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

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Abstract.—We 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). Our 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 95.5% in 2005. The relative contribution of gravid capelin to murre chick diets decreased by an order of magnitude between years (41.1 and 4.9% 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. *Received 20 September 2007, Accepted 24 November 2007.*

Key words.—auks, chick diets, forage fish, offspring condition.

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 throughout the Northwest Atlantic provision their chicks with a variety of prey including capelin of all sizes and maturity stages, sandlance *Ammodytes* spp., 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 influence 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 = ~1,000 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. Central place foraging theory predicts that 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 movement of maturing 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 respond quickly to changes in ocean temperatures (Carscadden *et al.* 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 influenced their availability to seabirds (Carscadden *et al.* 2002). 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 following a southward shift in the distribution of capelin, murres and puffins switched to alternative prey species (e.g., Daubed Shanny *Lumpenus maculates* and 0-group *Ammodytes* spp. Bryant *et al.* 1999; Ballie and Jones 2004) without incurring any reproductive costs and murres also increased their foraging effort (Bryant *et al.* 1999). By contrast, murre chicks at Funk Island, the species' largest colony, exhibited a decline in condition over the decade (1990-2000) that was related to a corresponding decline in the size and nutritional quality of capelin in their diets (Davoren and Montevecchi 2003b). For murres that have a short chick-rearing period (~3 weeks; Ainley *et al.* 2002), good temporal overlap in the inshore migration and spawning of capelin is one of the most important factors determining suc-

cessful reproduction. By contrast, puffins provision their chicks nearly twice as long as murres (38-44 d; Lowther *et al.* 2002), and this increases the likelihood that a portion of the chick-rearing period will not coincide with capelin spawning (~2-3 week duration; Nakashima and Wheeler 2002; Penton 2006). Consequently it may not be adaptive for puffins to specialize on capelin.

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 and overlap of parental prey deliveries to murre and puffin chick diets during 2004 and 2005 at Funk Island; and, 2) the performance of murre and puffin chicks between years.

STUDY AREA AND METHODS

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 (Fig. 1). Funk Island supports the world's largest common murre colony estimated at 340,000 to 400,000 pairs, or approxi-
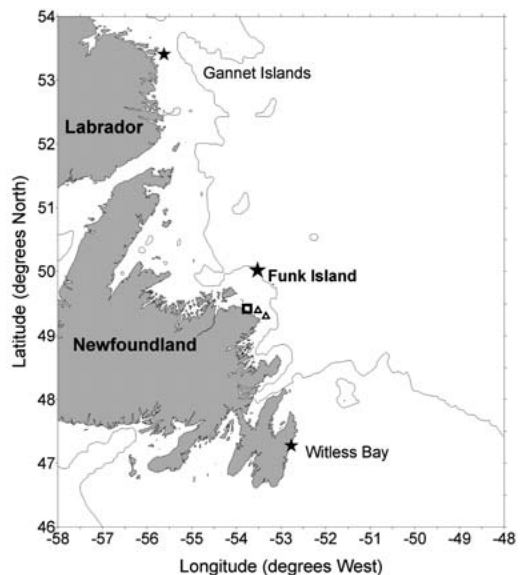

Figure 1. Map of the Northwest Atlantic showing the Funk Island Seabird Ecological Reserve (large black star) and the other major seabird colonies where Common Murres and Atlantic Puffins share breeding sites in the Northwest Atlantic (small black stars). The location of the beach (black square) and demersal (black triangles) capelin spawning sites that were monitored independently during 2003-2005 are also shown.

mately 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 2,000 pairs (Cairns *et al.* 1989).

Information is presented on the timing and duration of capelin spawning during an independent study in 2003-2005 (Penton 2006) at two demersal sites (persistent since their discovery in 2000; Davoren *et al.* 2006) and one beach site, all located within the foraging range of seabirds at Funk Island (Fig. 1).

Chick Diets

Parental prey loads were collected from murres and puffins over 8 d in 2004 (N = 163 for murres; N = 62 for puffins) and 10 d in 2005 (N = 112 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 5×20 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 h 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 into small (100-140 mm) and large (>140 mm) size classes that correspond roughly one to two and three to four 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 ($N_i = (n_i/n_t) * 100$) 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). The % IRI index was not used to describe murre diets because as single prey loaders, the values for % FO and % N do 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.

Dietary Overlap

Differences in chick diets 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 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).

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) and two nights in 2005 (2, 6 August). 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.

RESULTS

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 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 95.5% N in 2005 (106 of 111). Male capelin were rare (one in 2004; two in 2005) and in both years there were a few capelin that could not be sexed (unknowns; Table 1). There were also some partial (i.e., broken)

capelin in the diets in 2004 (N = 10) and 2005 (N = 3) that could only be identified to sex and information on stage of maturity, total length (mm) and mass (g) was not known. There were also four intact capelin in 2005 that had incomplete morphometric information.

Most capelin in murre chick diets were in spent condition in 2004 (53.6%) and 2005 (69.7%; Table 2). During 2005, the percentage of spent capelin increased daily accounting for 93.3% of total capelin in the chick diets on the final sampling day (Table 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). Gravid capelin were uncommon in 2005 and constituted less than 4.6% of chick diets. Immature capelin were rare accounting for less than 5% of the diets in each year. Capelin described as spent/immature (i.e., condition unknown) were not present in 2004 but accounted for 12.8% of chick diet in 2005.

All capelin fed to murre chicks in both years were larger than 100 mm (Fig. 2) with the exception of a single capelin 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 64.4% in 2005 (67 of 104 prey loads). Small capelin

Table 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 (1)	9	1	1	0
3-Aug-05	26 (1)	24	1	1	0
8-Aug-05	44	43	0	1	0
9-Aug-05	31 (1)	30	0	0	0
Totals-2005	111 (3)	106	2	3	0

Table 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	10	40.0	20.0	0.0	20.0	20.0
3-Aug-05	25	52.0	0.0	8.0	16.0	24.0
8-Aug-05	44	70.5	4.5	2.3	18.2	4.5
9-Aug-05	30	93.3	3.3	3.3	0.0	0.0
2005	108	69.7	4.6	3.7	12.8	9.2

(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 36.2% of all capelin (38 of 105 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; Fig. 2) though the mean mass of capelin were 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).

Puffin Chick Diets

Figure 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 in Table 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 transpar-
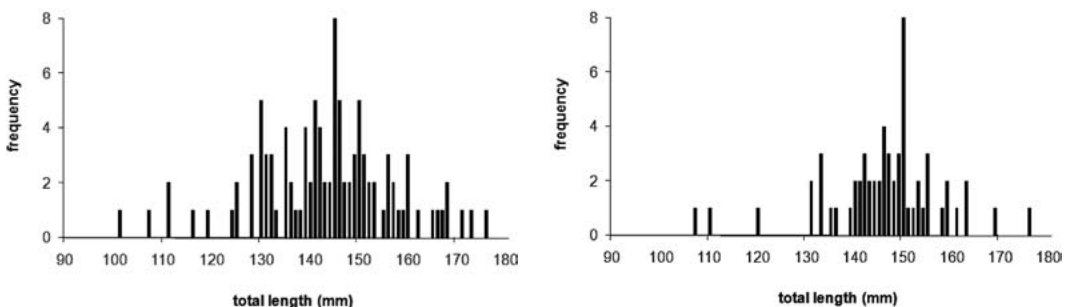

Figure 2. Length frequency distribution (mm) of capelin in murre chick diets in 2004 (left) and 2005 (right).

Table 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 San	%FO Cap	%FO Larval	%M San	%M Cap	%M Larval	%N San	%N Cap	%N Larval
27-Jul-04	8 (4)	100.0	0.0	75.0	87.7	0.0	12.3	66.0	0.0	34.0
28-Jul-04	4	75.0	0.0	75.0	47.5	0.0	52.5	42.9	0.0	57.1
29-Jul-04	7 (2)	100.0	0.0	0.0	100.0	0.0	0.0	100.0	0.0	0.0
30-Jul-04	15 (3)	100.0	0.0	6.7	99.7	0.0	0.3	98.3	0.0	1.7
31-Jul-04	5 (2)	100.0	0.0	40.0	99.2	0.0	0.8	94.7	0.0	5.3
2-Aug-04	4 (1)	100.0	0.0	0.0	100.0	0.0	0.0	100.0	0.0	0.0
3-Aug-04	6 (1)	100.0	0.0	33.3	98.8	0.0	1.2	93.2	0.0	6.8
2004	49 (13)	98.0	0.0	28.6	95.6	0.0	4.4	89.0	0.0	11.0
4-Aug-05	3	0.0	100.0	0.0	0.0	100.0	0.0	0.0	100.0	0.0
7-Aug-05	19	0.0	100.0	0.0	2.9	97.1	0.0	35.7	64.3	0.0
8-Aug-05	10	20.0	100.0	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	100.0	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

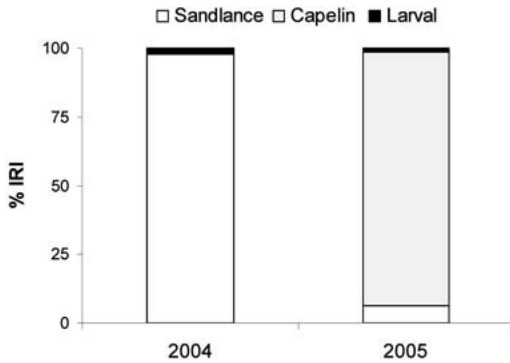Partial loads are excluded from dietary indices.

Figure 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.

ent capelin were included in the 'larval prey' category.

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 (Fig. 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 in-
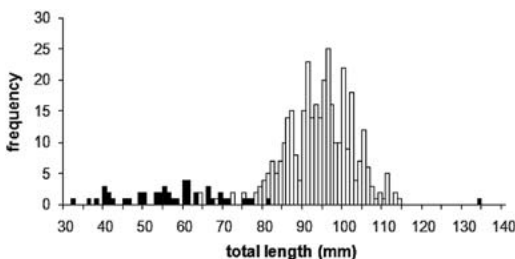
creased significantly over the sampling period (length = 74.4 + 4.8 day, r^2 = 0.87, P < 0.001) suggesting that puffins may select larger sandlance as the nutritional needs of the chick increases with age. The increase in size could also reflect daily growth in these 0-group fish. During 2005, sandlance were smaller (58.0 ± 16.0 mm; Fig. 4) and much less important in puffin chick diets accounting for less than 6.2% IRI compared to 92.5% IRI in 2004 (Fig. 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.

Capelin replaced sandlance as the most important prey item in puffin chick diets in 2005 accounting for 92.3% IRI (Fig. 3). Capelin were present in 97.9% of parental prey deliveries (46 of 47 prey loads) and accounted for 94.4% of total diet by mass (Table 3) and 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 (Fig. 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; Fig. 5).

'Larval prey' were of minor dietary importance in 2004 (2.4% IRI) and 2005 (1.5%

Figure 4. Length frequency (mm) distribution of sandlance in puffin chick diets in 2004 (white bars) and 2005 (black bars).
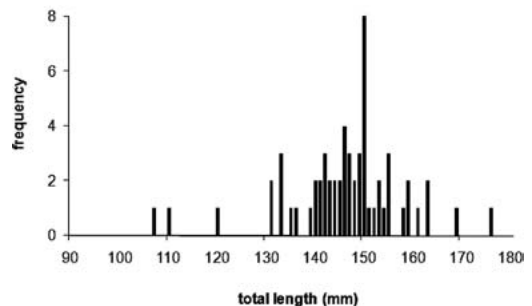

Figure 5. Length frequency distribution of capelin in puffin chick diets in 2005.

IRI; Fig. 3). Prey loads containing only larval prey were very rarely observed (only one 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 and less than 1% N in 2005 and ranged in size from 51-88 mm. 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 1 capelin (146.1 ± 12.1 mm) versus >1 capelin (146.1 ± 11.5 mm).

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 4). In contrast, overlap was high in 2005 (GOI_{adj} 0.838) 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 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).

Murre Offspring Performance

Inspection of the interaction term: (ANCOVA; $F_{1, 65} = 0.78$ P = 0.38) indicated no dif-

Table 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
Puffin 2004	0	0	48	14		P < 0.001
B Murre 2005	38	67	0	1	0.838	U = 28.3
Puffin 2005	13	38	10	5		P < 0.001
Inter-annual GOI_{adj}						
C Murre 2004	76	75	na	2	0.980	U = 5.1
Murre 2005	38	67	na	1		P = 0.16
D Puffin 2004	0	0	48	14	0.317	U = 126.1
Puffin 2005	13	38	10	5		P < 0.001

[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.

ference in the regression slopes between mass and wing length of murre fledglings in 2004 and 2005 (Fig. 6). 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)).

Puffin Offspring Performance

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; Fig. 7). 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).

<center>DISCUSSION</center>

Murre Chick Diets and Condition

The diets of murre chicks observed during this study were typical of the diets

Figure 7. Regression between body mass (g) and wing length (mm) of puffin chicks at Funk Island Newfoundland in 2004 (solid line): slope = 2.12 g mm^{-1}, r^2 = 0.39, N = 25 and 2005 (dashed line): slope = 1.94 g mm^{-1}, r^2 = 0.47, N = 30).

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 (Fig. 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 d in 2005, 8 ± 1 d in 2004 and 9 ± 1 d in 2003; Penton 2006). Beach spawning was also earlier and brief in 2005 (3 July for 2 d) relative to 2004 (10 July for 3-4 d; 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 colo-
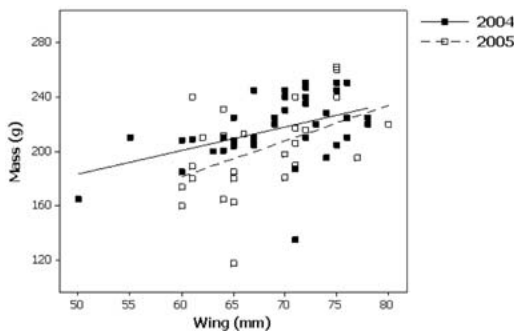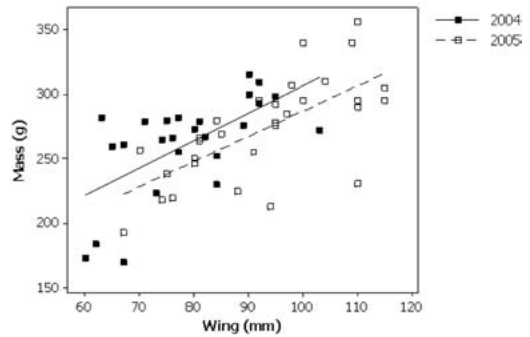

Figure 6. Regressions between body mass (g) and wing length (mm) of murre fledglings at Funk Island Newfoundland in 2004 (solid line): slope = 1.72 g mm^{-1}, r^2 = 0.20, N = 40, and 2005 (dashed line): slope = 2.61 g mm^{-1}, r^2 = 0.24, N = 29.

nies (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 lifetime 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 (Varoujean *et al.* 1979; Ydenberg 1989), 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). This early departure strategy could be effective for murres at Funk Island considering the availability of an important nursery area for adult-fledging pairs located north of the colony (Davoren *et al.* 2002).

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.

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). Adult sandlance collected at several Newfoundland colonies (Russell 1998) had mean energy densities (6.0 kJ. g^{-1}) that exceeded those reported for mature male (3.8kJ. g^{-1}) and female 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. 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 less available because more time and energy are required to maintain current information about prey availability.

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