COMPARATIVE FORAGING ECOLOGY OF PARENTAL COMMON MURRES (URIA AALGE) AND ATLANTIC PUFFINS (FRATERCULA ARCTICA) IN RESPONSE TO CHANGES IN FORAGE FISH AVAILABILITY

CHANTELLE BURKE

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RESPONSE TO CHANGES IN FORAGE FISH AVAILABILITY

by

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ABSTRACT

To ensure successful reproduction, seabirds must make continuous and adaptive foraging decisions in the face of uncertain prey conditions. I compared the foraging behavior (foraging ranges and diet choices) of parental common murres and Atlantic puffins at a high density, offshore colony (Funk Island) during 2 years of different forage fish availability. In a poor food year (2005), characterized by an order of magnitude decline in forage fish densities and smaller fish, murres and puffins increased the mean distance they traveled to forage by 36% and preferentially selected larger fish. These responses show flexible foraging behavior, but significantly lighter murre fledglings in 2005 (203.0 ± 4.6 g) relative to 2004 (215.0 ± 3.9 g) suggests that specialized feeding on unpredictable prey can have consequences for reproductive success. Puffins that are generalist foragers and have multiple prey load capacity were more resilient to declines in prey availability.

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Chapter 1:   General Introduction

During breeding seabirds are central-place foragers that collect prey at sea and have the additional constraint to return to the colony to feed their chick (Orians and Pearson 1979). Ultimately during this time seabirds are limited by the availability of suitable prey around the colony that determines the amount of time and energy involved in capturing and transporting prey to their chick at the colony and finding enough food for self maintenance. When prey conditions deteriorate, seabirds may allocate more time to foraging and less time to resting in order to maintain normal provisioning rates and successfully rear their chicks (Burger and Piatt 1990; Harding et al. 2007). Seabirds may also opt to provision their offspring with alternative prey (Bryant et al. 1999; Ballie and Jones 2004; Abraham and Sydeman 2006), but this option is limited by nutritional requirements and the availability of suitable alternatives. How these foraging decisions take shape is determined by a wide range of factors including the individuals experience, physiology (e.g. body size; Piatt 1990), life history traits (e.g. clutch size; Stearns 1992; Litzow and Piatt 2003), colony location and size (Parrish et al. 1998), oceanographic setting (Montevecchi 2008) and the biological and behavioural characteristics of the exploited prey (Obst et al. 1995; Davoren et al. 2003). Understanding how these factors influence foraging behaviour is important for interpreting seabird responses to changes in prey availability.

In this thesis, I compare the foraging behaviour of two closely-related, pursuit-diving auks with different foraging capabilities and strategies, the Common Murre *Uria aalge* (hereafter murres) and the Atlantic Puffin *Fratercula arctica* (hereafter puffins), to

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gain insights into how species-specific constraints influence the foraging decisions of seabirds under different forage fish conditions (Montevecchi et al. 2006). I also discuss how colony-related constraints at a high-density, offshore colony (Funk Island) influence the foraging efficiency and reproductive success of these two seabirds.

1.1.   Study species and study site

Murres and puffins are the two most abundant auks in the Northwest Atlantic (Nettleship and Birkhead 1985). They are long-lived seabirds that lay single-egg clutches and typically breed in large colonies, often sharing breeding and foraging habitat throughout much of their range (Harris and Birkhead 1985; Figure 1.1). Murres chicks are provisioned by both parents for 21 days and depart the colony at approximately 25% of adult body mass, accompanied at sea by the male parent (Ainley et al. 2002; Harris and Birkhead 1985). Puffins chicks are provisioned by both parents for approximately 38-44 days and depart the colony at approximately 75% of adult body mass at which time they are independent at sea (Lowther et al. 2002; Harris and Birkhead 1985).

Both species are pursuit-divers that forage through the water column and in the Northwest Atlantic, murres and puffins rely heavily on capelin to provision their offspring (Brown and Nettleship 1984; Piatt 1987; Cairns et al. 1987; Davoren and Montevecchi 2003b; Rodway and Montevecchi 1996; Nettleship 1991). While the amount of capelin in puffin chick diets tends to be variable (Baille and Jones 2004; Davoren and Montevecchi 2003b; Russell 1998; Piatt 1987), murres in Newfoundland specialize on capelin with chick diets consisting almost exclusively of female capelin larger than 100 mm (Davoren

and Montevecchi 2003b). The designation of capelin specialist applied to murres in Newfoundland implies that they will select capelin over other prey that may be equally available. In contrast, puffins that are described as generalist foragers may exhibit a more opportunistic foraging strategy whereby the most accessible suitable prey will be selected, which may or may not be capelin.

Dietary differences between these seabirds may be related to physiological constraints associated with body size and prey loading that influence the range and depth over which each species can forage. Murres are larger than puffins (murres = ~1000 g and puffins = ~ 400-450 g; Ainley et al. 2002; Lowther et al. 2002), and can dive deeper (maximum 180 m compared to maximum 60-70 m for puffins; Piatt and Nettleship 1985; Burger 1991) and consequently may have more prey options available to them. Moreover, flight costs are higher for murres that have a higher wing loading (2.06 g cm^{-2}; Spear and Ainley 1997) relative to puffins (1.34 g cm^{-2}; Livezey 1988) and as a result murres may be more discriminating in their diet choices. Finally as a single-prey loader, murres must optimize the value of a parental provisioning load by selecting a high-quality prey item when provisioning offspring. Puffins can carry multiple prey and have the option of selecting a single or a few large prey and/or many smaller ones. Ultimately these differences can determine the breeding success (or not) of these seabirds during large-scale fluctuations in prey availability.

This study was conducted at the Funk Island Ecological Reserve (49°45'N, 53°11'W; Figure 1.1). This colony is unique from others in the Northwest Atlantic in terms of its offshore location (60 km off the northeast coast of Newfoundland). Consequently, the foraging commutes for murres and puffins tend to be longer at Funk

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Island especially since capelin (*Mallotus villosus*) have a primarily coastal distribution during the summer in Newfoundland when they migrate inshore to spawn (Templeman 1948, Nakashima and Wheeler 2002, Davoren et al. 2006). This is potentially a significant limitation for murres and puffins at Funk Island. These seabirds are notoriously poor flyers due to a wing design that is a compromise between underwater and aerial flight (Pennycuick 1987; Burger, 1991) and expend significant energy during flight (Birt-Friesen et al. 1989). Davoren and Montevecchi (2003a) hypothesised that longer foraging trips contribute to the low provisioning rates and poor condition of murre offspring at Funk Island relative to other colonies; with some exceptions in extreme poor food years (e.g. Uttely et al. 1994). Furthermore, murre offspring at Funk Island exhibited a decline in condition over the 1990s (Davoren and Montevecchi 2003b) associated with changes in capelin availability, while murres at other smaller, inshore colonies showed no signs of reproductive stress under similar prey declines (Bryant et al. 1999; Wilhelm and Storey 2004). Similarly for puffins, the proportion of larval fish and invertebrates (low nutritional value) in prey loads at Funk Island was consistently higher in comparison to those at an inshore colony adjacent to Funk Island (James Island) where mature capelin dominated chick diets (1992-1995; Russell 1998).
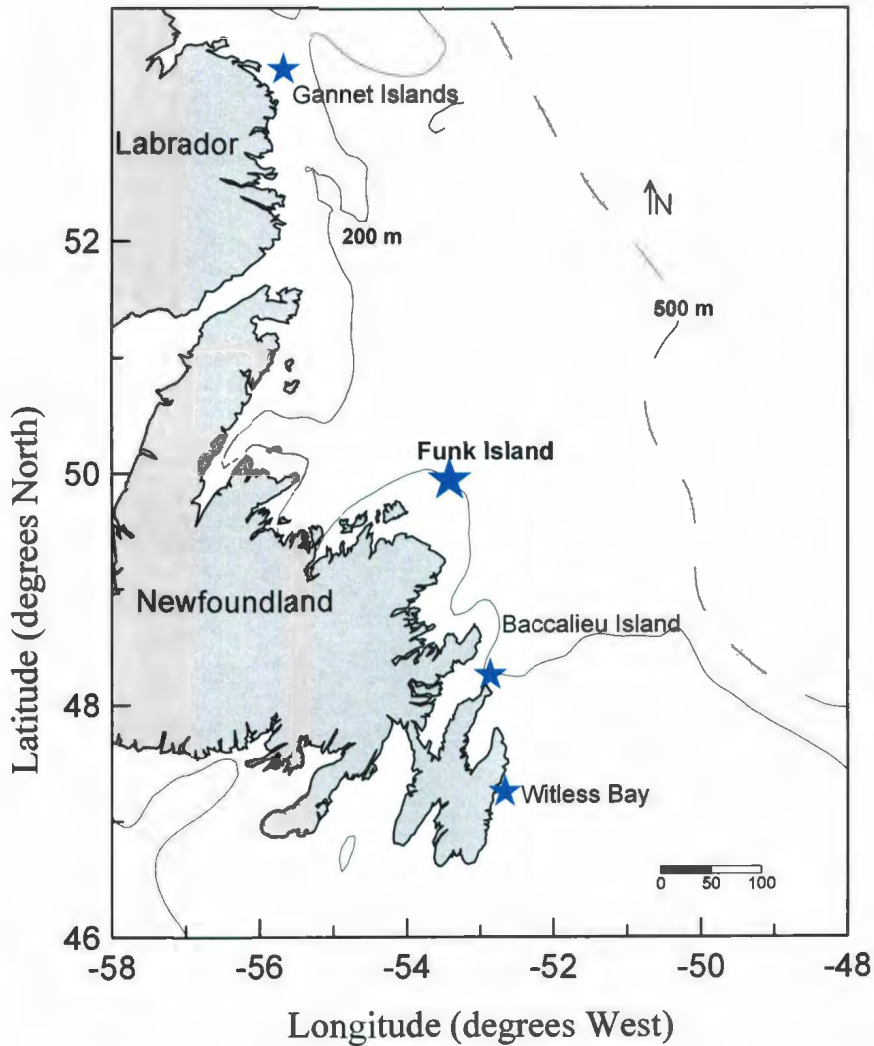
Figure. 1.1. Map of the Northwest Atlantic showing the Funk Island Seabird Ecological Reserve located off the northeast coast of Newfoundland as well as three other colonies where Common Murres and Atlantic Puffins share breeding habitat. The 500 m (dashed line) and 200 m (solid line) depth contours are shown. Scale bar (km).

1.2.   Seabirds and forage fish in the NW Atlantic

Forage fish play pivotal roles in marine food webs by creating major avenues of energy transfer between lower and upper trophic levels and supporting large vertebrate predators (Lavigne 1996; Springer and Speckman 1997). Oceanographic and fishing perturbations (and their interactions) often induce major shifts in forage species abundance and in turn alter food web dynamics in profound and unpredictable ways (Benson and Trites 2002; Chavez et al. 2003; Cury and Shannon 2004; Montevecchi et al. 2006).

Capelin are the focal forage fish of the Northwest Atlantic ecosystem and are the main prey of the large vertebrate food web including many species of seabirds, whales, seals and cod (Lavinge 1996; Montevecchi 2001). Capelin in the Northwest Atlantic have undergone dramatic shifts in their behaviour and biology since the early 1990s that have been linked to an unprecedented cold water perturbation in 1991 (Drinkwater 1996). Changes included reduced somatic body condition (Carscadden and Frank 2002), reduced size and younger age at spawning, and delayed (by one month) and more protracted spawning chronology (Carscadden and Nakashima 1997). In addition, shifts in the horizontal and vertical distributional of capelin have been observed including a shift southward and offshore (Miller and Lilly 1991) and a shift from high-density pelagic schools to low-density demersal schools (Mowbray 2002).

These changes have had consequences for the availability of capelin to seabirds during breeding as was evidenced in dietary shifts (gannets: Montevecchi and Myers 1996; murres: Bryant et al. 1999; puffins: Ballie and Jones 2003, 2004), delays in

breeding chronology (murres, puffins, kittiwakes: Hipfner et al. 2000; Davoren and Montevecchi 2003b) and declines in breeding success (kittiwakes: Regehr and Montevecchi 1997) and offspring condition (murres: Davoren and Montevecchi 2003b).

Overall, there is a high level of uncertainty about the mechanisms that are driving these changes in capelin availability and the potential consequences of these changes on the energetics and population dynamics of top marine predators (Davoren et al. 2007). This uncertainty is evident in the fact that water temperatures have been warming since the mid 1990s (Colbourne 2001) but capelin biology and behaviour has not returned to pre-perturbation levels. This thesis uses a multi-species approach in combination with independent and synoptic measurements of forage fish availability to develop a better understanding of the importance of capelin availability on the reproductive success of seabird predators in a dynamic marine ecosystem.

1.3.   Thesis objectives

The goal of my thesis is to examine the parental foraging decisions of murres and puffins in relation to forage fish availability during chick-rearing. My research addresses two important questions: 1) how do co-existing seabirds with different constraints respond to changes in forage fish availability during chick rearing, and 2) what are the reproductive consequences of changes in fish availability and the resulting behavioural responses by seabirds?

In chapter 2, I compared the chick diets of murres and puffins sampled over two years (2004-2005) at Funk Island. I quantified the composition of prey types and sizes in

the diets of each species and the degree of dietary overlap between the two species. Offspring condition, assessed as body weight (g) at a given wing length (mm), is compared between years and is related to diet. In Chapter 3, I described the availability of important forage fish in the diets of murre and puffin chicks and inter-annual changes in the foraging distances of provisioning adults to measure seabird responses to changes in prey availability. Estimates of forage fish availability were obtained from trawl surveys within the foraging ranges of murres and puffins from Funk Island. Differences in the distance that murres and puffins traveled to forage were estimated on the basis of observations of the locations of birds foraging at sea. I also assessed differences in the foraging locations of murres at sea by recording the direction of murres returning to the colony from foraging trips. Chapter 4 involved an integration of chick diets (chapter 2) and forage fish availability (chapter 3) data to assess the relative prey preferences and prey switching behaviour of murres and puffins during chick-rearing. This involved a comparison of the relative densities of two prey types in the environment with the relative proportion of two prey types in the diets. Prey switching behaviour was determined on the basis of whether or not prey preferences changed with changes in the relative densities of the prey.

The results of these studies provide an important comparison of how different seabird species cope with changes in forage fish availability. Findings are considered in the context of the NW Atlantic ecosystem and how seabirds are coping with ongoing changes in capelin availability.

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1.5.   Co-Authorship Statement

In the chapters of my thesis, my supervisor (Dr. WA Montevecchi) and committee members (Dr. Koen-Alonso and Dr. Anderson) assisted me in the generation of my research questions, the design of certain aspects of the colony and vessel studies and in determining suitable statistical analysis techniques. I was solely responsible for the collection and/or supervision of the colony data whereas assistance was provided for the vessel data from DFO personnel and research assistants hired to conduct seabird observations at seal. My committee assisted in the statistical analysis of the data where necessary, particularly in Chapter 4 where Dr. Koen-Alonso contributed significantly, but for the most part I was responsible for determining the appropriate statistical tests and executing the analysis. I was solely responsible for the writing of the manuscript and upon finalization of the completed manuscript; comments were obtained from my supervisor and committee members prior to submission to the School of Graduate Studies.

Chapter 2:   Fish and Chicks: Forage Fish and Chick Success in Co-existing Auks

2.1   Abstract

I compared the composition and overlap in the chick diets of the two most abundant auks in the Northwest Atlantic, the Common Murre (*Uria aalge*; hereafter murres) and the Atlantic Puffin (*Fratercula arctica*; hereafter puffins). My objective was to assess how auks with different foraging strategies (dietary specialization among murres vs. generalization among puffins) and physiological constraints imposed by differences in body size and prey-loading meet the energy demands of reproduction. Murres provisioned chicks with female capelin (>100 mm): 98.8 % by number in 2004 and 94.5 % in 2005. The relative contribution of gravid capelin to murre chick diets decreased by an order of magnitude between years (41.1 and 4.5 % by number in 2004 and 2005, respectively) and was related to the timing of capelin spawning. Puffins provisioned chicks with high proportions of forage fish in both years with the focal species changing from sandlance *Ammodytes spp.* in 2004 (97.6 % by index of relative importance, IRI) to capelin (> 100 mm) in 2005 (92.3 % IRI). Murre fledglings were significantly lighter in 2005 (203.0 ± 4.6 g) compared to 2004 (215.0 ± 3.9 g) whereas puffins chicks exhibited no such differences. These results suggest that generalized feeding is a viable strategy for puffins but that specialized feeding by murres can lead to poor offspring condition when there is low overlap between peak food availability (i.e. capelin spawning) and chick-rearing.

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2.2. Introduction

Divergence in ecological requirements among closely related, sympatric species is taken as evidence of niche partitioning that facilitates coexistence (e.g. Wiens 1989). Throughout the Northwest Atlantic, Common Murres *Uria aalge* (hereafter murres) and Atlantic Puffins *Fratercula arctica* (hereafter puffins) overlap in their breeding and foraging ranges but often exhibit striking dietary differences. Murres are considered capelin (*Mallotus villosus*) specialists (Piatt 1987; Burger and Piatt 1990; Montevecchi 2000; Davoren and Montevecchi 2003a, b) with chick diets consisting almost exclusively of female capelin larger than 100 mm (Davoren and Montevecchi 2005; but see Bryant et al. 1999). Puffins are considered generalist foragers and throughout the Northwest Atlantic they provision their chicks with a variety of prey including capelin of all sizes and maturity stages, sandlance *Ammodytes* ssp., larval pelagic fishes, gadids and crustaceans, and the occurrence of these prey in their diets is variable across years and colonies (Piatt 1987; Nettleship 1991; Rodway and Montevecchi 1996; Russell 1998; Ballie and Jones 2003, 2004).

The mechanisms explaining the dietary differences between these closely related pursuit-divers are likely associated with differences in their physiology that influences their ability to exploit prey over a range of distributions. Body size in piscivorous alcids is positively correlated to diving depth and duration (Piatt and Nettleship 1985; Piatt 1990) and murres that are considerably larger than puffins (murres = ~1000 g, puffins = ~ 400 g; Ainley et al. 2002; Lowther et al. 2002) can dive deeper (maximum 180 m compared to maximum 60-70 m for puffins; Piatt and Nettleship 1985; Burger 1991) and may have

more prey options available to them. On the other hand, murres have a higher wing-loading (2.06 g cm^{-2}; Spear and Ainley 1997) than puffins (1.34 g cm^{-2}; Livezey 1988) resulting in higher flight costs that can lead to more discriminating diet choices when suitable prey are less available around the colony. In addition, differences in prey-loading may influence how murres and puffins select prey under different prey availability scenarios. Under similar prey conditions, single-prey loaders should be more selective than multiple prey loaders that have the option of selecting a single or a few large prey and/or many smaller ones (Orians and Pearson 1979).

Capelin is the most important forage fish in the Northwest Atlantic and the timing of breeding for most seabirds coincides with the inshore availability of mature capelin (Harris and Birkhead 1985). During early summer (June-July), capelin migrate inshore from over-wintering areas on the edge of the continental shelf and prior to spawning on suitable gravel beaches or demersal sites (deep water; Davoren et al. 2006; Penton 2006) they form dense aggregations of sex-specific schools in coastal waters (Templeman 1948). Some seabirds return repeatedly to the same foraging sites to minimize search time (Irons 1998; Benvenuti et al. 1998; Davoren et al. 2003) and the availability of spatially predictable, dense concentrations of nutritious capelin may increase the foraging efficiency of seabirds when they are rearing offspring.

Capelin are cold blooded fish that respond quickly to changes in ocean temperatures (Carscadden and Nakashima 1997; Rose 2005) and following an extreme cold-water event in 1991 (Drinkwater 1996) capelin in the Northwest Atlantic exhibited changes in their behavior and biology that have been linked to declines in the condition of

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northern cod (Rose and O'Driscoll 2002) and to changes in seabird community dynamics (Regehr and Montevecchi 1997; Stenhouse and Montevecchi 1999; Massaro et al. 2000; Carsscadden et al. 2002; Davoren and Montevecchi 2003b). This involved major shifts in their distribution (Frank et al. 1996; Mowbray 2002), delays in the timing of spawning by approximately one month (Carscadden and Nakashima 1997) and decreased size at age (Carscadden et al. 2002). In southern Labrador, capelin ceased to spawn following a southward shift in distribution (Carscadden et al. 2001a) and became unavailable within the foraging range of seabirds at the Gannet Islands. Murres at this colony responded by switching to an alternate prey, the daubed shanny *Lumpenus maculates*, without incurring any reproductive costs but the time that parents spent paired at the colony (i.e. off-duty rest time) declined suggesting that murres did allocate more time to foraging (Bryant et al. 1999). Puffins in southern Labrador showed no signs of reproductive stress despite striking changes in their diets from capelin to alternative prey species such as 0-group sandlance (Ballie and Jones 2003, 2004). Puffins and murres at colonies in southern Newfoundland (Witless Bay) exhibited no marked differences in their diet or reproductive success following changes in capelin biology and behavior (Ballie and Jones 2003; Davoren and Montevecchi 2003a; Wilhelm and Storey 2004) but evidence from an earlier study in the mid-1980s showed that murres at Witless Bay increased their foraging effort and successfully buffered chicks from an order of magnitude decline in capelin abundance (Burger and Piatt 199). Murres at Funk Island, the species' largest colony, delayed breeding by approximately 3 weeks relative to pre-1990s timing and there was a decline in the condition of chicks over the decade that was related to smaller and poorer quality

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capelin (Davoren and Montevecchi 2003b). Long foraging trips at this high-density, offshore colony relative to smaller inshore colonies (e.g. Witless Bay and Gannet Islands) may limit the additional time that parents can dedicate to foraging without incurring long-term fitness costs.

To gain a better perspective on how co-existing murres and puffins cope with changes in forage fish availability during the breeding period we compared: 1) the dietary composition of parental prey deliveries to murre and puffin chick diets during 2004 and 2005 at Funk Island; and, 2) the condition of murre and puffin offspring between years.

2.3. Methods

2.3.1. Study site

This study was conducted at the Funk Island Ecological Reserve (49°45'N, 53°11'W), the most offshore colony in the Northwest Atlantic, located approximately 60 km off the northeast Newfoundland coast (Figure 2.1). Funk Island supports the world's largest common murre colony estimated at 340 000 to 400 000 pairs, or approximately 75 % of the Northwest Atlantic population (Chardine et al. 2003; Cairns et al. 1989). The Atlantic puffin colony on Funk Island is very small by comparison with an estimated 2000 pairs (Cairns et al. 1989) and expansion may be limited by the availability of habitat. The extent of suitable habitat in which to construct burrows is defined by a small grassy meadow in the center of the island that was generated from the composted remains of extinct Great Auks that were slaughtered there in the late 1700s (Montevecchi and Tuck 1987, Montevecchi and Kirk 1997). Funk Island also supports an expanding population of Northern Gannets *Sula bassanus* (~10 000 bp) and smaller numbers of Northern Fulmar *Fulmarus glacialis*, Black-legged Kittiwakes *Rissa tridactyla*, Herring Gull *Larus argentatus*, Great Black-backed Gull *Larus marinus*, Thick-billed Murre *Uria lomvia* and Razorbill *Alca torda* (Montevecchi and Tuck 1987).

Information is presented on the timing and duration of capelin spawning from an independent study conducted in 2003-2005 (Penton 2006) at two demersal sites (persistent since their discovery in 2000; Davoren et al 2006) and one beach site, located within the foraging range of seabirds at Funk Island (Figure 2.1).
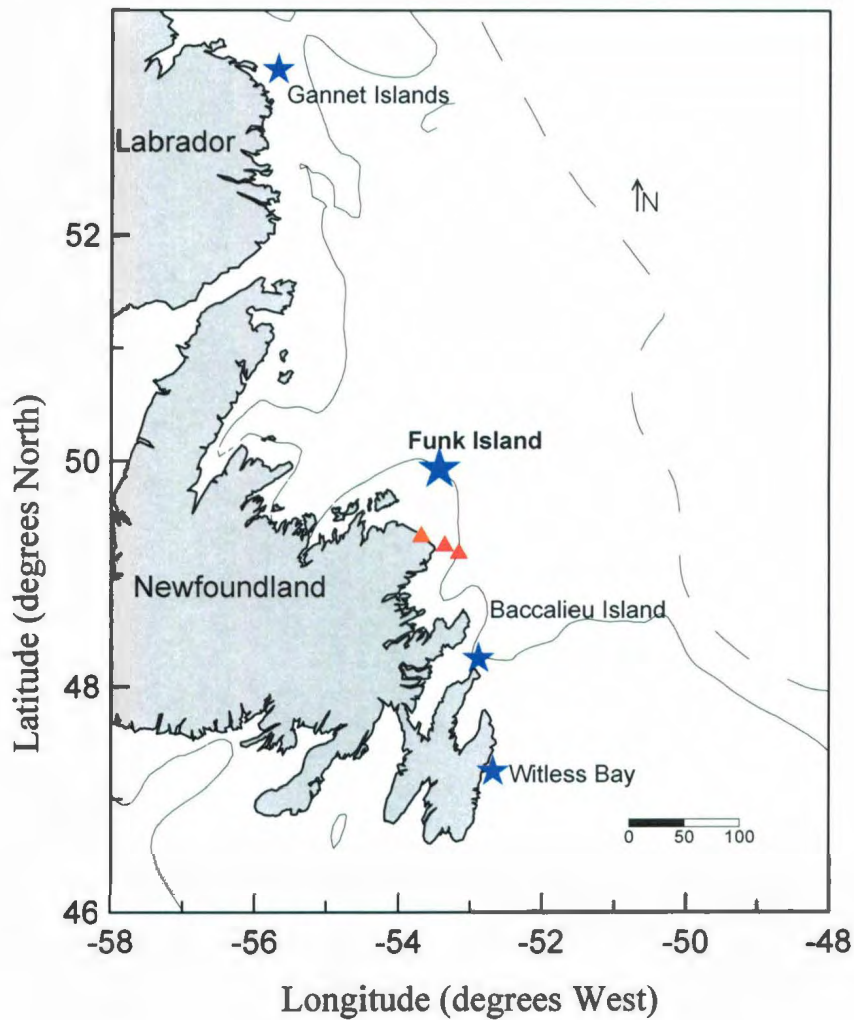
Figure. 2.1. Map showing the Funk Island Seabird Ecological Reserve (large blue star) and the other colonies as well as three other colonies where murres and puffins share breeding habitat. The location of the beach (orange triangle) and demersal (red triangles) capelin spawning sites that were monitored independently during 2003-2005 are also shown. Scale bar (km).

2.3.2. Chick diets

Parental prey loads were collected from murres and puffins over 8 days in 2004 (n = 163 for murres; n = 62 for puffins) and 10 days in 2005 (n = 110 for murres; n = 47 for puffins). Murre prey loads were collected from adults by intercepting them with a 3 m pole-net as they returned to the colony from foraging trips. Puffin prey loads were collected from adults after foraging trips by laying a large ground net (approximately 5 x 20 m) over burrow entrances. Puffins dropped their prey loads after several attempts at entering their burrows and flew away. The ground net was laid out for a maximum of 2 hr per sampling period to reduce disturbance. In 2004, only a portion of the total prey was accounted for in 13 of 62 puffin parental prey deliveries because not all items that had been dropped were found, or portions of the loads were scavenged by gulls during collection.

Where possible, prey items were identified to species, measured (total length, mm) and weighed (using 10 and 30 g Pesola spring scales for larval and mature fish respectively). Total prey load mass was measured (30 g Pesola), and the total number of prey items per load was recorded for puffins. Mature capelin were identified to sex and stage of maturity (i.e. gravid versus spent). Gravid capelin were defined as having a gonad sac containing eggs and spent females were identified on the basis of having flaccid undersides and gonad sacs that were empty or contained fewer than 10 eggs (Davoren and Montevecchi 2005). Capelin that could not be conclusively identified as being spent or immature were pooled into a category described as spent-immature (Davoren and Montevecchi 2003b). Given the importance of size in determining energy content and prey suitability for seabirds (Swennen and Duiven 1991), capelin in chick diets were also sorted

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into small (100-140 mm) and large (> 140 mm) size classes that correspond roughly to 1-2 and 3-4 year olds in the population (Carscadden et al. 2001).

The composition of prey categories (capelin sex, maturity stages, size classes) in murre chick diets were described according to a numerical percentage index ($Ni = (n_i/n_t) *$ 100) where n_i is the total number of individuals of prey category i in all prey loads (n_t) in a given year (Pierce and Boyle 1991). For puffins that deliver a broad range of prey types with widely divergent mass and numerical values, prey composition was described using an index of relative importance (expressed as a percentage % IRI; Cortes 1997) calculated as:

$$\% \ IRI = \% \ FO \ (\% \ M + \% \ N)$$

where FO = frequency of occurrence percentage, % M = mass percentage and % N = numerical percentage. The % IRI is a composite index that reduces bias in the description of dietary data that can arise using a single dietary index (Pinkas et al. 1971) For example, the numerical percentage index (% N) can overestimate the importance of small, abundant fish and overshadow larger less abundant fish. The % IRI is particularly useful for predators with a broad diet breath that include large and small prey items with widely divergent mass and numerical values. The %IRI index was not used to describe murre diets because as single prey loaders, the values for % FO and %N did not differ. Values for % FO, % M and % N are also provided separately for all prey categories in puffin chick diets according to sampling dates in each year. Results for % M include some estimated values

for individuals without recorded weights. These were generated using the mean mass for a species of a given size range (e.g. shannies 30-60 mm) generated from individuals that were weighed in each year. Intra-annual differences in the mean total length (mm) and mass (g) of individual prey, overall prey load mass and the mean number of prey items per prey load (puffins only) were tested using one-way ANOVA (*Minitab* statistical analysis package). Data summarizing prey and prey load mass (g), prey lengths (mm) and total number of prey per load are presented throughout as mean ± SD.

2.3.3. Dietary overlap

Differences in chick diets between species and years were evaluated using Petraitis (1979) General Overlap Index expressed as the adjusted general overlap index (GOI_{adj}; Smith 1984) that provides a value of dietary overlap ranging between 0 (no overlap) and 1 (complete overlap). The GOI_{adj} index evaluates the probability that the utilization curves of two or more species are drawn from a common curve, where the 'utilization curve' is defined as the relative use of all prey categories in the diets (Ludwig and Reynolds 1988). Prey categories in murre and puffin chick diets are described according to frequency of occurrence (i.e. number of prey loads containing a given prey). The null hypothesis of complete overlap ($GOI_{adj} = 1$) between species (inter-specific) and between years (inter-annual) was tested with the Mann-Whitney U-statistic that follows a chi-square distribution. When U exceeds the critical value for chi-square at $P < 0.5$, the null hypothesis is rejected (Ludwig and Reynolds 1988).

2.3.4. Offspring condition

Sampling dates at Funk Island in 2004 and 2005 corresponded to the peak fledgling period for murres and the mid-to-late chick-rearing period for puffins. This resulted in assessments of offspring at different developmental stages (i.e. murre fledglings versus puffin chicks). Murre fledglings were intercepted in dip nets as they jumped from departure ledges to go to sea with an accompanying male parent over three nights in 2004 (27, 30-31 July; n = 40) and 2 nights in 2005 (2, 6 August; n =30). They were weighed in nylon bags with a 500 g Pesola spring scale and flattened wing chord was measured to the nearest mm with a wing ruler, after which they were immediately released into the ocean.

Puffin chicks were removed from burrows during one day in 2004 (1 August) and 2005 (2 August). Body mass and wing length were measured following the same procedure described for murres. Hatching dates of puffins are typically asynchronous and as a result there is potential to have a wide range of ages within the sample population. To limit variability in the development stages among the measured chicks, wing lengths of less than 50 mm and greater than 115 mm, corresponding to individuals outside the linear phase of growth, were removed prior to analysis. This was done because 1) measurement error is greater during the early phase of growth when down plumage precedes the growth of primary feathers (Ricklefs 1967) and 2) because wing growth follows a sigmoidal trajectory with slower growth during the early and later (near fledging) stages of growth; whereas, the fastest rate of growth occurs during the linear phase (Gaston 1985).

Offspring condition for both species was gauged using a 'developmental condition index' (Bertram et al. 2002) that compares individual body mass (g) in relation to wing

length (mm) using an analysis of covariance (ANCOVA) that tests for differences in mass (response variable) between years (explanatory variable) while holding wing length constant (covariate). Homogeneity of slopes was tested by inspecting the significance of the interaction term between the covariate and the explanatory variable (ANCOVA: mass = constant + wing + year + *wing * year*) where a non-significant interaction term indicated homogeneity of slopes. Differences in the elevation of slopes were investigated using the adjusted mean masses, reported as the adjusted least square means (ALS) ± standard error (SE). Inter-annual differences in mean wing lengths were assessed using a one-way ANOVA.

2.4. Results

2.4.1. Murre chick diets

Capelin were the dominant prey in murre chick diets, accounting for 98.8 % by number in 2004 and 100 % in 2005 (Table 2.1). Other prey consisted of sandlance and alligator fish (order Scorpaeniformes) in 2004 (0.9 % N). Capelin in murre chick diets were predominately females accounting for 98.8 % by number in 2004 (159 of 161) and 94.5 % N in 2005 (104 of 110). Male capelin were rare (1 in 2004; 4 in 2005) and in both years there were a few capelin that could not be sexed (unknowns; Table 2.1). There were also some partial (i.e. broken) capelin in the diets in 2004 (n = 10) and 2005 (n = 4) that could only be identified to species and sometimes sex (if capelin). Information on stage of maturity, total length (mm) and mass (g) was not known for these individuals. There was

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also 1 intact capelin in 2005 without information on total length but for which condition and sex are known.

Table 2.1. Prey species in murre chick diets according to sampling date. Values are total number of prey loads collected, total number of capelin (sorted by sex) and total number of other prey. Values in parentheses are broken fish.

Date	# Preyloads	# Capelin by Sex			Other Prey
		Female	*Male*	*Unknown*	
26-Jul-04	15	15	0	0	0
28-Jul-04	27	24	1	1	1 (*sandlance*)
29-Jul-04	24 (2)	24	0	0	0
30-Jul-04	26 (4)	25	0	0	1 (*alligatorfish*)
31-Jul-04	26 (1)	26	0	0	0
1-Aug-04	24	24	0	0	0
2-Aug-04	21 (3)	21	0	0	0
Totals-2004	**163 (10)**	**159**	**1**	**1**	**2**
2-Aug-05	11 (2)[1]	7	3	1	0
3-Aug-05	25 (1)	24	1	0	0
8-Aug-05	44	43	0	1	0
9-Aug-05	30 (1)	30	0	0	0
Totals-2005	**110 (4)**	**104**	**4**	**2**	**0**

[1] one additional capelin with no length measurement

Most capelin in murre chick diets were in spent condition in 2004 (53.6 %) and 2005 (69.1 %; Table 2.2). During 2005, the percentage of spent capelin increased daily accounting for 90.0 % of total capelin in the chick diets on the final sampling day (Table 2.2). Gravid capelin were well represented in the chick diets in 2004 (41.1 %) with numbers peaking on the second day of sampling (61.5 % on 28 July) and declining thereafter (Table 2.2). Gravid capelin were uncommon in 2005 and constituted 3.6 % of

chick diets. While the difference in the amount of gravid capelin in the diets could be related to later sampling dates in 2005, there was a higher percentage of gravid capelin during 2 August in 2004 (33.3 % by number) than on the same date in 2005 (18.2 % by number) suggesting a real difference in availability between years. Immature capelin were rare accounting for less than 1 % of the diet in and less than 10% in 2005. Capelin described as spent/immature (i.e. condition unknown) were not present in 2004 but accounted for 12.7 % of chick diet in 2005.

Table 2.2. Relative proportions of capelin by maturity stages in murre chick diets according to sampling date. Values are numerical percentage (% N). N = number of capelin prey loads per day.

Date	N	Spent %N	Gravid %N	Immature %N	Spent/Imm %N	Unknown %N
26-Jul-04	15	46.7	40.0	0.0	0.0	13.3
28-Jul-04	26	19.2	61.5	3.8	0.0	15.4
29-Jul-04	22	50.0	50.0	0.0	0.0	0.0
30-Jul-04	21	57.1	38.1	0.0	0.0	4.8
31-Jul-04	25	64.0	36.0	0.0	0.0	0.0
1-Aug-04	24	75.0	25.0	0.0	0.0	0.0
2-Aug-04	18	66.7	33.3	0.0	0.0	0.0
2004	**151**	**53.6**	**41.1**	**0.7**	**0.0**	**4.6**
2-Aug-05	11	36.4	18.2	9.1	18.2	18.2
3-Aug-05	25	52.0	0.0	28.0	16.0	4.0
8-Aug-05	44	72.7	4.5	2.3	18.2	2.3
9-Aug-05	30	90.0	3.3	3.3	0.0	3.3
2005	**110**	**69.1**	**4.5**	**9.1**	**12.7**	**4.5**

All capelin fed to murre chicks in both years were larger than 100 mm (Figure 2.2) with the exception of one individual in 2005 (55 mm). The number of large capelin (i.e. > 140 mm) in the diets increased from 49.7 % in 2004 (75 of 151 prey loads) to 63.5 % in 2005 (66 of 104 prey loads). Small capelin (100-140 mm) accounted for 50.3 % (76 of 151 prey loads) of all capelin in murre chick diets in 2004; they were less common in 2005 accounting for only 36.5 % of all capelin (38 of 104 prey loads).

The mean total length of capelin in murre chick diets was significantly longer ($F_{1, 253} = 4.7$, $p = 0.03$) in 2005 (143 ± 11.4) than in 2004 (140.1 ± 13.9; Figure 2.2) while the mean mass of capelin was significantly lower ($F_{1, 253} = 19.8$; $p < 0.001$) in 2005 (9.9 ± 3.0) compared to 2004 (11.6 ± 3.0). Spent female capelin were also significantly longer in 2005 (145.4 ± 11.8) relative to 2004 (141.6 ± 10.5; $F_{1,155} = 4.5$; $p = 0.04$). Inter-annual differences in the size of gravid capelin could not be tested due to the small sample in 2005 (n = 5).
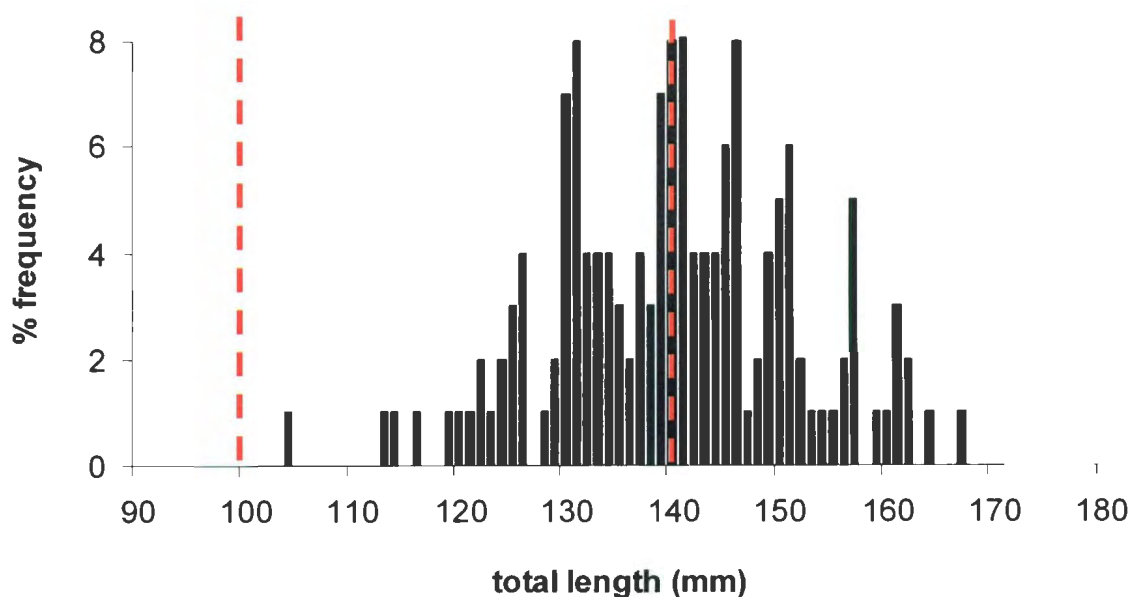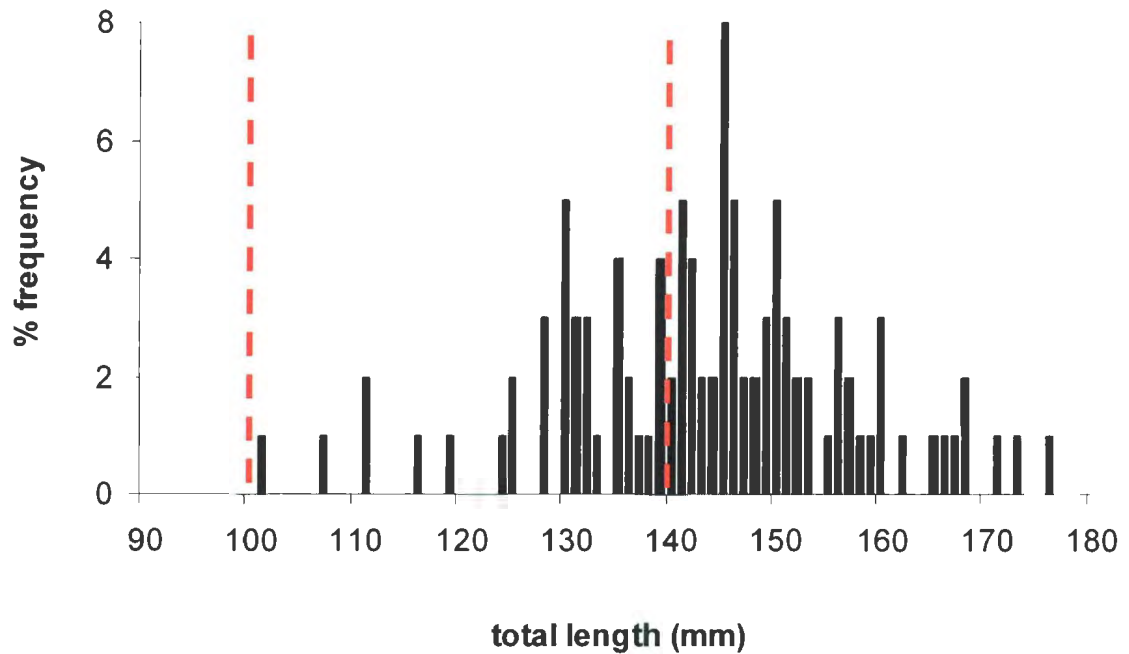
Figure 2.2. Length frequency distribution (mm) of capelin in murre chick diets in 2004 (top; n = 151) and 2005 (bottom; n = 104). The red dashed lines show the frequency of capelin distributed around the small (100-140 mm) and large (> 140 mm) size categories.

2.4.2. Puffin chick diets

Figure 2.3 illustrates the index of relative importance (% IRI) for puffin chick diets in 2004 and 2005. The contribution of prey categories according to each dietary index (% FO, % M, % N) is given by sampling date and for the overall sampling period for each year in Table 2.3. Puffin chick diets consisted of forage fish in both years but the main fish species shifted from sandlance in 2004 (97.6 % IRI) to capelin in 2005 (92.3 % IRI). In both years, diets containing forage fish were supplemented by small amounts of 0-group fish and crustaceans described collectively as 'larval prey'. Sandlance measuring < 30 mm (size

below which schooling behavior is not observed, Smigielski et al. 1984) and transparent capelin were included in the 'larval prey' category.
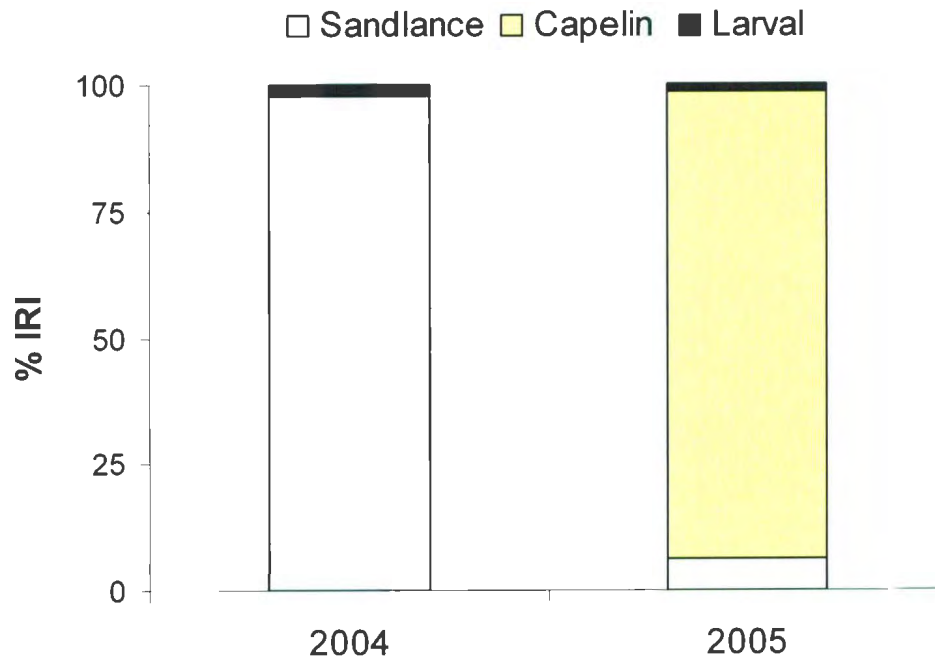
Figure 2.3. Composition of puffin chick diets expressed as percent index of relative importance (% IRI) during 2004 and 2005 at Funk Island. Partial loads are excluded.

Table 2.3. Relative proportions of the main prey in puffin chick diets according to frequency of occurrence percentage (% FO), mass percentage (% M) and numerical percentage (% N). N = number of prey loads per day with the number of partial loads shown in parentheses.

Date	N	%FO			% M			%N		
		San	Cap	Larval	San	Cap	Larval	San	Cap	Larval
27-Jul-04	8 (4)	100	0	75	87.7	0	12.3	66.0	0	34.0
28-Jul-04	4	75	0	75	47.5	0	52.5	42.9	0	57.1
29-Jul-04	7 (2)	100	0	0	100	0	0	100	0	0
30-Jul-04	15(3)	100	0	6.7	99.7	0	0.3	98.3	0	1.7
31-Jul-04	5 (2)	100	0	40.0	99.2	0	0.8	94.7	0	5.3
2-Aug-04	4 (1)	100	0	0	100	0	0	100	0	0
3-Aug-04	6 (1)	100	0	33.3	98.8	0	1.2	93.2	0	6.8
2004	**49 (13)**	**98.0**	**0**	**28.6**	**95.6**	**0**	**4.4**	**89.0**	**0**	**11.0**
4-Aug-05	3	0	100	0	0	100	0	0	100	0
7-Aug-05	19	26.3	100	0	2.9	97.1	0	35.7	64.3	0
8-Aug-05	10	20.0	100	10.0	3.9	93.6	2.5	34.3	25.7	40.0
9-Aug-05	7	28.6	85.7	28.6	10.8	88.5	0.7	70.3	24.3	5.4
11Aug-05	8	12.5	100	25.0	3.7	91.6	4.7	4.0	32.0	64.0
2005	**47**	**21.3**	**97.9**	**10.6**	**4.2**	**94.4**	**1.4**	**38.0**	**43.0**	**19.0**

Partial loads are excluded from dietary indices.

In 2004, sandlance were the most important prey in puffin chick diets (97.6 % % IRI) and constituted the highest relative proportion of the diet in terms of frequency of occurrence (98.0 % FO), mass (95.6 % M) and number (89 % N). Sandlance could not be identified to species and are referred to as *Ammodytes* spp., a designation typically used in fisheries research to describe *Ammodytes dubius* and *A. americanus* in the Northwest Atlantic (Liem and Scott 1966; Auster and Stewart 1986). The mean length of sandlance in puffin chick diets in 2004 was 93.6 ± 8.7 mm with a range of 61 – 114 mm (Figure 2.4).

This size corresponds to post-larval, young of the year (0-group) fish that would have spawned in January and February (Auster and Stewart 1986; Scott and Scott 1988) and are no longer transparent. The mean length of post-larval, 0-group sandlance collected in 2004 increased significantly over the sampling period (length = 74.4 + 4.8 day, r^2 = .87, p < 0.001) suggesting that puffins may select larger sandlance as the nutritional needs of the chick increases with age, The increase in size could also reflect daily growth in these 0-group fish. During 2005, sandlance were smaller (58.0 ± 16.0 mm; Figure 2.4) and much less important in puffin chick diets accounting for less than 6.2 % IRI compared to 97.6 % IRI in 2004 (Figure 2.3). The relatively high contribution of sandlance by number (38 % N) in 2005 resulted from a high number of small sandlance in a few prey loads.
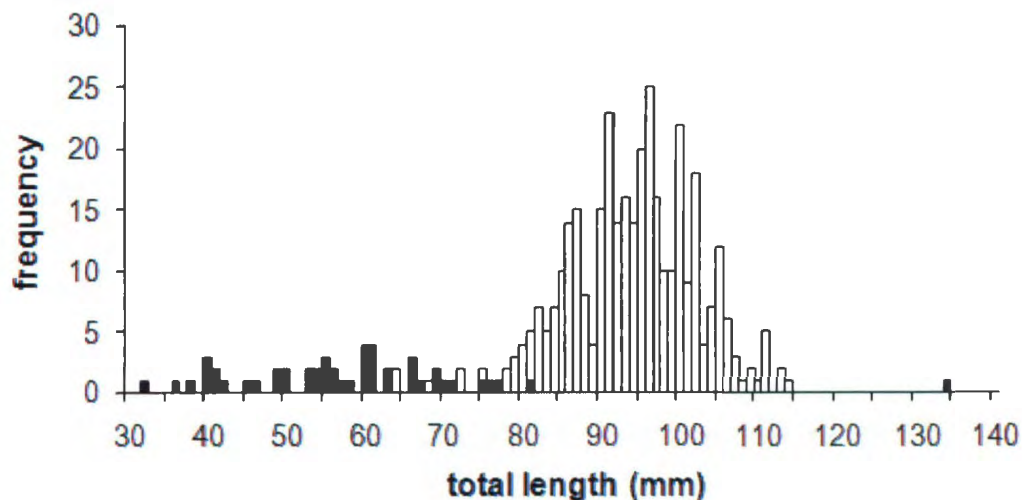
Figure 2.4. Length frequency (mm) distribution of sandlance in puffin chick diets in 2004 (white bars) and 2005 (black bars).

Capelin replaced sandlance as the most important prey item in puffin chick diets in 2005 accounting for 92.3 % IRI (Figure 2.3). Capelin were present in 97.9 % of parental

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prey deliveries (46 of 47 prey loads) and accounted for 94.4 % of total diet by mass (Table 2.3) but the percentage of capelin by number (% N) was relatively low (43.0 %). All capelin in puffin chick diets were females in predominately spent condition (83.6 % N) with a small percentage of spent/immatures (16.4 % N). Puffin chicks did not consume any gravid capelin. Capelin in puffin chick diets in 2005 ranged in size from 107 to 176 mm with a mean length of 146.1 ± 11.7 mm (Figure 2.5); these included a high occurrence of large capelin (> 140 mm) in 2005 (80.9 % FO, 38 of 47 prey loads) and fewer small capelin (27.7 % FO, 13 of 47 prey loads; Figure 2.5).
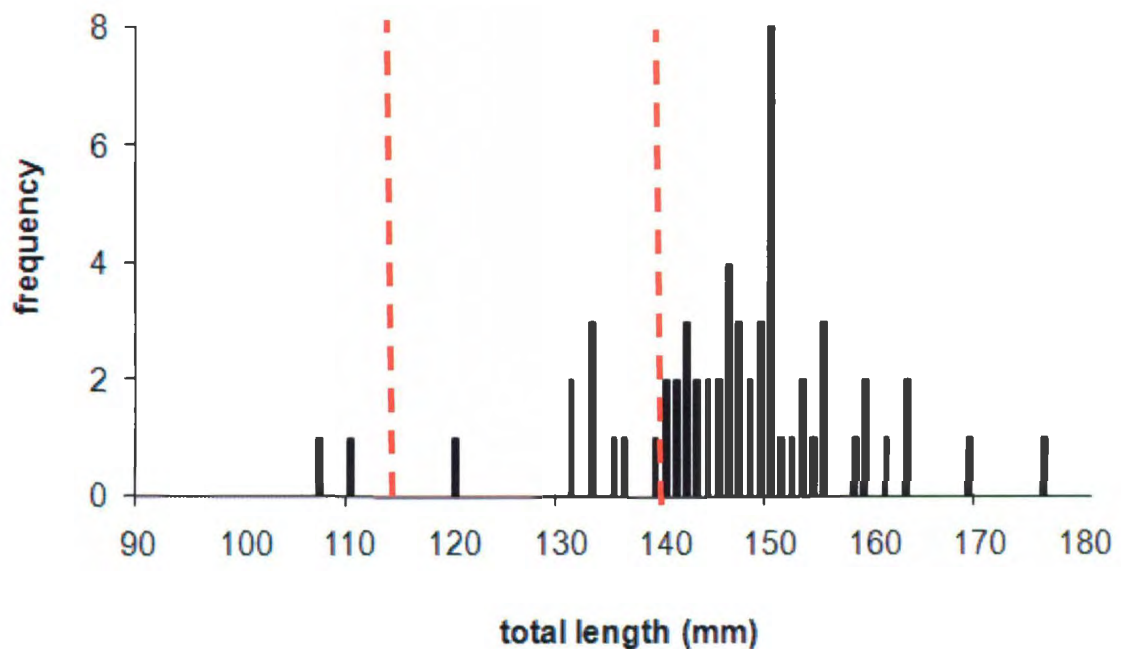
Figure 2.5. Length frequency distribution of capelin in puffin chick diets in 2005. The red dashed line illustrates the frequency of capelin distributed within the small (100-140mm) and large (> 140 mm) size categories.

'Larval prey' were of minor dietary importance in 2004 (2.4 % IRI) and 2005 (1.5 % IRI; Figure 2.3). Prey loads containing only larval prey were very rarely observed (only 1 prey load in 2004); rather larval prey occurred in combination with forage fish and was more frequently observed with sandlance than capelin > 100 mm. The contribution of larval prey by mass was very low in 2004 (4.1 % M) and 2005 (1.4 % M). Larval capelin (i.e. transparent) accounted for 1.7 % N of the total chick diet in 2004 ranging in size from 51 – 88 mm and less than 1 % N in 2005. Larval shannies consisting of both radiated shanny (*Ulvaria subbifurcata*) and daubed shanny (*Lumpenus maculatus*) were the most common species in the larval prey category with a mean total length of 43.6 mm ± 13.7. Small amounts of the remainder were juvenile fish, including gadids (Order Gadiformes), eelpouts and wolfish (Order Perciformes) and alligator fish.

The mean number of prey items per load was significantly higher ($F_{1,95}$ = 33.6, p <0.01) in 2004 (7.2 ± 2.6) when the smaller sandlance dominated chick diets compared to 2005 (3.0 ± 4.8). Mean prey load mass was not significantly different between 2004 (11.9 ± 5.1) and 2005 (13.8 ± 4.9). There was no difference in the mean length of capelin in puffin prey loads containing one capelin (146.1 ± 12.1 mm) versus > 1 capelin (146.1 ± 11.5 mm).

2.4.3. Dietary overlap

Dietary overlap in murre and puffin chick diets was very low in 2004 (GOI_{adj} 0.035) when puffin chicks consumed sandlance, and murre chicks consumed capelin (Table 2.4). In contrast, overlap was high in 2005 (GOI_{adj} .838) when large capelin dominated the chick diets of both species ($U = 28.3$; 3 df; $p < 0.001$). There was complete dietary overlap in murre chick diets between years (GOI_{adj} 0.980; $p = 0.16$; Table 2.4) but inter-annual dietary overlap was low (GOI_{adj} 0.317) for puffins.

During 2005, when capelin were the dominant prey in chick diets, there was no difference in the mean length of capelin delivered to murre (143.5 ± 13.9 mm) and puffin chicks (146.1 ± 11.7 mm). There was also no difference in the mean mass of capelin in murre (9.9 g ± 3.1 g) and puffin (10.1 g ± 2.3 g) prey loads in 2005. Puffin prey loads were however, significantly heavier than murre prey loads in 2005 ($F_{1, 147} = 32.2$, $p < 0.001$), because puffins often delivered more than one mature capelin per prey load (16 of 46 prey loads).

Table 2.4. Adjusted General Overlap Index (GOI$_{adj}$) results for interspecific (A and B) and inter-annual (C and D) dietary overlap. Values are frequency of occurrence of prey categories, GOI$_{adj}$ = adjusted general overlap index (0-1) and U = test statistic.

Prey Categories	Small Capelin (FO)	Large Capelin (FO)	Sand-lance (FO)	Other [a] Larval [b] (FO)	GOI$_{adj}$	U-test significance
Inter-specific GOI$_{adj}$						
A Murre 2004	76	75	0	2	**0.035**	U = 246.2 p < 0.001
Puffin 2004	0	0	48	14		
B Murre 2005	38	67	0	1	**0.838**	U = 28.3 p < 0.001
Puffin 2005	13	38	10	5		
Inter-annual GOI$_{adj}$						
C Murre 2004	76	75	na	2	**0.980**	U = 5.1 p = 0.16
Murre 2005	38	67	na	1		
D Puffin 2004	0	0	48	14	**0.317**	U = 126.1 p < 0.001
Puffin 2005	13	38	10	5		

[a] other refers to murres only and describes all fish in the diets other than capelin > 100 mm.

[b] larval prey refers to puffins only and describes 0-group fish and shrimp

2.4.4. Murre offspring condition

The residual versus fits plot for the ANCOVA analysis of wing length versus body mass indicated an extreme outlier in the data (blue point; Figure 2.6) that corresponded to a bird with a wing length of 55 mm and a body mass of 80 g in 2005. The probability of a fledgling weighing 80 grams is highly unlikely given that the mean mass of fledgling from 2000-2005 at Funk Island was 198.0 ± 28.2 and there were no fledglings in any of these

years that weighed less than 100 g. Therefore the outlier was removed from any further analysis given the high probability that a chick was mistakenly measured (versus a fledgling) or a measurement error occurred.
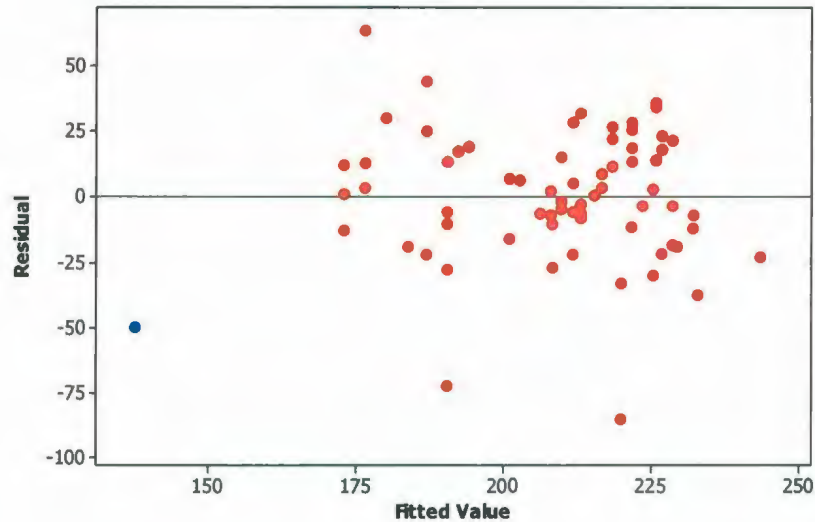
Figure 2.6. The residuals versus fits plot from the analysis of covariance on murre fledgling body mass and wing length in 2004 and 2005. The blue point (far left) indicates the outlier discussed in the text.

Inspection of the interaction term: (ANCOVA; $F_{1, 65} = 0.78$ p = 0.38) indicated no difference in the regression slopes between mass and wing length of murre fledglings in 2004 and 2005 (Figure 2.7). Given that the assumption of homogeneity of slopes was met, the model was re-run without the interaction term to test for main effects (Engqvist 2005). The mean mass of fledglings at a given wing length was different between years with significantly heavier fledglings in 2004 (215.1 ± 3.9 g) compared to 2005 (203.0 ± 4.6 g;

$F_{1, 68} = 4.1$ p =0.047). Mean wing lengths did not differ between years (2004: 68.9 ± 5.5 mm, 2005: 67.7 ± 6.0 mm; (ANOVA; p = 0.42).
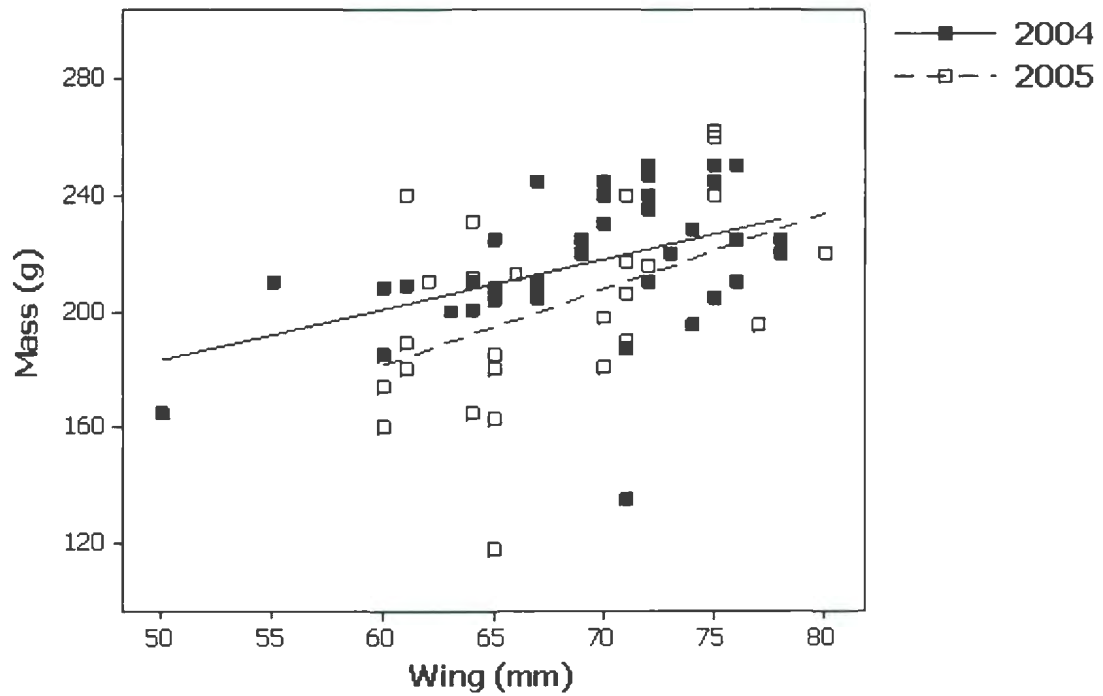
Figure 2.7. Regressions between body mass (g) and wing length (mm) of murre fledglings at Funk Island in 2004 (solid line): slope = 1.72 g mm^{-1}, r^2 = .20, n = 40, and 2005 (dashed line): slope = 2.61 g mm^{-1}, r^2 = .24, n = 29.

2.4.5. Puffin offspring condition

The mass of puffin chicks at a given wing length did not differ between years. The slopes of mass versus wing length were statistically indistinguishable between years (interaction term: $F_{1, 51} = 0.07$, $p = 0.79$; Figure 2.8). Chicks were lighter at a given wing length in 2005 (258.8 ± 5.9 g) than in 2004 (277.9 ± 7.3) but the difference was not significant ($p = 0.07$). Mean wing lengths were significantly longer in 2005 (92.7 ± 13.9 mm) compared to 2004 (78.8 ± 11.3 mm; $F_{1, 54} = 16.1$; $p = 0.001$).
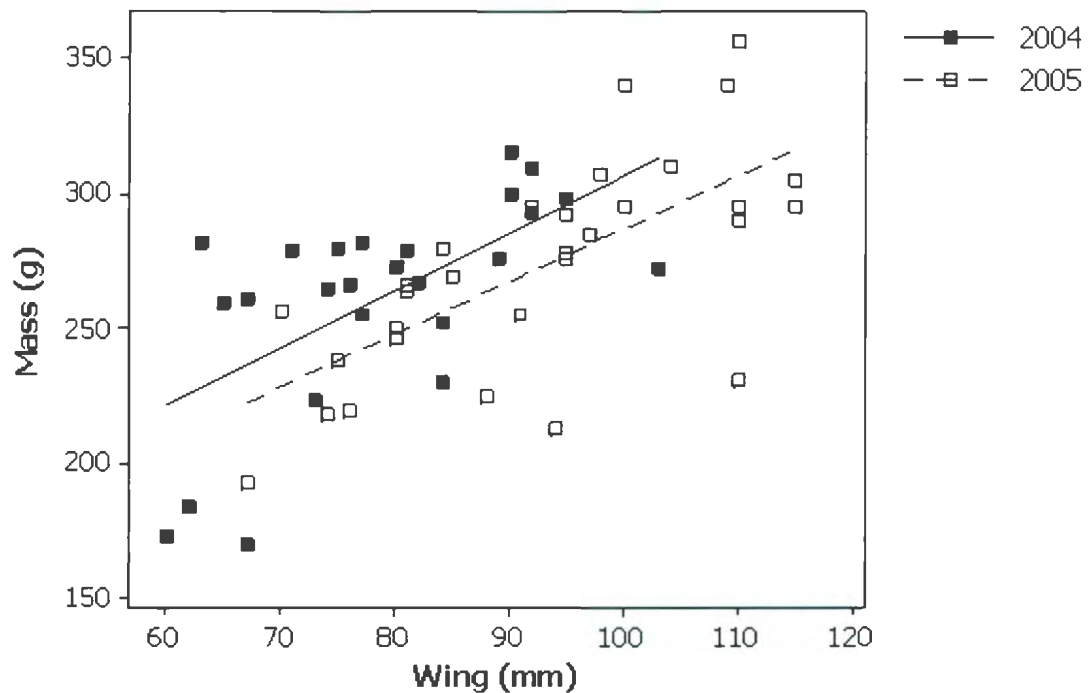
Figure 2.8. Regression between body mass (g) and wing length (mm) of puffin chicks at Funk Island in 2004 (solid line): slope = 2.12 g mm^{-1}, r^2 =. 39, n = 25 and 2005 (dashed line): slope = 1.94 g mm^{-1}, r^2 = .47, n = 30).

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2.5. Discussion

2.5.1. Murre chick diet and condition

The diets of murre chicks observed during this study were typical of the diets throughout the Northwest Atlantic with a strong bias for female capelin larger than 100 mm (Birkhead and Nettleship 1987; Burger and Piatt 1990; Piatt 1990; Davoren and Montevecchi 2003b, 2005; Wilhelm and Storey 2004). The relative contribution of gravid capelin to the diets of murre chicks declined by an order of magnitude from 2004 to 2005 and was related to the timing of capelin spawning. Independent data on the timing and duration of capelin spawning within the foraging range of seabirds at Funk Island (Figure 1) indicated that demersal spawning began on 13 July in 2005, approximately two weeks earlier than during 2004 (28 July) and 2003 (30 July), and was shorter in duration (6 ± 1 days in 2005, 8 ± 1 days in 2004 and 9 ± 1 days in 2003; Penton 2006). Beach spawning was also earlier and brief in 2005 (3 July for 2 days) relative to 2004 (10 July for 3-4 days; Penton 2006). Presumably, gravid female capelin that have higher energy densities relative to spent capelin (Montevecchi and Piatt 19984), were unavailable to murres during the sampling period in 2005 (2-9 August), which coincides with late chick-rearing phase. This in addition to the fact that capelin in the chick diets were significantly lighter in 2005, likely contributed to lighter fledglings in 2005 (Litzow et al. 2002; Davoren and Montevecchi 2003b).

The mean masses of murre fledglings at Funk Island in 2004 and 2005 (215 g ± 3.9 and 203.0 g ± 4.6 respectively) are low in comparison to other colonies (Piatt 2002; Davoren and Montevecchi 2003a) with the exception of some poor food years (212 g; Uttley et al. 1994 and 211 g; Hatchwell 1991), and this is consistent with other records for Funk Island (e.g. 191 ± 4.0 g in 2000; Davoren and Montevecchi 2003a). Long foraging trips at Funk Island, due to the predominantly coastal distribution of mature capelin (Davoren et al 2003), could potentially constrain parental provisioning rates if the time required to forage exceeds a maximum threshold beyond which the life-time fitness of the parent is compromised (Stearns 1992). However, murres may compensate for greater foraging effort in poor food years by departing the colony early to continue their development at sea. Growth rates are faster at sea (Ydenberg 1989; Varoujean et al. 1979), so it may be more advantageous to both offspring (faster growth) and the accompanying male parent (maintain reserves) to depart the colony as soon as possible (Sealy 1973; Hipfner and Gaston 1999). Upon departure from the colony, the male parent accompanies the fledgling at sea for a period of 1-2 months (Varoujean et al. 1979, Hope Jones and Rees 1985), during which the adult molts their flight feathers and the juvenile and parent remain flightless for a period (Birkhead and Taylor 1977). Davoren et al (2000) documented an important nursery area (i.e. an area characterized by high densities of juvenile-adult pairs and high prey densities; Hatch et al 2000; Davoren et al. 2002) north of Funk Island that is utilized by murres throughout the NW Atlantic. The relative close proximity of this important nursery area for Funk Island murres may allow them to compensate for early

departure from the colony by moving into this productive feeding area within close proximity of the colony.

Before murre chicks can depart the colony successfully they must attain adequate wing growth to glide from ledges into the sea and to propel themselves underwater to forage and evade aerial predators once they go to sea (Hedgren 1979; Hatch 1983; Ainley et al. 2002; Benowitz-Fredericks et al. 2006). Inspection of the mean wing lengths of murre fledglings at Funk Island over all years when fledglings were sampled (2000 – 2005) indicates no inter-annual differences (ANOVA; $F_{1, 222}$ = 1.67; P = 0.14) suggesting that departure times at this colony may depend on attaining a critical wing length (mean ± SD; 67.6 ± 6.9). This strategy could result in fledglings departing the colony in poor condition during years when food is limited, resulting in reduced survival and recruitment of juveniles (Hatch 1983), however the relationship between fledgling condition and over-winter survival is not well documented (Zador and Piatt 1999). Recent population estimates indicate that the murre population at Funk Island has stabilized while other murre colonies in the Northwest Atlantic are undergoing population increases associated with a reduction in bycatch mortality following the large-scale removal of gill nets after the ground fish moratorium in 1992 (Robertson et al. 2004). The relationship between fledgling condition and juvenile recruitment into the population deserves further research attention given the documented decline in murre chick condition associated with changes in capelin biology and behavior during the 1990s (Davoren and Montevecchi 2003b) and the significance of the Funk Island murre colony to the rest of the Northwest Atlantic's breeding population.

2.5.2. Puffin chick diet and condition

Consistent with previous studies in the Northwest Atlantic (Rodway and Montevecchi 1996; Russell 1998; Ballie and Jones 2004), there was high inter-annual variability in the composition of forage fish in puffin chick diets. Mature capelin and post-metamorphic sandlance are key prey components in puffin chick diets, with an alternating trend between these two prey (Rodway and Montevecchi 1996; Russell 1998). Post-larval, 0-group sandlance collected at several Newfoundland colonies (Russell 1998) had energy densities (7.3 kJ. g^{-1}) that exceeded those reported for mature capelin (including gravid capelin; 4.6 kJ. g^{-1}; Montevecchi and Piatt 1984; Lawson et al. 1998). Compared to bulkier capelin, the elongate shape of sandlance facilitates the carrying of many fish in a puffin's bill-load (Harris and Hislop 1978; Hislop and Harris 1985). Despite these attributes, the amount of sandlance in puffin diets at Funk Island fluctuates considerably (Russell 1998; this study), implying that sandlance are not consistently available to puffins. Sandlance recruitment is highly variable and large fluctuations in abundance are observed every few years (Robards et al. 1999).

Puffin chicks did not exhibit differences in mass at given wing lengths in 2004 and 2005, suggesting that chicks performed equally well on post-larval 0-group sandlance and mature female capelin. This is not unexpected given that the nutritional quality of both their main prey is high and both are schooling prey that can be captured using similar foraging tactics. Longer wing lengths in 2005 could reflect later sampling (by approximately one week) but it could also suggest preferential allocation to wing growth in 2005 (Oyan and Anker-Nilssen 1996) to facilitate earlier colony departure (Thick-billed

Murres; Hipfner and Gaston 1999) that may be advantageous in poor food years. Consequently, while puffin chicks showed no decline in condition between 2004 and 2005, longer wings in 2005 could be indicative of poorer food conditions in that year.

Presumably, the puffin's more generalized strategy characterized by switches between prey types and multiple prey-loading allows them to cope with fluctuations in forage fish during breeding. In contrast, the specialized strategy of the murre is less efficient when capelin conditions are stochastic because more time and energy are required to maintain current information about prey availability.

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Chapter 3: Flexible Foraging in Response to Changes in Forage Fish Availability

3.1. Abstract

I studied the at sea foraging behavior of Common Murres (*Uria aalge*) and Atlantic Puffins (*Fratercula arctica*) during chick-rearing in 2004 and 2005 in relation to synoptic estimates of forage fish availability. Flexible adjustments in foraging tactics by murres and puffins closely reflected changes in forage fish availability between years. The availability of capelin (> 100mm) as measured during trawl surveys declined in 2005 by an order of magnitude (mean density ± SE in 2004: 20410.7 ± 12684.9 9 above 60 m per km^2 and 2005: 3645.7 ± 1731.8 9 above 60 m per km^2) and capelin were smaller (2004: 132.8 ± 22.1 mm and 2005: 92.5 ± 23.0 mm) and more dispersed in 2005. Murres and puffins increased the mean distances they foraged from the colony by 36% in 2005 and murres significantly expanded the area over which they searched for capelin. These results demonstrate that during periods of reduced food availability, murres and puffins allocate more time to foraging to mitigate the effects on their offspring.

3.2. Introduction

The foraging strategies of seabirds differ in many respects during the breeding and non-breeding season. When rearing offspring, seabirds forage from a central place to collect prey at sea and they have an additional constraint to return to the colony to feed their chick (Orians and Pearson 1979). Consequently, foraging effort is restricted to some specific distance from the colony that varies by species. By contrast, outside breeding, seabirds are "free" to track patchily distributed, ephemeral prey to meet their nutritive requirements and balance their energy budgets.

Ultimately, the time and energy allocated to provisioning chicks at the colony is directly influenced by prey availability (Uttely et al. 1994; Monaghan et al.1994; Burger and Piatt 1990, Piatt et al 2007). For piscivorous seabirds that rely on pelagic prey (i.e patchy and ephemeral), unpredictable foraging conditions are not uncommon and reproductive success is dependent on the capacity to make continuous and adaptive foraging decisions (Harding et al. 2007). Many seabirds have evolved foraging tactics that allow them to adjust to current prey conditions and optimize foraging efficiency by minimizing time spent locating and transporting prey. These tactics involve but are not limited to memory-based foraging (Davoren et al. 2003), area restricted search tactics (Grumbaum and Viet 2003), the exploitation of public information from other predators (Ward and Zavi 1973; Davoren et al. 2003), different foraging and capture techniques for different prey (Garthe et al. 2007; Montevecchi et al. under revision), prey-switching (Ostrand et al. 1998; Suryan et al. 2000; Abraham and Sydeman 2006) and/or combinations of these activities (Davoren et al. 2003). These responses are influenced by

a number of factors including physiology (e.g. body size; Piatt 1990), life-history traits (e.g. clutch size; Stearns 1992; Litzow and Piatt 2003) and geographic context (e.g. colony location: Parrish et al. 1999), that influence a seabird's ability to exploit prey under variable conditions. For example, when capelin in the Northwest Atlantic underwent a dramatic shift in their vertical distribution towards the seabed during the early 1990s (Mowbray 2002), Black-legged Kittiwakes *Risa tridactyla* were the only seabirds to experience breeding failures (Regehr and Montevecchi 1997) due to their inability as surface-feeders to exploit capelin distributed in deep water.

In some species, flexible time-activity budgets may be used to moderate the effects of fluctuations in prey availability during chick-rearing. Provisioning adults may allocate more time to foraging when prey availability declines and less time to non-foraging related activities such as rest and maintenance (Burger and Piatt 1990, Harding et al 2007). Consequently, provisioning rates and offspring condition do not always accurately reflect prey conditions (Cairns 1987, Piatt et al. 2007). Estimates of parental foraging effort (i.e. foraging range, dive depth and duration) provide useful information regarding seabird responses to changes in prey availability (Burger and Piatt 1990; Uttley et al. 1994; Monaghan et al. 1994; Suryan et al. 2000; Harding et al. 2007) that are sensitive to moderate prey fluctuations (Cairns 1987). For alcids, including murres and puffins that have high wing loading ratios (body mass to wing area), flight is a more limiting factor, and therefore foraging range is a sensitive indicator of temporal and spatial shifts in prey availability. Assessments of the foraging behavior of seabirds at sea in combination with independent assessments of prey density are useful in understanding how changes in prey availability influence the foraging decisions of seabirds. Furthermore, multi-species

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studies involving closely related, co-existing seabirds provide comprehensive insights into how species-specific constraints influence the foraging decisions of seabirds under different prey conditions (Montevecchi et al. 2006).

This study investigates the foraging tactics of murres and puffins at an offshore colony (Funk Island) in the Northwest Atlantic in association with synoptic and independent measurements of forage fish availability. The major objectives of the study were: 1) to describe changes in forage fish availability within the foraging ranges of chick-rearing murres and puffins at Funk Island in 2004 and 2005; 2) to assess the foraging strategies of murres and puffins in response to changes in forage fish availability.

3.3. Methods

3.3.1. Study area and survey design

A meso-scale vessel survey was conducted during 8-17 August 2004 and 15-22 August 2005 around the Funk Island Ecological Reserve (49°45'N, 53 °11'W) aboard the CCGS research vessel *Wilfred Templeman*. Information on seabird diets and offspring performance was collected at Funk Island over a comparable time frame (26 July- 3 August 2004 and 2-11 August 2005) providing relatively synoptic information on diet and prey availability. The survey included a series of transects that extended from near the coast, oriented to the northeast, across the inner Newfoundland Shelf (Figure 3.1), and was designed to encompass the maximum foraging ranges of murres at Funk Island (123 km during incubation and 80 km during chick-rearing; Cairns et al. 1987). This design also encompasses the smaller foraging range of puffins.
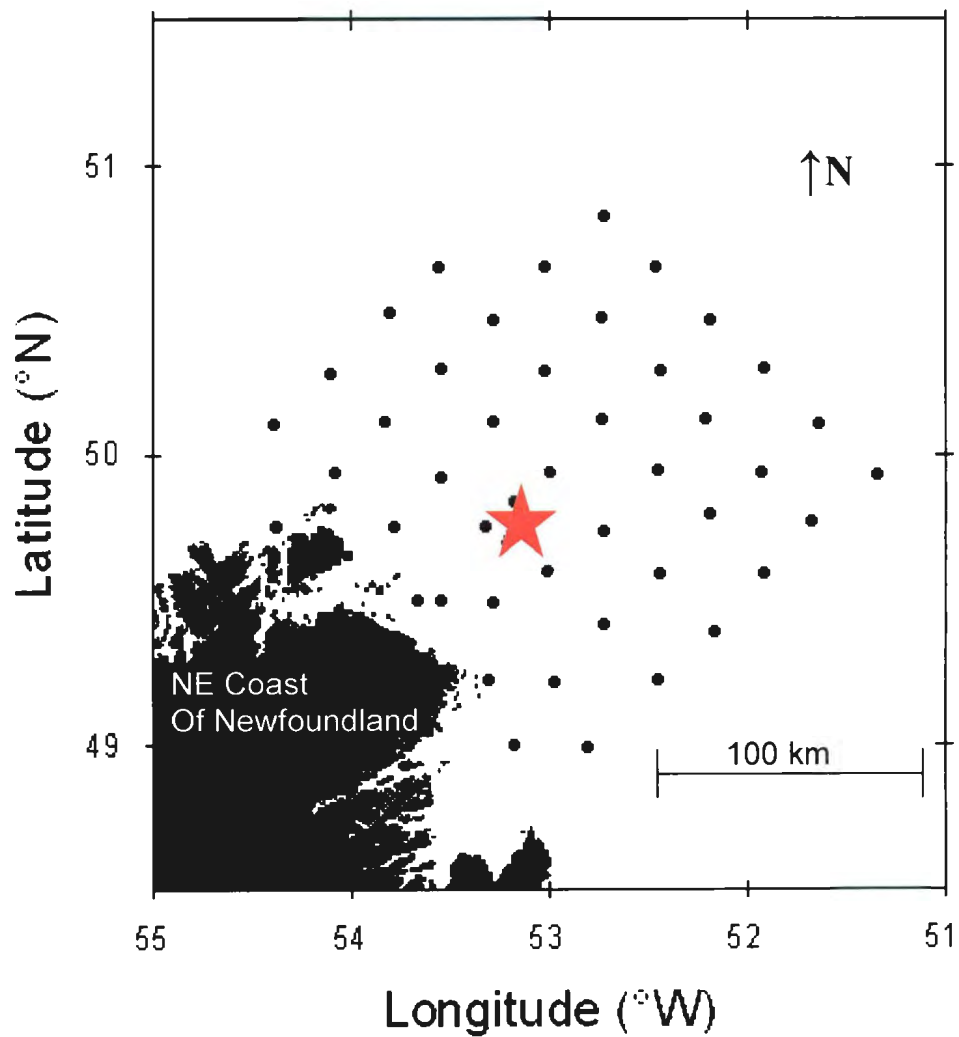
Figure 3.1. Meso-scale survey design in 2004 and 2005. The red star indicates the Funk Island seabird colony and the red dots show the locations of the trawl sets. Scale bar (km).

3.3.2. Forage fish availability

Forage fish availability was estimated from systematic trawl samples over the meso-scale survey during 2004 (n = 45) and 2005 (n = 49). Samples were collected using the International Young Gadoids Pelagic Trawl (IYGPT), a standard research trawl designed to catch pelagic juvenile gadoids (range 10-200 mm). The maximum vertical sampling range of the IYGPT is 60 m, corresponding to the range over which murres and puffins take the bulk of their prey (Tremblay et al. 2003; Croll et al. 1992; Hedd et al. unpubl. data). While murres can dive considerably deeper (Piatt and Nettleship 1985) than 60 m, new information gathered from time-depth recorders (TDRs) attached to murres at Funk Island (2007) indicate that over 80% (by number) of dives occur in the upper 50 m (Hedd et al. unpub data). Puffins are smaller birds with mean dive depths of 26.4 ± 15.3 m (Barrett and Furness 1990) and maximum dive depths recorded between 41-68 m (Burger and Simpson 1986).

All IYGPT catches were processed at sea and whenever possible all fish were identified to species. When catches were high, a random sample of 200 capelin was measured to generate information on length frequency distributions. No information was available for the maturity stages of capelin (e.g. gravid versus spent) in 2004; therefore changes in the composition of capelin between years are described in terms of length as was done for capelin in the diets (Chapter 2). Capelin were classified according to two size classes: small capelin (100-140 mm) and large (> 140 mm) corresponding roughly to 1-2 and 3-4 year fish (Carscadden et al. 2001). Capelin that were < 100 mm are not considered suitable prey for murres (Barret 2002; Davoren and Montevecchi 2005) and are not included in the estimates for total capelin. Estimates of large and small capelin

were generated from the recorded lengths of the random sub-samples of capelin. Abundance estimates for size classes per trawl were calculated as the total number of capelin in each set multiplied by the proportion (by number) of each class. The top ranking species in the trawls were described according to percent by number (% N) and by percent frequency of occurrence (% FO; percent of the total trawls containing a given species).

For the purposes of this study, availability is assumed to be proportional to density (# individuals above 60 m per km^2). Forage fish density was estimated as the number of forage fish (per species and size categories) sampled by the IYGPT trawl (60 m depth) over a mean horizontal area (0.026 km^2), calculated using the mean distance towed (standardized to 2.8 km) times the average horizontal opening of the net (9.3 m). Trawl depth and configuration (i.e. net depth, net opening, and wing and door widths) monitored during the survey using acoustic net sensors (Scanmar) indicated low variability in the horizontal opening of the net between sets.

The distribution of trawl catch data is commonly characterized by many zeros and some extreme values, resulting in a highly skewed distribution and large variance to mean ratios that may reflect the patchy distributions of fish. The arithmetic mean was used to estimate density as it is deemed to be a robust abundance estimator for trawl catch data that are not log normally distributed (Myers and Pepin 1990). The Lilliefors test for normality (Statistica software) on the non-zero trawl estimates indicated that capelin did not follow a log normal distribution in 2004 ($p < 0.05$) or 2005 ($p < 0.05$). The distribution of total capelin (> 100 mm) are shown using maps created with Surfer

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software 8 using a smoothed kriging method to show prey density over surface area ($\log_{10}$ number 10^4 m^{-2}).

3.3.3. Avian foraging distances

During the meso-vessel surveys, observations of seabirds were recorded continuously during daylight hours using standard strip methods (Tasker et al. 1984). An observer on the bridge of the vessel recorded all birds out to 300 m in a 90° arc from the bow to the port side of the vessel. Counts and behavioral descriptions (on the water, foraging, flying, flying with fish) were entered on a laptop computer connected to the navigational system of the vessel. Counting software (designed by D. Senciall Fisheries and Oceans Canada) was used to append a position (latitude, longitude) and GMT to each observation. Murres and puffins observed on the water were assumed to be foraging. The distance (km) from the colony to where individual birds were observed on the water was used to approximate the foraging distances of murres and puffins from the colony in 2004 and 2005. Birds on the water may include non-breeders that may travel further from the colony than provisioning adults and therefore estimates of distances traveled from the colony for breeding adults could be overestimated.

Measurements of the distance that parental murres and puffins traveled from the colony to foraging sites were summarized by constructing cumulative frequency distributions (CDFs) with cumulative percentage of total birds plotted against distance from Funk Island. A pairwise two-sample Kolmogorov-Smirnov test (KS-test) was used to detect differences in the distance of foraging birds from the colony (using Statistic

software). Two null hypotheses were tested: 1) the maximum distance between the CFDs of each species was not different between years, and, 2) the maximum distance between species was not different within years. The KS-test provides an estimate of the maximum vertical deviation between the curves of the cumulative frequency distributions using the D statistic (reported as D_{max}).

3.3.4. Directions of foraging flocks returning to the colony

Many species of alcids that breed in large colonies form conspicuous flocks when commuting between the colony and foraging areas, and the flight directions of alcids to and from the colony are good indicators of where the birds have been foraging (Schneider et al. 1990; Wanless et al. 1990; Davoren et al. 2003). The flight directions of incoming flocks of murres and puffins to Funk Island were recorded during 360° scans conducted daily in 2004 and 2005. Observers on the highest point on the island recorded the species, number and return directions of seabirds within 45° sectors (8 in total) over 1 min intervals using compass equipped binoculars. Three repetitions of the 360° scan were conducted during a single session which lasts approximately from 24 to 30 minutes. Wind speed and direction were recorded at the outset and after each session.

Data are presented as the percentage of total birds, by number within four 90° sectors representing northeast (0° - 90°), southeast (90° - 180°), southwest (180° - 270°) and northwest (270° - 360°). The quadrants were grouped into four 90° sectors as opposed to the original eight 45 ° quadrants in order to refine the resolution of the data. Chi-square analysis was used to test whether the direction of returning birds was different between

years. Differences in mean flock sizes of murres between years were also tested using ANOVA analysis (Minitab).

3.4. Results

3.4.1. Forage fish composition

Total numbers of fish captured in the IYGPT were higher in 2004 (28,924) than in 2005 (16,680). Capelin was the most abundant species accounting for 86.8 % and 92.4 % (by number) of the total catch in 2004 and 2005 respectively (Table 3.1). While total numbers of capelin were higher in 2004 (25,109) than in 2005 (15419 total capelin), the frequency of occurrence of capelin was lower (40 % FO and 79.6 % FO in 2004 and 2005 respectively). Sandlance accounted for a small proportion of the total catch in 2004 (2.9 % by number) but occurred in 60 % FO of the trawls (29 of 45 sets). Sandlance were extremely rare in 2005, accounting for less than 0.06 % of the total catch (by number) and occurring in 12.2 % FO of the trawls (6 of 49 sets). Many of the lower ranked species in 2004 and 2005 (Table 3.1) were young fish of the year including redfish (*Sebastes* sp.), Arctic cod (*Boreogadus saida*) and Atlantic cod (*Gadus morhua*) and a variety of sculpins (Cottidae spp.) Most of these species that ranged in size from 40 – 60 mm and are in the pelagic life stage prior to settling to the bottom during autumn, hence they are accessible to pursuit-diving seabirds.

Table 3.1. Fish species captured in the IGYPT in 2004 (A) and 2005 (B) according to relative abundance by number (% N) and % frequency of occurrence (%FO). Ns – refers to not speciated.

A) Prey Species	Total Number	% Number	% Frequency of Occurrence (n = 45 sets)
Capelin	25109	86.81	40.00
Redfish (ns)	1312	4.54	64.44
Sandlance	841	2.91	60.00
Atlantic Cod	831	2.87	84.44
Daubed Shanny	426	1.47	66.67
Seasnail (ns)	81	0.28	55.56
Mailed Sculpin	59	0.20	44.44
Northern Alligatorfish	55	0.19	46.67
Hookear Sculpin	47	0.16	42.22
Striped Wolffish	45	0.16	28.89
Other (17 species)	118	0.41	range: 2.22 – 26.7

B) Prey Species	Total Number	% Number	% Frequency of Occurrence (n = 49 sets)
Capelin	15419	92.44	79.59
Arctic Cod	650	3.90	75.51
Atlantic Cod	139	0.83	40.82
Daubed Shanny	108	0.65	28.57
Hookear Sculpin	59	0.35	46.94
Striped Wolffish	50	0.30	26.53
Northern Alligatorfish	46	0.28	36.73
American Plaice	39	0.23	16.33
Seasnail (ns)	37	0.22	20.41
Redfish (ns)	32	0.19	22.45
Sandlance	10	0.06	12.24
Other (11 species)	91	0.55	range: 0.02 - 0.22

The mean total length of capelin was significantly different between years ($F_{1, 4068}$ = 2783.6; p <0.0001) with larger capelin in 2004 (132.8 ± 22.1 mm) relative to 2005 (92.5 ± 23.0 mm). Capelin ranged in length from < 50 mm to > 170 mm in both years, the modal size of capelin was > 100 mm in 2004 and at < 100 mm in 2005 (Figure 3.2).

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Large capelin (i.e. > 140 mm) were more abundant in 2004 accounting for 39.7 % (by number) of total capelin compared to only 5.2 % (by number) in 2005. Capelin <100mm were the most abundant prey in 2005 accounting for 68 % (by number) of all capelin.
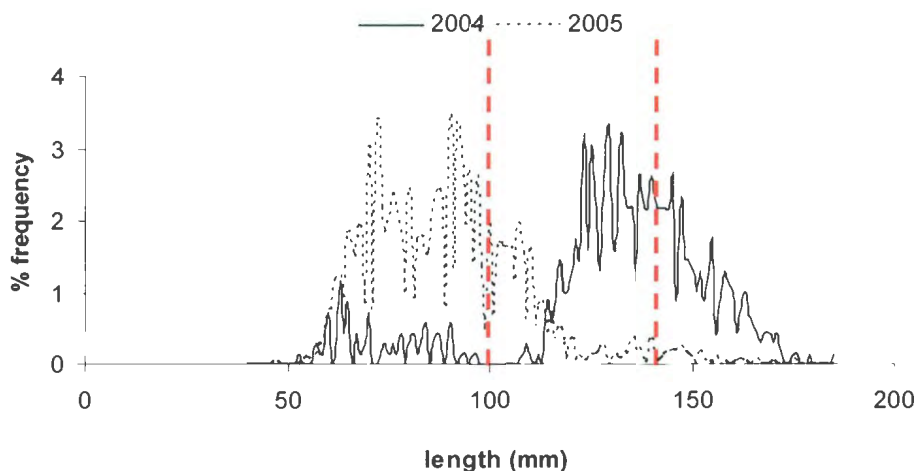
Figure 3.2. Length frequency distributions of capelin sampled in the IYGPT trawl during 2004 (n = 1302) and 2005 (n = 2767). Red vertical lines delineate the distribution of capelin according to the small (100-140 mm) and large (> 140 mm) size class categories.

Sandlance sampled in the IYGPT in 2004 ranged in size from 50 mm to 135 mm (Figure 3.3). The length frequency distribution was bimodal with peaks observed around 50-80 mm and 100-130 mm. Sandlance abundance was too low in 2005 to discriminate modes in the length frequency distribution.
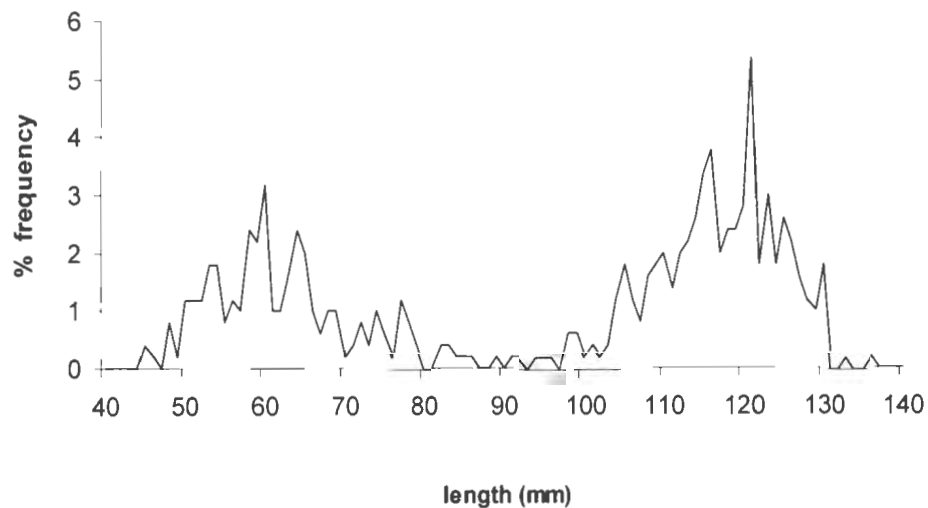
Figure 3.3. Length frequency distribution of sandlance sampled in the IYGPT trawl during 2004. Lengths of sandlance in 2005 were only recorded for 9 fish all less than 80 mm.

3.4.2. Forage fish densities

There was a six-fold decline in the average density of capelin > 100 mm from 2004 (20410.7 ± 12684.9 above 60 m per km^2) to 2005 (3645.7 ± 1731.8 above 60 m per km^2). Large (> 140 mm) and small capelin (100-140 mm) were available in both years but the mean densities of both size classes of capelin declined in 2005 (Table 3.2), with large capelin showing a 50-fold decline in density. Sandlance density was low compared to capelin in both years, and sandlance densities declined in from 2004 (723.4 ± 453) to 2005 when there were fewer than 10 individuals above 60 m per km^2. There was a seven-fold increase in the mean density of capelin < 100 mm from 2004 to 2005 (Table 3.2), the only prey to increase in density in 2005.

Table 3.2. Differences in the density (individuals in the upper 60m/km^2) of forage fish over the meso-scale survey in 2004 and 2005. Values are mean ± SE.

PREY SPECIES	YEAR	DENSITY (#/km^2) MEAN ± SE
Total capelin (> 100 mm)	2004	20410.71 ± 12684.9
	2005	3645.7 ± 1731.8
Large capelin (> 140 mm)	2004	7022.6 ± 3996
	2005	129.7 ± 45.2
Small capelin (100–140 mm)	2004	13388.1 ± 8961
	2005	3516.0 ± 1772
Capelin (< 100 mm)	2004	1187.7 ± 799
	2005	8534.2 ± 3329
Sandlance	2004	723.4 ± 453
	2005	7.9 ± 3.4

3.4.3. Forage fish distributions

Figure 3.4 shows the distributions of total capelin (i.e. > 100 mm) in 2004 (A) and 2005 (B). Capelin had a predominantly coastal distribution during 2004, with the highest densities occurring within 60 km south of Funk Island (Figure 3.4 A). Capelin (> 100mm) were highly dispersed in 2005 with the exception of a few high-density areas adjacent to and south of Funk Island (Figure 3.4 B). The distributions of total capelin in both years reflect the distributions of large (> 140 mm) and small capelin (100-140 mm). Figure 3.5 shows the distribution of sandlance in 2004. Densities of sandlance were too low in 2005 to show distribution.
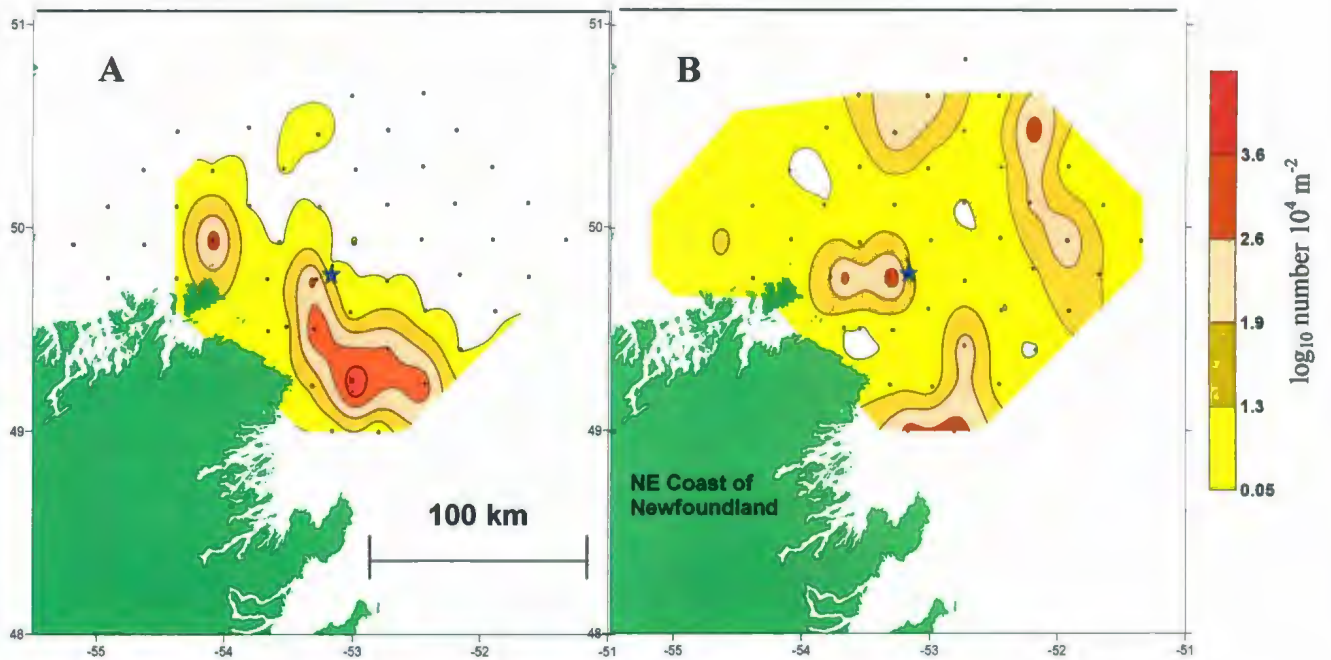
Figure 3.4. Distributions of capelin >100 mm during 2004 (A on the left) and 2005 (B on the right) represented as density in the upper 60 m of the water column ($\log_{10}$ number 10^4 m^{-2}). The blue star represents Funk Island.
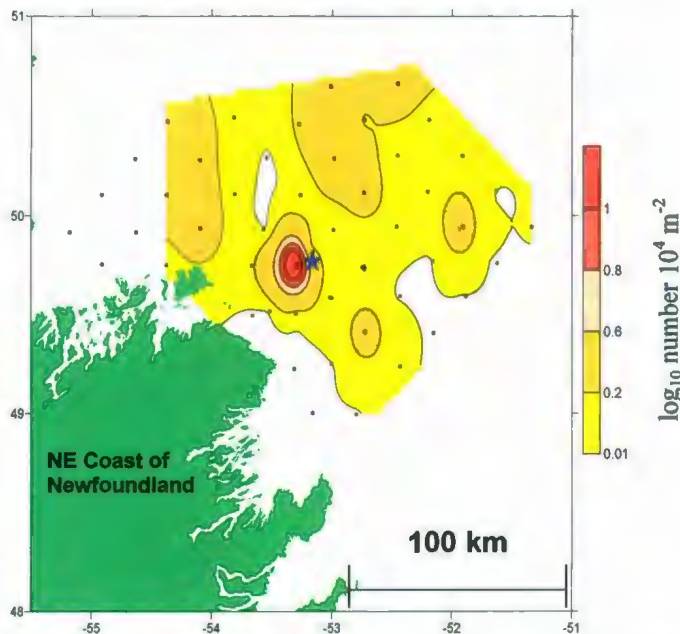
Figure 3.5. Distribution of sandlance during 2004 represented as density in the upper 60 m of the water column ($\log_{10}$ number 10^4 m^{-2}; note scale is different than for capelin). The blue star represents Funk Island.

3.4.4. Estimated avian foraging distances

There were striking differences in the distributions of murres and puffins at-sea during 2004 and 2005. The mean distance that murres traveled from the colony to forage increased significantly (D_{max} = 0.02, p <0.001; Figure 3.6) from 2004 (46.5 ± 18.5 km) to 2005 (63.1 ± 31.2 km). Similarly, the mean distance that puffins traveled from the colony to forage increased significantly (D_{max} = 0.05, p <. 01; Figure 3.6) from 2004 (44.1 ± 22.8 km) to 2005 (59.3 ± 28.2 km). Maximum foraging distances were just less than 60 km for both species in 2004 (58.2 km for murres; 57.5 for puffins) and increased to 88.2 km (murres) and 77.5 km (puffins) during 2005 representing a 50% increase. There were no differences in the mean travel distances between species in either year.
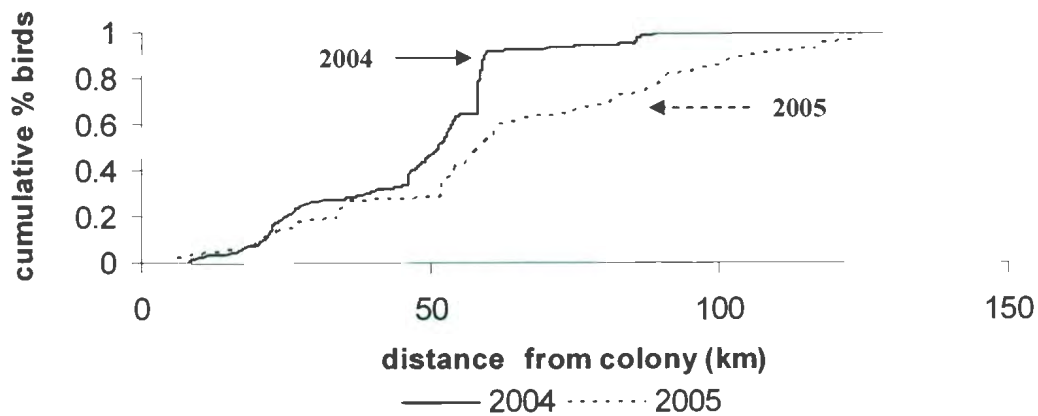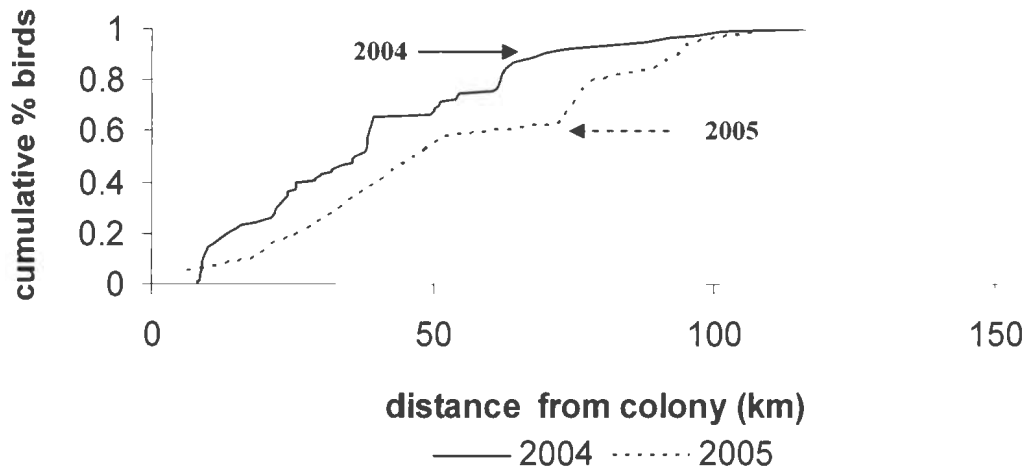
Figure 3.6. Comparative distributions of murres (top graph) and puffins (bottom graph) observed on the water during the meso-scale surveys in 2004 and 2005. Data are cumulative frequency distributions, with cumulative percentage of total number of birds plotted against distance from Funk Island.

3.4.5. Directions of foraging flocks returning to the colony

During 2004, 65 % of murres returned to the colony from the southwest ($180°-270°$) but in 2005, there was a relatively even distribution of murres returning to the colony from all directions (Figure 3.7). Chi-square tests indicated a significant difference between years in the directions from which murres returned to the colony from foraging trips (X^2 = 6784.6, df = 3, p = 0.000). The flock sizes of returning murres were also significantly different between years (D_{max} 0.2 = p<0.001) with higher mean flock sizes in 2004 (11.6 ± 14.6) relative to 2005 (6.5 ± 7.6). Maximum flock size was 200 in 2004 compared to 60 in 2005.

Puffins returned to the colony from the northern sector in 2004 (100 %) and 2005 (87 %). This suggests that the foraging locations of puffins did not overlap with those of the murres; however, the sample sizes for puffins were too small to infer this conclusively (n = 16 and 30 in 2004 and 2005). The puffin colony at Funk Island is small (~ 2000 pairs; Montevecchi unpub data) relative to the murre colony (412,000 pairs; Chardine et al. 2003), and as a result, individuals and small groups of puffins are much less conspicuous in flight and are difficult to detect during the 360° scans. Therefore, information on puffins gathered from scans is largely descriptive.
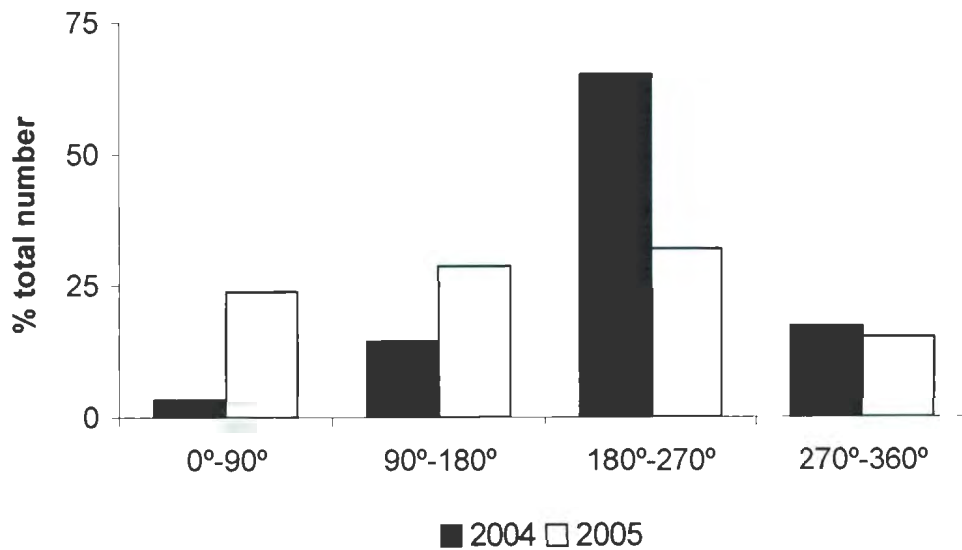
Figure 3.7. Distributions of murres returning to Funk Island during 360° scans in 2004 and 2005. Data are % total number across 4 sectors representing NE (0°-90°), SE (90°-180°), SW (180°-270°) and SE (270°-360°) in 2004 and 2005.

3.5. Discussion

3.5.1. Behavioral responses to changes in forage fish availability

Information on forage fish availability collected from trawl surveys within the foraging range of murres and puffins at Funk Island indicated very different foraging conditions characterized by high and low forage fish availability in 2004 and 2005 respectively. Overall capelin (> 100 mm) and sandlance were more abundant in 2004, and capelin were larger and distributed in higher-density concentrations. In contrast, both capelin (> 100 mm) and sandlance were more scarce in 2005, and capelin were smaller and were dispersed at lower densities over the entire survey area. These changes in forage fish availability corresponded to significant adjustments in the foraging strategies of murres and puffins.

Murres and puffins increased the maximum distances they traveled to forage by approximately 50 % in 2005 (60 km in 2004 to 80-90 km in 2005) presumably in an effort to locate suitable prey for their chicks during low forage fish availability. Both species delivered primarily large capelin (>140 mm) to their chicks in 2005, despite the fact that large capelin were extremely scarce.

For alcids that have high wing-loading relative to other seabirds and use muscle-powered flapping flight, longer foraging trips entail significantly higher energy expenditures (Birt-Friesen et al. 1989). Following this line of reasoning, it seems that murres and puffins selected the largest prey available to them in 2005 in an effort to offset the costs associated with longer foraging trips. During 2004, when forage fish were more

abundant and foraging trips were significantly shorter, there was presumably less pressure on adults to find the largest available prey during provisioning trips.

The return directions of murre flocks to the colony also indicated a shift in foraging strategies between years that was linked to the density and distribution of capelin. In 2004, 65 % of the murres returned to the colony from the southwest (180°-270°) corresponding to an area where the highest densities of capelin were recorded during the meso-scale survey. In 2005, when capelin densities were low and capelin were dispersed over the study area, murre flock sizes were significantly smaller and murre flocks returned to the colony from all directions suggesting a more random foraging strategy.

There is evidence that murres use memory or local enhancement (or a combination of both) at sea to locate 'hotspots' that are defined as locations that consistently have an abundance of accessible prey over days, weeks and years (Irons 1998; Benvenuti et al. 1998; Cairns and Schneider 1990; Davoren et al. 2003). During a previous study at Funk Island during 1998-2000, the return directions of murre flocks indicated a modal southwest direction that was consistent among years (Davoren et al. 2003). The southwest region corresponds to the Straight Shore of Bonavista Bay where persistent aggregations (over days, weeks and years) of capelin shoals have been documented (Davoren et al. 2006). These capelin aggregations are associated with demersal spawning areas that are persistent (over days, weeks and years) due to favorable habitat (Penton 2006; Rose-Taylor 2006; Davoren et al. 2006). The availability of these persistent capelin aggregations near spawning sites could increase the foraging efficiency of murres at Funk Island, provided there is a good temporal overlap between spawning and chick-rearing.

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Capelin in the study area spawned approximately 2 weeks earlier in 2005 relative to previous years (2003 and 2004: Penton 2006) potentially resulting in an earlier dispersal of surviving females from spawning sites to post-spawning staging areas (100-150 m: Davoren et al. 2006) where they remain at depth during the day and migrate into surface waters at night. The low densities of capelin sampled in the IYGPT (sampling range at 60 m), the dominance of spent capelin in the diets and the random foraging patterns of murres in 2005 all support this notion.

For puffins, the availability of these capelin hotspots is evidently less important given that they did not deliver any capelin to their chicks in 2004 when availability was high. Competition for capelin may be intense at these foraging sites given the high densities of murres at Funk Island and the smaller puffin may be excluded by the larger more robust murre (Piatt 1990). As generalists, puffins can forage on a variety of prey and therefore may forego the interactions with murres when a suitable alternative (i.e. sandlance) is available.

3.5.2. Consequences of long foraging trips

Increased foraging effort can reduce the survival and long-term reproductive output of adult seabirds (Golet et al. 1998). Long foraging trips increase the daily energy expenditure of adults and also compromise the time available for mates to spend together at the colony; time that is critical for the maintenance of pair bonds and breeding sites that influence future reproductive success (Harris et al. 1996).

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Using estimates of mean foraging range (this study) and flight speed (69 km h^{-1} and 63 km h^{-1} for murres and puffins respectively; Pennycuick 1987) I estimated the minimum time spent flying to and from the colony by murres and puffins in 2004 and 2005 (Table 3.3).

Table 3.3: Estimates of the time spent flying per foraging trip (h) for murres and puffins in 2004 and 2005 at Funk Island.

Parameter	Murres		Puffins	
	2004	2005	2004	2005
Flight time/ foraging trip $\dfrac{2 * km}{km/h}$	1.3 h	1.8 h	1.4 h	1.9 h

Using the estimate of mean foraging trip duration of 4.1 h (Davoren and Montevecchi 2003) for murres at Funk Island, the time allocated to flight by murres in 2004 and 2005 represents 33 % and 44 % of the total foraging trip in 2004 and 2005 respectively. This is strikingly different from the time allocated to flight at other, smaller colonies located close to shore. Direct measurements of the time allocated to flight for murres in Witless Bay (Cairns et al. 1990), Newfoundland and at Sumburg Head, Shetlands (Monaghan et al. 1994) using electronic timers (Witless Bay) and radio telemetry (Sumberg Head) indicated that murres at these colonies spent less than 10 % of their time away from the colony in flight. During a year when the main prey of murres at Sumberg Head declined by 40-fold, murres flew for 6.9 % of the total time of a 3-h foraging trip t (Monaghan et al. 1994), however diving effort increased substantially (34 % of time away from the colony) resulting in reduced chick feeds (Uttley et al. 1994).

There have been very few studies of the distributions of Atlantic puffins feeding around their colonies during the breeding season, particularly for the Northwest Atlantic (but see Cairns et al. 1987). Under normal prey availability conditions, puffins typically forage within 10 km of the colony when rearing chicks (Wanless et al 1990) and puffins at a nearshore colony in Newfoundland (Gull Island, Witless Bay) foraged within < 5 km of the colony during chick-rearing (Cairns et al. 1987). Extreme foraging distances have also been documented and following a crash of herring stocks in the North Sea, at Røst I., Norway, traveled at least 137 km to fishing grounds and experienced broad-scale breeding failures (Anker-Nilssen and Lorentsen 1990).

The relatively high proportion of time allocated to flight by murres and puffins at Funk Island may constrain their ability to allocate time to other activities when prey is scarce. Consequently, when capelin availability declines, parents may have few options but to engage in longer and fewer foraging trips per day. Davoren and Montevecchi (2003) hypothesized that free time for murres at Funk Island is compromised by the challenges associated with maintaining a breeding site at the world's largest colony. Breeding murres at Funk Island nest side by side over flat terrain and aggressive interactions with neighbors are common resulting in increased pressure to maintain their breeding site in order to breed again in the following year (Harris et al 1996). As a result, murres at Funk Island may spend the minimum amount of time required to maintain a pair bond and breeding site that cannot be further compromised. The constraints of site maintenance at the world's largest colony and unusually long foraging commutes may limit the murres' ability to provision their chicks without incurring high individual fitness costs that could compromise their own survival and future reproductive opportunities.

3.6. Conclusions

Murres and puffins at Funk Island exhibited flexible foraging behavior in response to declines in forage fish availability. Both species increased the distance they traveled from the colony, and murres significantly expanded the area over which they searched for food during a year when forage fish availability was lower. Longer foraging trips can potentially limit the number of feeds that a chick receives if the adult is unable to increase the time spent away from the colony. The distances that murres and puffins traveled during this study suggest that they may be operating at a maximum threshold above which they would incur long-term reproductive costs.

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Chapter 4: Parental Diet Choices in Response to Forage Fish Availability

4.1. Abstract

I studied the prey preferences and prey switching behavior of Common Murres (*Uria aalge*) and Atlantic Puffins (*Fratercula arctica)* during two years of different forage fish availability, characterized as good (2004) and poor (2005) food years. Murres' preference for large capelin (relative to small capelin) increased from 2004 ($\alpha_{1,2} = 1.9$) to 2005 ($\alpha_{1,2} = 47.8$) despite a greater than 50-fold decline in the availability of large capelin, resulting in negative prey switching. Puffins exhibited a complete shift in their choice of prey between years: 2004 (98 % FO for sandlace) and 2005 (78.7% FO for large capelin) and showed a strong preference for large capelin ($\alpha_{1,2} = 100.2$) in 2005. Specialization for energy rich prey is a predicted response of central place foraging theory that states as travel distances increase, predators optimize their net energetic intake by selecting prey with higher energy values. The results of this study support this prediction and also suggest that murres and puffins exhibit discriminating diet choices when forage fish availability is low in order to optimize their foraging efficency.

4.2. Introduction

Seabirds that rely on unpredictable and ephemeral prey must decide continuously about where to forage, for how long and which prey to select (MacArthur and Pianka 1966; Stephens and Krebs 1986), and maintaining current information about the status of potential prey species facilitates adaptive decision-making. This is more challenging when seabirds are breeding on land and they are physically separated from their prey for extended periods. In addition, central place foraging increases time and energy investments thereby limiting the amount of available time/energy to sample their foraging environment and maintain current knowledge of prey conditions (Orians and Pearson 1979).

Seabirds employ a variety of foraging tactics to cope with the challenges of self-and-offspring provisioning during breeding that are influenced by the physiological and life history traits of the predator as well as the biological and behavioral characteristics of the prey they exploit (Obst et al 1995; Shaffer et al. 2001; Davoren et al. 2003). One strategy is to specialize on one or very few prey species (Fryxell and Lundberg 1994). The advantage of specializing is that a predator can minimize the amount of information (i.e. sampling) required to maintain current knowledge of foraging conditions, provided that the patterns of availability for the principle prey are relatively stable over time. In addition, specializing on one or a few prey species narrows the tactics that a predator must learn to forage successfully. Alternately, a predator can forage more opportunistically and consume a variety of prey types (i.e. a dietary generalist). While

there are obvious advantages to this strategy in terms of a seabird's flexibility to fluctuations in prey availability and abundance, there is potential to incur information costs associated with the additional time required for the predator to sample and maintain current knowledge of more than one prey species (Dall and Cuthill 1997). This is particularly important if different prey require different foraging tactics or skills to capture.

The generalist foraging strategy is often associated with prey switching behavior which describes the scenario in which a predator feeds disproportionately on the most abundant prey (P_1) and switches to an alternative prey (P_2) when the relative density of P_1 changes and declines below a threshold density of P_2 (Murdoch 1969; Murdoch et al. 1975). The behavioral mechanisms that lead to prey switching are elusive and require insights into the behavior of both the predator (i.e. preferences) and the prey (i.e. availability). The concept of prey switching in the seabird literature is often used to describe a change of prey species in the diet over time (e.g. Suryan et al. 2000; Lehikoinen 2005; Abraham and Sydeman 2006) rather than the classical definition of prey switching (Murdoch 1969) that explores the functional response of seabirds to changes in the density of their prey. While prey preferences and prey switching are influenced by prey availability and the pressure to forage optimally, other factors not related to behavior can influence these behaviors such as morphology (e.g. gape size; Schmitt and Holbrook 1984). In the context of this study however, I am interested only in those foraging tactics used by seabirds to cope with shifts in prey availability.

Assessments of the prey preferences and switching behavior also provide useful and much needed information regarding potential bias in studies that use seabirds as

indicators of changes in local fish composition, abundance and distribution. Strong dietary preferences are indicative of non-random sampling by seabirds that violate the assumptions required to accurately assess changes in prey availability from seabird diets; unless functional responses can be elucidated (Harding et al. 2007). The conditions under which seabirds switch between prey types is not well known and as a result their dietary indices of changes in prey availability can be confounded (Montevecchi 1993). Assessing the foraging decisions of seabirds with different foraging strategies is useful for understanding the ecological relationships between changes in prey availability and reproductive success (Vader et al. 1990; Barrett 2002).

In this chapter, I assess the prey preferences and prey switching behavior of provisioning murres and puffins at Funk Island through a comparison of the relative use (i.e. consumption) of important forage fish species with their relative availability in the environment. My primary objectives are: 1) to compare the relative preferences of parental murres and puffins during chick rearing at Funk Island in 2004 and 2005; 2) to investigate whether the prey preferences of parental murres and puffins change in response to changes in the relative densities of the most important prey in their diets (i.e. prey switching) and 3) to discuss the mechanisms that form the diet choices of murres and puffins.

4.3.   Methods

4.3.1.   Estimating diet and prey availability

The composition of murre and puffin chick diets was determined from parental prey deliveries collected at Funk Island during 2004 and 2005. Parental prey loads were collected over eight days in 2004 (n = 163 prey loads for murres; n = 62 for puffins) and over ten days in 2005 (n = 110 for murres; n = 47 for puffins). Murre prey loads were collected by intercepting adult murres with a 3 m pole-net as they returned to the colony from foraging trips. Prey loads were collected from adult puffins after foraging trips by intercepting them at burrow entrances using a large ground net (approximately 5 x 20 m). Puffins dropped their prey loads after several attempts at entering their burrows and then flew off.

The dominant prey species in the diets of murre and puffin chicks are described according to percent frequency of occurrence (% FO), an index that calculates the percentage of all prey loads containing one or more individuals of prey category *i* (Pierce and Boyle 1991). 95% confidence intervals were constructed by re-sampling the original diet observations 50,000 times (Efron and Tibshirani 1993). When there is no overlap in the confidence intervals representing the different prey categories, the percentage that each prey contributed to the diet in a given year is significantly different.

Forage fish availability was estimated from systematic trawls over a meso-scale vessel survey during 8-17 August in 2004 and 15-22 August in 2005. The spatial scale of the survey was designed to encompass the maximum foraging range of murres and puffins from Funk Island. Fish samples were collected using the International Young

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Gadoids Pelagic Trawl (IYGPT), a standard research trawl designed to catch pelagic juvenile gadoids (n = 45 trawl sets in 2004 and n = 49 trawl sets in 2005). Density was calculated as the total number of prey i divided by the area (km^2) swept by the trawl (area km^2 = distance towed 2.8 km X mean horizontal net opening 9.3 m = 0.026 km^2). The arithmetic mean was used to estimate density as it is deemed to be a robust abundance estimator for trawl catch data that are not log normally distributed (Myers and Pepin 1990). The Lilliefors test for normality (Statistica software) on the non-zero trawl estimates indicated that capelin did not follow a log normal distribution in 2004 ($p < 0.05$) or 2005 ($p < 0.05$).

Capelin in the trawls are described according to size classes rather than maturity stages (i.e. gravid versus spent): 1) to avoid inaccurate representations of the availability of gravid versus spent capelin that could potentially arise due to small lags in sampling dates for diets and forage fish density and the highly transient nature of maturity stages in capelin and; 2) to investigate the role of prey size in preference and prey switching behavior. Capelin were characterized according to two size-classes that included small (100-140 mm) and large (> 140mm) capelin corresponding roughly to the 1-2 and 3-4 year olds in the population (Carscadden et al. 2001). Capelin that were < 100 mm are not considered suitable prey for murres (Barret 2002; Davoren and Montevecchi 2005) but are occasionally present in puffin chick diets and, therefore, were incorporated into a separate category defined as 'larval prey' which describes prey loads consisting of quantities of 0-group fish and invertebrates. Sandlance measuring less than 30 mm were also included in the 'laval prey' category but all other sandlance (i.e. > 30 mm with no maximum size limit) were considered separately. Sandlance develop into juveniles with

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adult coloration when they are only a few centimeters long (29 mm for *Americanus*;

Smigielski et al. 1984) at which point they exhibit schooling behavior and like adults,

begin burrowing into the sand during inactive periods (Robards et al. 1999). Given that

the appearance and behavior of juvenile and adult sandlance are similar which likely

influences a puffin's ability to detect and discriminate them from other prey, smaller

sandlance (30 – 60 mm) are considered in the same category as larger individuals (60 -

115 mm).

4.3.2. *Prey preference and prey switching*

Prey preference reflects the likelihood of a given prey being chosen over   others

that are equally available (Murdoch 1969; Manly et al. 1972; Murdoch et al. 1975;

Chesson 1978, 1983). Preference implies a multi-prey species scenario in which the

predator has a number of prey options available and therefore reflects a 'relative

preference' (Koen-Alonso 2007). I assessed the relative pairwise preferences of murres

and puffins in 2004 and 2005 using an index derived by Manly et al. (1972) and further

developed by Chesson (1978, 1983) that relates the relative proportion of a given prey in

the diet to its relative availability in the environment as:

$$P_1/P_2 = \alpha_{1,2} N_1/N_2 \qquad \qquad \textbf{equation} \qquad \textbf{4.1}$$

where P_1 and N_1 are the proportional consumption and density of prey 1 respectively, and

$\alpha_{1,2}$ is a proportionality constant that measures the "pairwise relative preference" of P_1

with respect to P_2. In graphical terms, P_1/P_2 as a function of N_1/N_2 will produce a line that passes through the origin where the slope of the line is equal to the pairwise relative preference, denoted as $\alpha_{1,2}$ (Figure 4.1). When the consumption ratio P_1/P_2 is equal to the ratio of prey available N_1/N_2, there is no preference for prey 1 relative to prey 2 and the slope of the line (i.e. the relative preference) equals 1 and both species are equally preferred (Figure 4.1: blue line). Alternately when the diet is biased in favor of one of the two prey, the slope of the line increases above or below 1 depending on the orientation of the preference (Figure 4.1: red line).
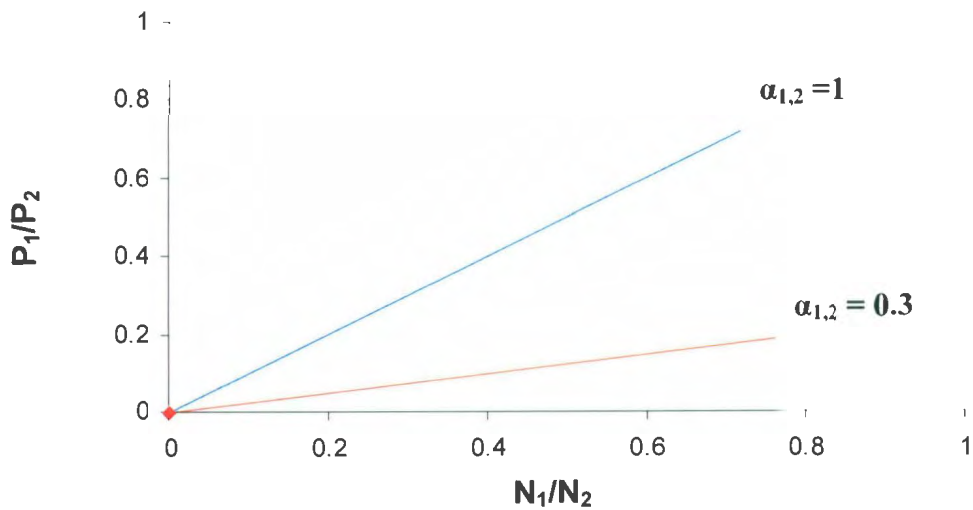
Figure 4.1. A conceptual illustration of relative pairwise preference in the case of equal preference ($\alpha_{1,2} = 1$: represented by the blue line) and when there is a higher preference for P_2 relative to P1 ($\alpha_{1,2} < 1$: red line).

The advantage of this relative index is that preference does not change with prey density unless there is a corresponding change in the behavior of the predator (Chesson 1978, 1983). This permits the detection of prey switching behavior by solving equation 1 for $\alpha_{1,2}$:

$$\alpha_{1,2} = P_1 N_2 \ / \ N_1 P_2 \qquad\qquad \textbf{equation 4.2}$$

When the consumption ratio (P_1/P_2) changes as a consequence of a change in the prey density ratio (N_1/N_2), $\alpha_{1,2}$ will remain constant indicating no prey switching. In other words, given that $\alpha_{1,2}$ is the slope of the relationship between P_1/P_2 and N_1/N_2; multiple observations of $\alpha_{1,2}$ at different density ratios will align along a straight line that also passes through the origin when there is no prey switching (Figure 4.2). Alternately, when a change in the consumption ratio is not in proportion to a corresponding change in the prey density ratio, $\alpha_{1,2}$ will be variable (i.e. at each specific ratio of prey densities, $\alpha_{1,2}$ will be different) indicating prey switching. Therefore, a variable $\alpha_{1,2}$ will transform the linear relationship between these ratios into a non-linear one (Figure 4.2) thereby providing evidence of the presence of prey switching.
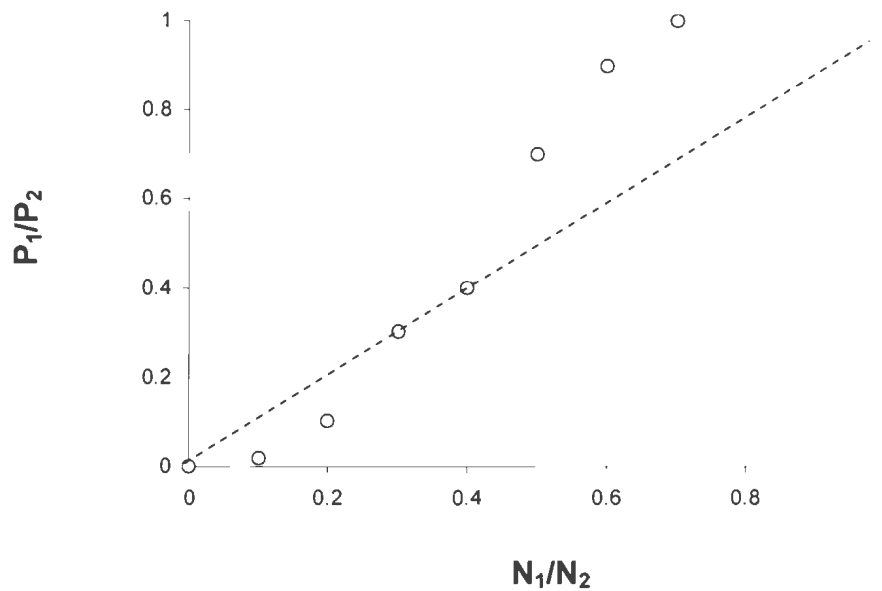
Figure 4.2. Conceptual illustration of the classical form of prey switching (adapted from Murdoch 1969). The dashed line indicates the expected ratio in the diet in the case of no switching and the circles indicate the general form of the expected ratios when classical prey switching occurs.

4.4.   Results

4.4.1.   Forage fish availability

The overall availability of capelin in the size range consumed by murre chicks (i.e. > 100 mm) declined from 2004 (20410.7 ± 12684.9 above 60 m per km^2) to 2005 (3645.7 ± 1731.8 above 60 m per km^2; Figure 4.3). There was also a decline in the availability of large capelin in 2005 (129.7 ± 45.2 above 60 m per km^2) relative to 2004 (7022.6 ± 3996 above 60 m per km^2) as well as small capelin that declined from 2004 (13388.1 ± 8961 above 60 m per km^2) to 2005 (3516.0 ± 1772 above 60 m per km^2).

Small capelin were the most abundant size class of capelin available to murres and puffins in both years (Figure 4.3). Sandlance, the most important prey in puffin chick diets in 2004 experienced a decline in availability in 2005 (7.9 ± 3.4 above 60 m per km^2) from 2004 (723.4 ± 453.0 above 60 m per km^2) and in 2005 it was the least available of the prey types represented in puffin chick diets. Laval prey was the only prey category that increased in availability from 2004 ($2577.3.0 \pm 866.0$ above 60 m per km^2) to 2005 (9337.6 ± 3380.0 above 60 m per km^2). This increase in larval prey is largely due to an abundance of immature and larval capelin (i.e. < 100 mm) in 2005.
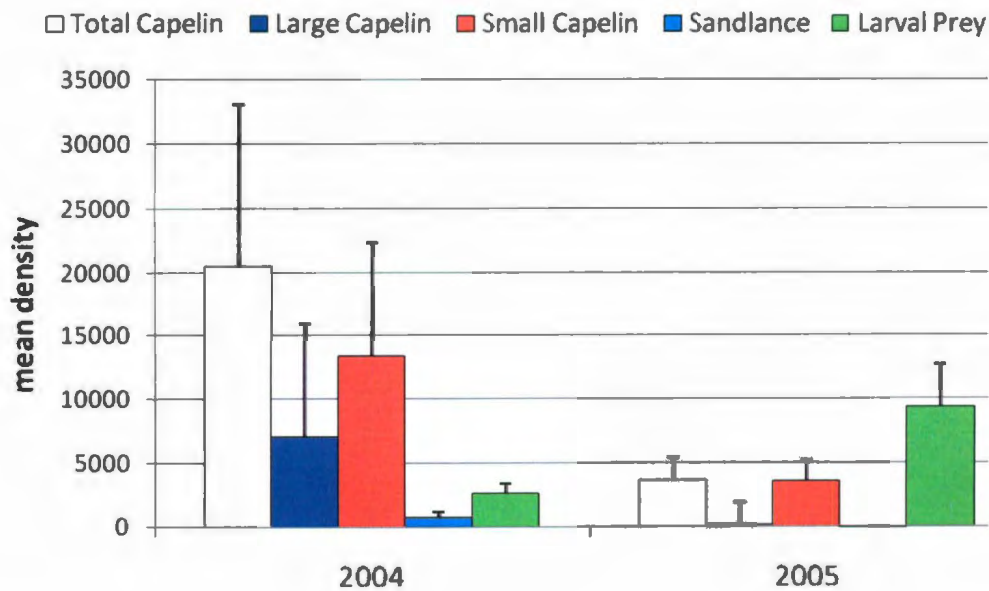
Figure 4.3. Mean densities of forage fish during 2004 and 2005 from trawl estimates during the meso-scale surveys. Forage fish categories include total suitable capelin (> 100mm), small capelin (100-140 mm), large capelin (> 140 mm) sandlance and larval prey. Values are mean (arithmetic) ± SE.

4.4.2. Murre chick diet composition

Murre chick diets were dominated by capelin > 100 mm in both years. In 2004, there was no difference in the consumption of large (49.7 % FO) and small (50.3 % FO) capelin (Figure 4.4; note overlapping CI) but the consumption of 'other prey' (1.3 % FO) was significantly lower. During 2005, large capelin were consumed in significantly higher proportions (62.9 % FO) relative to small capelin (36.2 % FO) and other prey (capelin < 100 mm; 0.9 % FO) despite a corresponding decline in their availability.
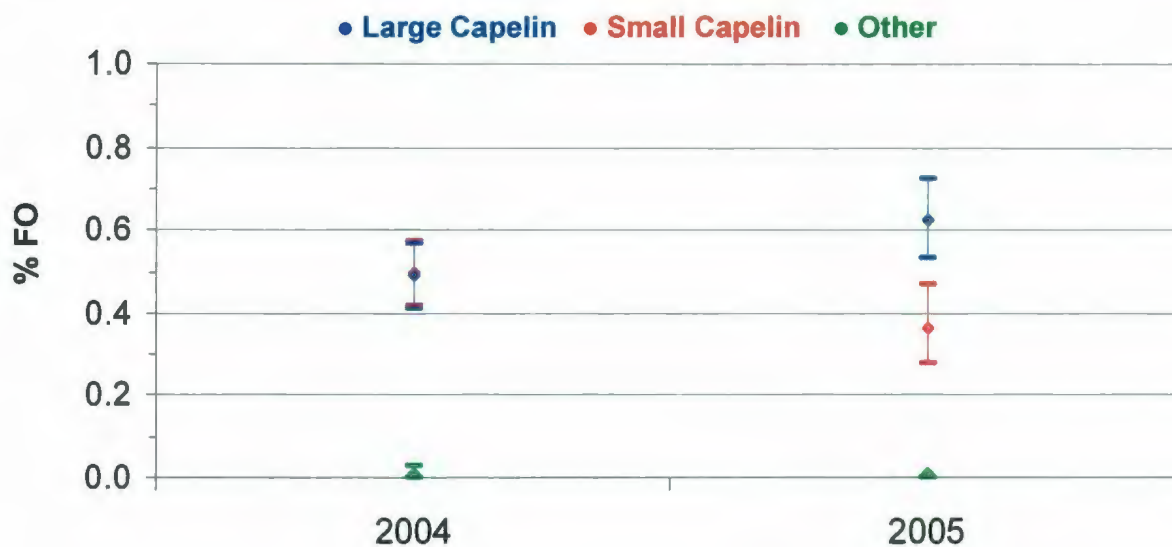
Figure 4.4. Composition of murre prey loads in 2004 (n = 153) and 2005 (n = 105) according to prey categories (i.e. large and small capelin and other prey) by frequency of occurrence percentage (%FO). Bars indicate 95% CI.

4.4.3. Puffin chick diet composition

The composition of prey types in puffin chick diets was very different between years (Figure 4.5). In 2004, puffin chicks consumed sandlance (98.0 % by frequency of occurrence) and larval prey (28.6 % FO) with significantly higher proportions of

sandlance relative to larval prey (Figure 4.5). In 2005, large capelin were the most common prey in puffin chick diets (78.7% FO) and were consumed in significantly higher proportions relative to all other prey categories (small capelin, sandlance and larval prey; Figure 4.5). There were no significant differences in the consumption of sandlance, small capelin and larval prey in 2005.
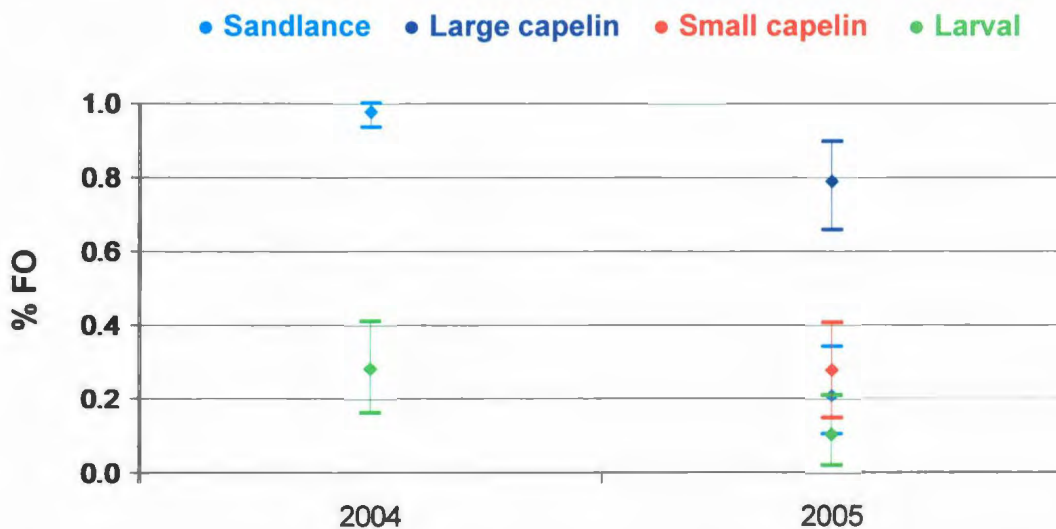
Figure 4.5. Composition of prey types in puffin prey loads in 2004 (n = 49) and 2005 (n = 47) according to percent frequency of occurrence (%FO). Bars indicate 95% CI.

4.4.4. Murres: Relative prey preferences and prey switching behavior

Murres preferred large capelin relative to small capelin in 2004 ($\alpha_{1,2}$ = 1.9) and 2005 ($\alpha_{1,2}$ = 47.8; Figure 4.6). Even though the consumption of large capelin was slightly lower than the consumption of small capelin in 2004 (Figure 4.4), there was a preference for large capelin because its relative availability was approximately half that of small

capelin. The relative consumption of large capelin increased in 2005 from the previous year, in association with a corresponding decline in the relative availability of large capelin from 2004 to 2005. This result is consistent with negative prey switching behavior, whereby a predator responds to a decrease in the relative abundance of a given prey by consuming relatively more of it and consequently less of the other prey (Figure 4.6).
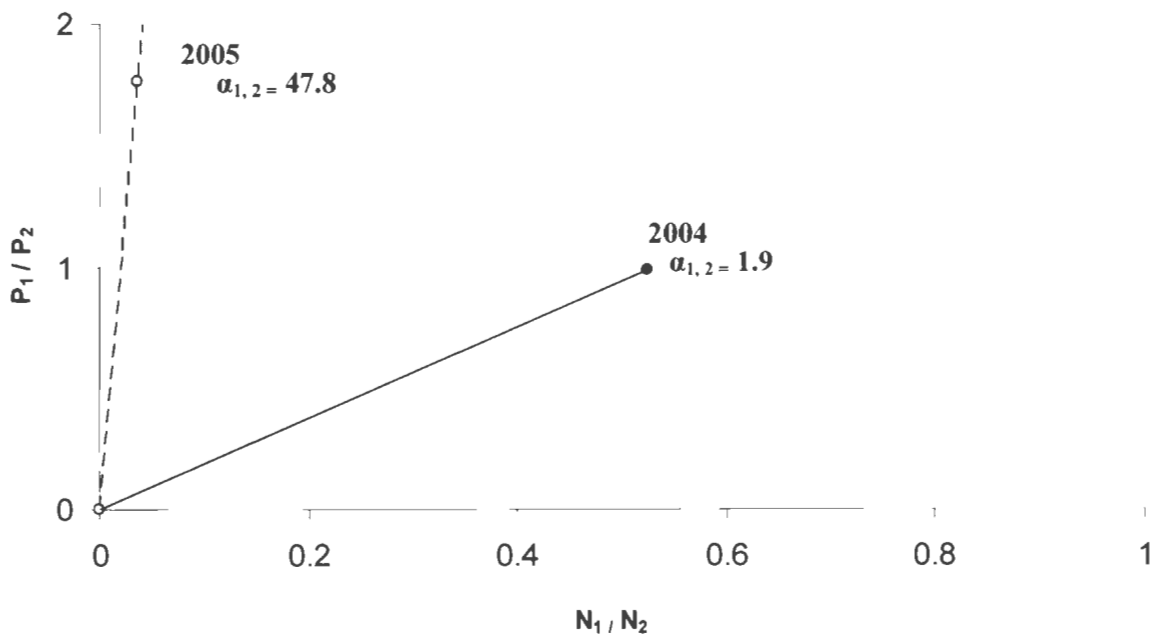
Figure 4.6. Murres' preference for large capelin relative to small capelin in 2004 (solid circle) and 2005 (open circle). The lines indicate the expectation for multiple observations of $\alpha_{1,2}$ under the hypothesis of no prey switching based on the relative preferences estimated for 2004 (solid line) and 2005 (dashed line). It is clear that these two observations do not follow a linear trajectory, providing a clear indication of prey switching.

Although Figure 4.6 clearly indicates negative prey switching, if the high variability associated with the prey density estimates are considered, it is possible that this

apparently clear pattern can be obscured. To address this point, I ran a Monte Carlo simulation to generate an approximate distribution for the ratio between the relative preferences in 2004 and 2005 ($\alpha_{1,2}$ 2004/ $\alpha_{1,2}$ 2005). This distribution can then be used to evaluate the probability of the ratio ($\alpha_{1,2}$ 2004/ $\alpha_{1,2}$ 2005) being larger or smaller than any given value. If there were no differences in relative preference between years, the expectation would be that the probability of a ratio being larger than one should be similar to that of a ratio smaller than one.

The data used in the Monte Carlo simulation were assumed to be normally distributed based on the central limit theorem (Sokal and Rohl 2003). To avoid unrealistic results (i.e. negative densities), these distributions were truncated according to reasonable expectations of the data. The diet values were bounded by 0 and 1 given that the data are relative proportions (by number) and the prey density estimates were bounded by 0 and an upper value that was 10 times the estimated mean. Table 4.1 shows the values used in the Monte Carlo simulations.

Table 4.1. Parameter estimates for Monte Carlo simulation to test the differences in murres' relative pairwise preferences of large capelin (P_1) relative to small capelin (P_2) between years.

Year	Prey	Proportion %FO	Precision (1/VAR)[a]	Diet Bounds	Mean Density	Precision (1/VAR)	Density Bounds
2004 n = 151	Large Capelin	0.497	633.5	0, 1	7022.6	0.000000001	0, 70000
	Small Capelin	0.503	625.1	0, 1	13388.1	0.000000003	0, 140000
2005 n = 104	Large Capelin	0.635	457.7	0, 1	129.7	0.00001	0, 1300
	Small Capelin	0.365	463.5	0, 1	3516.0	0.000007	0, 3500

[a] values of variance generated from 50,000 bootstrap of the original diet observations

The probability of the outcome of the relative pairwise preference ratios being less than one (i.e. $\alpha_{1,2}\,2004/\,\alpha_{1,2}\,2005 < 1$) was 96.4%. A plot of the frequency distribution of the ratios for ($\alpha_{1,2}2004/\,\alpha_{1,2}\,2005$) shows that majority of the ratios were distributed below one (Figure 4.7), thus supporting the initial finding that murres' exhibited negative prey switching behavior (i.e. preference changed in response to a change in prey density).
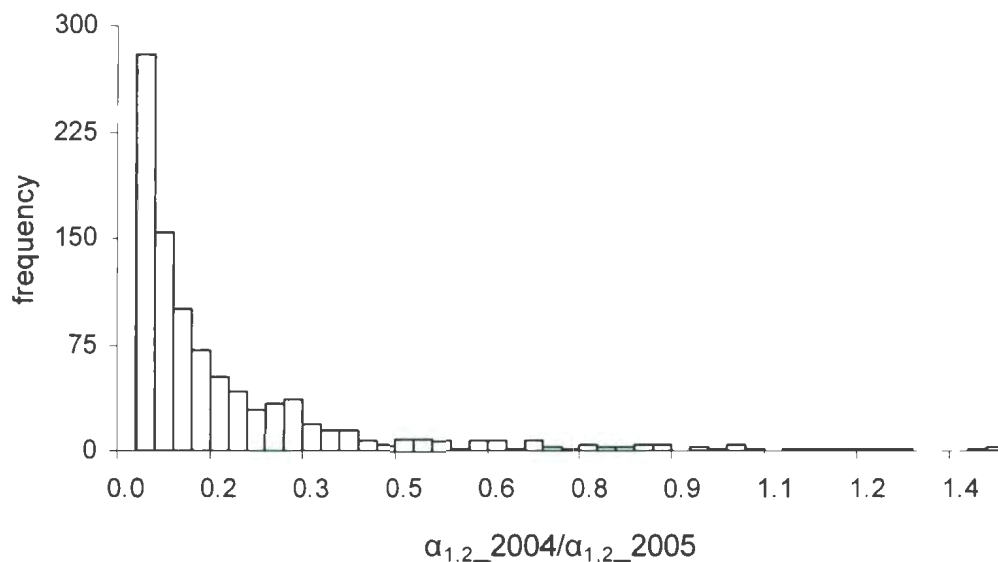
Figure 4.7. Distribution of the relative preference ratios ($\alpha_{1,2}\_2004\,/\alpha_{1,2}\_2005$) obtained from the Monte Carlo model from 50000 simulations.

4.4.5. Puffins: Relative prey preference and prey switching behavior

Puffin chicks consumed sandlance and larval prey in 2004 and there was a strong preference for sandlance relative to larval prey ($\alpha_{1,2} = 26.9$; Table 4.2). Given that puffins did not consume any capelin in 2004, I was unable to measure their preference for sandlance relative to capelin in that year. However, the fact that puffins fed sandlance to

their chicks when both prey were available implies a preference for sandlance over capelin, at least in the case where overall prey availability is high. Puffins consumed both large and small capelin in 2005, but similar to murres there was a very strong preference for large capelin ($\alpha_{1,2}$ = 100.2; Table 4.2). Unfortunately, I was unable to quantify puffin prey switching behavior because: 1) capelin were not present in the diets in 2004 and 2) sandlance availability was too low in 2005 to accurately estimate relative preference. Despite this, it is apparent that puffins underwent a change in their diet choices between years and that this shift was associated with the decline in sandlance availability in 2005.

Table 4.2. The relative pairwise preferences of puffins in 2004 and 2005 for the most common prey categories in puffin chick diets in these years.

YEAR	PREY CATEGORIES	PAIRWISE RELATIVE PREFERENCE
2004	Sandlance (P_1) vs Goop (P_2)	$\alpha_{1,2} = 26.9$
2005	Large capelin (P_1) vs Small capelin (P_2)	$\alpha_{1,2} = 100.2$

4.5. Discussion

4.5.1. Diet choices of parental murres

In this study, the relative consumption of large capelin, the preferred prey of murres in both years, increased as its relative availability declined, resulting in negative prey switching behavior. Reports of negative prey switching are uncommon in the literature (but see Rindorf et al 2006) and to my knowledge has never been documented for seabirds. However, the behavior is likely a consequence of central

place foraging (Orians and Pearson 1979) and therefore may be an important strategy for seabirds during breeding, and in particular for species that undergo long and/or energetically costly foraging commutes.

Central place foraging theory predicts that the prey energy selected by a predator increases as distance traveled from the central place increases (Orians and Pearson 1979). The results of this study strongly support this prediction, and explain the murres' strong preference for large capelin in 2005 that was extremely scarce and presumably difficult to find. In 2005, the maximum foraging distances of murres at Funk Island was 50% greater than during 2004 (from maximum 60 km in 2004 to 90 km in 2005; see Chapter 3) and was associated with an order of magnitude decline in the availability of suitable capelin (> 100 mm). Consequently, murres expended significantly more energy while foraging in 2005 and in order to compensate for this increase in expenditure, they had little choice but to select the highest energy prey available to them, which in 2005 was large capelin. By contrast in 2004, when the murres' maximum foraging distances were 50% shorter, small capelin (100-140mm) that were nearly twice as abundant relative to large capelin, were presumably sufficient to cover the cost of foraging. While the intrinsic profitability of a small capelin would presumably not be different between years, its overall profitability is negatively influenced by the additional energy required to capture and deliver it to the colony. Therefore the net value of a small capelin would have been lower in 2005 when the energy required to locate it was 50% greater.

This study also suggested that murres might exhibit a less specialized strategy when capelin is abundant and the risk of hunger or poor reproductive success is reduced. Murres consumed small and large capelin in relatively equal proportions in 2004 even though there appeared to be no shortage of large capelin. On the other hand, this might also suggest that murres are less capable of discriminating between size classes of capelin at higher densities.

4.5.2. Diet choices of parental puffins

The foraging behavior of puffins in both years did not conform to the behavior usually associated with generalist predators. While puffins did feed their chicks a variety of prey in both years, they exhibited very strong preferences (2004: sandlance and 2005: large capelin) and the preferred prey were consumed in significantly higher proportions to the other less important prey in their diets. Interestingly, the possible mechanisms behind the discriminating prey choices strategy of puffins in both years may be very different.

In 2004 puffins delivered sandlance to their chicks even though capelin was a much more abundant prey. High overall forage fish availability in 2004 would result in a decreased risk of hunger and therefore facilitate a specialized foraging strategy whereby puffins could allocate more 'free' time to finding their preferred prey. The energy densities of post-larval, young of the year sandlance (7.3 kJ. g^{-1}) exceed those of mature capelin (including gravid capelin; 4.6 kJ. g^{-1}; Montevecchi and Piatt 1984; Lawson et al. 1998) and therefore are likely preferred by parental puffin when they

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are available. In 2005, puffins' relative preference for large capelin was very strong (stronger than murres). However, in 2005 discriminating prey choices may have been associated with longer foraging distances resulting in puffins' choosing the most profitable prey available (i.e. large capelin) to compensate for the increase in energy expenditure. Furthermore, when foraging conditions are relatively poor, there may be an information cost (Dall and Cuthill 1997) associated with being a generalist whereby a puffin foraging on multiple prey types would incur additional time costs associated with sampling and maintaining current information about the status of multiple versus one prey type.

Whether or not puffins (seabirds in general) are more or less discriminating during poor years is an important behavioral question but addressing this question requires very high quality information about their prey field. Unfortunately this information is difficult to collect for puffins given the wide range of prey in their diets and the limitations of sampling gear for some forage species.

4.5.3. *Alternate explanations for prey switching*

The mechanisms that influence how a predator responds to changes in prey density are not always a case of a more or less prey resulting in a change in consumption rates. Changes in the predator's perception of prey or the detectability of prey at different densities can result in prey switching behavior that is not apparent from the analysis used in this study. For example, an alternative hypothesis to explain the prey choices of murres in 2004 (i.e. relatively equal proportions of

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small and large capelin) could be related to the decline in the ability of murres to discriminate between capelin sizes at higher densities. Alternately, the behavior of the prey (e.g. escape mechanisms) may vary at different densities that could influence the predator's ability to capture the prey (Turesson and Bronmak 2004). For example there is evidence that at high densities, sand lance schools compact in formation under the threat of predation and the large sand lance remain at the center of the school (Meyer et al. 1979) thereby affecting the success rate of a predator. Finally, prey characteristics (e.g. taste; Stanger-Hall et al. 2001 and detectability; Jackson 2000) can also influence a predator's preferences for a specific prey and need to be considered in the interpretation of prey preference and prey switching behavior.

An important consideration in the interpretations of prey switching is the recognition that sampling designs rarely (if ever) produce true availability estimates of the prey. While these biases are difficult to address due to the prohibitive logistics and cost associated with marine research programs, they should always be considered in the interpretation of findings. For example, in this study the catchability of different prey types and different prey densities are assumed to be constant. Yet if the sampling gear is less efficient at capturing prey at lower densities (e.g. large capelin in 2005) or at capturing a specific prey species (e.g. sandlance), estimates of relative preference for these prey could be exaggerated.

4.6. Conclusions

For murres and puffins to forage optimally during periods of reduced availability, they need to be very discriminating to ensure that they have the most profitable single prey item available. Given the high cost of flight for auks (Pennycuick 1987; Burger, 1991), longer foraging trips would have resulted in higher energy costs and thus greater pressure to deliver larger, more energetically profitable prey to the offspring. In this study, the highest quality prey was also the least available prey which resulted in negative prey switching by murres. This response could represent an important behavioral mechanism for seabirds at Funk Island where competition for food is high and foraging trips are long (Davoren and Montevecchi 2003).

These findings are significant in contributing to our understanding of the behavior mechanisms that form the diet choices of seabirds under variable food conditions. Discriminating foraging behavior is important to consider when using diets to assess changes in forage fish availability given that poor food years resulted in the paradoxical result of larger capelin in the diets. When the diets are evaluated in combination with information on foraging effort, given these finding, larger prey may be indicative of declines in overall forage fish availability. For puffins, the diets were good indicators of declines in sandlance availability, given that the occurrence of sandlance in the diets declined in 2005 when it became unavailable. However,

given the issues with low sandlance catchability in trawls surveys, this result deserves further investigation.

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Chapter 5: General Discussion

Reproduction is an intense time for seabirds that rear their young at large, dense, oceanic colonies. One of the greatest challenges for seabirds during reproduction is to find enough food to successfully raise offspring without compromising their own fitness. As long-lived animals with estimated life spans of about 20-35 years, seabirds can buffer fluctuations in of food resources by adjusting the time and effort allocated to foraging (Burger and Piatt 1990; Harding et al 2007) or alternatively pursuing long-term reproductive strategies (Ydenberg 1989; Ricklefs 1990).

The process of finding food during chick rearing involves different foraging tactics then during self-provisioning as seabirds become physically separated from their prey for extended periods of time. This makes finding prey much more difficult especially for piscivorous seabirds whose primary prey is ephemeral and patchy. This explains why many seabirds adjust the time of egg-laying to coincide with the seasonal peak of prey availability (Lack 1968; Harris and Birkhead 1985). In Newfoundland, the seabird breeding period has traditionally coincided with the peak availability of capelin *Mallotus villosus* which occurs in association with spawning (Cairns et al. 1987), however since the early 1990s, capelin spawning chronology has been delayed (Carscadden and Nakashima 1997) and less predictable between years (Penton 2006).

This thesis investigated how Common Murres and Atlantic Puffins, the most abundant auks in the Northwest Atlantic, negotiate the challenges associated

with reproduction and central place foraging in a cold ocean ecosystem, that has been undergoing major shifts in its demersal and pelagic foodwebs in recent decades, including significant changes in the biology and behaviour of capelin, the major forage fish (Carscadden et al. 2002).

5.1. Chick diets

The diets of murre chicks observed during this study were typical of the diets throughout the Northwest Atlantic with a strong bias for female capelin larger than 100 mm (Birkhead and Nettleship 1987; Burger and Piatt 1990; Piatt 1990; Davoren and Montevecchi 2003b, 2005). For murres that have a relatively short chick-rearing period (~ 3 weeks; Ainley et al. 2002), good temporal overlap in the inshore migration and spawning activity of capelin (estimated at approximately one month; Carscadden and Nakashima 1997) relative to chick-rearing is one of the most important factors determining peak food availability. There is a precedent for murres at Funk Island to adjust the timing of egg-laying in response to changes in the inshore arrival of capelin. Davoren and Montevecchi (2003b) documented a significant delay in the timing of breeding of murres at Funk Island (by approximately 3 weeks) corresponding to major delays (4-6 weeks) in the timing of capelin spawning in Newfoundland (Carsscadden and Nakashima 1997). Adjustments in breeding chronology represent a significant behavioural adjustment that highlights the importance of capelin to murres at

Funk Island and it also supports the premise that there is no suitable alternative prey to capelin for murres at the species largest colony.

The results of this study confirm previously held assumptions that puffins in Newfoundland do not rely on capelin to the same extent as murres (Russell 1998; Ballie and Jones 2004; but see Piatt 1987). Capelin were totally absent from puffin chick diets during one year when post larval, young of the year sandlance dominated their diets and puffin chicks performed equally well on sandlance (2004) and capelin (2005). Atlantic puffins provision their chicks nearly twice as long as murres (Harris and Birkhead 1985) and this increases the likelihood that the inshore migration of capelin will not fully overlap with chick rearing. Thus, it may be non adaptive for puffins to specialize on capelin.

Dietary overlap between sympatric, co-existing species has shown to be high when food is superabundant and low when food is scarce (Schoener 1982; Wiens 1989) implying increased competition for food when resources are very scarce. Interestingly, during this study, the opposite pattern was observed whereby the chick diets of murres and puffins converged (GOI_{adj} .838; see Chapter 2) during a year (2005) when forage fish availability was shown to be very low. Furthermore, the preferred prey choice for both species in 2005 was directed towards a prey item that was extremely scarce (large capelin) relative to other presumably suitable prey (e.g. small capelin). This finding suggests that while competition for food may have been high in 2005, murres and puffins were forced to share a common resource, despite its scarcity, due to 1) the absence of a suitable

alternative for puffins (i.e. sandlance) and 2) the need to select the highest energy prey available due to the long foraging trips in 2005.

5.2. Avian foraging distances

Information on forage fish availability collected from trawl surveys during this study show that forage fish availability can be highly variable between years and that parental murres and puffins adjust their foraging effort in response to this variability (see also Burger and Piatt; Harding et al. 2007) When seabirds experience moderate changes in the availability of prey during chick rearing they can respond by 1) increasing time and effort they allocate to locating their principle prey (Burger and Piatt 1990) or 2) selecting an alternative prey, if a suitable alternative is available (Bryant et al 1999, Ballie and Jones 2004). The results of this study showed that both murres and puffins significantly increased the distance that they traveled to find suitable prey during a year when forage fish availability was very low.

Murres that have a very specialized strategy and are single prey loaders are more constrained and have more difficulty coping with changes in capelin availability. Increasing their foraging effort is likely the only viable option for murres when capelin is scarce. This strategy is somewhat constrained at Funk Island where intense competition for breeding sites requires that parents spend a minimum amount of time to guard the nest to ensure a breeding site in the following year (Davoren et al 2003a). The overall impression from this study is

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that puffins are extremely robust and are well adapted to coping with extremes in the availability of forage fish. This resilience is attributed primarily to generalist strategy that allows to switch between different prey species and to carry multiple items during a foraging trip.

5.3.   Parental diet choices

This study documented negative prey switching by murres, a response associated with a significant reduction in the overall availability of suitable capelin in 2005 and a 50% increase in the maximum distance traveled from the colony to forage. Central place foraging predicts that predators must select prey with higher energy values as the distance from the colony to the foraging area increases (Orians and Pearson 1979). In this study, large female capelin was presumably the prey with the highest energy densities that were available in 2005 and as a result, they were preferentially selected by provisioning adults. This finding has implications for using murre chick diets as indicators of capelin abundance in the absence of independent measures of foraging effort and chick condition, given that murres were still capable of provisioning their chicks with suitable capelin even when capelin were extremely scarce.

Atlantic Puffins showed a complete shift in their choice of prey between years, delivering sandlance when it was available to them but choosing primarily large capelin and relatively small proportions of alternate prey types in 2005 when sandlance was unavailable. The importance of sandlance to puffins was an

important issue to come out of this thesis. There was some evidence that puffins prefer sandlance to capelin, based on the fact that they choose capelin over sandlance in 2004 when both prey were available. Unfortunately, I was unable to quantify this preference due to a lack of capelin the diets in one year and poor sample sizes of sandlance in the next year. The biology and recruitment of sandlance in the Northwest Atlantic has received little research attention because 1) it is difficult to monitor with tradition research tools and 2) it is not commercially harvested. The results of this thesis suggest that puffins can provide information on the recruitment of sandlance based on the fact that they seem to select it over other prey when it is available. Therefore, information on this forage fish (e.g. length frequency data) collected from puffin diets could be useful in monitoring the recruitment of these elusive forage fish.

5.4. Offspring condition

Murre fledglings were lighter at a given wing length in 2005 when large capelin was less available and murres traveled farther to provision their chicks. This suggests that the increase in foraging effort in 2005 due to poor capelin availability may have potentially constrained the provisioning capability of parental murres. The consequences of increased foraging effort could also potentially compromise the fitness of the breeding adults resulting in a decline in reproductive success at the world's largest colony. This effect could be measured

with information on adult body condition during years of low and high capelin availability as were observed during this study.

Considering that Funk Island is the largest murre colony in the world, it seems obvious that murres at this colony are well adapted to extreme variability in capelin. However, the murre population at Funk Island has stabilized during the last few decades while other murre colonies are undergoing population increases resulting from a reduction in bycatch mortality from the gill net fishery since the ground fish moratorium in 1992 (Robertson et al. 2004). Fledgling condition reported during this study were low relative to those documented at other colonies (Piatt 2002) and support previous reports of poor offspring condition at Funk Island (Davoren and Montevecchi 2003a). Lighter fledglings have been associated with lower survival and recruitment rates (Gaston 1997) and considering that Funk Island supports 75% of the Northwest Atlantic population, future research should be directed at estimating the survival and recruitment rates of juvenile murres at Funk Island.

Puffins in this study, exhibited no change in their condition between years despite significantly increasing their foraging range in one year (2005). These results suggest that puffins switch with relative ease between different prey and consequently are more resilient to changes in the availability of forage fish.

5.5. Conclusions

The dynamics of predator-prey relationships and the foraging behaviour of predators under different prey conditions are critical to understanding the potential effects of climate-induced changes on ecosystems. Seabirds are reliable samplers of forage fish populations that are key links in marine ecosystems, and their foraging behaviour can provide information about changes in marine food webs (e.g. Wanless et al. 2005). Yet, if seabird indicators are to be used effectively, bias associated with prey preferences, prey switching and buffering mechanisms need to be addressed. The consolidation of predator and prey information using the type of integrated approach (synoptic colony and vessel measurements) outlined in this thesis can provide valuable insights into the behavioural decisions that drive seabird responses to changes in forage fish communities.

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