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Food Resource Use and Diet Overlap of Common and Thick-billed Murres at the Gannet Islands, Labrador

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Abstract.—We studied food resource use by two similar seabird species, Common (*Uria aalge*) and Thick-billed murres (*U. lomvia*), breeding sympatrically at the Gannet Islands, Labrador, to examine the overlap in their chicks' diet and thus to indirectly evaluate whether the two species were in competition for food. We used Monte Carlo randomization to establish whether murre chick diet overlap in 1996 and 1997 were greater than would be expected by chance. Diet overlap was higher than 75% in both years and was not lower than that predicted by the null model. To determine whether the two murre species' chick food resource use converged in ways other than diet composition, we compared timing of breeding, sizes of fish delivered to chicks, maximum dive depths and diurnal feeding patterns. In both years, the murres' chick-rearing periods overlapped almost exactly. The size of the principal item in their chicks' diets did not differ significantly. During one of two all-day feeding watches in 1997, the murres' chick-feeding peaks were concurrent, but during the other they were not. In 1997, foraging Common and Thick-billed murres dove to similar maximum depths. Taken together, these results suggest that chick food resource partitioning might have been negligible between Common and Thick-billed murres breeding at the Gannet Islands in 1996 and 1997. Received 5 November 1998, accepted 21 January 1998.

Key words.—Capelin, Common Murre, competition, competitive exclusion, daubed shanny, diet, Labrador, *Lumpenus maculatus*, *Mallotus villosus*, Thick-billed Murre, *Uria aalge*, *Uria lomvia*.

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Gause's Law, or the competitive exclusion principle, states that in sympatry, species that are closely related will differentiate ecologically (Gause 1934). A testable hypothesis derived from the principle is that sympatric species that are similar along one niche dimension will differ along another, effectively diminishing resource-use overlap (the niche complementarity hypothesis; Schoener 1974). This hypothesis has been supported by several bird studies, including Cody's (1968, 1974) work on grassland bird communities, and by Lack's (1947) studies of Darwin's finches. Cody (1973) addressed the question of resource partitioning in auks and posited that different species foraged at predictably different distances from their colonies.

Not all studies have produced results that are consistent with the niche complementarity hypothesis. Cody's interpretation of his data was contentious (Bedard 1976) and studies of Common and Thick-billed murre (*Uria aalge* and *U. lomvia*) chick diet in the Barents Sea offered only ambivalent support for the hypothesis (Furness and Barrett

1985; Barrett and Furness 1990; Barrett *et al.* 1997). These studies recorded high degrees of chick-diet overlap, nearly identical maximum dive depths and foraging ranges, and similar patterns of diurnal chick-feeding of both murre species. Although the birds' chick-rearing periods overlapped to an extent, the Common Murre median hatch date was earlier than that of the Thick-billed Murres and, during some months, breeding Common Murres dove to shallower maximum depths than did Thick-billed Murres. At present, there is no incontrovertible evidence for interspecific competition between murre species, even though competition may be expected, given the species' known ecological and morphological similarities (Storer 1952; Gaston and Jones 1998).

Like the Barents Sea colonies, the Gannet Islands in the Labrador Sea are one of few places in the Atlantic where the congeneric Common and Thick-billed murres breed syntopically in large numbers (Nettleship and Evans 1985; Birkhead and Nettleship 1987a). At the Gannet Islands, the two murre species could minimize their poten-

tial for competition for food resources in at least six ways: 1. breeding at different times; 2. taking different fish species; 3. taking different sizes or sexes of fish; 4. foraging at different locations; 5. foraging at different depths; or 6. foraging during different times of day. We looked for evidence of niche partitioning by investigating possibilities 1, 2, 3, 5, and to some extent 6, by determining the timing of Common and Thick-billed Murre chick rearing, and by quantifying chick diet overlap, the sizes and sexes of prey delivered to chicks, the maximum dive depths of brooding birds, and the diurnal pattern of feeds to chicks, during the 1996 and 1997 breeding seasons. We used Monte Carlo randomizations to determine the significance of observed overlap values.

METHODS

Study area

We conducted our study at the Gannet Islands, Labrador (53°56'N, 56°32'W), where there were breeding populations of approximately 40,000 pairs of Common Murres and 2,000 pairs of Thick-billed Murres (Lock *et al.* 1994). We made observations at several murre breeding plots used previously by Birkhead and Nettleship (1987a, 1987b, 1987c).

Timing of Breeding

To determine the timing of Common and Thick-billed murre chick-rearing periods, we used the type I methods of Birkhead and Nettleship (1981), recording the hatch and fledge dates of chicks on productivity plots in 1996 and 1997 (Common Murres, 1996, $n = 180$; 1997, $n = 140$). J. Mark Hipfner monitored the hatch and fledge dates of Thick-billed Murres (1996 and 1997, $n = 150$). In calculating median hatch dates (MHDs), we used only hatch dates which were known to within 24 hours.

Diet Overlap

To establish the chick diet composition used to calculate diet overlap, we conducted feeding watches at murre breeding sites. At regular intervals throughout the chick-rearing period, we recorded the types of fish delivered to 10-50 Common and 15-30 Thick-billed murre chicks between 1400 and 1800 h. In 1996 we conducted eight four-hour feeding watches of Common and Thick-billed murres. In 1997, we conducted 11 four-hour feeding watches of Common Murres and nine of Thick-billed Murres. Watches were conducted simultaneously for both species. As recommended by Wolda (1981), we used Horn's (1966) adaptation of Morisita's (1959) index of resource use overlap to characterize the similarity of Common and Thick-billed murre chick diets. This index is standardized and ranges from 0 to one.

The proportions of each item used in the indices were derived from percentages by number of the items in the chicks' diets. Because each chick meal consisted of a single fish, and because the sizes of these fish did not vary much, percentage by number approximated percentage by mass (Bryant 1998). We considered a diet item to be the lowest taxon to which we could identify a meal from our observation blind (Table 1). Most items comprised species of fish, while a few comprised genera or families.

Following Tokeshi (1986), we used randomization tests to establish whether diet overlap differed significantly from those calculated from randomly-generated diets (i.e., showed evidence of differential partitioning of the food resource between the two murre species). We used the "Resampling Statistics" program (Simon 1997) to perform Monte Carlo randomizations. For each murre species in each year, we created 5,000 randomly constructed diets (Adams and Anthony 1996). Each of these diets consisted of the same number of feeds observed in that year and composed of the same diet items we recorded during feeding watches. From the 5,000 randomly-generated diets for each year, we calculated 5,000 diet diversities and niche breadths for each murre species. Then, from the random distributions of each index, we calculated the proportion of values that were more extreme than those observed. The set of items used for randomization of Thick-billed Murre chick diets was larger than the set of items they actually delivered to their chicks in each year because we assumed that any item fed by one species of murre during either year of the study and fed by the other during the year in question was available to both during the year in question. From the 5,000 randomly-generated Common and Thick-billed murre diets for each year, we derived 5,000 chick diet overlap scores. We found p values for the observed diet overlaps by calculating the proportion of values in the random distribution that were more extreme than those observed.

Chick meal fish size, sex and reproductive state

Once every two to five days during the chick-rearing period, we collected chick diet samples from Common Murres in 1996 and 1997. These were collected from parents as they returned to their sites from the sea. In 1997, J. Mark Hipfner collected Thick-billed Murre samples from ledges on which breeding birds held sites. To eliminate the possibility of disturbance effects, no diet samples were collected from birds nesting on or near productivity or feeding watch plots. We measured the masses of intact fish to the nearest gram with an electronic balance and their length to the nearest millimeter. The fork length of fish with forked tails (such as sandlance *Ammodytes* sp. and capelin *Mallotus villosus*) was taken, along with their total length. In 1997, we also examined the reproductive states of capelin and daubed shannies *Lumpenus maculatus* fed to murre chicks.

We used two-tailed, unpaired t -tests to compare the mean masses and lengths of daubed shannies delivered to the two species. We used ANOVA to determine whether the mean masses and lengths of daubed shannies delivered to Common Murre chicks varied significantly between years. To compare the ratios of gravid and non-gravid daubed shannies delivered to Common Murres with those delivered to Thick-billed Murres, we used a Chi-square test of the homogeneity of means. To

Table 1. Common and Thick-billed murre chick diets and diet overlaps in 1996 and 1997.

Prey item	Percentage by number 1996		Percentage by number 1997	
	Common N = 373	Thick-billed N = 110	Common N = 380	Thick-billed N = 148
Capelin (<i>Mallotus villosus</i>)	11.8	1.8	44.7	6.3
shannies (Sticheidae)	84.0	97.2	52.9	93.7
fish doctor (<i>Gymnelis viridis</i>)	1.4	0.9	—	—
gadids (Gadidae)	0.6	—	0.8	0.7
sandlance (<i>Ammodytes hexapterus</i>)	1.6	—	1.0	—
sculpin (<i>Myoxocephalus</i> sp.)	0.6	—	0.3	—
squid (<i>Illex</i> sp.)	—	—	0.3	—
Niche overlap	0.982		0.769	

compare the proportions of male to female capelin delivered to Common Murre chicks, as well as the proportions of gravid to not gravid female capelin, we used Chi-squared tests of independence.

Temporal Patterns of Food Delivery

In addition to four-hour watches, with the help of other researchers, we conducted feeding watches that included all daylight hours. These lasted 16-17 hours, from approximately 0430 h until 2130 h. Four all-day watches of Common Murres were done in 1996 (on August 4, 9, 16 and 21) and four were done in 1997 (August 5, 9, 11 and 21). Two all-day watches of Thick-billed Murres were done in 1997 (these were simultaneous with the August 5 and 11 all-day watches of Common Murres). During all-day watches, observers' shifts in the blind never exceeded four hours. To determine whether the frequency of feeds delivered during these four periods varied or differed between Common and Thick-billed murre chicks, we performed Chi-square analyses.

Maximum Dive Depths

In order to estimate the portion of the water column exploited by breeding murres, we measured the birds' maximum dive depths. We used noose poles to capture birds at their sites to deploy or retrieve depth gauges. In 1996, we deployed 74 capillary-tube maximum depth gauges (MDGs; Burger and Wilson 1988) on brooding and incubating Thick-billed Murres. In 1997 we deployed 19 MDGs on Thick-billed Murres and 14 MDGs on Common Murres. The gauges were retrieved within 48 hours in 1996 and within 24 hours in 1997. We only gauged birds of known reproductive status (egg or chick). No birds were caught on the plots monitored for productivity or chick diet. No birds were gauged more

than once. We interpreted the depth gauge readings following the protocol used by Burger and Wilson (1988).

RESULTS

Timing of Breeding

For the birds with known hatch and fledging dates, the chick-rearing periods of Common and Thick-billed murres were highly synchronous in both 1996 and 1997 (Fig. 1). In 1996, the Common Murre chick-rearing period began on July 20 and lasted until September 1. Thick-billed Murres reared chicks between July 21 and September 5. The median hatch date (MHD) of chicks reared on the productivity plots was July 29, the same for both species. The median hatch dates of those birds reared on the feeding plots differed only slightly between species; The Common Murre MHD was July 30 and that of Thick-billed Murres was July 31. July 31 was the MHD of the Common Murres and July 30 the MHD of Thick-billed Murres reared on the productivity plots. On the feeding plots, the Common Murres' MHD was July 30, and the Thick-billed Murres' was July 31.

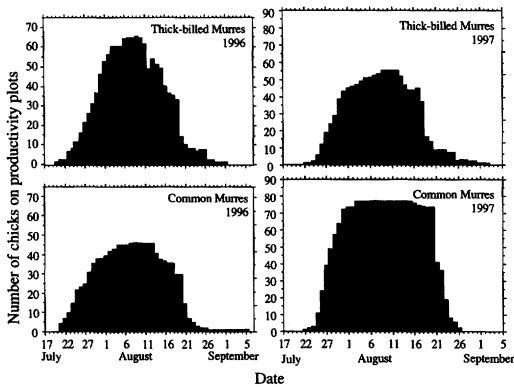


Figure 1. Numbers of Thick-billed and Common murre chicks present on representative productivity plots during 1996 and 1997.

Niche Breadth, Diet Diversity and Diet Overlap

For both species in both years, chicks diets were composed principally of shannies (fish of the family Stichaeidae, primarily daubed shannies). Thick-billed Murres seemed more reliant than Common Murres on shannies (Table 1). In addition to shannies, capelin accounted for a sizable proportion of Common Murre chick diets. Other items included sandlance, sculpins (family Cottidae), fish doctors (*Gymnelis viridus*), gadids (*Gadus* spp., *Boreogadus saida*) and squid (*Illex* spp.; Table 1).

In 1996, Common and Thick-billed murre chick diets were virtually identical (Table 1); the observed overlap was 0.98. The mean of the 5,000 overlaps calculated from randomly-generated chick diets was 0.90. The 95% confidence limits around this mean were narrow; the *p* value corresponding to the observed overlap was less than 0.001 (Fig. 2). The chick diets were less similar in 1997 than they were in 1996. The observed value fell well within the 95% confidence levels of the mean (*P* = 0.8; Fig. 2).

Size of Fish Delivered to Chicks

We measured 170 Common Murre chick meals in 1996; 124 (73%) of these were daubed shannies and 20 (12%) of them were capelin. In 1997 we measured 124 meals of Common Murre chicks, 59 (48%) of daubed shannies and 45 (36%) of capelin. The re-

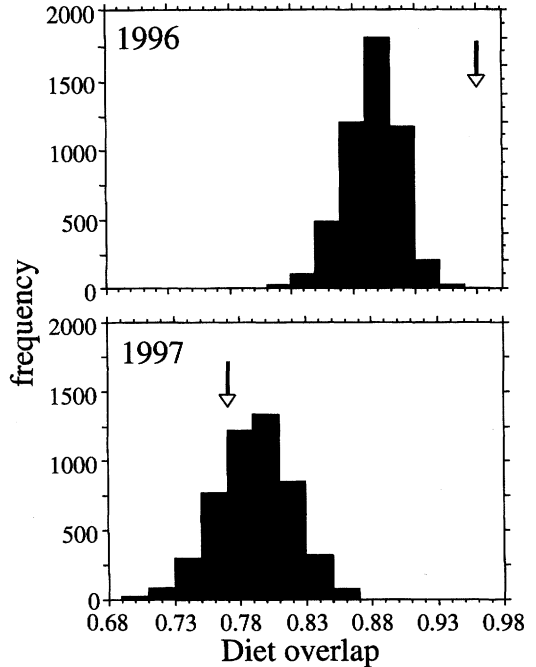


Figure 2. Frequency distribution of overlap (Morisita 1959; Horn 1966) in the diets of Common and Thick-billed murre chicks, calculated from diets generated randomly, given the number of fish deliveries and species of fish fed to chicks in 1996 and 1997. Arrows indicate observed overlaps.

maining fish were sculpin, sandlance, fish doctor and arctic cod. In 1997 we measured 28 meals of Thick-billed Murre chicks, all of which were daubed shannies.

In 1997, the size of daubed shannies delivered to Common and Thick-billed murre chicks did not differ significantly (Table 2; mass, $t_{74} = 1.0$, *P* = 0.3; length, $t_{83} = 1.2$, *P* = 0.2). The mean mass of daubed shannies delivered to Common Murre chicks did not differ between 1996 and 1997 (Table 2; $t_{176} = 1.1$, *P* = 0.2). The mean total lengths of daubed shannies did not vary significantly between 1996 and 1997 (Table 2; $t_{181} = 0.2$, *P* = 0.9). Common Murres fed their chicks larger capelin in 1996 than in 1997. In 1996 capelin mean mass was 30 per cent higher (Table 2; $t_{63} = 2.5$, *P* < 0.0001) and mean fork-length was six per cent longer (Table 2; $t_{60} = 3.1$, *P* = 0.003).

In 1997 we examined the reproductive state of 51 daubed shannies delivered to Common Murre chicks; 86% were gravid. Of the remaining seven, four were males and three

Table 2. Mean lenths and masses of capelin and daubed shannies delivered to Common and Thick-billed murre chicks in 1996 and 1997.

Fish species	Murre species	Year	N	Length		N	Mass (g)	
				X	SD		X	SD
Daubed Shanny	Common Murre	1996	124	152	10	122	10.2	1.6
	Common Murre	1997	59	151	8	56	10.6	2
	Thick-billed Murre	1997	26	154	11	20	10.1	1.8
Capelin	Common Murre	1996	11	144	10	20	17	4
	Thick-billed Murre	1997	39	135	11	45	12.9	3.5

were of unknown sex but were not gravid. Of the 24 daubed shannies delivered to Thick-billed Murre chicks, 71% were gravid. The seven fish that were not gravid included one male and six fish of unknown sex. The ratios of gravid to not gravid daubed shannies delivered to Common and Thick-billed murre chicks did not differ significantly ($X^2_2 = 2.6$, $P = 0.3$). Among 49 known-sex capelin brought to Common Murre chicks, 98% were female ($X^2_1 = 45.1$, $P < 0.0001$). Only two percent of the 42 female capelin with known reproductive state was gravid ($X^2_1 = 38$, $P < 0.0001$). Of the females that were not gravid, seven had a few eggs in their body cavities, which suggests that they had already spawned.

Temporal Patterns of Food Delivery

When analyzed at a one-hour scale, Common Murre chicks feeding rates varied with time of day for three of four all-day feeding watches in 1996 (Fig. 3; 4 August, $X^2_{15} = 39.2$, $P = 0.006$; 9 August, $X^2_{15} = 23.5$, $P = 0.7$; 16 August, $X^2_{16} = 50.3$, $P < 0.0001$; 21 August, $X^2_{15} = 34.2$, $P = 0.003$) and three of four feeding watches in 1997 (5 August, $X^2_{16} = 42.3$, $P = 0.0004$; 9 August, $X^2_{16} = 34.3$, $P = 0.005$, 11 August, $X^2_{16} = 62.8$, $P < 0.0001$; 21 August, $X^2_{16} = 15.7$, $P = 0.5$). Feeding rates to Thick-billed Murre chicks varied significantly with time of day during one of two all-day feeding watches in 1997 (5 August, $X^2_{16} = 14.6$, $P = 0.6$; 11 August, $X^2_{16} = 89.2$, $P < 0.0001$). When fish deliveries varied with time of day, there were high early morning peaks and lower evening peaks for both species. The daily pattern of feeds did not differ significantly between murre species during one of two simultaneous all-day watches (5 August watch, $X^2_{16} = 8.8$, $P = 0.9$; 11 August watch, $X^2_{16} = 26.6$, $P = 0.05$; Fig. 3).

Maximum Dive Depths

Of the 40 incubating Thick-billed Murres fitted with depth gauges in 1996, 25 were recaptured. Sixteen gauges yielded readable data. Thirty-two chick-rearing Thick-billed Murres were fitted with depth gauges in 1996, and 18 were recaptured. Eleven of these still bore readable gauges. In 1996, the mean maximum dive depth of incubating Thick-billed Murres (110 ± 35 m) did not differ significantly from that of brooding Thick-billed Murres (100 ± 23 m; $t_{25} = 0.9$, $P = 0.4$). In 1997, we recaptured seven of the 19 chick-rearing Thick-billed Murres that carried depth gauges. All the gauges were readable. The mean maximum dive depth of Thick-billed Murres in 1997 (94 ± 34 m) was not significantly different from that in 1996 (104 ± 28 m; $t_{32} = 0.6$, $P = 0.6$). Of the 14 depth gauges deployed on Common Murres in 1997, we retrieved only two. The depths they recorded (85 m and 158 m) were near the high and low limits of the range of Thick-billed Murre depths (40 m - 178 m; Fig. 4).

DISCUSSION

We found little or no evidence of food resource partitioning by Common and Thick-billed murre during the chick-rearing period at the Gannet Islands in 1996 and 1997. This is in keeping with the results of other studies of high-latitude seabirds (Trivelpiece *et al.* 1987; Barrett and Furness 1990). However, from the point of view of ecological theory, the lack of overlap we observed is somewhat surprising, because sympatric congeners are expected to use resources differently (Gause 1934; Lack 1971). This expectation was met by murre at the Gannet Islands in 1982-1983,

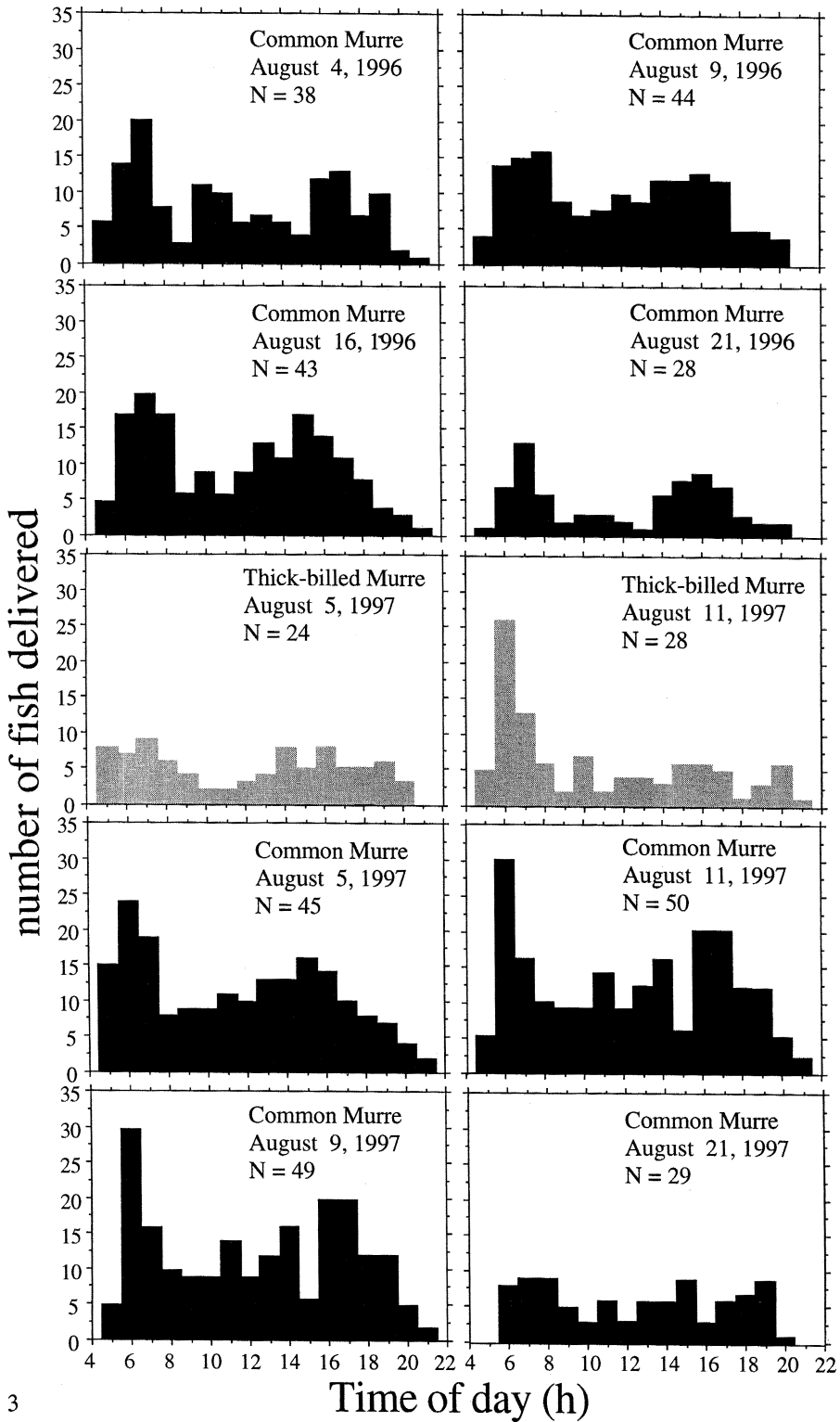


Figure 3. Numbers of fish delivered per hour to Common and Thick-billed murre chicks on feeding watch plots during 0430h-2130 h feeding watches in 1996 and 1997. Sample sizes are number of sites observed.

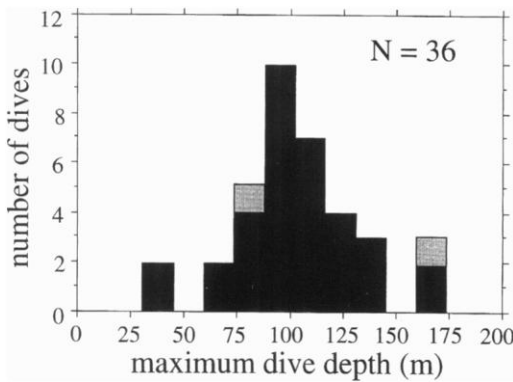


Figure 4. Maximum dive depths of breeding Thick-billed Murres in 1996 and 1997 (black bars) and breeding Common Murres in 1997 (grey bars).

when they seemed to partition their food resources by feeding their chicks different suites of prey items and by staggering their chick rearing periods (Birkhead and Nettleship 1987a, c). We attribute the apparent lack of partitioning during our study to changes in the relative and absolute local abundances of capelin and daubed shannies. High overlap in chick diets is not unusual for murres; it was over .88 for two years, during a study in the Barents Sea (Barrett and Furness 1990).

Although chick diet overlap was high in both years of our study, only in 1996 was such convergence higher than expected by chance. Yet in both 1996 and 1997, the two species' chick diets did not overlap less than predicted by the null model, implicating a lack of partitioning. In contrast, chick diet overlap scores in 1982 and 1983 (0.62 and 0.41, respectively) were lower than predicted by the null model, suggesting partitioning (calculated from Birkhead and Nettleship's 1987c data). In the 1980s, the diet of Common Murre chicks was more diverse and had a higher capelin-to-shanny ration than that of Thick-billed Murre chicks (Birkhead and Nettleship 1987c).

There is evidence that between the mid-1980s and mid-1990s, the distribution of capelin shifted away from the Gannet Islands (Miller and Lilly 1991; Miller 1993). This could partially account for the murres' more similar, shanny-dominated diet in the latter period. However, no data are available on the abundance of daubed shannies in southern Labrador.

Conclusions about resource partitioning drawn from diet overlap estimates depend on the assumption that each item in murre chicks' diets is equally available to their parents. If this assumption is true, lack of adherence of an overlap value to the null model would suggest resource partitioning. However, if shared rare items (such as gadids) were highly available to the parents, or if shared common items (such as shannies) were relatively unavailable to the parents, then lack of adherence to the null model could occur even in the absence of partitioning.

In 1996, when diet overlap was significant, the only other possibility of resource partitioning we examined was the timing of the chick-rearing period, and the two murre species overlapped entirely. This held true in 1997, as well. During the period 1981-1983, murre chick-rearing periods overlapped, but were not identical; Common and Thick-billed murres median hatch dates differed by two to ten days (Birkhead and Nettleship 1987a). During two years at Hornøya the median hatch dates of syntopic murres differed by 12 and 17 days (Barrett *et al.* 1997).

In 1997, Common and Thick-billed murres use of chick food resources converged along a greater range of parameters, including reproductive state and size of fish, dive depth and, possibly, time of foraging. For instance, the lengths, masses and reproductive states of daubed shannies, the principal item in both murre species' chick diets, did not vary significantly between species. Gravid daubed shannies comprised the greatest portion of the chick diets of both species. As at the Gannet Islands, at Hornøya in the Barents Sea, Common and Thick-billed murres fed their chicks fish of the same size (Furness and Barrett 1985; Barrett and Furness 1990; Barrett *et al.* 1997). Yet these similarities are not universal, as there is evidence that sympatric adult Common and Thick-billed murres partition resources by eating fish of different sizes (Erikstad and Vader 1989).

The disproportionate frequency of non-gravid females among capelin delivered to Gannet Islands Common Murre chicks was remarkable. Most of the capelin fed to

murre chicks in the Barents Sea were gravid (Furness and Barrett 1985; Barrett and Furness 1990; Barrett *et al.* 1997). The energy and protein content of gravid females is higher than those of other capelin (Montevecchi and Piatt 1984), suggesting that the former would be preferred. If the murres' chick-rearing period was late with respect to capelin spawning, this could explain the preponderance of spent and not-gravid females among the capelin that chicks ate.

The diurnal feeding pattern data do not wholly support the hypothesis that Common and Thick-billed murres forage for their chicks at different times of day. During both simultaneous all-day feeding watches, early morning and afternoon feeding peaks characterized the feeding patterns of both species. Yet during one watch, significant differences were detected between Common and Thick-billed murres in the frequency of feeds over time. Timing of feeding is an important niche dimension on which to gather more information, because, more than other organisms, vertebrate predators tend to partition resource use by varying their time of activity (Schoener 1974).

Our information on diving behavior indicated that Common and Thick-billed murres exploited the same portion of the water column (diving to maximum depths between approximately 80 and 180 meters). Gannet Islands murre diving behavior was similar to that of Thick-billed Murres at Coats Island (Croll *et al.* 1992) and of Common Murres in Witless Bay (Piatt and Nettleship 1985). Nevertheless, our Common Murre sample size ($N = 2$) was too small to make powerful comparisons. Moreover, even if both species dove to the same maximum depths, as these data imply, they might have fed at different depths.

Inferring competition from the effects of one species on the population size or productivity of another is more rigorous than measuring resource-use overlap (Pianka 1981; Schoener 1983). We were not able to test the effects of one murre species on the other at Gannet Islands. However, we can compare published estimates of colony attendance and productivity during a period

when the murres partitioned their resources with estimates made during our study. Neither the breeding success of Common Murres nor that of Thick-billed Murres was lower in 1996 or 1997 than in 1981, 1982 or 1983 (Bryant *et al.* in press; Birkhead and Nettleship 1987b). Likewise, in 1996 and 1997, the mean numbers of Common and Thick-billed murres present on count plots were the same as or higher than those recorded in 1981, 1982 and 1983 (Bryant *et al.* in press; Birkhead and Nettleship 1987b). Hence, we detected no evidence of increased interspecific competition between the 1980s and 1990s.

The apparent lack of chick food resource partitioning by Common and Thick-billed murres at the Gannet Islands might be partially explained by the bio-oceanographic conditions of the Southern Labrador Sea, which supports an arctic marine ecosystem. Most studies that have lent credence to the competitive exclusion principle have been conducted in the tropics or in temperate regions (Schoener 1983). The Arctic's relatively high summertime marine productivity but lack of diversity might facilitate high resource use overlap between ecologically similar predators. When they failed to detect strong evidence of competition between alcids breeding on Hornøya, in North Norway, Furness and Barrett (1985) suggested that, in summer, high-latitude marine ecosystems might foster interspecific ecological similarity. Our data support this hypothesis.

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