

Responses to changes in prey availability by Common Murres and Thick-billed Murres at the Gannet Islands, Labrador

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Abstract: We quantified Common Murre (*Uria aalge*) and Thick-billed (*Uria lomvia*) Murre chick diets, chick-feeding rates, breeding success, chick growth, adult masses, and pair members' time spent together at site at the Gannet Islands, Labrador, in 1996 and 1997, after a decline in capelin (*Mallotus villosus*) abundance along the coast of southern and central Labrador. These results, with the exception of time spent at the site, were compared with those collected by other researchers at the Gannet Islands in 1981–1983, before the capelin decline. The two species responded similarly to the decline. After the decline, murres fed their chicks up to 75% fewer capelin and up to 65% more daubed shannies (*Lumpenus maculatus*). Feeding rates of both murre species varied among years, without respect to changes in the proportion of capelin. We found no evidence for declines in colony attendance, breeding success, chick growth, and adult mass. No data on time spent at the site were available before the decline in capelin abundance, but after the decline, off-duty murres of both species spent a mean of 10 min at their sites per feeding visit. This amount of time was short with respect to that recorded for Common Murres elsewhere, suggesting that murres' foraging effort at the Gannet Islands was high and buffered the effects of prey availability on other parameters measured. Taken together, our results suggest that murres responded to changing capelin abundance by changing their chicks' diet, but were otherwise little affected.

Résumé : Nous avons procédé à l'analyse quantitative du régime alimentaire des poussins, de leur taux d'alimentation, du succès de la reproduction, de la croissance des poussins, de la masse des adultes et de la durée de cohabitation des couples au site de nidation situé dans les îles Gannet, Labrador, en 1996 et 1997, chez des Guillemots marmettes (*Uria aalge*) et des Guillemots de Brünnich (*Uria lomvia*) après le déclin du Capelan (*Mallotus villosus*) le long de la côte centrale et australe du Labrador. Toutes les variables, sauf le temps passé au site, ont été comparées à celles obtenues au cours d'une étude entreprise par d'autres chercheurs dans les îles Gannet en 1981–1983 avant le déclin du Capelan. Les deux espèces ont réagi de la même façon au déclin de la population de poissons. Après le déclin, les guillemots ont utilisé 75% moins de capelans et 65% plus de Lompénies tachetées (*Lumpenus maculatus*) pour nourrir leurs poussins. Les taux d'alimentation variaient d'une année à l'autre chez les deux espèces, indépendamment de la proportion de capelans dans le régime. La fréquentation de la colonie, le succès reproducteur, la croissance des poussins et la masse des adultes n'ont pas diminué. Il n'existe pas de données sur la durée des visites au site avant le déclin de la population de capelans, mais, après le déclin, les guillemots passaient en moyenne 10 min au site pour s'alimenter. Cette durée est courte comparativement à celle enregistrée ailleurs pour le Guillemot marmette, ce qui semble indiquer que les efforts de quête de nourriture dans les îles Gannet sont importants et temporisent les effets de la disponibilité des proies sur les autres variables mesurées. Dans l'ensemble, nos résultats indiquent que les guillemots ont réagi à la diminution de l'abondance des capelans en modifiant le régime alimentaire de leurs poussins, mais ont été peu affectés autrement.

[Traduit par la Rédaction]

Introduction

Changes in food availability can profoundly affect the reproductive parameters of breeding animals. Breeding seabirds have been shown to respond to variation in availability of their marine prey with changes in chick diet composition (e.g., Cullen et al. 1992; Hobday 1992; Montevecchi and

Myers 1995), feeding rates (e.g., Uttley et al. 1994), productivity (e.g., Crawford and Dyer 1995; Barrett 1996), colony attendance (e.g., Crawford and Dyer 1995), time-activity budgets (e.g., Burger and Piatt 1990; Cairns 1992; Monaghan et al. 1994, 1996), chick growth (e.g., Cullen et al. 1992; Barrett 1996), adult mass (e.g. Monaghan et al. 1996), and survival (e.g., Vader et al. 1990).

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Alcids are long-lived birds with delayed maturity, and thus can afford to adjust their reproductive effort as environmental conditions change (Lack 1968). As pursuit-diving alcids with obligate one-egg clutches, murrens could be expected to adjust foraging effort and chick diet composition before limiting their clutch size or chick's growth. In fact, in the wake of less than catastrophic changes in prey availability, this has been evinced (Burger and Piatt 1990; Monaghan et al. 1994, 1996; Uttley et al. 1996). Nevertheless, further multiyear studies of seabird reproductive performance and prey abundance are required to test hypotheses about the birds' responses to changes in prey availability. This type of integrated research was possible at the Gannet Islands, Labrador, where, during the early 1980s, Birkhead and Nettleship (1987a, 1987b, 1987c) systematically gathered data on chick diet composition, feeding rates, and productivity of Common and Thick-billed murrens. They also collected information pertaining to chick growth, colony attendance, and adult mass. In the 1980s, capelin (*Mallotus villosus*), an important prey for murre species at many colonies (Bradstreet and Brown 1985; Gaston and Jones 1998), predominated in the Common Murre chick diet and was an important component of the Thick-billed Murre chick diet (Birkhead and Nettleship 1987c). After the conclusion of their research 1983 and before the inception of this study in 1996, capelin virtually evacuated southern and central Labrador waters and ceased spawning on beaches near the Gannet Islands (Miller and Lilly 1991; Miller 1993; J. Anderson, personal communication; Cartwright residents, personal communication).

The objective of our study was to determine the extent to which Common and Thick-billed murre productivity, chick diet composition, and feeding rates reflected changes in capelin availability at the Gannet Islands. We also assessed, indirectly, the effects of such changes on colony attendance, chick growth, adult mass, and time allocated to foraging. Since Common Murre chicks had previously depended more heavily on capelin than Thick-billed Murre chicks, we hypothesized that Common Murre breeding parameters would exhibit more sensitivity to changes in the abundance of this fish species.

Methods

Study site

We conducted our research on GC4, one of seven small islands among the Gannet Islands (53°57'N, 56°31'W), the site of Labrador's largest and most diverse seabird colony. A recent survey showed that 19 394 and 1320 pairs of Common and Thick-billed murrens, respectively, breed on the four islands that make up the main cluster of the Gannet Islands (G.J. Robertson and R.D. Elliot, unpublished data). Co-occurrence of large numbers of the two murre species is relatively rare at colonies in the North Atlantic (Tuck 1960).

Breeding success

We monitored the breeding chronology and breeding success of Common and Thick-billed murrens using the type I methods of Birkhead and Nettleship (1980). Sites for productivity monitoring were located in the same part of the colony as Birkhead and Nettleship's (1987a, 1987b) plots Common Murre A and Thick-billed Murre A and B because these plots could be observed without noticeably disturbing birds. We mapped both Common and

Thick-billed murre study plots and numbered the nest sites on them. Every day during the breeding season we checked each site on the plots and recorded whether there was an egg, a chick, or nothing present. We defined hatching success as the percentage of eggs laid that hatched, fledging success as the percentage of chicks fledged from eggs that hatched, and breeding success as the product of hatching and fledging success.

We monitored 139 Common Murre sites for productivity in 1996 and 109 sites in 1997. These sites occupied about 15 m² of a boulder-strewn rock platform approximately 5 m above sea level and 30 m from the sea. Using 7× binoculars and a 20× spotting scope, we watched the birds from a blind perched approximately 15 m above the plot.

We monitored 144 Thick-billed Murre pairs in 1996 and 143 pairs in 1997. These birds occupied sites on cliff ledges and steep rocky slopes above and to the south of the Common Murre plot. The occupied portions of the cliffs and slopes stood about 25 m above sea level. Using a 20× spotting scope, we watched Thick-billed Murrens from a blind that was situated across a gulch and approximately 15–30 m from their sites.

We used χ^2 tests to make interyear and interspecies comparisons of Common and Thick-billed murre productivity.

Colony attendance

We counted adult murrens present on three count plots at 16:00 every 2–3 days during the breeding season in 1996 and 1997. These plots were identical with those described by Birkhead and Nettleship (1987a; Thick-billed Murre plots A and C and Common Murre plot C). On each plot, we tallied the number of murrens twice. If the two counts were within 5% of each other, we averaged them. If not, we made third or fourth counts and then averaged the two most similar counts.

Diet composition and feeding rates

We determined chick diets and feeding rates by direct observation following the methods of Birkhead and Nettleship (1987c), except that we did not estimate the lengths of fish delivered to chicks and did not conduct additional Thick-billed Murre watches. All watches lasted from 14:00 to 18:00 and were performed by two observers, one watching Common Murrens and one watching Thick-billed Murrens. In 1996, we conducted 8 Common and 8 Thick-billed murre feeding watches and in 1997 we conducted 11 Common and 9 Thick-billed murre feeding watches.

To account for differences in mass among prey items, we converted the percentages by number of chick diet items to percentages by mass. To collect Common Murre chick meals, we used a fleyg net with a long pole to startle birds returning to the colony, causing them to drop their fish. We collected Thick-billed Murre chick meals directly from breeding ledges. We did not collect meals from birds nesting on or near feeding watch/productivity plots. We used the mean masses of intact capelin ($n = 20$), daubed shannies (*Lumpenus maculatus*, $n = 121$), and other fish ($n = 17$), such as sandlance (*Ammodytes hexapterus*), sculpins (*Myoxocephalus* spp.), and fish doctors (*Gymnelis viridis*), collected from Common Murrens returning to the colony in 1996 to make the conversions for 1996, and the mean masses of intact capelin ($n = 45$) and daubed shannies ($n = 56$) collected in 1997 to make the conversions for 1997. Some of the prey species relegated to the "other" category (such as squid (*Illex* sp.) and Atlantic cod (*Gadus morhua*)) recorded during feeding watches were never collected from adults; these were not used to calculate mean percentages by mass. Daubed shannies ($n = 20$) were the only intact fish collected from Thick-billed Murre breeding ledges in 1997. We assumed that masses of these fish were the same in 1996 as in 1997 (this assumption held true for Common Murrens' daubed shannies ($t = 1.40$, $df = 176$, $p = 0.16$)) and that masses of capelin delivered to

Thick-billed Murre chicks were the same as those delivered to Common Murre chicks.

From the vantage point of our blinds, it was difficult to distinguish daubed shannies from other members of the genus *Lumpenus* (specifically stout and slender eelblennies, *Lumpenus fabricii* and *Lumpenus medius*, respectively). Thus, lumpenids are grouped as "shannies" in our analyses. However, 99% ($n = 220$) of the lumpenids we collected from murrens in 1996 and 1997 were daubed shannies.

We calculated the odds in favour of capelin and shanny deliveries in order to compare the predominance of the most important items in the diets of chicks between years and between species. To compare feeding rates among years we used ANOVAs.

Chick growth

In 1996, we took both a single mass and a single wing measurement from 36 Common Murre chicks of unknown age. Chicks chosen for measurement occupied sheltered sites, where they could be handled without causing premature fledging. Five chicks measured in 1996 had wing lengths of 60 mm or greater. Following Birkhead and Nettleship (1985), we assumed that these chicks were at least 20 days old, and considered their masses to be fledging masses. In 1997, we weighed and measured 9 Common Murre and 8 Thick-billed Murre chicks of known age every 3 days from hatching until fledging. From these measurements, we calculated the chicks' maximum growth rates (g/day) and midpoint masses (median of hatching and fledging masses). In both years, mass measurements were taken to the nearest gram using a 300-g spring scale. Wing measurements were made to the nearest millimetre, from the carpal joint to the tip of the longest primary.

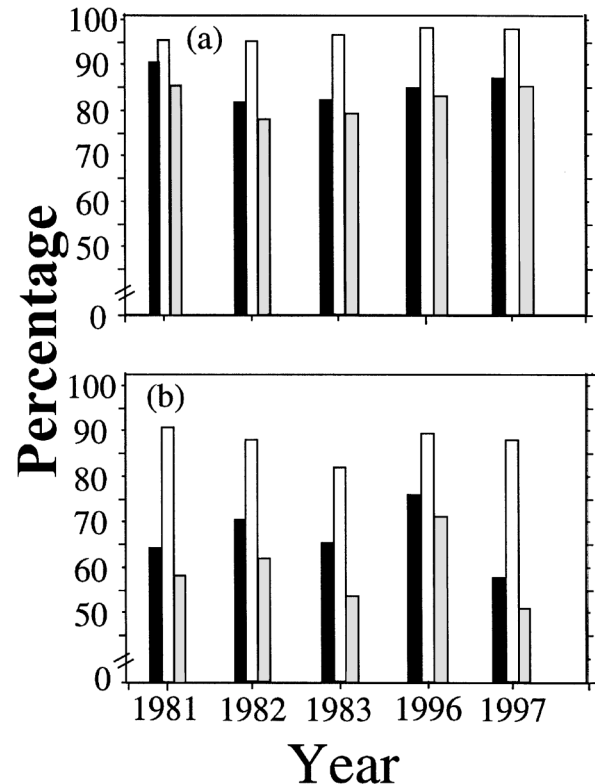
Adult mass

Within-season changes in adult murrens' mass might result from adaptive mass loss, an increase in exercise, or a combination of both (Croll et al. 1991). If murrens' mass varies inversely with the amount of energy they expend, then mass differences between years could result from interyear differences in prey availability (Monaghan 1996). To compare the masses of murrens during incubation with those during chick rearing, and to compare the masses of chick-rearing murrens between years, we weighed adults of both Common and Thick-billed murrens throughout their breeding seasons in 1996 and 1997. We used noose poles to capture Thick-billed Murrens. In 1996, 71 incubating and 46 brooding Thick-billed Murrens were weighed. In 1997, 23 incubating and 11 brooding Thick-billed Murrens were weighed. Only the masses of the Thick-billed Murrens of whose breeding stage (incubating or brooding) we were certain were included in the analyses. We used both noose poles and fleyg nets to capture Common Murrens. In 1996, no incubating Common Murrens were weighed but 106 brooding Common Murrens were weighed. In 1997, 13 incubating and 64 brooding Common Murrens were weighed. We assumed that the Common Murrens caught in the fleyg net were brooding chicks because they were all carrying fish to the colony and we rarely saw nonbrooding Common Murrens bring fish to the observation plots during the chick-rearing period. Murrens were not caught near feeding watch/productivity plots. To compare murrens' incubation and brooding masses, we used unpaired two-tailed t tests. To compare brooding masses for each murre species between years, we used one-way ANOVAs.

Time at site

As an index of the amount of time murrens allocated to foraging, we measured the time during which the two members of a pair remained together at their site (time at site; TAS) after the parent on foraging duty arrived with a chick meal. We assumed that this time would vary inversely with the time and energy allocated to foraging by the individuals, because TAS has been shown to indicate

Fig. 1. The percentages of eggs laid that hatched (solid bars), chicks hatched that fledged (open bars), and eggs laid that produced a fledgling (shaded bars), on the productivity plots at the Gannet Islands for Common Murrens in 1981 ($n = 308$), 1982 ($n = 320$), 1983 ($n = 307$), 1996 ($n = 139$), and 1997 ($n = 109$) (a) and Thick-billed Murrens in 1981 ($n = 222$), 1982 ($n = 254$), 1983 ($n = 219$), 1996 ($n = 144$), and 1997 ($n = 143$) (b). Data for 1981–1983 are from Birkhead and Nettleship (1987b).



both foraging-trip length and foraging effort (Monaghan et al. 1994). To establish mean TAS for Thick-billed and Common murrens, we conducted focal pair (FP) watches during all daylight hours. We began a FP watch when a bird arrived at its site with a fish, thus ensuring that the birds we were watching were truly a breeding pair. FP watches ended when one of the pair members left the site. We never saw Common or Thick-billed murrens spend time at the colony away from the vicinity of their sites, except for the short time Common Murrens sometimes spent walking directly from their site to the water or vice versa. However, if the murrens frequented parts of the colony away from their sites without first spending time at their sites, we would not have detected it. To determine whether off-duty Common or Thick-billed murrens varied the amount of time they spent at their sites with respect to time of day (grouped into three 4-h periods) or part of chick-rearing period (grouped into three periods for Thick-billed Murrens and five periods for Common Murrens), we used ANOVAs. We used two-tailed unpaired t tests to compare the amounts of time Common and Thick-billed murrens spent at their sites.

Results

Breeding success

In 1996 and 1997, Common Murre breeding success was 83% ($n = 136$) and 85% ($n = 109$), respectively, while Thick-billed Murre breeding success was 71% ($n = 144$) and

Fig. 2. Mean numbers ($\pm 95\%$ confidence limits) of adult murrelets counted throughout the breeding season during 1981 and 1996. Data for 1981 are from Birkhead and Nettleship (1982).

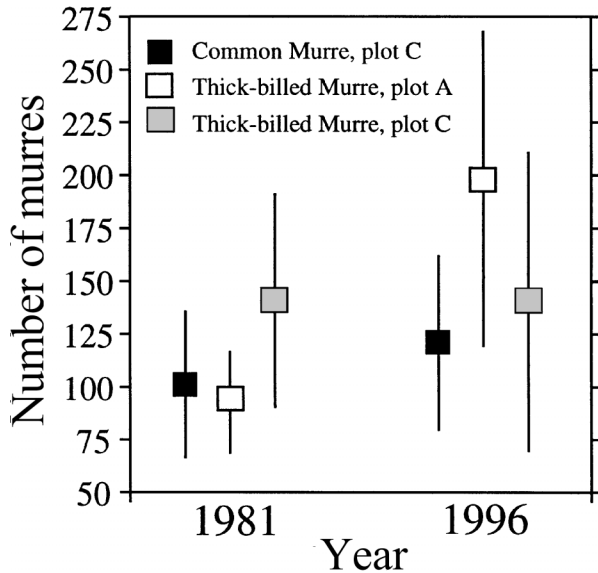


Table 1. Common Murre chicks' diet composition in 1996 and 1997.

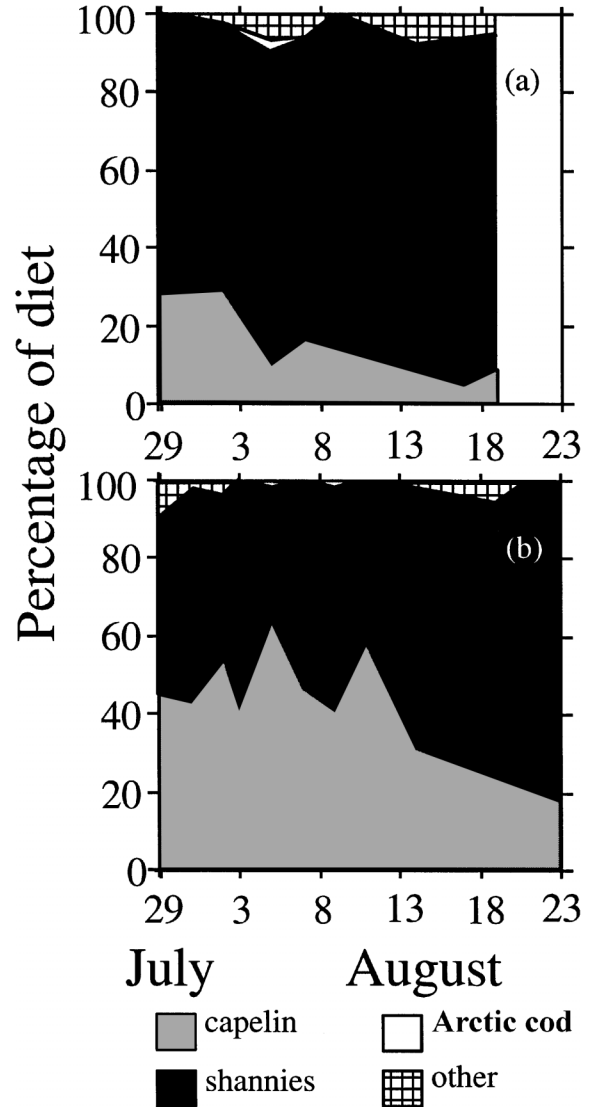
Diet item	Year	<i>n</i>	% by number	Total mass (g)	% by mass
Capelin	1996	43	12	731	18
	1997	170	45	2193	50
Daubed shanny	1996	313	84	3193	79
	1997	200	53	2120	48
Other	1996	17	4	136	3
	1997	10	2	80	2
Total					
Known fish	1996	373		4060	
	1997	380		4393	
Unknown fish	1996	24			
	1997	24			

Note: *n* is the number of feeds of the diet item delivered at Common Murre plot A during 10 feeding watches (14:00–18:00). Total mass was estimated from the mean masses of each diet item collected from Common Murre parents. "Other" items include sandlance, Arctic cod, sculpin, and squid. Unknown fish were those delivered to chicks but not identified to species.

51% (*n* = 143), respectively. The difference in breeding success between Common and Thick-billed murrelets was not significant in 1996 ($\chi^2 = 0.80$, *df* = 1, *p* = 0.38) but was significant in 1997 ($\chi^2 = 6.37$, *df* = 1, *p* < 0.01; Fig. 1). Likewise, the difference in hatching success between Common and Thick-billed murrelets (Fig. 1) was not significant in 1996 ($\chi^2 = 14.13$, *df* = 1, *p* < 0.001) but was significant in 1997 ($\chi^2 = 0.81$, *df* = 1, *p* = 0.34). In both years, between-species differences in fledging success were not significant (1996, $\chi^2 = 0.83$, *df* = 1, *p* = 0.38; 1997, $\chi^2 = 0.04$, *df* = 1, *p* = 0.85).

Neither Common nor Thick-Billed murre breeding success varied among the years 1981, 1982, 1983, 1996, and

Fig. 3. Seasonal variation in percentages by number of capelin, daubed shanny, Arctic cod, and other fish in Common Murre chicks' diets in 1996 (*n* = 373) (a) and 1997 (*n* = 380) (b).



1997 (Fig. 1; Common Murres: hatching success, $\chi^2 = 1.09$, *df* = 6, *p* = 0.99; fledging success, $\chi^2 = 0.16$, *df* = 6, *p* = 0.99; Thick-billed Murres: hatching success, $\chi^2 = 1.86$, *df* = 6, *p* = 0.99; fledging success, $\chi^2 = 0.6$, *df* = 6, *p* = 0.99).

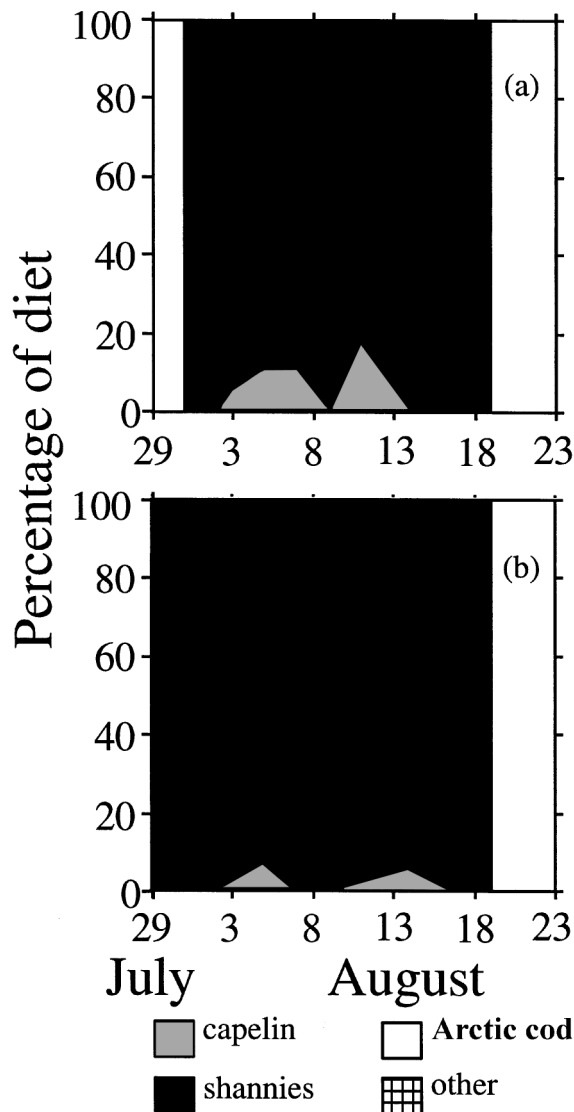
Colony attendance

The mean number of Common Murres present on Common Murre plot C increased significantly from 101 in 1981 to 121 in 1996 (*t* = 16.38, *df* = 66, *p* < 0.001). The mean number of birds present on Thick-billed Murre plot A (Fig. 2) increased significantly from 93 in 1981 to 196 in 1996 (*t* = 16.77, *df* = 69, *p* < 0.0001). On Thick-billed Murre plot C, the mean number of birds did not vary between years (*t* = 0.1, *df* = 67, *p* = 0.9).

Diet composition

We recorded a striking change in murre chick diet between the early 1980s and 1996–1997. Common Murre

Fig. 4. Seasonal variation in percentages by number of capelin, daubed shanny, Arctic cod, and other fish in Thick-billed Murre chicks' diets in 1996 ($n = 110$) (a) and 1997 ($n = 148$) (b).



chicks, which were fed mostly capelin in 1981–1983, were fed mostly daubed shanny in 1996 and almost equal proportions of capelin and shannies in 1997 (Table 1, Fig. 3). The chance that a Common Murre would feed a capelin to its chick was smaller in 1996 than in 1997 (Table 3). Conversely, the chance that a shanny would be fed was greater in 1996 than in 1997. In both years, fish other than capelin and shannies accounted for small proportions of the diet of Common Murre chicks. Other fish in the Common Murre chicks' diet in 1996 and 1997 included sandlance, fish doctor, Atlantic cod, Arctic cod (*Boreogadus saida*), sculpin, and squid.

The diet of Thick-billed Murre chicks was composed of more shannies and fewer capelin than that of Common Murre chicks (Fig. 4, Table 2). The odds in favour of a capelin were extremely low in both years, but more so in 1996 (Table 3).

In 1982 and 1983, Thick-billed Murre chicks were sometimes fed Arctic cod, fish doctor, and sandlance (Birkhead

Table 2. Thick-billed Murre chicks' diet composition in 1996 and 1997.

Diet item	Year	n	% by number	Total mass (g)	% by mass
Capelin	1996	2	2	34	3
	1997	9	6	116	7
Daubed shanny	1996	107	97	1070	96
	1997	139	94	1473	93
Other	1996	1	1	8	1
	1997	0	0	0	0
Total					
Known fish	1996	110		1112	
	1997	148		1589	
Unknown fish	1996	125			
	1997	241			

Note: n is the number of feeds of the diet item delivered at Thick-billed Murre plot A during 8 (1996) and 10 (1997) feeding watches (14:00–18:00). Total mass was estimated from the mean masses of each diet item collected from Thick-billed Murre parents. "Other" items include sandlance, Arctic cod, sculpin, and squid. Unknown fish were those delivered to chicks but not identified to species.

and Nettleship 1987c), but capelin and shannies alone accounted for 100% of the fish delivered during feeding watches. In 1996 and 1997, however, we made rare ($n < 10$) observations of Thick-billed Murres feeding Arctic cod to their chicks, but these feeds were not concurrent with feeding watches.

In 1996 and 1997, as in the 1980s, the odds in favour of a chick being fed a capelin were greater for Common Murres than Thick-billed Murres. The opposite was the case for shanny feeds. In each year, the odds in favour of a Thick-billed Murre delivering a shanny to its chick were higher than those of a Common Murre delivering one to its chick. Despite these consistent interspecies differences in the ratios of chick diet items, changes in the diets of chicks of the two murre species exhibited similar patterns. Parents of both species fed their chicks substantially more shannies and fewer capelin and Arctic cod in 1996 and 1997 than in 1982 and 1983 (Table 3).

Feeding rates

Thick-billed Murres fed their chicks more frequently in 1996 than in 1997 ($t = 5.49$, $df = 16$, $p < 0.0001$; Fig. 5). Common Murres exhibited a similar between-year difference in feeding rates, but the difference was not significant ($t = 1.97$, $df = 18$, $p = 0.06$). Thick-billed Murres fed their chicks at a significantly higher rate than Common Murres in 1996 ($t = 6.58$, $df = 14$, $p < 0.00001$). In 1997, however, feeding rates did not differ significantly between species ($t = 1.5$, $df = 20$, $p = 0.15$).

Common and Thick-billed murres' feeding rates varied significantly among the years 1981, 1982, 1983, 1996, and 1997 (Fig. 5; Common Murres, $F_{[4,48]} = 58$, $p < 0.0001$; Thick-billed Murres, $F_{[4,47]} = 69.2$, $p < 0.0001$). Between-year differences in feeding rates did not consistently correspond to the amount of capelin in the birds' diets.

Chick growth

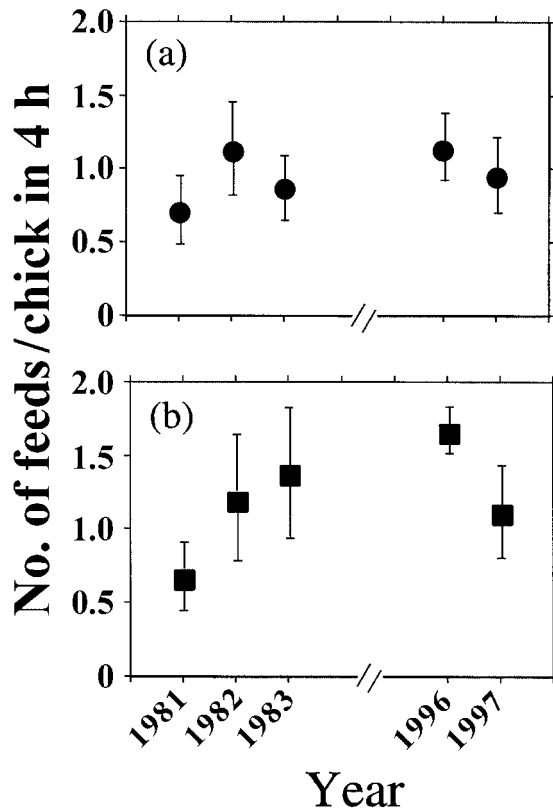
In 1996, the mean mass of previously undisturbed Common Murre chicks with wing lengths greater than or equal to

Table 3. Odds in favour of capelin and shanny deliveries to Common and Thick-billed murre chicks.

Year	Species	Odds in favour of:		n
		a capelin delivery	a shanny delivery	
1982	Common Murre	3.2	0.10	2085
	Thick-billed Murre	0.24	2.6	241
1983	Common Murre	3.1	0.18	1640
	Thick-billed Murre	0.43	2.0	409
1996	Common Murre	0.14	5.0	364
	Thick-billed Murre	0.02	35.7	110
1997	Common Murre	0.81	1.1	380
	Thick-billed Murre	0.06	12.6	

Note: The odds in favour of a delivery are equal to the number of deliveries of that fish observed during 4-h feeding watches divided by the number of deliveries of other fish.

Fig. 5. Rates of food delivery (mean \pm SD) during 4-h feeding watches (14:00–18:00) to Common Murre chicks in 1981 ($n = 8$ watches), 1982 ($n = 11$), 1983 ($n = 12$), 1996 ($n = 8$), and 1997 ($n = 11$) (a) and Thick-billed Murre chicks in 1981 ($n = 12$ watches), 1982 ($n = 11$), 1983 ($n = 12$), 1996 ($n = 8$), and 1997 ($n = 9$) (b). Data for 1981–1983 are from Birkhead and Nettleship (1982, 1985).



60 mm was 233 ± 21 (SD) g ($n = 5$), or 24% of the mean adult mass. In 1997, the mean fledging mass of regularly handled Common Murre chicks was 223 ± 21 g ($n = 8$), or 23% of the mean adult mass in that year. The mean fledging mass of regularly handled Thick-billed Murre chicks in 1997 was 224 ± 25 g ($n = 8$), or 24% of the mean adult mass in that year.

Because of differences in methodology, we could make a direct comparison of fledging masses only for Common

Murre chicks at the Gannet Islands, and for only one pair of years: 1981 (238 ± 26 g, $n = 141$) and 1996. There was no significant difference between the mean fledging masses in these years ($t = 0.79$, $df = 1$, $p = 0.57$); however, the sample size was small (5) in 1996.

In 1983, the mean mass of previously undisturbed fledging Thick-billed Murres was 228 ± 30 g ($n = 10$), only 0.2% higher than that of the eight regularly handled Thick-billed Murre chicks in 1997.

Adult mass

For both Common and Thick-billed murre adults, masses during chick rearing tended to be lower than during incubation (Table 4). In 1996, the mean mass of adult Thick-billed Murres was 5% higher during incubation than during chick rearing ($t = 3.64$, $df = 115$, $p = 0.004$). However, in 1997, the mean mass of Thick-billed Murres during incubation did not differ significantly from that during chick rearing ($t = 1.03$, $df = 32$, $p = 0.31$). In 1997, the mean mass of Common Murres during chick rearing was 5% lower than the mean mass during incubation ($t = 2.30$; $df = 75$, $p = 0.02$).

The mean mass of chick-rearing Thick-billed Murres varied significantly among the years 1981, 1982, 1996, and 1997 ($F_{[3,103]} = 2.91$, $p = 0.04$), owing to an exceptionally high mean mass in 1997. There was no significant interyear variation in the masses of chick-rearing Common Murres ($F_{[4,249]} = 1.55$, $p = 0.19$).

Time at site

In 1997, the median TAS for Common Murre pair members during single feeding visits was 9 min, with an interquartile range spanning from 6 to 12 min ($n = 41$; for comparison with other studies, mean = 10.5 ± 7.5 min). TAS for Thick-billed Murres was similar but more variable; they stayed with their mates for a median time of 7 min per feeding visit, with an interquartile range of from 3–17 min per feeding visit ($n = 27$; mean = 11.3 ± 11.0 min). Neither Common nor Thick-billed murres on foraging duty varied TAS with respect to time of day or season (for Common Murres with respect to season, $F_{[4,36]} = 1.69$, $p = 0.17$; for Common Murres with respect to time of day, $F_{[2,38]} = 1.12$, $p = 0.37$; for Thick-billed Murres with respect to season, $F_{[2,24]} = 0.86$, $p = 0.44$; for Thick-billed Murres with respect to time of day, $F_{[2,24]} = 0.35$, $p = 0.71$). Thus, we pooled the

Table 4. Mean masses of incubating and chick-rearing Common and Thick-billed murres in 1981, 1982, 1983, 1996, and 1997.

Year	Species	Incubating			Chick-rearing		
		Mean mass (g)	SD	<i>n</i>	Mean mass (g)	SD	<i>n</i>
1981	Common Murre	980	61	30	909	64	24
	Thick-billed Murre	943	51	30	899	57	30
1982	Common Murre	993	61	31	944	56	30
	Thick-billed Murre	971	68	30	903	47	20
1983	Common Murre	975	56	31	960	50	30
	Thick-billed Murre	955	58	20	—	—	—
1996	Common Murre	—	—	—	945	66	106
	Thick-billed Murre	945	64	71	900	68	46
1997	Common Murre	1011	64	13	960	74	64
	Thick-billed Murre	943	65	23	919	59	11

Note: Data for 1981–1983 are from Birkhead and Nettleship (1987a).

data for each species and made an interspecific comparison of TAS. We found no significant difference in the mean amounts of time that off-duty Common and Thick-billed murres spent at their sites ($t = 0.36$, $df = 66$, $p = 0.72$).

Discussion

Changes in capelin abundance apparently had little effect on breeding Common and Thick-billed murres. Contrary to our hypothesis that Common Murres would exhibit greater sensitivity to changes in capelin abundance, breeding parameters for both murre species seemed equally robust to such changes.

Breeding success

Breeding Common and Thick-billed murres were remarkably resilient to varying availability of their supposedly preferred prey. Despite interyear variability in prey-species availability and chick diet composition, neither Common nor Thick-billed murres' breeding success changed significantly between the early 1980s and the mid-1990s. We concur with Monaghan et al. (1994) that murre breeding success is relatively insensitive to changes in prey availability. During our study, Common Murres consistently experienced higher breeding success than Thick-billed Murres as a result of their higher hatching success. In 1981, 1982, and 1983, Thick-billed Murres at the Gannet Islands experienced both lower hatching success and lower fledging success than Common Murres (Birkhead and Nettleship 1987b). This difference was attributed to the murres' use of different breeding habitats (cliff ledge vs. flat terrace).

Colony attendance

Murres' attendance at the Gannet Islands colony did not fall in response to a decreased abundance of capelin. In fact, the numbers of both species attending the colony probably increased between the early 1980s and 1996. Unlike those of murres at the Gannet Islands, counts of murres breeding in the Barents Sea varied in response to capelin abundance over a 22-year period (Vader et al. 1990). Concurrent with a collapse of the Barents Sea capelin stock, numbers of Common Murres breeding at three colonies in northern Norway

plummeted by about 80%. Thick-billed Murres at the same colonies fared better, although their numbers also fell substantially (33–63%; Vader et al. 1990).

Because murres are long-lived and can "choose" to forgo a breeding season at little cost to their lifetime fitness, adult survival will only be affected by extreme shortages of prey (Monaghan 1996). The Gannet Islands murres did not exhibit declines in colony attendance similar to those of their conspecifics in the Barents Sea, probably because their food resource base changed less adversely and (or) because both Common and Thick-billed murres from the Gannet Islands were able to supplement their winter diets sufficiently with fish other than capelin.

Diet composition

The predominance of a benthic fish, the daubed shanny, in Common Murre chick diets in 1996–1997 is highly unusual. Although their chicks' diets often include some demersal species, Common Murres tend to prey less upon benthic animals than on pelagic schoolers. For instance, the most prevalent item in Common Murre chicks' diets in the northwest Atlantic has been the capelin (Bradstreet and Brown 1985; Birkhead and Nettleship 1987c; Burger and Piatt 1990) and, less recently, the sandlance (Tuck 1960). Chick diets in the Barents Sea consisted of capelin, herring, and sandlance (Furness and Barrett 1985; Barrett and Furness 1990; Barrett et al. 1997). In the North Sea, Common Murre chicks' diets consisted mainly of sandlance (Harris and Wanless 1995) and, in the Irish Sea, sprat (*Sprattus sprattus*) (Hatchwell 1991). Although Common Murre chicks' diets very rarely deviate from this trend, a benthic fish prevailed in chicks' diet at the Farallon Islands (Ainley et al. 1996); Common Murres at this colony fed their chicks juvenile rockfish (*Sebastes* spp.), which supposedly become demersal by the time they are large enough to appear in chicks' diets (Moser and Boehlert 1991).

The change in Common Murre chicks' diet between 1982–1983 and 1996–1997 was striking, not only for its magnitude but for the behavioural shift it might have required. If daubed shannies live solitarily in the benthos, as purported (Makushok 1986; Scott and Scott 1988), murres must employ a different strategy to catch them than they do

to catch the pelagic schooling capelin. Although the dietary shift was similar for Thick-billed and Common murre chicks, a predominantly benthic diet is less unusual for Thick-billed Murre chicks (Tuck 1960; Bradstreet and Brown 1985; Gaston 1985*a*). Demersal fish are especially common in chicks' diets in the more southerly reaches of the Thick-billed Murre's Atlantic range, including the Gannet Islands (Bradstreet and Brown 1985; Birkhead and Nettleship 1987*c*), but a schooling fish, the Arctic cod, is the most prevalent item at both low and high Arctic colonies in eastern Canada (Gaston and Nettleship 1981; Gaston 1985*a*).

The change in composition of the Common Murre chicks' diet was not necessarily accompanied by a change in diet quality. Analyses of the proximate composition (proportions of protein, lipid, ash, and water) and energy density of 12 daubed shannies and 2 capelin that we collected from chick-rearing Common Murres on the Gannet Islands in 1996 revealed that the lipid and protein contents and energy density of daubed shannies were as high as those of capelin (Magalhães 1998). These parameters vary widely with season, fish sex, and reproductive state; the energy densities of capelin collected from Gannet Islands murres were higher than those of one larger sample and much lower than those of another sample taken at different locations and (or) different times of the year (Montevicchi and Piatt 1984; Lawson et al. 1998). During both years of this study, the majority of the capelin that murres fed to their chicks on the Gannet Islands were non gravid females (Bryant and Jones 1999), which tend to have a lower nutritional value than gravid ones (Montevicchi and Piatt 1984). Birkhead and Nettleship (1987*c*) reported that in 1982 and 1983, the capelin collected from the Gannet Islands murres had higher energy densities than daubed shannies. However, this difference was based on the results of bomb calorimetry, and the sexes and reproductive states of the fish were not reported.

Little research has been conducted on daubed shanny abundance, distribution, behaviour, or ecology. The depths at which daubed shannies have been captured (0–120 m) fall within the range used by chick-rearing murres at the Gannet Islands (Scripps Institute of Oceanography Oceanographic Collections 1997; National Museum of Natural History (Smithsonian Institution) Fish Collection 1998; Bryant and Jones 1999). The results of North Atlantic Strategic Assessment Project (SAP) trawls indicated that daubed shannies are abundant along most of the coast between northern Labrador and the southern Gulf of Maine, but are more abundant in the southwestern Gulf (East Coast of North America Strategic Assessment Project 1998). Nonetheless, few of SAP's trawls contained daubed shannies, and the mean number caught per tow was too small to afford reasonable estimates of the fish's real abundance.

In 1996, when chicks' diets were composed principally of daubed shannies, we estimate that Gannet Islands murres fed 2.8 million of these fish (ca. 290 t) to their chicks before their departure from the colony. This does not account for adult consumption, which is probably much greater (Gaston and Jones 1998). However, because we had no estimates of daubed shanny abundance near the Gannet Islands for any year, we were unable to assess whether the patterns we ob-

served related to variation in the abundance or distribution of this important benthic species. Our results underline the importance of further research on the behaviour, ecology, and abundance of the daubed shanny.

Feeding rates

The rates at which both Common and Thick-billed murres provisioned their chicks at the Gannet Islands varied among years, but not in accordance with changes in the proportion of capelin in the chicks' diets. Similarly, Burger and Piatt (1990) found that in spite of within- and among-season fluctuations in capelin availability in and near Witless Bay, Newfoundland, Common Murres breeding there did not adjust the rates at which they fed their chicks. Feeding rates did not differ significantly between Common Murre chicks reared at breeding sites in areas of different forage fish availability in Cook Inlet, Alaska (Zador and Piatt 1999). In contrast, at the Shetland Islands, the feeding rates for Common Murre chicks were twice as high during a year in which the independently estimated abundance of their only available chick food (sandlance) was high than during a year when it was low (Kunzlik 1989 in Uttley et al. 1996; Monaghan et al. 1996; Uttley et al. 1996). In both Witless Bay and the Shetland Islands, breeding murres spent more time foraging when prey availability was low (Burger and Piatt 1990; Monaghan et al. 1994, 1996). In conjunction with the fact that feeding rates at the Gannet Islands and in Witless Bay did not fluctuate with capelin availability, this suggests that when alternative prey are available, murre chicks' feeding rates are not primarily regulated by the availability of "preferred" prey. Thus, at the Gannet Islands, the feeding rates of murres did not reflect capelin availability.

Chick growth

We have little reason to believe that the growth rates of murre chicks differed before and after local declines in capelin availability. In 1996–1997, the fledge masses of Common and Thick-billed murre chicks from the Gannet Islands were similar to those recorded in the early 1980s. In 1997, observers often saw Thick-billed Murre chicks refuse fish from their parents, which is consistent with the contention that their chicks grew well. Likewise, in 1997, murre chicks grew well in comparison with those from other colonies in other years (data compiled by Gaston 1985*b*). Nevertheless, intercolony differences in chick growth can be affected by factors other than diet composition. Such factors might include feeding rates, temperature, humidity, and genetic constraints, although Gaston (1985*b*) showed that for Thick-billed Murres, between-colony differences in temperature did not correspond to differences in fledge masses.

Adult mass

While the masses of adult Common and Thick-billed murres were lower during chick rearing than during incubating, they were not lower during either period in 1996–1997 than in the 1980s. Therefore, we found no evidence that the decrease in capelin abundance increased the physical stress on breeding adult murres, or that adult mass correlated with capelin abundance.

Time at site

Although breeding murres spend a substantial portion of "free time" at sea (Cairns et al. 1987; Benvenuti et al. 1998), the amount of free time they spend on land seems to reflect the proportion of time they allocate to foraging, which, in turn, reflects the availability of supposedly preferred prey items. Although Cairns et al. (1987) showed that the proportion of time Common Murres spent diving decreased with the duration of the foraging trip, Monaghan et al. (1994) demonstrated that trip duration, and hence TAS, provides a reliable index of the foraging effort of murres.

While Common Murres' TAS might reflect foraging effort (Monaghan et al. 1994), the link between Thick-billed Murres' TAS and foraging effort is less obvious. This is because there are few published data on Thick-billed Murres' TAS in relation to changing prey availability or chicks' diets. Like Common Murres, Thick-billed Murres might adjust TAS as feeding conditions change. If this is the case, then Common Murres seem to expend no greater effort foraging than Thick-billed Murres do, despite the fact that Common Murre chicks' diets change more drastically. Alternatively, as Thick-billed Murres behave less gregariously toward their mates and chicks than Common Murres do (R. Bryant, personal observation; see Birkhead 1985), the former might keep TAS constant, increasing only their free time spent at sea as feeding conditions improve. This possibility is more likely because, unlike Common Murres at the Gannet Islands, Thick-billed Murres tend to nest shoulder to shoulder on narrow cliff ledges, where adults often have difficulty sharing the small space available at their site.

TAS for Gannet Island murres was lower than values recorded at other colonies during years when the availability of "preferred" prey was moderate or high (Burger and Piatt 1990; Monaghan et al. 1996; Zador and Piatt 1999), which suggest a relatively high foraging effort. No measurements or estimates were made of the time murres spent together at the Gannet Islands in the 1980s. However, based on the analysis of brooding-shift durations for Common Murres in 1983, Verspoor et al. (1987) surmised that even in that year, TAS for off-duty murres was low.

In conclusion, with respect to each of the parameters we measured, Common and Thick-billed murres responded similarly to changes in capelin abundance. For both species, chicks' diets, and possibly parental TAS, changed. Yet we detected no appreciable differences in breeding success, feeding rates, chick growth, or adult mass.

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