

# The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions

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## Keywords

central place foraging; diet choice; fitness; foraging seabirds; parental behavior; prey availability.

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## Abstract

During reproduction, seabirds need to balance the demands of self- and offspring-provisioning within the constraints imposed by central place foraging. To assess behavioral adjustments and tolerances to these constraints, we studied the feeding tactics and reproductive success of common murrelets (also known as common guillemots) *Uria aalge*, at their largest and most offshore colony (Funk Island) where parents travel long distances to deliver a single capelin *Mallotus villosus* to their chicks. We assessed changes in the distance murrelets traveled from the colony, their proximate foraging locations and prey size choice during two successive years in which capelin exhibited an order of magnitude decrease in density and a shift from aggregated (2004) to dispersed (2005) distributions. When capelin availability was low (2005), parental murrelets increased their maximum foraging distances by 35% (60 to 81 km) and delivered significantly larger capelin to chicks, as predicted by central place foraging theory. Murrelets preferred large (> 140 mm) relative to small capelin (100–140 mm) in both years, but unexpectedly this preference increased as the relative density of large capelin decreased. We conclude that single prey-loading murrelets target larger capelin during long foraging trips as parents are 'forced' to select the best prey for their offspring. Low fledgling masses suggest also that increased foraging time when capelin is scarce may come at a cost to the chicks (i.e. fewer meals per day). Murrelets at this colony may be functioning near physiological limits above which further or sustained adjustments in foraging effort could compromise the life-time reproductive success of this long-lived seabird.

## Introduction

During breeding, seabirds have to balance the demands of self- and offspring-provisioning within the constraints imposed by foraging from a fixed colony site (Orians & Pearson, 1979). Seabirds rear their offspring on land and the additional time and energy associated with traveling between the colony and feeding areas represents a major limitation in their ability to adequately provision themselves and their offspring. This may be more intense at large colonies where prey depletion and competition can potentially result in longer foraging trips (Birt *et al.*, 1987; Lewis *et al.*, 2001). In addition, seabirds are physically separated from their food sources for extended periods making it difficult to maintain current information about prey availability.

Many seabirds exhibit considerable behavioral flexibility in response to moderate and short-term fluctuations in food availability. Picivorous auks, for instance, have flexible activity budgets (Burger & Piatt, 1990; Uttley *et al.*, 1994; Harding *et al.*, 2007; Ronconi & Burger, 2008), whereby parents modify foraging time at the expense of time at the colony to maintain normal provisioning rates. An alternate

strategy, consistent with expectations for long-lived seabirds (Stearns, 1992) is to maintain constant foraging effort in the face of declining food availability rather than compromise future reproductive success (e.g. chinstrap penguins; Croll *et al.*, 2006).

Many studies have investigated behavioral flexibility by seabirds, but much less is known about how foraging adjustments influence diet choices. A key prediction from central place foraging theory is that as travel distance increases, birds that carry prey in their bill will attempt to maximize the rate of energy provisioning to offspring by selecting larger, higher quality prey (Orians & Pearson, 1979). Consequently, parents are predicted to select different sized prey at varying distances from the colony.

We studied common murrelets (also known as common guillemots) *Uria aalge* at their largest North American and most oceanic colony (Funk Island, Newfoundland) where parents provision their chicks almost exclusively with a single female capelin (Davoren & Montevecchi, 2003; Burke & Montevecchi, 2008) that is carried lengthwise in the bill. Capelin has a primarily coastal distribution in Newfoundland during summer (Nakashima, 1992) resulting in long foraging commutes from this offshore colony (Davoren &

Montevecchi, 2003). Long foraging trips are costly for murre that expend considerable energy during flight (Birt-Friesen *et al.*, 1989) owing to wing design that is a compromise between aerial and underwater flight (Pennycuik, 1987; Burger, 1991). Moreover, as single-prey loaders, they are compromised in their ability to supplement the energy they can deliver to offspring during a foraging trip. The digestive anatomy of murre evolved to minimize mass (via rapid digestion) at the cost of digestive efficiency (i.e. energy that becomes available for metabolism) may also promote strong selectivity for high-quality prey that are readily digestible and provide optimal metabolizable energy (Hilton, Houston & Furness, 2000). These circumstances provide a compelling context in which to test behavioral adjustments of a central place foraging seabird to fluctuations in food availability.

We estimated the distances that parental murre traveled from the colony to forage (via vessel surveys around the colony) and their return directions to the colony (via 360° scans) during successive chick-rearing seasons in which capelin availability was very different. Using a pair-wise relative preference index (Manly, Miller & Cook, 1972; Chesson, 1978) we investigated whether changes in foraging effort influenced the murre's preference for different size classes of capelin, corresponding to immature (100–140 mm) and mature (>140 mm) capelin, respectively (Anderson, Dalley & Carscadden, 1999). Given the murre's reliance on capelin and their ability to adjust activity budgets, we expected that murre would adjust their foraging tactics (travel distances, search area) to find suitable capelin over moderate fluctuations in availability. Furthermore we expected that the size of the capelin delivered to offspring would reflect the effort invested in delivering it to the chick (i.e. larger capelin associated with greater effort). The biological consequences of these responses were examined by measuring inter-annual changes in the condition of murre fledglings. Finally we discuss how constraints at this globally significant colony determine the murre's ability to

adjust to uncertainty about prey and environmental conditions.

## Materials and methods

### Study area

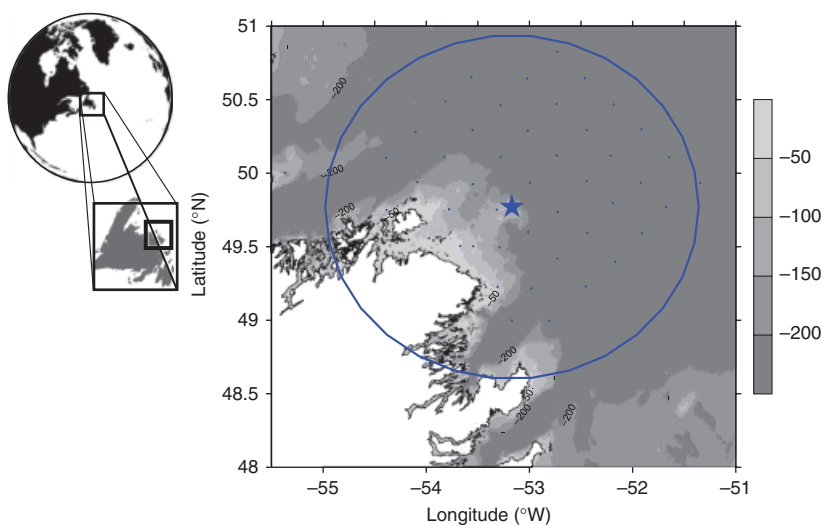
Research was conducted during 2004 (26 July–3 August) and 2005 (2–11 August) at the Funk Island Seabird Ecological Reserve (49°45'N, 53°11'W) located *c.* 60 km off the north-east Newfoundland coast in eastern Canada (Fig. 1). Funk Island supports an estimated 340 000–400 000 pairs of Common Murres, representing *c.* 75% of the north-west Atlantic population (Chardine *et al.*, 2003).

Vessel surveys were run in 2004 (8–17 August) and 2005 (15–22 August) aboard the Canadian Coast Guard research vessel *Wilfred Templeman*. Surveys encompassed a 360° area centered on Funk Island, extending to 130 km from the colony at its maximum extent (Fig. 1). The survey was designed to encompass the primary foraging area and maximum foraging range of murre at this large colony where foraging ranges likely exceed those estimates documented at smaller colonies (e.g. 80 km; Cairns, Bredin & Montevecchi, 1987).

### Prey availability

Murre at Funk Island very rarely deliver capelin smaller than 100 mm to their chicks (Davoren & Montevecchi, 2003; Burke & Montevecchi, 2008), hence we defined suitable capelin for murre to include only those that are equal to or longer than 100 mm.

The availability of suitable capelin was indexed using the standard mid-water International Young Gadoids Pelagic Trawl (IYGPT) along systematic sampling stations throughout the survey area (15 nm spacing; Fig. 1). The IYGPT samples pelagic prey in the upper 60 m of the water column where murre take most of their prey (Tremblay *et al.*, 2003).



**Figure 1** Chart of the study area off the north-east Newfoundland coast showing the Funk Island Ecological Reserve (blue star) and scope of the vessel survey during 2004 and 2005 (blue circle represents a 130 km radius around Funk Island), with the locations of the trawl sets indicated by the blue dots. Shaded depth contours (m) are shown in legend.

Though murres can dive considerably deeper than 60 m (Piatt & Nettleship, 1985; Burger, 1991), new information from time-depth recorders (Hedd *et al.*, 2009) indicate that 60% of the presumed 'chick-provisioning' dives of murres at Funk Island occur above 60 m (terminal dive depth: mean  $\pm$  SD = 46.7  $\pm$  40.1 m).

Density was estimated as the total number of suitable capelin sampled by IYGPT (60 m depth) over a mean horizontal area (0.026 km<sup>2</sup>), using the mean distance towed (standardized to 2.8 km) times the average horizontal opening of the net (9.3 m). Trawl catch data are commonly characterized by many zeros and extreme values, resulting in highly skewed distributions with large variance to mean ratios that likely reflect the patchy distributions. The arithmetic mean was used to estimate capelin densities, as it is the most robust abundance estimator for trawl catch data that are not log normally distributed (Myers & 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 ( $P < 0.05$ ). Distributions of suitable capelin over the survey area are illustrated using density contour maps (Surfer 8) by applying a smoothed kriging method to log-transformed volumetric capelin densities (log<sub>10</sub> number 10<sup>4</sup> m<sup>-2</sup>).

### Murre foraging patterns

During vessel surveys, murres were recorded continuously during daylight hours using standard strip methods (Tasker *et al.*, 1984). An observer on the vessel's bridge recorded murres to 300 m in a 90° arc from the bow to the port side. The distance (km) from the colony to individual bird locations was used to approximate the murres' foraging distances. Travel distances from the colony to foraging areas were assessed by constructing cumulative frequency distributions of the percentage of total murres plotted against distance from the colony. A pair-wise two-sample Kolmogorov–Smirnov test was used to detect inter-annual differences in the foraging distances of murres (Statistica software).

We used birds on the water as a proxy for foraging individuals, because birds spend considerable time on the surface following successful feeding bouts to digest (Ropert-Coudert *et al.*, 2004). While murres from a nearby colony (Cabot Island; 49°16'N, 53°28'W) could represent a small number of birds observed on the water; Funk Island birds outnumber these by an order of magnitude and account for the vast majority of birds in the study.

The flight directions of incoming flocks of murres were recorded during daily 360° scans in 2004 and 2005 to assess foraging areas. Many auk species at large colonies form conspicuous flocks when commuting between the colony and foraging areas and flight directions to and from the colony are useful indicators of where the birds have been foraging (Davoren, Montevecchi & Anderson, 2003). Observers on the highest point on the island recorded the number and return directions of murres within 45° sectors (eight in total) during 1-min intervals using compass binoculars. Three repetitions of the 360° scan were conducted

during a session (24–30 min). Wind speed (km h<sup>-1</sup>) and direction were recorded at the outset and after each session. The return directions of flocks are independent of wind direction and velocity below sustained speeds of 25 km h<sup>-1</sup> (Davoren *et al.*, 2003), so we did not include scans when sustained winds were higher than 25 km h<sup>-1</sup>.  $\chi^2$  analysis was performed on the percentage of total birds, by number within the north-east (0–90°), south-east (90–180°), south-west (180–270°) and north-west (270–360°) sectors to determine whether the direction of returning birds differed between years.

### Murre diet choices

We used a pair-wise relative preference index to test whether murres exhibited a preference for capelin of two different size classes (corresponding to maturity stages). Capelin in chick diets and trawl data were classified according to large (>140 mm) and small (100–140 mm) size classes that approximate 'mature' and 'immature' capelin, respectively. These classifications were based on capelin life-history characteristics and the sizes of capelin landed by murres at Funk Island (i.e.  $\geq 100$  mm). Capelin larger than 140 mm are considered to be 3 years or older (Anderson *et al.*, 1999), the age of maturity (Winters, 1982). At <140 mm, capelin are typically younger than 3 years and considered immature (Anderson *et al.*, 1999).

The pair-wise relative preference index relates the relative proportion of a given prey in murre chick diet to its relative availability in the environment as:

$$P_1/P_2 = \alpha_{1,2}N_1/N_2$$

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 'pair-wise relative preference' of  $P_1$  with respect to  $P_2$ . In this case,  $P_1$  refers to large capelin and  $P_2$  to small capelin, and therefore  $\alpha_{1,2} > 1$  indicates a preference for large capelin, 0 indicates no preference and  $< 0$  indicates a preference for small capelin.

To collect chick diets, a 3 m pole-net was used to intercept adult murres returning to the colony with fish. Sampling occurred over 9 days (26 July–3 August) in 2004 ( $n = 163$  prey) and 10 days (2–11 August) in 2005 ( $n = 110$  prey). The composition of large and small capelin in murre chick diets was described according to per cent total number (% $N$ ) and 95% confidence intervals were constructed by re-sampling original diet observations 50 000 times (Efron & Tibshirani, 1993). Confidence intervals were used to test differences in diet composition between years. Non-overlapping confidence intervals indicated that the percentage that each size class of capelin contributed to diet differed significantly within a given year.

### Murre fledgling condition

Murre fledglings were intercepted in dip nets as they jumped from ledges on their way to sea with an accompanying male parent over three nights in 2004 (27, 30–31 July;  $n = 40$ ) and

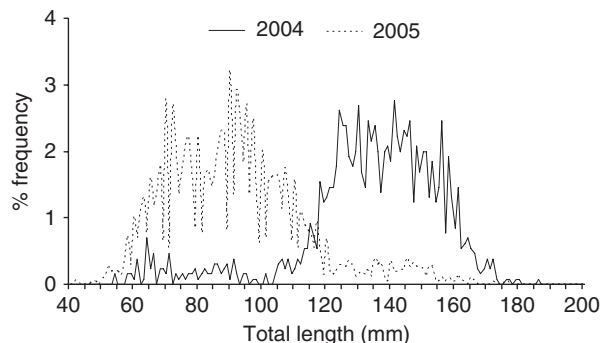
two nights in 2005 (2, 6 August;  $n = 30$ ). They were weighed in nylon bags with a 500 g Pesola spring scale (Pesola AG Baar, Switzerland) and flattened wing chord was measured to the nearest millimeter with a wing ruler, after which they were immediately released into the ocean. Offspring condition was gauged using a 'developmental condition index' (Bertram *et al.*, 2002) that relates body mass (g) to wing length (mm). Differences in developmental condition indices were assessed with an ANCOVA (see Burke & Montevecchi, 2008).

## Results

### Inter-annual capelin availability

Capelin was the most abundant fish species sampled around Funk Island, representing 86.8 and 92.4% of total catch (by numbers) in 2004 and 2005, respectively. Capelin was significantly ( $F_{1,4068} = 2783.6$ ;  $P < 0.0001$ ) larger in 2004 ( $132.8 \pm 22.1$  mm) relative to 2005 ( $92.5 \pm 23.0$  mm). While the length range of capelin sampled by the IYGPT ( $< 50$  to  $> 170$  mm) was similar in both years, their length frequency histograms differed, with most capelin measuring  $> 120$  mm in 2004 and  $< 120$  mm in 2005 (Fig. 2).

The density and distribution of suitable capelin (i.e.  $\geq 100$  mm) was also very different between years with a sixfold decline in average density above 60 m in the water column from 2004 (mean  $\pm$  SE:  $20\,410.7 \pm 12\,684.9$  km $^{-2}$ ) to 2005 (mean  $\pm$  SE:  $3947.4 \pm 1881.0$  km $^{-2}$ ). Capelin ( $\geq 100$  mm) had a predominantly inshore distribution in 2004, with high densities occurring at the southern extent of the survey area (Fig. 3a). In 2005, capelin ( $\geq 100$  mm) was highly dispersed over most of the survey area and no notable concentrations were available to murre (Fig. 3b). Large ( $> 140$  mm) and small capelin (100–140 mm) was available in both years but large capelin exhibited a 50-fold decrease in density from 2004 (mean  $\pm$  SE:  $7022.6 \pm 3996$  per km $^2$ ) to 2005 ( $120.6 \pm 48.8$  per km $^2$ ). Moreover, large capelin was highly dispersed in 2005 and no large capelin was found concentrated over the survey area (Fig. 3d).



**Figure 2** Length frequency distributions of capelin *Mallotus villosus* sampled by IYGPT trawl during 2004 ( $n = 1302$ ) and 2005 ( $n = 2767$ ). IYGPT, International Young Gadoids Pelagic Trawl.

### Murre foraging patterns

A significantly higher proportion of murre foraged farther from Funk Island in 2005 ( $D_{\max} = 0.02$ ,  $P < 0.001$ ; Fig. 4). Mean foraging distances increased from (mean  $\pm$  SD:  $46.5 \pm 18.5$  km in 2004 to  $58.11 \pm 27.2$  km in 2005). Maximum distances traveled by 75% of murre recorded on vessel surveys increased from 60 km in 2004 to 81 km in 2005 (Fig. 4), representing a 35% increase in maximum distance traveled from the colony to forage.

A major shift in the murre's foraging areas occurred between years as indicated by the directions of birds returning to the colony. During 2004, 65% of murre returned from the south-west ( $180$ – $270^\circ$ ; inshore) whereas in 2005, murre returned to the colony from all directions (Fig. 5).

### Murre diet choices

Consistent with long-term dietary trends at Funk Island, murre delivered primarily female capelin  $\geq 100$  mm to chicks (Davoren & Montevecchi, 2003). Significantly larger capelin were delivered in 2005 (mean  $\pm$  SD;  $143.5 \pm 11.4$  mm) compared with 2004 ( $140.1 \pm 13.9$  mm;  $F_{1,254} = 4.7$ ,  $P = 0.03$ ), even though capelin available to murre in 2005 was significantly smaller (mean  $\pm$  SD;  $116.5 \pm 16.2$  mm). Additionally, during 2004, the consumption of small (50.3% FO) and large (49.7% FO) capelin did not differ (Fig. 6; note CI). During 2005, large capelin was consumed in significantly higher proportion (63.5% FO) relative to small capelin (36.5% FO).

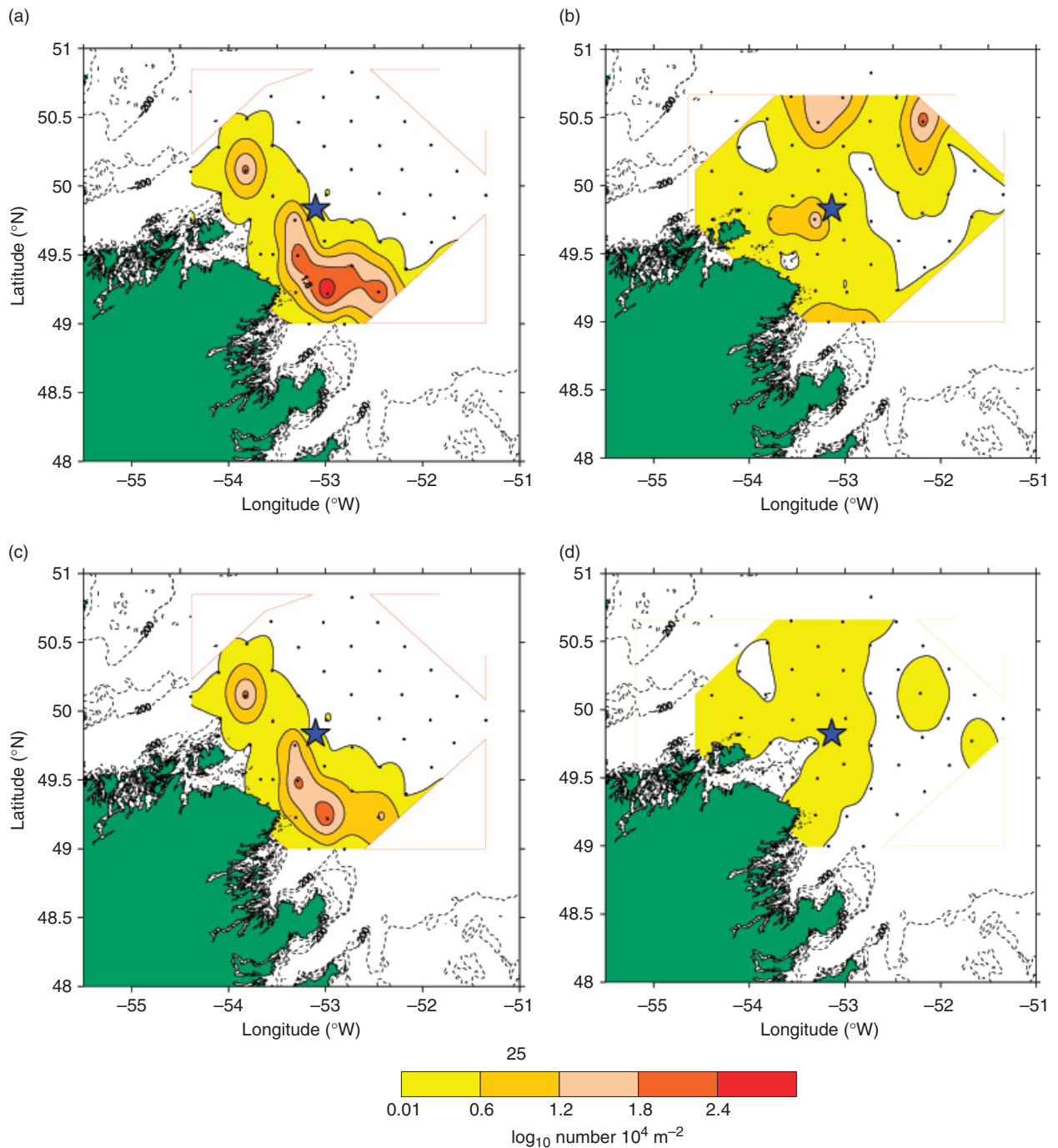
Pair-wise relative preference analysis indicated that murre preferentially selected large over small capelin in 2004 ( $\alpha_{1,2} = 1.9$ ) and in 2005 ( $\alpha_{1,2} = 55.1$ ; Table 1). Interestingly, the relative preference for large capelin was 29 times higher in 2005 despite the fact that the availability of large capelin within the murre's foraging environment was extremely low.

### Murre fledgling condition

Fledglings at given wing lengths were significantly heavier in 2004 ( $215.1 \pm 3.9$  g) compared with 2005 ( $203.0 \pm 4.6$  g;  $F_{1,68} = 4.1$   $P = 0.047$ ). Mean wing lengths did not differ between years (2004:  $68.9 \pm 5.5$  mm, 2005:  $67.7 \pm 6.0$  mm; ANOVA,  $P = 0.42$ ).

## Discussion

Capelin ( $\geq 100$  mm) density within the murre's foraging range around Funk Island varied fivefold between 2004 ( $20\,410 \pm 12\,684.9$ ) and 2005 ( $3947.4 \pm 1881.0$ ) and shifted from aggregated (2004) to dispersed (2005) distributions. In addition, capelin was significantly smaller in 2005. These differences were likely associated with inter-annual variability in the timing of capelin spawning ( $\sim 2$  weeks difference in peak spawning between 2004 and 2005; Penton, 2006) relative to the murre's chick rearing period. This variability reflects recent stochastic trends in capelin spawning behavior precipitated by an anomalous cold-water event in 1991 (Carscadden, Frank & Leggett, 2001).



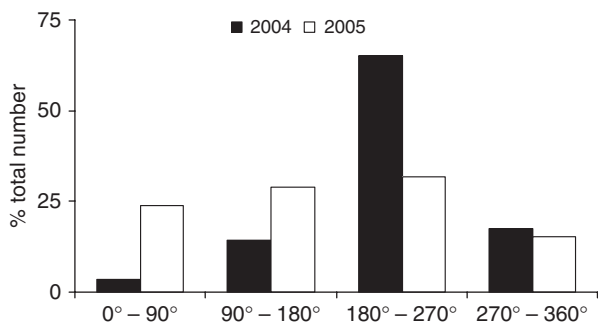
**Figure 3** Capelin *Mallotus villosus* distributions in 2004 and 2005 represented as volumetric density in upper 60 m of water column ( $\log_{10}$  number  $10^4 \text{ m}^{-2}$ ). Panels illustrate the distribution of all suitable capelin ( $\geq 100 \text{ mm}$ ) in 2004 (a) and 2005 (b) and large capelin ( $> 140 \text{ mm}$ ) in 2004 (c) and 2005 (d). Blue star represents Funk Island.

As predicted, murres flew 35% further from the colony to forage (60 to 81 km) and searched over more of the available foraging area (Fig. 5) in response to a fivefold decrease in suitable capelin density and a distributional shift. Density-dependent effects involving prey depletion, disturbance and

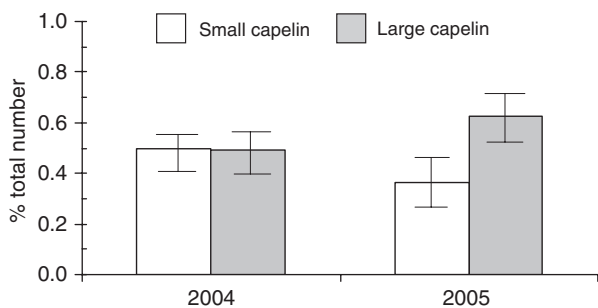
interference could contribute to long foraging trips (Birt *et al.*, 1987; Lewis *et al.*, 2001), yet we observed a substantial change in foraging distances during successive years in which density-dependent effects would remain constant. Inter-annual shifts in prey availability exert major influences



**Figure 4** Comparative cumulative frequency distributions of murre *Uria aalge* on water recorded from vessel surveys in avian foraging ranges in 2004 and 2005. Cumulative percentages of total numbers of murre are plotted against distance from Funk Island.



**Figure 5** Distributions of murre *Uria aalge* returning to Funk Island during 360° scans in 2004 and 2005. Data are per cent total number across north-east (0–90°), south-east (90–180°), south-west (180–270°) and north-east (270–360°) quadrants.



**Figure 6** Composition of murre *Uria aalge* prey loads in 2004 ( $n=153$ ) and 2005 ( $n=105$ ) according to capelin *Mallotus villosus* size classes (large and small) by percentage total number (%FO). Bars indicate 95% CI.



**Figure 7** Common murre *Uria aalge* colony at Funk Island, Newfoundland. Photo credit: W. A. Montevecchi.

on time and energy constraints and foraging distances (e.g. Garthe *et al.*, 2006) at this globally significant murre colony.

The murre's ability to adjust time budgets is well documented (Burger & Piatt, 1990; Monaghan *et al.*, 1994; Harding *et al.*, 2007), but our study is the first to show different diet choices in response to adjustments in foraging effort. Murre delivered larger capelin to chicks in 2005 when availability was low and maximum travel distances from the colony increased by 35%, a response predicted by central place foraging theory (Orians & Pearson, 1979). For single-prey loading murre, size is likely an important determinant in the selection of capelin whose lipid and energy values are an increasing function of size (Montevecchi & Piatt, 1984).

The murre also exhibited a preference for large, mature capelin (>140 mm) relative to small, immature (100–140 mm) capelin in both years. Interestingly, their preference for large capelin *increased* in association with a corresponding *decrease* in relative availability in 2005. The scarcity of large capelin in 2005 and the paradoxically high proportion of this prey in the chick diets suggests that murre were exploiting concentrations of large capelin not detected in the trawl survey (i.e. below 60 m). Capelin make extensive vertical migrations to surface waters at night (Davoren, Montevecchi & Anderson, 2006), so we expect that capelin sampled at night provide a representative sample of concentrations that are located in deeper waters during the day. Therefore if large capelin was located in deeper water (i.e. beyond 60 m) during daylight, we would expect a higher proportion of larger individuals in night catches relative to day catches. Contrary to this expectation,

**Table 1** Inter-annual values for the consumption and density of large capelin relative to small capelin used to calculate pair-wise relative preference of murre in 2004 and 2005

Year	Relative consumption of large capelin ( $P_1/P_2$ )	Mean (SE) density of large capelin ( $N_1/N_2$ )	Relative preference for large capelin ( $P_1/P_2 = \alpha_{1,2} N_1/N_2$ )
2004	0.50	7022.6 ± 3996	1.9
2005	0.63	120.6 ± 48.8	55.1

capelin captured at night was significantly smaller ( $X + \text{sd}$  length =  $90.6 \pm 20.3$ ;  $P = 0.001$ ) than capelin captured during the day ( $93.3 \pm 23.1$ ), suggesting that murre were not finding larger capelin in deeper water below 60 m.

The alternative explanation for discriminating prey choice by murre is explained by the fact that murre invested significantly more foraging effort in 2005 and to compensate they likely had little choice but to select the best prey for chicks (i.e. large capelin), regardless of availability. By contrast, when large capelin was abundant, murre consumed small and large capelin in relatively equal proportions in 2004 suggesting that they exhibit less discriminating prey choices when capelin is abundant and the risk of hunger or poor reproductive success is reduced. Our findings highlight the important role of adaptive prey choices in buffering offspring from short-term fluctuations in prey availability and enhance our understanding of behavioral mechanisms that drive prey choices by seabirds.

Murre fledgling condition in 2005 ( $203.0 \pm 4.6$  g) was low relative to other colonies even in extremely poor food years (e.g. 211 g: Hatchwell, 1991; 212 g: Uttley *et al.*, 1994). This finding suggests that additional time spent foraging came at a cost to offspring (i.e. fewer meals per day) that could not be reconciled by eating larger capelin. Murre in other regions also exhibit strong reliance on large and lipid-rich prey and major breeding failures have been associated with declines in prey quality (Wanless *et al.*, 2005) and abundance (Uttley *et al.*, 1994). As single-prey loaders that require rich prey for digestive efficiency (Hilton *et al.*, 2000), murre may be highly sensitive to declines in the availability of high-quality prey (Osterblom *et al.*, 2008) when foraging time is limited during breeding.

We suggest that longer foraging commutes during poor food years at this densely populated, offshore colony represents a substantial time-limiting factor in murre parents' ability to buffer offspring by increasing provisioning effort. This idea is supported by a recent study showing that murre at Funk Island forage throughout the night while murre at a nearby colony (Gull Island, ~100 000 pairs) spend this time resting (Hedd *et al.*, 2009). Consequently, parental murre at the species' largest North American colony could be functioning near maximum physiological capability above which further adjustments in foraging effort during periods of limited food availability would compromise the life-time fitness of parents (Stearns, 1992).

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