarcoids
Sculpins
Capelin
Cod
Sandlance
Crustacea

Figure 1.7. Proportion of prey types in relation to distances of return flights.

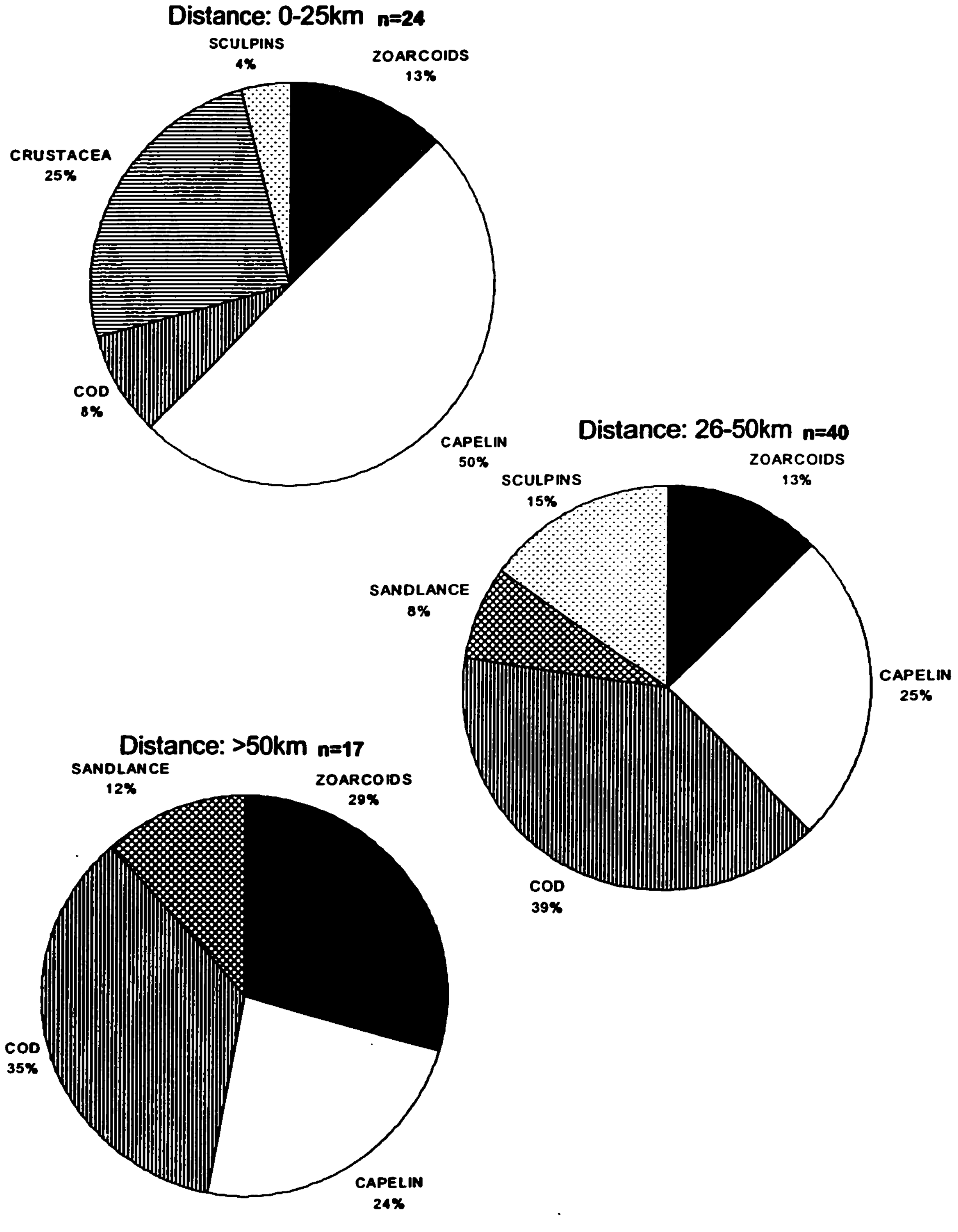

Distance: 0-25km n=24
SCULPINS 4%
ZOARCOIDS 13%
CRUSTACEA 25%
COD 8%
CAPELIN 50%
Distance: 26-50km n=40
ZOARCOIDS 13%
SCULPINS 15%
SANDLANCE 8%
CAPELIN 25%
COD 39%
Distance: >50km n=17
SANDLANCE 12%
ZOARCOIDS 29%
COD 35%
CAPELIN 24%

Figure 1.8. Average distances of return trips in relation to prey type. Boxes represent mean ± std. error. Error bars represent std. deviations. There were significant differences between prey classes. ANOVA: $F_{5,75}=6.565$ $R^2=0.304$ $p<0.001$

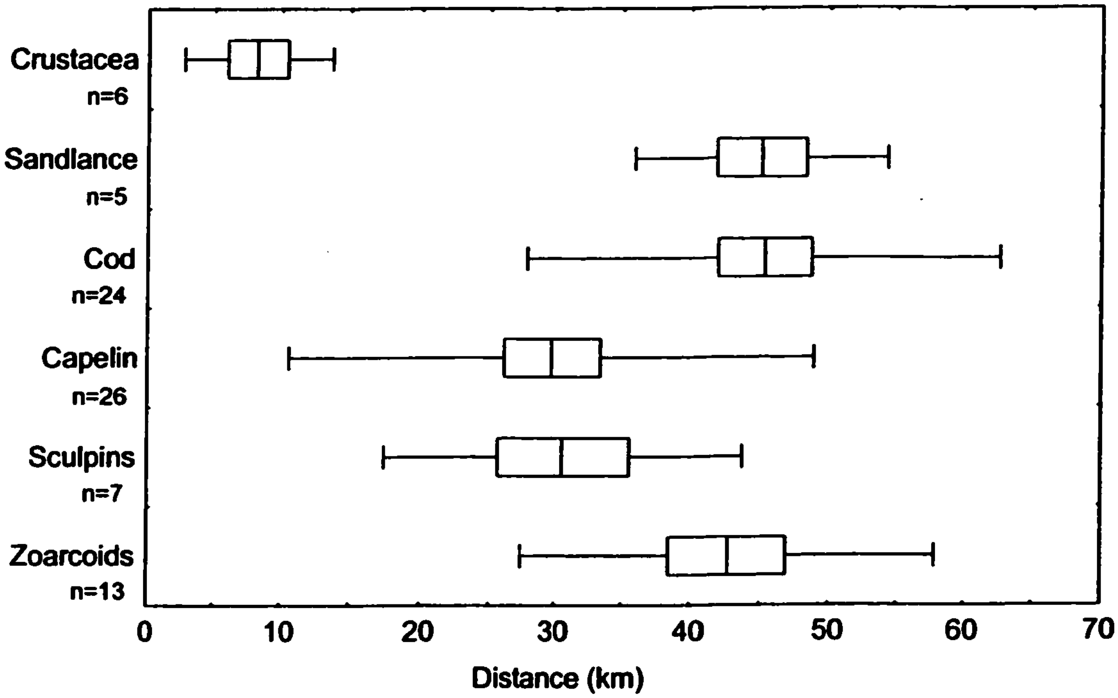
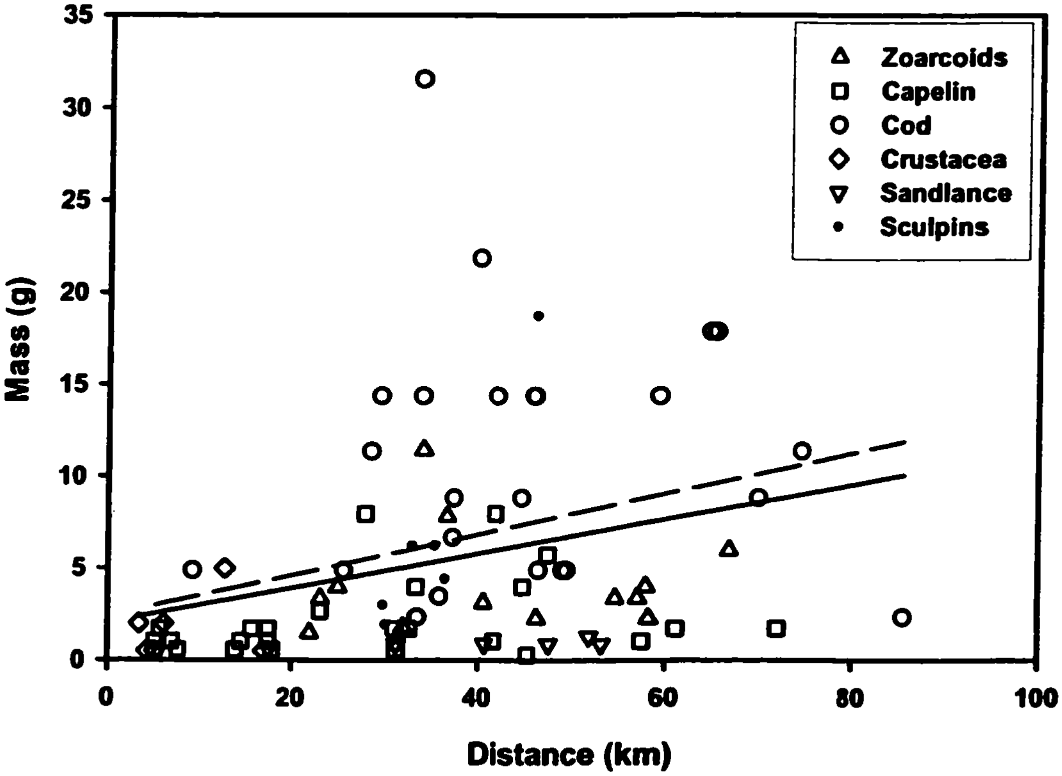

Crustacea
n=6
Sandlance
n=5
Cod
n=24
Capelin
n=26
Sculpins
n=7
Zoarcoids
n=13
0
10
20
30
40
50
60
70
Distance (km)

Figure 1.9. Mass of prey items in relation to distance of return flight. Positive correlations between mass and distance were significant based on log transformed values for mass. Solid line represents slope of the regression for all prey types. ($y = 0.007x + 0.403$; $F_{13.938}$ $R^2=0.155$ $p<0.001$). Dashed line represents slope of the regression for Arctic cod and capelin only.



Zoarcoids
Capelin
Cod
Crustacea
Sandlance
Sculpins
Mass (g)
Distance (km)
0
5
10
15
20
25
30
35
0
20
40
60
80
100

3. Trends in species composition and patterns of specialisation in adult Thick-billed Murres (*Uria lomvia*) delivering prey to nestlings

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note: this chapter has been formatted in preparation for journal submission

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Trends in species composition and patterns of specialisation in adult Thick-billed Murres (*Uria lomvia*) delivering prey to nestlings

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3.1. Abstract

We examined data collected from observations of adult Thick-billed Murres delivering food to nestlings at a colony in northern Hudson Bay, Canada from 1994 to 2000 to investigate patterns of prey species composition and individual specialisation. Uniquely marked birds allowed for identification of known individuals between years. Diet items included a variety of small benthic and pelagic fishes and invertebrates. Arctic cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) together, accounted for over 50% of deliveries in all years. There were trends for an increase in capelin (31% to 50%) and a decrease in cod (32% to 15%) during the period of the study. Sandlance (*Ammodytes* spp.) and sculpins also were frequent in chick diets with zoarcoids (< 16%) and invertebrates (< 8%) occurring less frequently and with greater variability. Cluster analyses indicated clearly identifiable groups of individuals within our sample with a tendency for specialisation. Specialisations were most evident on prey species which were less abundant in overall composition such as sculpins or as an absence of common prey (cod and capelin) in some diets. Some individuals showed a distinct preference for rare diet items such as certain types of zoarcoids. In many individuals, these tendencies for specialisation persisted between years suggesting active behavioural mechanisms. Trends in prey composition and individual specialisation are discussed in relation to patterns in Thick-billed Murre foraging behaviour as well as to the ecology, availability and distribution of prey items in the vicinity of the colony. We discuss the implications of diet specialisation when using seabirds as sampling

devices for prey species in their local marine environments and for the interpretation of trends over time.

3.2. Introduction

Diet studies of adult seabirds provisioning nestlings have been widely reported in the literature (Gaston and Noble 1985; Gaston 1985; Barrett and Furness 1990; Wanless et al. 1992; Gaston and Bradstreet 1993; Robinson and Hindell 1996; Chapdelaine and Brousseau 1996; Kirkwood and Robertson 1997; Cherel et al. 1999; Bryant et al. 1999). A key component of these studies of foraging ecology is the presentation of general trends in diet composition. While several studies have looked at differences in diet between colonies or within seasons (Chapdelaine and Brousseau 1996), fewer have examined differences in diet between individuals (but see: Cairns 1987b). In some populations that prey on a wide variety of prey items, it has been demonstrated that individuals can exhibit a high degree of variation (Beissinger et al. 1994).

Many studies of seabird foraging ecology and prey trends have been based on observations of birds returning to breeding sites at their colonies with food for their nestlings. As top level predators in their marine environments, seabirds have often been used as indicator species to provide information on prey populations within their foraging areas (Cairns 1987a). Knowledge of variation in the way in which individuals sample from their environment is of interest when interpreting information from birds on foraging behaviour and trends in prey selection at the population level. Behaviour of specialists within a population may affect our interpretation of results for the population at large and the relative effects on the prey community. Examination of inter-individual trends within a population may also provide insight into variation in patterns of bird behaviour and ecology of prey species and provide insights into the way that individual foraging strategies develop.

The Thick-billed Murre (*Uria lomvia*), a robust, medium-sized seabird, is an important component of Arctic ecosystems. It is one of the most abundant bird species breeding in polar regions and it congregates in large numbers at several colonies throughout the Arctic in the summer. As such, it has the potential to exert large pressure on the marine environments around its colonies. During the breeding season adult birds forage on a variety of fishes and invertebrates while provisioning for their chicks.

We examined general trends in prey composition at a colony of Thick-billed murres at Coats Island, Nunavut from 1994 to 2000. Prey items delivered by adults to their nestlings were identified and recorded. In addition to description of overall species composition we analysed diet patterns of marked individuals between years. Because the diet of birds at Coats island is very varied, compared to most other Thick-billed Murre populations studied, it provided excellent material for the evaluation of individual specialisations. Results of specialisation patterns are interpreted with regards to individual foraging behaviour as well as ecology of prey types. Implications of specialisation within a population are discussed in relation to the interpretation of overall diet trends and the use of such information when using seabirds as indicators of marine environments.

3.3. Materials and Methods

The data used in this study were collected over a period of seven years, from 1994 to 2000, as part of a long term research and population monitoring program on the colony of Thick-billed Murres at Coats Island, Nunavut (62°57'N, 82°00'W). The colony, located in northern Hudson Bay, provides seasonal breeding habitat for approximately 30,000 pairs of Thick-billed Murres. Research and observations have been conducted at this study site by the Canadian Wildlife Service since 1984 (Gaston 1991). The study site has been described in detail in other papers (De Forest and Gaston 1996). An intensive annual banding program since 1984, concentrated at several locations within the colony, has resulted in the presence of many individually marked birds, distinguished by combinations of colour bands and by easily readable numbered stainless steel bands. Hence, we have been able to identify specific individuals and collect information on their behaviour throughout several successive breeding seasons. All data used in the present analysis were collected on birds within a single study plot in the colony (Plot Q).

Observations of birds were made from a wooden blind just above the study plot. Birds under observation were all within 6 m of the blind. Approximately 69 breeding pairs, involving a total of 138 marked individuals were observed over the course of the study period. Information on adult foraging behaviour was collected throughout the chick rearing period in all years from 1994 to 2000 using a series of continuous observational watches, each lasting between 24hrs, 48hrs or 72hrs. In all years, the timing of observations ranged over a period beginning as early as 23 July and continuing through 14 August (Appendix 1). Effort was distributed in all years so that observations covered similar periods of nestling development (roughly from when half the chicks had hatched, to just prior to the first chicks departing). During these observational watches, information was collected on the identity of birds delivering prey items to their chicks. Timing of deliveries, to the nearest minute, as well as identification of prey to species were noted.

3.3.1. Prey items

The range of prey items observed over the study were classified into ten categories that were easy to recognise from the observation blind: capelin (*Mallotus villosus*), Arctic cod (*Boreogadus saida*), crustaceans (shrimp and amphipods – mostly *Parathemisto* spp.), sandlance

(*Ammodytes* spp.), sculpins (mostly *Triglops* spp., but also *Myoxocephalus* spp. and *Gymnocanthus* spp.), squid (*Gonatus* spp.), fish doctor (*Gymnelus viridis*), daubed shanny (*Leptoclinus maculatus*), fourline snakeblenny (*Eumesogrammus praecisus*) and Arctic shanny (*Stichaeus punctatus*). For some analyses, all prey classes except cod and capelin were grouped together and referred to as 'others'.

3.3.2. Sample for analysis of individual preference

To maximize the total number of prey observations per individual we combined information from different years. Because information on individual birds could not be obtained in all years, either because they were absent or because they failed to rear a chick, and because the frequency of different prey species varied from year to year, we selected a combination of individuals and years from the entire set of observations from 1994 to 2000 that yielded an adequate number of individuals for which information was available for several years. This sample (individual preference sample) was used in order to investigate individual patterns in delivery of prey items.

Individuals were selected based on being present and active in 3 of the 7 years of study. The combination of years that resulted in the largest sample of identifiable individuals was from 1998, 1999 and 2000. This subset comprised 12 individuals (Table 2.1), of which 8 were males and 4 were females (information on sex were determined through behavioural and molecular genetic techniques, Appendix 2.).

3.3.3. Statistical analyses

Trends in overall prey composition and inter-annual variation were examined for all ten prey categories by calculating relative proportions for each prey type delivered by all of the birds under observation across all watches in a given year. Prey totals were calculated for both the total sample of years from 1994 to 2000 (Table 2.2) and for the smaller subset of 12 birds from 1998 to 2000 (individual preference sample). All analyses on individual trends were based only on the subset of observations for the 12 selected individuals. As no observations of *Eumesogrammus praecisus* were recorded in the individual preference samples, this prey category was not included in any further analyses.

Before investigation of prey patterns attributable to individual birds, the selected sample was analysed for variation in prey due to time of delivery and for differences due to sex. To test for variation in prey delivered in relation to time of day, prey were grouped into three main categories (cod, capelin and others) and the 24hr day was partitioned into six 4hr blocks (00:00-03:59, 04:00-07:59, 08:00-11:59, 12:00-15:59, 16:00-19:59, 20:00-23:59). A contingency test was performed to examine variation in prey representation between time periods. Differences in the contribution of each sex were tested separately for each of the nine prey categories using Kruskal-Wallis analysis of variance. Critical p-values (at the level of 0.05) were corrected using the Bonferonni adjustment to account for the number of prey categories.

Analysis of individual prey patterns were investigated using three different statistical procedures. An initial test of individual prey distributions was conducted by comparing individual prey totals (cod, capelin and others) to the overall total of all other birds in the sample (Appendix 3). A Chi-square analysis was carried out for each of the 12 selected individuals.

Having obtained evidence that individuals differed significantly in the mixture of prey delivered to their nestlings, we then employed cluster analyses to examine groupings of individuals and prey types based on similarity and dissimilarity indices. For the cluster analyses, all prey categories were used as factors except for *Stichaeus punctatus* and squid due to their small sample sizes (inclusion of these prey types did not contribute sufficient variation to overall groupings). All cluster analyses were performed on the percentage contributions of each prey type to the diet of each individual bird. Hierarchical classification schemes were conducted using Ward's method to generate groupings. Tree clusters were created for individuals based on prey type, as well as for prey groupings based on individual contributions. K-means cluster analyses were also performed on the sample to separate individuals based on prey types, using an ANOVA to calculate maximum variation between groupings.

In an attempt to identify whether individuals maintained similar preferences from year to year, the proportions of prey types delivered for each individual were calculated within each year sampled and compared to the average proportion of deliveries made per individual in each year.

All cluster analyses were performed using STATISTICA 5.1 (StatSoft Inc.). All other analyses were conducted using SYSTAT 8.0 (SPSS Inc.).

3.4. Results

3.4.1. Prey trends – whole sample

A total of 3,322 prey items were observed and identified from 1994 to 2000. In all years, Arctic cod and capelin predominated, contributing over 50% of all deliveries (Table 2.2). Other items that occurred frequently in most years were sculpins (3.7-23.0%) and sandlance (0.4-24.5%). Prey items such as the zoarcoids (*Eumesogrammus praecisus, Leptoclinus maculatus,* *Gymnelus viridis*, *Stichaeus punctatus*) occurred in much lower proportions, usually less than 8.0% and were sometimes completely absent in some years. Invertebrates (crustaceans and squid) were also present in small numbers. There was a general trend for an increase in the number of capelin in the chick diet over the seven year period, rising from 31.5% in 1994 to 50.1% in 2000. In contrast, the proportion of cod declined over the study period, most sharply since 1996, falling from a high of 57.0% to a low of 15.8% in 2000. Numbers of sculpins in the diet also tended to decline, from 23.0% in 1995 to 3.7% in 2000. Sandlance showed a relatively steady increase in numbers from less than 1% in 1994 to over 24% in 2000.

3.4.2. Prey trends – individual preference sample

As in the larger data set, cod and capelin comprise over 50% of prey deliveries in all three years, with capelin occurring in consistently higher proportions than cod (Table 2.3). No clear trends were apparent in cod or capelin, with variation in totals between years. As in the larger sample, sandlance increased from 6.7% in 1998 to 21.9% in 2000. *Eumesogrammus praecisus* was completely absent from this sample of individuals. The rest of the zoarcoids were present in smaller proportions (less than 3%) with the exception of *Leptoclinus maculatus* which occurred in relatively high proportions in 1998 and 1999 (17.0% and 10.1%, respectively, but mainly because of one individual - see below).

3.4.3. Individual preferences

Deliveries of prey items to chicks were observed at all hours of the day. Peak hours of activity were between 04:00 and 12:00 (Figure 2.1). Total number of deliveries were low between 20:00 and 04:00. Analysis of the differences in distribution of prey types throughout the day indicated that the variety of prey items did not differ significantly ($\chi^2 = 7.46$, df = 10, p = 0.682). All further analyses were pooled over time of day.

The sample of selected individuals was composed of 8 males and 4 females. To test for the effects of sex, we compared the distribution of prey types between males and females. Results of Kruskal-Wallis analyses indicated no significant variation attributable to this factor (Table 2.4). As neither time of day nor sex appeared to affect the choice of prey delivered, these factors were not considered in further analyses.

3.4.3.1. Individual prey distributions

Comparison of individual prey distributions to group distributions indicated that 4 of the 12 birds in the sample differed significantly from the overall sample (Table 2.5). Birds for which individual prey distributions indicated a significant departure from the group as a whole were: 09445, 54043, 59567 and 62574. In order to avoid low cell values in the Chi-square analyses, this comparison only included three prey categories (capelin, cod, others; see Appendix 3). Consequently, this test was very conservative and served merely to demonstrate the existence of significant variation among individuals. Subsequent analyses attempted to describe these differences in detail.

3.4.3.2. Hierarchical classification

Classification analysis of birds based on individual prey percentages produced a tree diagram suggesting 4 groupings of individuals (Figure 2.2). Two individuals which were singled out separately from the rest, on branches of their own were birds 54043 (group 1) and 59567 (group 2). Birds 02110, 09445, 52526 and 62573 formed a distinct grouping (group 3) on a branch removed from the rest of the sample. The other 6 individuals in the sample clustered rather closely together with branching and linkage distances placing 01001, 54150, 04128, 10277, 07237 and 62574 together (group 4). The descriptive nature of this process is evident when, with a small re-interpretation of the branching, bird 59567 (group 2) could be considered as associated with group 4 instead.

Classification analysis of prey types based on contributions by individual birds generated a tree diagram with 3 distinct groupings (Figure 2.3). Cod and capelin occupy a branch to themselves (group 1b). Sculpins also fall out on a single branch (group 3b). The remaining prey types (crustacea, *Gymnelus viridis*, *Leptoclinus maculatus*, sandlance) comprise the final grouping (group 2b).

3.4.3.3. k-means clustering

For comparison of classification techniques, k-means clustering was also conducted to generate groupings of individuals based on prey type. A series of five clustering trials were performed on the sample of selected individuals, specifying models with parameters of 2 to 6 groups. Each k-means analysis produced an ANOVA table indicating variation among classification parameters (prey types). The classification scheme which resulted in the least number of groupings for individuals, with the most significant variation between them, consisted of 4 groups. Bird 54043 was singled out by itself (group 1c). Individuals 02110, 09445, 52526 and 62573 were placed in a separate group (group 2c). The third classification included 07237, 59567 and 62574 (group 3c). Another grouping was made up of the remaining birds (01001, 04128, 10277, 54150; group 4c). The ANOVA table for this classification scheme (Table 2.6) indicated that groupings were based on significant differences in individual contributions to prey types of cod, capelin and sculpins. A breakdown of the 4 classes of individuals with regards to relative prey proportions indicated that group 1c (bird 54043) was weighted heavily in capelin and *Leptoclinus maculatus*, it was characterised by an almost complete absence of cod among the prey delivered (Figure 2.4). Group 2c included individuals with high proportions of capelin and sculpins, while group 3c birds were high in both cod and capelin with very small proportions of other prey types. Group 4c contained individuals with a variety of all prey types.

3.4.3.4. Individual trends between years

To determine if individuals identified as potential specialists tended to bring in similar prey types between years we compared individual prey composition to average prey composition in each year (Table 2.7). From these comparisons it appears that bird 54043 consistently delivered higher than average proportions of capelin and *Leptoclinus maculatus* in all years sampled. Both 09445 and 52526 included higher than average proportions of sculpins in their nestling diet in all years, while 52526 delivered a higher than average percentage of *Leptoclinus maculatus* in 1998 and 1999. Bird 10277 delivered higher than average proportions of *Stichaeus punctatus* (otherwise rare) in both 1998 and 1999. Bird 04128 was the only bird to deliver *Gymnelus viridis* in 1998 (n = 4) and in 1999 delivered all but one of those seen (n = 4). This evidence suggests strongly that some specialisation's persisted from year to year.

3.5. Discussion

3.5.1. Species composition and trends

Descriptions of composition and proportions of prey items included in Thick-billed Murre nestling diets have been previously documented at the Coats Island colony and other locations (Bryant et al. 1999). The types of prey species identified in the current study are similar to those found in the diets of other colonies in the Canadian Arctic (Gaston and Noble 1985) and consistent with previous studies reported at our site (Gaston 1985; Woo et al. unpubl.). Unfortunately, although many observations have been made at the colony, independent measures of species distribution and abundance in the area of Hudson Bay surrounding our study site are lacking. The most abundant items in the chick diet at Coats Island were Arctic cod and capelin, which together comprised over 50% of identified deliveries in all years from 1994 to 2000. The consistently high proportions of these two diet items suggested that they were predictable in occurrence and readily available to foraging adults. The prominence of these prey species in the diet lends further support to previous claims that they are the general preferred diet items for murre nestlings at this colony (Gaston and Hipfner 2000). Although numbers of cod and capelin contributed a large percentage of the diet, there was some variability in the relative proportions of the two prey types and some clear trends were evident. Capelin showed a slight increasing trend in occurrence since 1994, while cod exhibited an overall decline over the same period. These trends in diet composition may reflect changes in the distribution or availability of these prey species to the birds due in part to ongoing environmental changes occurring throughout the Arctic. Recent studies of long term environmental trends indicate increases in Arctic air and sea surface temperatures, as well as changes in sea-ice cover (Morison et al. 2000). Parkinson (2000) has indicated that there has been a reduction in the amount of ice-cover and changes in the timing of break-up in the area of Hudson Bay surrounding the colony. As Arctic cod are known to be associated with ice edges and floes (Hop et al. 1997), where younger age classes (size classes which the birds target) find food sources in the form of summer algal blooms, changes in the distribution and occurrence of these physical structures may effect prey availability to the birds.

Less information is available about the biology of the small size class capelin which the birds take, but they are less dependent on ice formations, hence the slight increase in numbers may also be related to these environmental changes. Separate analyses by Gaston et al. (A.J. Gaston, K.Woo and M. Hipfner unpubl.) have indicated that the change in proportion of capelin in the diet is independent of the amount of cod, thus these changes most likely reflect real changes in availability rather than a simple switch from one dominant species to another.

Along with cod and capelin, sculpins and sandlance also appear regularly in the diet, identified in all years. Sculpins are benthic in nature and less far ranging than schooling species such as cod. As such, they are likely to be found on the sea floor of the shelf which extends 5 – 10 km away from the colony. A steady decline in the occurrence of sculpins since 1997 indicate that this prey type may be increasingly difficult to locate, possibly due to effects of local depletion associated with predation pressure around the colony (Ashmole 1963). Sandlance has exhibited an increase in the proportion of deliveries over the study period. Though little is known about the life cycle and behaviour of sandlance in Hudson Bay, sampling in Alaska by Robards et al. (1999a, 1999b) indicate that these fish utilise gravel or sandy beaches for spawning activity. A reduction in the amount of pack ice and earlier timing of break up may increase accessibility of these habitats to spawning sandlance in the areas around Coats Island, thus increasing availability to foraging murres.

Other prey items such as zoarcoids occur less often in the diet but with much more variability between years. As is the case with other diet items, detailed information on the biology of these demersal fish in the Arctic are sparse (Green and Mitchell 1997). We suggest that the pattern we see may be a reflection of relative abundances or availability within the local marine environment. The inclusion of these prey types and their relative ‘scarcity’ in observed deliveries, provides an opportunity to identify birds within our sample who tend to take higher than average amounts, and thus may be considered as 'specialising' on these items.

Comparisons of prey composition were made between the sample of 12 birds used for preference analyses and the overall sample. The dominance of cod and capelin was also evident in the individual sample, although between year trends were not readily identified in the smaller sample, covering only three years. Sculpins and sandlance occurred in similar proportions to the total sample, exhibiting similar decreasing and increasing trends respectively. Numbers of zoarcoids in the individual sample were also similar to the total sample, with a slightly increased variability. Overall, the relative composition of the individual sample generally reflects that of the larger sample. We considered this smaller sample to be representative of the larger sample when proceeding with investigations into individual trends and preferences.

3.5.2. Individual preference sample

Distribution of deliveries over a 24 hr period indicated most activity occurred during daylight hours (04:00 – 20:00). This diurnal pattern is similar to behaviour exhibited by other pursuit diving birds. For birds that rely on visual location of prey, it has been demonstrated that foraging activity has been related to varying levels of light (Cannell and Cullen 1998). Peak hours of arrival activity observed from our sample indicate that the majority of birds delivered meals to their chicks between 4:00 and 12:00. This uni-modal pattern is in contrast with patterns of activity observed previously (pers. obs.) and at other colonies (Bengston et al. 1993) where a bi-modal distribution in peak activity has been reported. Typical peaks in activity at Coats Island are usually observed in the morning (06:00 – 10:00) and in the evening (16:00 – 20:00). These activity peaks coincide with changes in brooding duties between partners as one arrives after a night of foraging and then later in the evening when the partner returns after foraging throughout the day. The absence of a two peak pattern of activity in our sample is most likely due to the sexual make-up of the individual sample. Brooding shifts at our study site lasted approximately 12 hrs per shift, with one partner tending the chick while the other partner was absent from the colony. We have found that the timing of these shifts appears to be associated with the sex of the birds (Kober unpubl.). Those birds present on the colony during the day are mostly males, while birds that arrive in the evening and attend the colony overnight are mostly females. Similar patterns in the difference in colony attendance based on sex have been shown by Gaston and Nettleship (1981). Since the composition of our smaller individual sample consisted mostly of males (8 males, 4 females), the single peak in delivery activity likely reflects the return of these birds after overnight foraging trips. The distribution of prey was not significantly affected by timing of deliveries, nor was prey composition different between the sexes. The absence of variation with sex or time of day was surprising, as during incubation males generally dive deeper than females (Woo et al. 1998). However, this variation refers to self-feeding dives. Apparently this distinction disappears when diving for prey to deliver to nestlings.

3.5.2.1. Identification of specialists

Most analyses and models involving identification of prey specialists within a population are based on a comparison of observed prey frequencies to those of known frequencies in the environment (Beauchamp et al. 1992). Unfortunately in our situation, there is little information available with regards to the distribution and abundance of prey species in the vicinity of our study site aside from what we can infer from diet observations of the birds themselves. For the purposes of our analyses we determine preference by comparing diet composition of individuals to the average composition of prey taken by all other individuals. We defined as specialists, those individuals which tended to include a higher than average proportion of specific prey items in their deliveries when compared to the percentage for the combined sample.

Comparison of the distribution of individual species composition for each bird sampled to the species distribution in the rest of the sample revealed that there were significant differences in individual prey patterns. From this general analysis of patterns in prey composition, 4 of the 12 individuals exhibited distributions different from the sample distribution. The prey groupings used to categorize these differences were not precise enough to provide insights into the mechanisms underlying differences in prey choice. However, our results provided preliminary evidence for the potential of individuals within our sample population to exhibit a tendency for specialisation and hence provided the basis for further investigation.

3.5.2.2. Outcome of classification analyses

Identification of distinct individual variation within the sample led to the use of classification analyses involving all prey categories to provide greater detail into potential specialisation. In the absence of any a priori predictions regarding preference related to specific prey taxa, we employed cluster techniques to test for natural groupings within our sample. These types of analyses are largely exploratory in nature, and were utilised to aid in elucidating patterns that existed within our data set. The exact probabilities of different groupings and classification trees cannot be calculated. Nonetheless, these procedures are useful when trying to identify individuals with unique or similar prey tendencies.

Hierarchical tree clustering using Ward's method of amalgamation produced a dendrogram suggesting 4 groups of birds based on individual prey proportions. Two groups included only single individuals (group 1: 54043 and group 2: 59567). Both of these individuals were also identified as specialists by the contingency table analyses. Visual analyses of the prey composition for each of the birds in the sample provide rationale for the groupings. Of the two birds singled out from the rest of the sample, 54043 is distinct from the other birds in delivering high numbers of *Leptoclinus maculatus* and in the near total absence of cod among its deliveries. Conversely, 59567 appears to have concentrated almost exclusively on cod when foraging for its chick. All of the birds included in group 3 (02110, 09445, 52526, 62573) included sculpins as a common component of their deliveries, while the rest of the birds in the sample (group 4: 01001, 54150, 04128, 10277, 07237, 62574) appear to incorporate a more general pattern of prey types in their deliveries, not highly concentrated in any one particular item.

A second method of classification analysis was also applied to the data set, using k-means clustering to group birds based on individual prey composition. Based on results of the hierarchical clustering we expected a four group model, but we ran a series of analyses, specifying from 2 to 6 groups to determine if other natural combinations existed. As expected, no significant increase in variation among groups was found, beyond four classes. Results of classification using k-means techniques produced slightly different groupings than the hierarchical methods, altering membership of 2 of the 4 groups. Bird 59567 was not singled out but was instead, grouped with 07237 and 62574 (group 3c), leaving birds 01001, 54150, 04128 and 10277 in a single group (group 4c). These differences in group membership do not differ strongly from those obtained from the dendrogram and can be arrived at with slightly different interpretation of the tree diagram. Variation between classification methods arise from differences in the algorithms which each technique employs to distinguish between groups. This is often a problem in the application of cluster analyses, especially when using multiple software packages, as each may apply slightly different classification rules (Afifi and Clark 1996). The differences between the two methods we used were most likely due to differences in sensitivity or ability of the ANOVA used to distinguish groups in k-means clustering from the average distance measures employed in tree clustering. As the differences in groupings using alternate methods in this study were small, with the majority of birds associated in a similar manner, we are confident that the classifications produced represent real differences within the data set. The similarity in the properties of groups is evident from examination of the percentage means of prey types upon which the groupings were based for k-means clustering, which provide statistical support for the visual analysis we conducted for hierarchical groups. Bird 54043 was isolated on the basis of its high representation of *Leptoclinus maculatus* and lack of cod, as before. Group 2c, which has identical individual make up as group 3 on the tree cluster, once again represents birds that take a sizeable proportion of sculpins in addition to capelin and cod. A group of generalist foragers (group 4c) is still present, while the grouping that now includes birds 59567, 07237 and 62574 is heavily weighted in cod and capelin.

From the classification scheme provided, it appears that the sample is made up of largely generalist feeders (6 of 12 birds), taking mostly cod and capelin but also including a range of most other prey types. The presence of a *Leptoclinus maculatus* specialist is strikingly evident, given the fact that this prey type makes up a small proportion of the overall sample and is considered a rare diet item in comparison to prey types such as cod and capelin. *Leptoclinus* is also ecologically different from cod or capelin, in its benthic lifestyle. Thus, tendency for preference on a prey type can also provide indirect insight into the foraging behaviour of a particular individual. Bird 54043 may actively search out this prey type, it may have located an area with a predictable supply of this species, or it may have developed a particular skill in capturing this type of prey. More detailed study at the individual level is required to discriminate between these alternatives, but the fact that this individual also included a large proportion of the more common capelin in its prey choices suggests more the latter options. The same type of inferences can be applied to the group of individuals which include sculpins in their take. Sculpins are also benthic fishes, but the typical prey composition of individuals in this group do not include a large proportions of *Leptoclinus maculatus*. This suggests that sculpins and daubed shannies are not necessarily associated, either by area or ecology, and hence are not equally accessible in the same areas. The simplest explanation seems to be that birds taking a high proportion of sculpins may not be utilising the same foraging areas as those that take *Leptoclinus maculatus*.

Comparison of species composition patterns of individuals between groups can be useful in drawing inferences about foraging behaviour or relative species distribution. Hierarchical cluster analysis of prey types based on individual proportions produced a tree diagram which classified prey types into two groupings. Cod and capelin were amalgamated into a single group (1b) while the rest of the prey types (crustaceans, *Gymnelus viridis*, *Leptoclinus maculatus*, sandlance and sculpins) comprised the second group (2b). This classification of prey types reflects the known ecology of these species. Cod and capelin are both pelagic, schooling species of fish, both are likely to be encountered over deeper waters away from the colony. The rest of the prey types are largely benthic. *Gymnelus viridis*, *Leptoclinus maculatus* and sculpins and sandlance are demersal fishes that permanently reside at or are closely associated with ocean substrate. Crustaceans are subject to diel vertical migration within the water column, and thus may also be found near the ocean bottom.

3.5.2.3. Preference between years

Analysis of prey trends, pooled over the entire individual sample, is necessary to provide large enough sample sizes for statistical analyses, but can obscure persistent tendencies over time. Having identified individuals and groups of birds with similar prey tendencies and apparent preferences, we examined patterns of deliveries for birds between the three years included in the preference sample to determine if prey choices were similar from year to year. In most cases, preferences did persist across years. This was despite the fact that many single-year samples were small and hence would have been strongly affected by stochastic variation.

Birds 09445 and 52526 both include high proportions of sculpins in their prey choices across years. Bird 54043, which was identified as a *Leptoclinus* specialist, consistently included this rare diet item in its deliveries in all years, while also taking higher than average amounts of capelin. These types of patterns provide further evidence of specialisation and indicate that some cases of repeated specialisation occur from season to season. Details of the behavioural mechanisms that individual birds may employ for these patterns to exist are not presently known. As discussed earlier, whether individuals exploit the same foraging locations from year to year, actively search for specific prey types or develop a proficiency for capturing certain items requires further study using methods which will provide direct information on individual foraging behaviour.

Although we have been able to demonstrate obvious patterns in specialisation from season to season, it is likely that we have underestimated the degree to which specialisation can occur. Small within year sample sizes mean that some specialisation has not been detected by us. It is apparent in the data set that seasonal specialisations can also occur, especially in the case of individuals that took a rare species several times in one year but not in another. For example, bird 04128 took high proportions of *Gymnelus viridis* in two years, but did not include any in a third year when this prey type was absent from all individuals in the sample entirely. Likewise, bird 62573 took several *Leptoclinus maculatus* in 1998, a year where the average proportion in the sample was very low, but did not include this item in any other years when other individuals did. This suggests that some individuals may develop specialisations in a particular year that do not persist in other years. These individuals may adjust their foraging behaviour to exploit prey patches opportunistically from year to year. Many of the specialisations identified, either in a single year or across years, tended to concentrate on zoarcoid species of fish. These fishes are benthic and sedentary in nature. Their prominence as markers of specialist diets suggests that they may be patchily distributed so that only birds foraging in specific areas or habitats are likely to encounter them.

3.5.3. Conclusions

The description and analysis of diet trends is a useful tool for investigating foraging behaviour of seabirds and is an important component in their use as monitors of their local environments. Diet information collected from birds at Coats Island, Nunavut can provide information on the distribution, availability and ecology of prey species in an area for which there are currently few other means of sampling. Identification of trends and changes over time are important in monitoring and assessing a northern ecosystem, such as Hudson Bay, which may be sensitive to changing environmental conditions. Cod and capelin appear to be dominant components of the northern Hudson Bay fish community, while zoarcoids appear less often in Thick-billed Murre nestling diets.

When using diet information to interpret trends in prey populations, it is of interest to know how individuals are sampling from their environment, as specialisation can effect results. In cases where independent methods of sampling environmental conditions are unavailable to directly measure prey abundance, application of multivariate clustering techniques can aid in classifying individual sampling patterns within a population. Though results of cluster analyses can often be subject to interpretation, the close agreement between the methods we employed allowed us to confidently identify specialists within our sample. Comparison of prey properties for the groupings and individuals we identified provide information on individual tendencies and foraging behaviour, as well as some insight into prey ecology. It is difficult to differentiate between mechanisms or patterns of behaviour birds use which result in the prey specialisations we have identified. Application of electronic data loggers and satellite telemetry to link at sea foraging behaviour with colony based observations would serve to provide insight into these areas. Knowledge of how individuals within a population sample from their environment are important when interpreting general trends in prey composition. The presence of cod and capelin in the diets of most of the birds in our sample suggest that they are items birds may encounter readily, thus trends identified for these prey types are likely be a good indication of real changes in abundance of these fish. Alternately, trends identified for items that appear less often in the sample and are considered 'rare', may be influenced by the specialisation of a relatively few individuals. This must be kept in mind when interpreting long term trends in these types of prey items.

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Table 2.1. List of birds included in the sample used for analyses on prey preferences. Each individual was uniquely identifiable by band number and colour band combinations. Sexes of birds were determined through observational and molecular genetic techniques.

Band #	left color bands	right color bands	sex
01001	DB/H8	LG/metal	M
02110	R/A9	LG/metal	M
04128	X	R/metal	M
07237	R/H9	DG/metal	F
09445	R/A1	OR/metal	F
10277	DB/A2	metal	M
52526	LG/metal	BK/DB	M
54043	BR	LG/metal	F
54150	BR/DB	LG/metal	M
59567	DB/W	LG/metal	M
62573	X	LG/metal	F
62574	DB/Y	LG/metal	M

Table 2.2. Summary of prey totals and species composition for deliveries made by all birds (c. 135) observed on watches lasting 24hr, 48hr or 72hr from 1994 through 2000.

	1994		1995		1996		1997		1998		1999		2000	
	total	%	total	%	total	%	total	%	total	%	total	%	total	%
Capelin	77	31.56	39	14.72	114	24.15	242	42.61	282	45.71	215	37.78	294	50.08
Arctic cod	79	32.38	102	38.49	269	56.99	124	21.83	111	17.99	176	30.93	93	15.84
Crustaceans	6	2.46	19	7.17	6	1.27	21	3.70	33	5.35	12	2.11	5	0.85
Fourline snake blenny	7	2.87	6	2.26	9	1.91	8	1.41	9	1.46	8	1.40	5	0.85
Fish doctor	9	3.69	11	4.15	4	0.85	12	2.11	16	2.59	9	1.58	2	0.34
Daubed shanny	17	6.97	23	8.68	7	1.48	20	3.52	40	6.48	42	7.38	17	2.90
Sandlance	1	0.41	1	0.38	41	8.69	18	3.17	37	6.00	43	7.56	144	24.53
Sculpins	44	18.03	61	23.02	20	4.24	98	17.25	74	11.99	54	9.49	22	3.75
Arctic shanny	0	0.00	2	0.75	0	0.00	10	1.76	9	1.46	3	0.53	3	0.51
Squid	4	1.64	1	0.38	2	0.42	15	2.64	6	0.97	7	1.23	2	0.34
total no. of deliveries	244		265		472		568		617		569		587	

Table 2.3. Summary of prey totals and species composition for deliveries made by a selected sample of birds (n = 12), used for detailed preference analyses (Individual preference sample).

Individual preference sample	1998 total	1998 %	1999 total	1999 %	2000 total	2000 %
Capelin	55	40.74	49	35.25	38	52.05
Arctic cod	21	15.56	34	24.46	10	13.70
crustaceans	4	2.96	3	2.16	1	1.37
Fourline snake blenny	0	0.00	0	0.00	0	0.00
Fish doctor	4	2.96	4	2.88	0	0.00
Daubed shanny	23	17.04	14	10.07	1	1.37
Sandlance	9	6.67	12	8.63	16	21.92
Sculpins	17	12.59	20	14.39	5	6.85
Arctic shanny	2	1.48	1	0.72	0	0.00
Squid	0	0.00	2	1.44	2	2.74
total no. of deliveries	135		139		73	

Table 2.4. Results of Kruskal-Wallis analysis for sex differences (8 male, 4 female) within each prey class. Probabilities were compared against the Bonferroni adjusted value (p= 0.006) to account for number of prey classes.

	Bonferonni adjusted p (α’ = 0.006)	
	Mann-Whitney U statistic	p
capelin	17.500	0.797
Arctic cod	8.000	0.165
crustaceans	13.000	0.543
Fish doctor	12.000	0.296
Daubed shanny	24.500	0.140
sandlance	24.500	0.140
sculpins	25.000	0.118
Arctic shanny	14.000	0.480
squid	18.500	0.514

Table 2.5. Comparison of individual prey distributions (capelin, cod, others) to the grouped prey distribution of other birds in the individual preference sample (n = 12).

	1998-2000	
Band no.	χ^2	p
01001	0.601	0.741
02110	1.379	0.502
04128	1.544	0.462
07237	4.697	0.095
09445	10.457	0.005*
10277	2.156	0.340
52526	2.053	0.358
54043	44.834	0.000*
54150	0.104	0.950
59567	20.739	0.000*
62573	4.613	0.100
62574	6.378	0.041*

Table 2.6. Results of ANOVA on groupings determined by k-means cluster analysis of individual prey proportions, for the individual preference sample, when maximum number of

k-means cluster ANOVA results for 12 selected individuals by prey type: groups = 4

factor	Between Groups SS	df	Within Groups SS	df	F	p
Capelin	0.153	3	0.026	8	15.640	0.001*
Cod	0.180	3	0.069	8	6.920	0.013*
crustaceans	0.009	3	0.011	8	2.488	0.134
Gymnelus	0.006	3	0.031	8	0.503	0.690
Leptoclinus	0.022	3	0.045	8	1.309	0.337
Sandlance	0.005	3	0.020	8	0.615	0.624
sculpins	0.233	3	0.041	8	15.117	0.001*

groups = 4.

Table 2.7. Individual yearly (1998, 1999, 2000) prey percentages for each bird in the individual preference sample (n=12), compared to average yearly percentages for the sample.

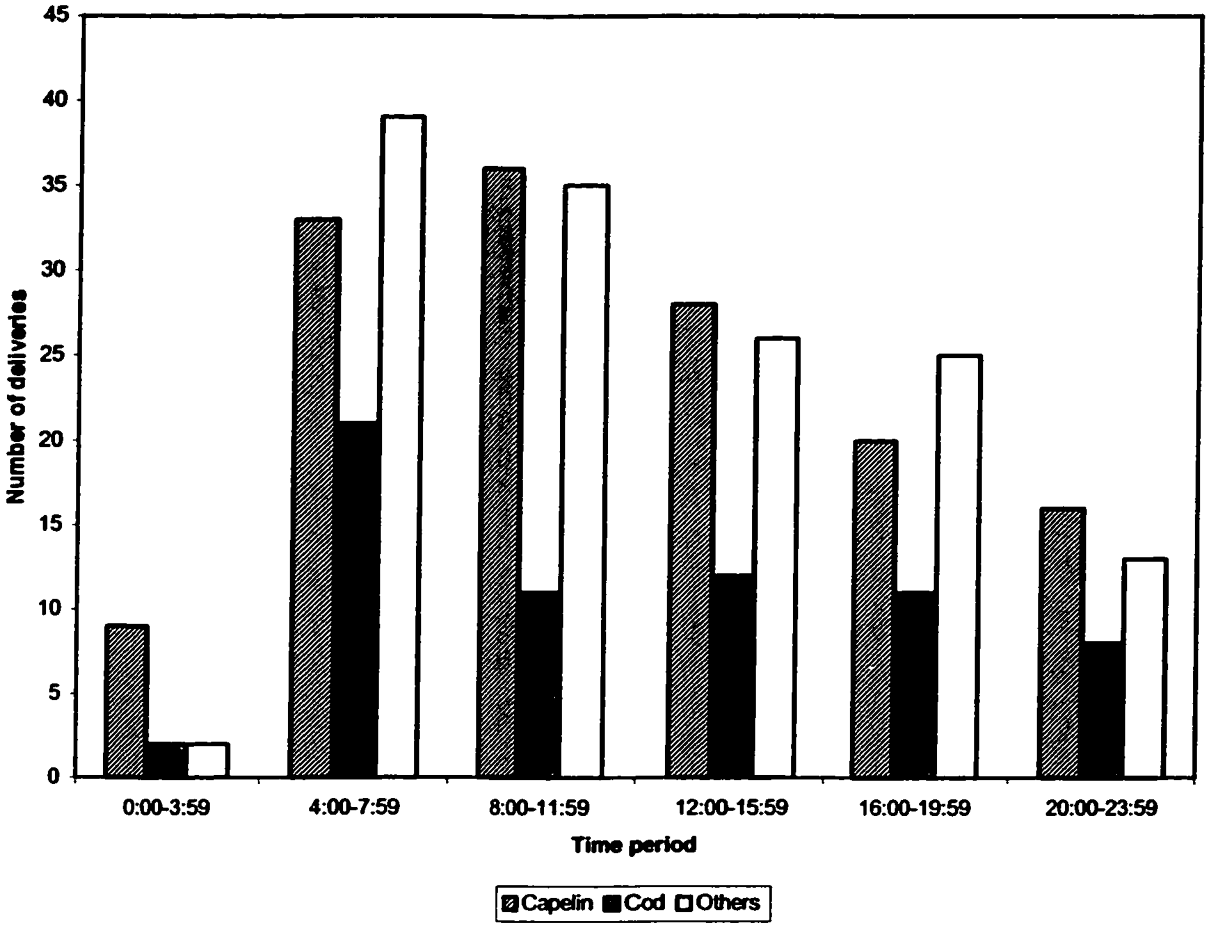
	Average prey proportions per bird for Individual preference sample (n = 12)		
Prey type	1998	1999	2000
Capelin	36.20	31.45	50.31
Arctic cod	18.55	29.42	12.64
crustaceans	1.89	1.88	2.78
Fish doctor	1.67	2.78	0.00
Daubed shanny	13.23	5.95	0.32
sandlance	9.61	7.80	27.34
sculpins	17.87	18.85	5.97
Arctic shanny	0.98	0.83	0.00
squid	0.00	1.04	0.64
Individual i.d. #	Proportion of deliveries by prey type for individual birds		
Prey type	1998	1999	2000
01001			
Capelin	50.00	40.00	33.33
Arctic cod	37.50	20.00	0.00
crustaceans	0.00	10.00	0.00
Fish doctor	0.00	0.00	0.00
Daubed shanny	12.50	0.00	0.00
sandlance	0.00	10.00	66.67
sculpins	0.00	10.00	0.00
Arctic shanny	0.00	0.00	0.00
squid	0.00	10.00	0.00
02110			
Capelin	0.00	0.00	100.00
Arctic cod	50.00	20.00	0.00
crustaceans	0.00	0.00	0.00
Fish doctor	0.00	0.00	0.00
Daubed shanny	0.00	0.00	0.00
sandlance	50.00	0.00	0.00
sculpins	0.00	80.00	0.00
Arctic shanny	0.00	0.00	0.00
squid	0.00	0.00	0.00
04128			
Capelin	45.00	0.00	66.67
Arctic cod	10.00	41.67	0.00
crustaceans	5.00	0.00	33.33
Fish doctor	20.00	25.00	0.00
Daubed shanny	5.00	0.00	0.00
sandlance	10.00	25.00	0.00
sculpins	5.00	8.33	0.00
Arctic shanny	0.00	0.00	0.00
squid	0.00	0.00	0.00

Individual i.d. #	Proportion of deliveries by prey type for individual birds		
Prey type	1998	1999	2000
07237			
Capelin	30.00	30.00	50.00
Arctic cod	30.00	50.00	16.67
crustaceans	0.00	0.00	0.00
Fish doctor	0.00	0.00	0.00
Daubed shanny	10.00	0.00	0.00
sandlance	10.00	10.00	16.67
sculpins	20.00	10.00	16.67
Arctic shanny	0.00	0.00	0.00
squid	0.00	0.00	0.00
09445			
Capelin	0.00	31.25	25.00
Arctic cod	0.00	0.00	25.00
crustaceans	0.00	0.00	0.00
Fish doctor	0.00	0.00	0.00
Daubed shanny	0.00	12.50	0.00
sandlance	0.00	25.00	25.00
sculpins	100.00	31.25	25.00
Arctic shanny	0.00	0.00	0.00
squid	0.00	0.00	0.00
10277			
Capelin	29.41	30.00	100.00
Arctic cod	23.53	40.00	0.00
crustaceans	17.65	10.00	0.00
Fish doctor	0.00	0.00	0.00
Daubed shanny	11.76	0.00	0.00
sandlance	5.88	10.00	0.00
sculpins	0.00	0.00	0.00
Arctic shanny	11.76	10.00	0.00
squid	0.00	0.00	0.00
52526			
Capelin	27.27	22.22	30.00
Arctic cod	27.27	11.11	30.00
crustaceans	0.00	0.00	0.00
Fish doctor	0.00	0.00	0.00
Daubed shanny	18.18	22.22	0.00
sandlance	0.00	11.11	10.00
sculpins	27.27	33.33	30.00
Arctic shanny	0.00	0.00	0.00
squid	0.00	0.00	0.00

Individual i.d. #	Proportion of deliveries by prey type for individual birds		
Prey type	1998	1999	2000
54043			
Capelin	64.86	65.00	65.38
Arctic cod	0.00	2.50	3.85
crustaceans	0.00	2.50	0.00
Fish doctor	0.00	0.00	0.00
Daubed shanny	27.03	20.00	3.85
sandlance	2.70	2.50	19.23
sculpins	5.41	5.00	0.00
Arctic shanny	0.00	0.00	0.00
squid	0.00	2.50	7.69
54150			
Capelin	42.86	100.00	33.33
Arctic cod	14.29	0.00	33.33
crustaceans	0.00	0.00	0.00
Fish doctor	0.00	0.00	0.00
Daubed shanny	14.29	0.00	0.00
sandlance	14.29	0.00	33.33
sculpins	14.29	0.00	0.00
Arctic shanny	0.00	0.00	0.00
squid	0.00	0.00	0.00
59567			
Capelin	100.00	22.22	57.14
Arctic cod	0.00	77.78	28.57
crustaceans	0.00	0.00	0.00
Fish doctor	0.00	0.00	0.00
Daubed shanny	0.00	0.00	0.00
sandlance	0.00	0.00	14.29
sculpins	0.00	0.00	0.00
Arctic shanny	0.00	0.00	0.00
squid	0.00	0.00	0.00
62573			
Capelin	25.00	20.00	0.00
Arctic cod	0.00	40.00	0.00
crustaceans	0.00	0.00	0.00
Fish doctor	0.00	0.00	0.00
Daubed shanny	50.00	0.00	0.00
sandlance	12.50	0.00	100.00
sculpins	12.50	40.00	0.00
Arctic shanny	0.00	0.00	0.00
squid	0.00	0.00	0.00

Individual i.d. # Prey type	Proportion of deliveries by prey type for individual birds 1998	 1999	 2000
62574			
Capelin	20.00	16.67	42.86
Arctic cod	30.00	50.00	14.29
crustaceans	0.00	0.00	0.00
Fish doctor	0.00	8.33	0.00
Daubed shanny	10.00	16.67	0.00
sandlance	10.00	0.00	42.86
sculpins	30.00	8.33	0.00
Arctic shanny	0.00	0.00	0.00
squid	0.00	0.00	0.00

Figure 2.1. Distribution of prey types (capelin, cod, others) delivered to chicks in relation to time of day. ($\chi^2 = 7.46$, df = 10, p = 0.682).



45
40
35
30
25
20
15
10
5
0
Number of deliveries
0:00-3:59
4:00-7:59
8:00-11:59
12:00-15:59
16:00-19:59
20:00-23:59
Time period
▨ Capelin ■ Cod □ Others

Figure 2.2. Hierarchical tree classification of birds (n = 12) based on individual proportions of prey types, using Ward's method. Prey classes of *Stichaeus punctatus* and squid were not used in the grouping scheme.

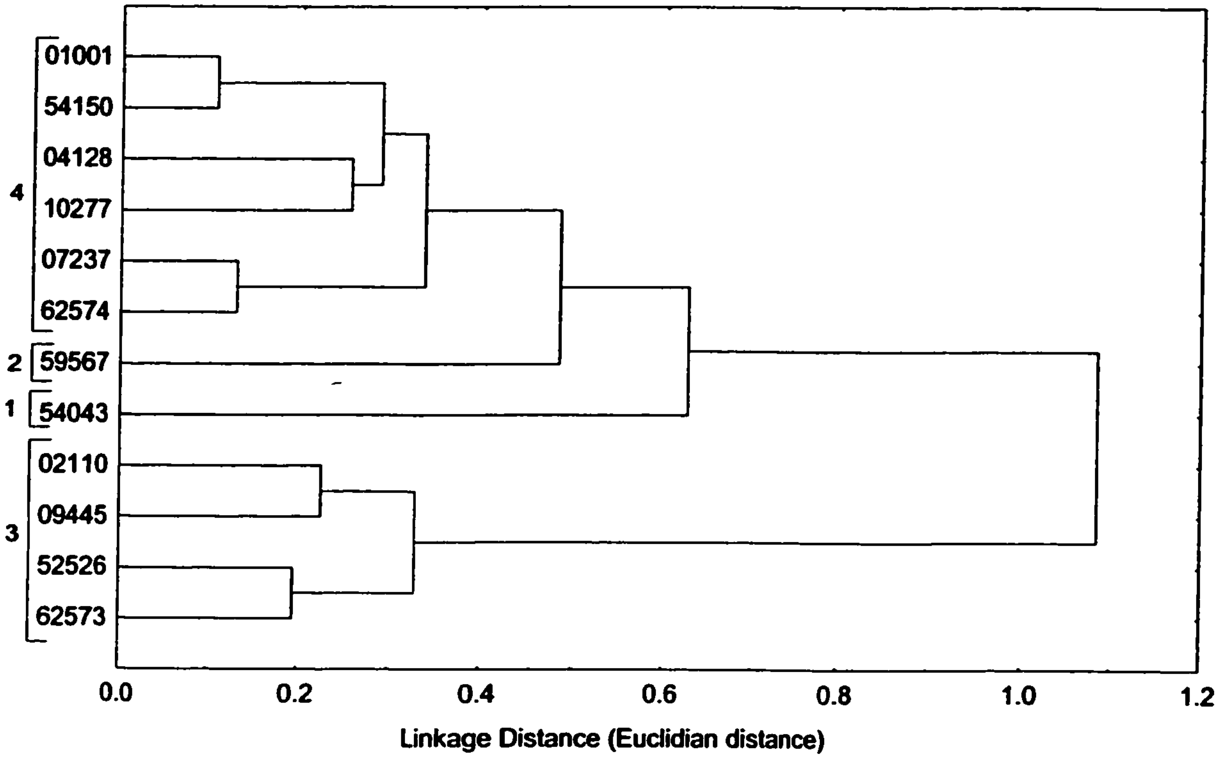

4
01001
54150
04128
10277
07237
62574
2
59567
1
54043
3
02110
09445
52526
62573
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Linkage Distance (Euclidian distance)

Figure 2.3. Hierarchical tree classification of prey types (excluding *Stichaeus punctatus* and squid) based on individual percentage compositions, using Ward's method.

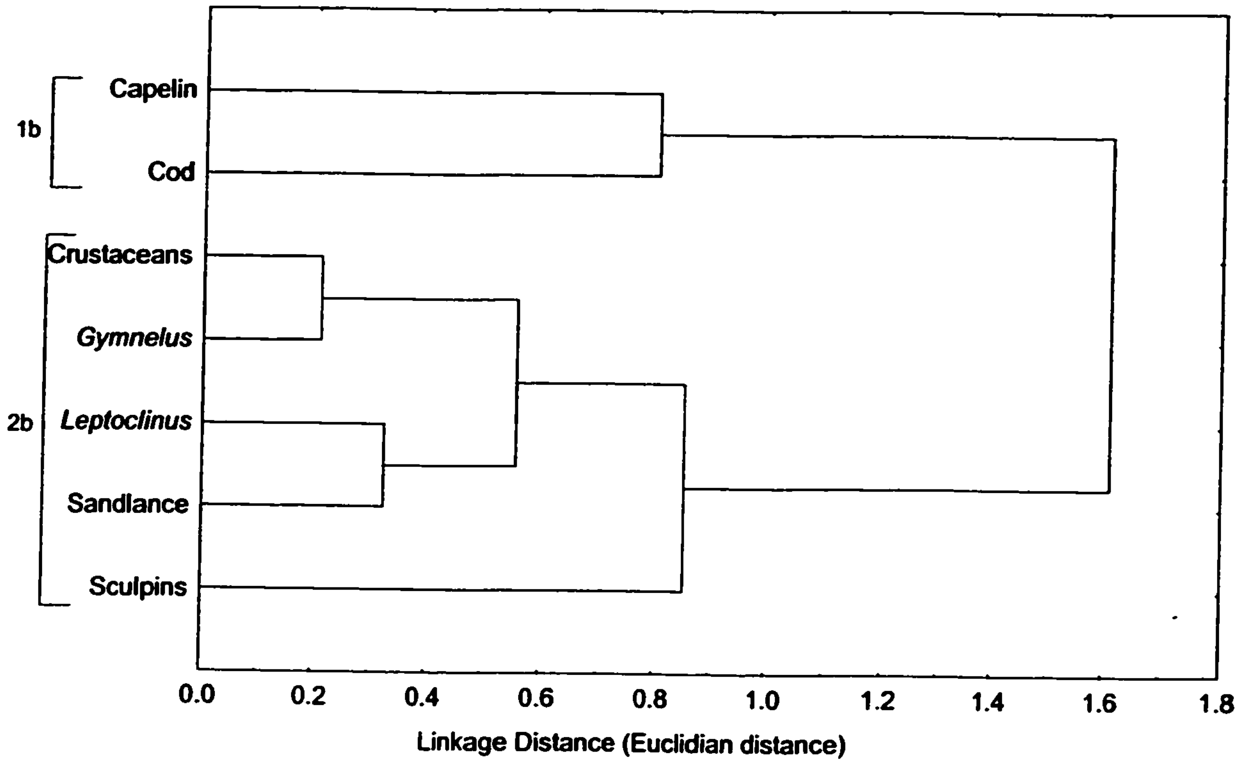
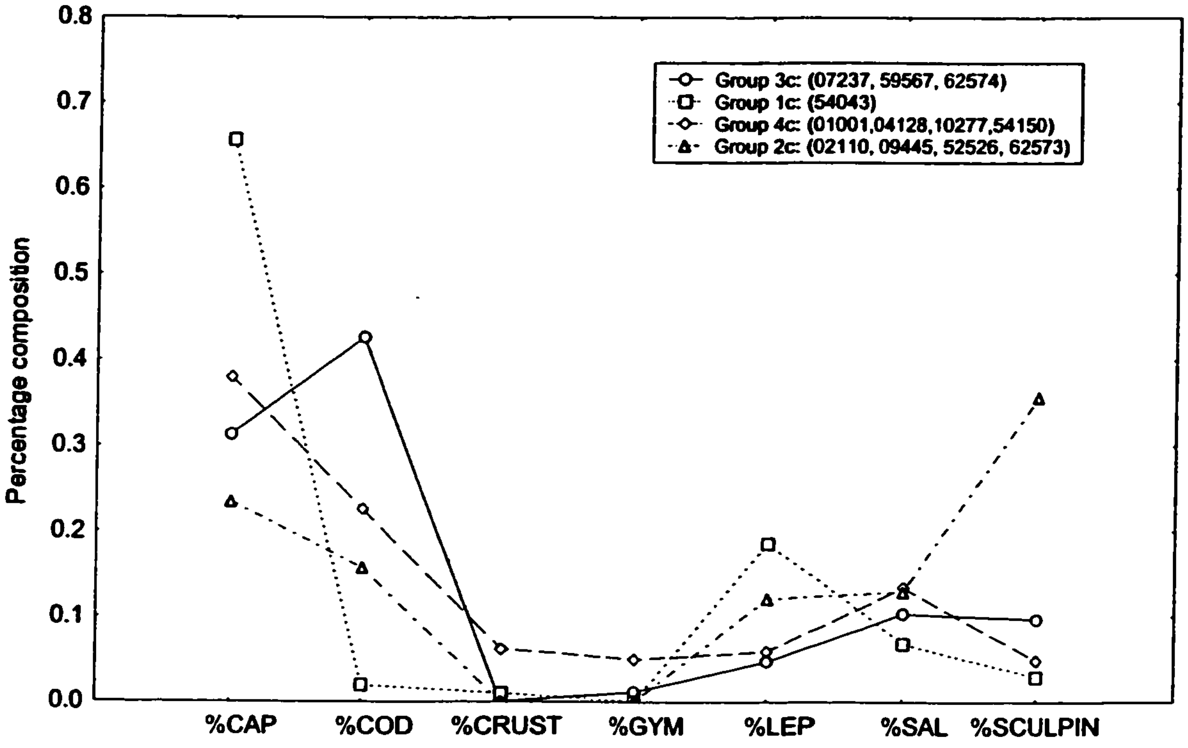

1b
Capelin
Cod
2b
Crustaceans
Gymnelus
Leptoclinus
Sandlance
Sculpins
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
Linkage Distance (Euclidian distance)

Figure 2.4. Group means of prey percentage contributions to each of four clusters as determined from k-means clustering analysis. Prey types *Stichaeus punctatus* and squid were excluded from analysis.


0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Percentage composition
Group 3c: (07237, 59567, 62574)
Group 1c: (54043)
Group 4c: (01001,04128,10277,54150)
Group 2c: (02110, 09445, 52526, 62573)
%CAP
%COD
%CRUST
%GYM
%LEP
%SAL
%SCULPIN

4. General Discussion

In this thesis I have attempted to provide insight into patterns of foraging behaviour and prey choice of adult Thick-billed Murres provisioning for nestlings. Results have been related to the ecology of prey species in the area of Hudson Bay surrounding the colony. The use of traditional observational techniques at the breeding site coupled with recently developed devices to quantify behaviour of birds while away from the colony allowed me to describe patterns of Thick-billed Murre behaviour which have been difficult to access until now. I have also attempted to provide information on the ecology, abundance and distribution of the fishes and invertebrates in an area of Hudson Bay, for which there is currently little known.

The use of electronic data recorders allowed me to describe dive patterns and travel activity. Although Thick-billed Murres have been known to dive to depths of over 200m (Croll et al. 1992), results from the current study suggest much shallower average dive depths of between 32.7 – 42.9m. These are in close agreement with other recent reports of murre dive depths using the same devices (Falk et al. 2000). However, I have shown that patterns of dive behaviour change when adults are foraging for themselves compared to when they take items for delivery to their chicks. Dives associated with self-feeding (the majority of dives) are significantly less deep than those dives associated with capture of prey items for transport to the colony (last dive before the return trip). It appears that foraging adults make a higher number of shallower dives to acquire resources for themselves, while expending extra effort when going after items for their nestlings. Under the assumption that diving is an energetically costly behaviour, these results agree with principles of energy maximisation and central place foraging theory. When individuals are not required to transport prey they can afford to conduct several shallow dives for smaller prey items which they can consume on the spot. As trips to and from the colony to provision chicks require expenditure of extra energy, birds actively undertake deeper dives (which may reflect an increase in search time) to capture larger (higher energy) prey items for nestling development.

Comparison of the size of prey items delivered to chicks in relation to distance of return flights provided further support for the predictions of central place foraging theory made by Orians and Pearson (1979). Mass of prey items delivered to nestlings were positively related to the distances from which they were transported, suggesting that individuals attempt to maximise energy returns to their chicks when foraging away from the colony. These results provide support for the application of theoretical models to predict observed patterns of behaviour for Thick-billed Murres.

Estimates of foraging ranges indicated that most birds fed within 100km of the colony. Overall, foraging ranges from Coats Island appeared to be smaller than those observed at other, larger colonies (Gaston et al. 1985c; Benvenuti et al. 1998). This suggests that food supply in the vicinity of the Coats Island colony may be more abundant than in the vicinity of larger colonies. This observation supports the suggestion of Gaston (1985a) and Gaston (1985b) that large colonies tend to deplete local food supplies, making it necessary for birds to fly further to feed.

Despite the fact that food resources do not appear to limit nestling development and population growth at the study site, associations of travel distances with prey species indicate apparent differences in patterns of distribution for these items. Arctic cod, a major component of nestling diets, which represents a significant proportion of feeds in both number and average mass, was associated with distances of greater than 25km from the colony. Capelin, which also compose a significant proportion of deliveries, were located mostly within 25km of the colony. Since both prey items were common in nestling diets these differences indicate that individuals may actively employ different patterns of behaviour and frequent different areas when foraging for prey. Associations of distance with prey types also provided evidence for possible cases of local prey depletion in the vicinity of the colony. There was an absence of benthic, mostly sedentary prey types such as zoarcoids among fish brought back from close to the colony. There was also a lack of sandlance (which is associated with sandy sea floors) nearby. These results suggest that certain prey types may have been reduced in areas close to the colony because of increased foraging pressure from a growing colony (although historical distributions of these species are lacking).

In addition to indications of local distribution of prey species in the vicinity of the colony, my results were able to contribute information on the general biology of some of the fish species in the area. Associations of prey species with dive depths provided a general picture of the vertical distribution of these organisms within the water column. Pelagic fish species such as cod and capelin were associated with a range of intermediate depths (21 – 60m), while zoarcoids and sculpins were located at deeper depths (average >40m). When coupled with bathymetric information of areas surrounding Coats Island, these results can provide further information on the distribution of species. The shallow depths at which sandlance were associated (<40m) may reflect their distribution along the narrow shelf that surrounds the island, while other benthic species (zoarcoids and sculpins) may be further offshore.

Trends in species composition of nestling diets presumably provide an indication of overall patterns in prey abundance and availability. Overall percentage composition, indicate the importance of cod and capelin as a persistent component of nestling diets. A sharp decline in the amount of cod fed to chicks in recent years was coupled with an increase in the occurrence of capelin in the diet. A decline in sculpins was also evident, while numbers of sandlance appear to be increasing. As there are no independent methods of sampling available in the vicinity of the colony, the birds provide the only tool with which to assess changes in prey populations. The changes in occurrence of specific species in the nestling diet may be an indication of changes taking place in this area due to the effects of climate change (Hansell et al. 1997). Studies by Stirling et al. (1999) have associated significant declines in the condition of adult polar bears in western Hudson Bay since 1981 with earlier timing of land-fast ice break-up, linked to a general warming trend in regional air temperatures. Continued monitoring of diet trends in association with environmental variables are required to determine if these changes are related.

The collection of diet information over a number of years allowed for the identification of groups of prey specialists within the population. This is an area of seabird foraging behaviour which has rarely been addressed, mostly because large data sets are required to detect these trends. Though a large proportion of birds appear to be generalist foragers, including a constant variety of prey items in their deliveries, other groups and individuals stand out as significantly different from average observed prey proportions. In particular, a group of sculpin specialists were identified in the sample as well as at least one individual which concentrated on the rarely seen *Leptoclinus maculatus*. Inspection of inter-year tendencies showed that some specialisations persisted between years, although there were also some cases of birds which exhibited intermittent or seasonal specialisation. When patterns of specialisation were examined with respect to information gathered on the distribution of prey species, it appears that these patterns may reflect differences in where individuals chose to forage.

Some birds who included mostly capelin and cod in their deliveries also included sandlance and sculpins. While capelin was represented widely throughout the foraging range, sculpins were associated most commonly with distances of less than 50 km with both sandlance and cod taken from distances beyond 50 km. This apparent lack of association between patterns of prey distribution and prey composition of specialist groupings suggest that specialisations may arise from distinct differences in behavioural patterns rather than from purely opportunistic encounters. Determinations of exactly where individuals were going to forage could only be crudely estimated from the current data: more precise methods of tracking individuals need to be applied to fully distinguish between trends in specialisation due to differences in foraging locations, search effort or handling proficiency.

Identification and understanding of trends in prey specialisation within a population are important when interpreting such information in relation to conditions of the local environment. When independent measures of prey species abundance are not available, knowledge of how individuals sample from their environment and their impact on overall trend analyses must be considered.

Throughout most of the analyses conducted in this research comparisons were made between sexes. No differences due to sex were detected in the data set with regards to any areas of Thick-billed Murre foraging behaviour while provisioning chicks. Significant differences were not detectable in dive depth, travel distance or prey choices between males and females. Differences dive depths were identified between males and females when dives were pooled over all categories (self-feeding and chick provisioning, unpubl. data), but these differences disappeared when considering only foraging behaviour related to chick rearing. This suggests that the increased stress involved in raising a chick affects both males and females in a similar manner with regards to provisioning, as both appear to adopt similar patterns of behaviour.

While many aspects of Thick-billed Murre biology and behaviour have been previously examined, there is still much to be known. I have been able collect and analyse data that provide information on patterns of behaviour which have been difficult to address hitherto. Analyses of a long term data set coupled with recent technological advances in remote data loggers have allowed me to quantify previously unknown behavioural patterns. Improving the understanding of bird behaviour in relation to local ecological conditions is important when using these animals as natural sampling tools and is key when interpreting results about their marine environments.

Findings of the studies included in this thesis have made significant contributions to extending the knowledge of Thick-billed Murre foraging patterns as well as providing information on the ecology of fish species in an area of Hudson Bay which is currently lacking.

Results discussed here may provide the basis for more detailed investigations of individual foraging behaviour, possibly with the development and miniaturisation of satellite tracking equipment to provide answers to questions which I was not able to fully address, such as exact locations of foraging birds. The relevance of the use of seabirds as indicators of their local marine environments, has been considered in relation to individual behaviour. With knowledge of how individuals can affect interpretation of prey trends observed at the colony, I believe that seabirds, such as Thick-billed Murres, will continue to be useful tools in the assessment of changes in marine environments. This is will be increasingly important in tracking long term effects in the face of global climate changes and increasing human pressure on our marine ecosystems.

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5. List of Appendices

5.1. Appendix 1.

Details of timing and duration of observational feeding watches (FW) at Coats Island, Nunavut from 1994 – 2000.

Year	Watch	Date	Duration
1994	FW1	July 27, 28	48hrs
	FW2	Aug. 5, 6	48hrs
1995	FW1	July 29	24hrs
	FW2	Aug. 8, 9	48hrs
	FW3	Aug. 14	24hrs
1996	FW1	July 27	24hrs
	FW2	Aug. 2	24hrs
	FW3	Aug. 8	24hrs
	FW4	Aug. 14	24hrs
1997	FW1	July 23	24hrs
	FW2	July 29	24hrs
	FW3	Aug. 4	24hrs
	FW4	Aug. 9	24hrs
1998	FW1	July 28, 29, 30	72hrs
	FW2	Aug. 4, 5, 6	72hrs
	FW3-1	Aug. 11	24hrs
	FW3-2	Aug. 13	24hrs
1999	FW1	July 28, 29, 30	72hrs
	FW2	Aug. 7, 8, 9	72hrs
	FW3	Aug. 12, 13, 14	72hrs
2000	FW1	July 30, 31	48hrs
	FW2	Aug. 8, 9, 10	72hrs

5.2. Appendix 2.

Genetic sexing of Thick-billed Murres:

In birds, females are the heterogametic sex, and carry ZW sex chromosomes, while males carry ZZ chromosomes. Efforts to sex birds genetically have involved targeting non-specific regions of nuclear DNA (e.g. using microsatellites; Longmire et al. 1993) or targeting regions within the sex chromosomes (e.g. Ellegren 1996, Griffiths et al. 1998). The regions targeted following techniques by Griffiths et al. (1998) are two homologous introns (non-coding segments) found within the CHD (Chromo-Helicase-DNA binding genes) coding regions of the W and Z chromosomes of birds. The introns differ in size in the W and Z chromosomes allowing discrimination of males and females. The technique involves amplification of the intron regions using specific primers (which bind to conserved regions within CHD, and are thus universal for most non-ratite birds sampled to date), amplification of the introns by the PCR (polymerase chain-reaction), electrophoresis through agarose gels, and visualization by staining. Using this technique, males are identified by having a single band (the product from the W chromosome) while females have two bands (the product from the W and Z chromosomes).

The following section outlines the protocol from Griffiths et al. (1998) optimized for sexing Thick-billed Murres (*Uria lomvia*). Some recipes for reagents were obtained from Dr. Rick Lanctot, Biological Resources Division, U.S. Geological Survey at Anchorage, Alaska.

5.2.1. Laboratory techniques

5.2.1.1. Extractions. DNA was extracted from blood of murres, following standard phenol/chloroform protocols (overnight digestion at 55°C in lysis buffer consisting of 0.1 M Tris-Cl pH 8.0, 0.01 M EDTA pH 8.0, 0.1 M NaCl, 0.1% SDS, and 0.134 to 0.267 mg/mL proteinase

K in a total volume of 750 µl; DNA was then extracted two times with phenol, once with 24:1 chloroform to isoamyl alcohol). DNA was then precipitated by addition of one-tenth the volume of 2.5 M NaAc and an equal volume of cold isopropanol. The DNA was looped out with a melted glass pipette, air-dried for 2-3 min., and resuspended in 50 µl ddH_20.

5.2.1.2. PCR conditions. A buffer was made to be used in the PCR (PCR buffer #2; R. Lanctot, unpublished) consisting of 0.1 M Tris-HCl pH 8.3, 15 mM $MgCl_2$, 0.5 M KCl, 0.1% gelatin solution, 0.1% IGEPAL solution, and 0.1% Triton X-100 solution, in a final volume of 1 mL. Reaction volumes were 4.8 µl ddH_20, 2 µl PCR buffer #2, 0.167 mM dNTP mix, 0.83 M primer CHD-P8, 0.83 M primer CHD-P2, 0.083 U Taq polymerase, and 2 µl of DNA diluted to 1:10 DNA to ddH_2O (typically 50 or more ng), in a final volume of 12 µl. (Primer sequences from Griffiths et al. 1998). The PCR mix was overlaid with oil. The PCR cycle was conducted as follows: initial denaturation for 1 min 30 sec at 94°C , 30 cycles of denaturation for 30 sec at 94°C, annealing for 45 sec at 54 °C, and extending for 45 sec at 72 °C, and a final extension of 2 min at 72 °C.

5.2.1.3. Gel electrophoresis. Prior to electrophoresis, 7.5 µl of bromophenol blue tracking dye were added to each product (50% glycerol, 5X TA buffer, trace of bromophenol blue powder). PCR products were visualized by electrophoresis through a 3% agarose gel (4.5 g agarose in 150 mls 1X TA buffer) previously stained with 7.5 µl GelStar (Mandel Scientific) or 4.5 µl ethidium bromide. Electrophoresis was conducted for approximately 3 hr 30 min at 100 V.

5.2.2. References

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5.3. Appendix 3.

Prey totals for birds included in the Individual preference sample

Band #	observed				
Prey type	1998	1999	2000	Individual total	sample total of all other birds
01001					
Capelin	4	4	1	9	133
Arctic cod	3	2	0	5	60
crustaceans	0	1	0	1	7
Fish doctor	0	0	0	0	8
Daubed shanny	1	0	0	1	37
sandlance	0	1	2	3	34
sculpins	0	1	0	1	41
Arctic shanny	0	0	0	0	3
squid	0	1	0	1	3
others	1	4	2	7	133
02110					
Capelin	0	0	2	2	140
Arctic cod	1	1	0	2	63
crustaceans	0	0	0	0	8
Fish doctor	0	0	0	0	8
Daubed shanny	0	0	0	0	38
sandlance	1	0	0	1	36
sculpins	0	4	0	4	38
Arctic shanny	0	0	0	0	3
squid	0	0	0	0	4
others	1	4	0	5	135
04128					
Capelin	9	0	2	11	131
Arctic cod	2	5	0	7	58
crustaceans	1	0	1	2	6
Fish doctor	4	3	0	7	1
Daubed shanny	1	0	0	1	37
sandlance	2	3	0	5	32
sculpins	1	1	0	2	40
Arctic shanny	0	0	0	0	3
squid	0	0	0	0	4
others	9	7	1	17	123

Band # Prey type	observed				
	1998	1999	2000	Individual total	sample total of all other birds
07237					
Capelin	3	3	3	9	133
Arctic cod	3	5	1	9	56
crustaceans	0	0	0	0	8
Fish doctor	0	0	0	0	8
Daubed shanny	1	0	0	1	37
sandlance	1	1	1	3	34
sculpins	2	1	1	4	38
Arctic shanny	0	0	0	0	3
squid	0	0	0	0	4
others	4	2	2	8	132
09445					
Capelin	0	5	1	6	136
Arctic cod	0	0	1	1	64
crustaceans	0	0	0	0	8
Fish doctor	0	0	0	0	8
Daubed shanny	0	2	0	2	36
sandlance	0	4	1	5	32
sculpins	4	5	1	10	32
Arctic shanny	0	0	0	0	3
squid	0	0	0	0	4
others	4	11	2	17	123
10277					
Capelin	5	3	1	9	133
Arctic cod	4	4	0	8	57
crustaceans	3	1	0	4	4
Fish doctor	0	0	0	0	8
Daubed shanny	2	0	0	2	36
sandlance	1	1	0	2	35
sculpins	0	0	0	0	42
Arctic shanny	2	1	0	3	0
squid	0	0	0	0	4
others	8	3	0	11	129

Band # Prey type	observed 1998	 1999	 2000	 Individual total	sample total of all other birds
52526					
Capelin	3	2	3	8	134
Arctic cod	3	1	3	7	58
crustaceans	0	0	0	0	8
Fish doctor	0	0	0	0	8
Daubed shanny	2	2	0	4	34
sandlance	0	1	1	2	35
sculpins	3	3	3	9	33
Arctic shanny	0	0	0	0	3
squid	0	0	0	0	4
others	5	6	4	15	125
54043					
Capelin	24	26	17	67	75
Arctic cod	0	1	1	2	63
crustaceans	0	1	0	1	7
Fish doctor	0	0	0	0	8
Daubed shanny	10	8	1	19	19
sandlance	1	1	5	7	30
sculpins	2	2	0	4	39
Arctic shanny	0	0	0	0	3
squid	0	1	2	3	1
others	13	13	8	34	107
54150					
Capelin	3	1	1	5	137
Arctic cod	1	0	1	2	63
crustaceans	0	0	0	0	8
Fish doctor	0	0	0	0	8
Daubed shanny	1	0	0	1	37
sandlance	1	0	1	2	35
sculpins	1	0	0	1	41
Arctic shanny	0	0	0	0	3
squid	0	0	0	0	4
others	3	0	1	4	136

	observed				
Band # Prey type	1998	1999	2000	Individual total	sample total of all other birds
59567					
Capelin	0	2	4	6	136
Arctic cod	1	7	2	10	55
crustaceans	0	0	0	0	8
Fish doctor	0	0	0	0	8
Daubed shanny	0	0	0	0	38
sandlance	0	0	1	1	36
sculpins	0	0	0	0	42
Arctic shanny	0	0	0	0	3
squid	0	0	0	0	4
others	0	0	1	1	139
62573					
Capelin	2	1	0	3	139
Arctic cod	0	2	0	2	63
crustaceans	0	0	0	0	8
Fish doctor	0	0	0	0	8
Daubed shanny	4	0	0	4	34
sandlance	1	0	1	2	35
sculpins	1	2	0	3	38
Arctic shanny	0	0	0	0	3
squid	0	0	0	0	4
others	6	2	1	9	130
62574					
Capelin	2	2	3	7	135
Arctic cod	3	6	1	10	55
crustaceans	0	0	0	0	8
Fish doctor	0	1	0	1	7
Daubed shanny	1	2	0	3	35
sandlance	1	0	3	4	33
sculpins	3	1	0	4	38
Arctic shanny	0	0	0	0	3
squid	0	0	0	0	4
others	5	4	3	12	128