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Recent changes in the winter diet of murres (*Uria* spp.) in coastal Newfoundland waters

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Abstract: We investigated the winter diet of murres (*Uria* spp.) in coastal Newfoundland waters in relation to environmental and ecological changes that have occurred in the Northwest Atlantic since the 1980s. We analyzed the contents of 371 stomachs (311 from Thick-billed Murres, *Uria lomvia*, and 60 from Common Murres, *Uria aalge*) of birds shot by hunters around the Newfoundland coast during the winters of 1996–1998. We observed that the frequency of empty stomachs was greater in our study than in a similar study conducted during 1984–1986. We found no difference in the proportion of fish in the diet between the 1980s and the 1990s, however, Arctic cod (*Boreogadus saida*; from 55 to 12%) and capelin (*Mallotus villosus*; from 28 to 6%) decreased in frequency of occurrence. The proportion of stomachs containing crustaceans and squid did not change between the 1980s and 1990s, but hyperiid amphipods (*Parathemisto* spp.) replaced euphausiids (*Thysanoessa* spp.) as the predominant crustacean. Changes in murre winter diet off the coast of Newfoundland corroborate other sources of information indicating that major changes in the distribution and biology of marine organisms occurred in the Northwest Atlantic during the 1990s.

Résumé : Nous avons étudié le régime alimentaire d'hiver des guillemots (*Uria* spp.) dans les eaux côtières de Terre-Neuve en relation avec les changements environnementaux et écologiques qui se sont produits dans l'Atlantique du Nord-Ouest depuis les années 1980. Nous avons analysé les contenus stomacaux de 311 Guillemots de Brünnich (*Uria lomvia*) et de 60 Guillemots marmettes (*Uria aalge*) tués par des chasseurs près des côtes de Terre-Neuve au cours des hivers 1996–1998. Nous avons observé que la fréquence des estomacs vides était plus grande dans nos études que dans une étude semblable durant les hivers 1984–1986. Nous n'avons pas observé de différence dans la proportion de poissons présents dans les estomacs entre les années 1980 et les années 1990, mais la fréquence du Saida franc (*Boreogadus saida*; de 55 à 12 %) et celle du Capelan (*Mallotus villosus*; de 28 à 6 %) ont diminué. La proportion d'estomacs contenant des crustacés et des calmars n'a pas changé entre les années 1980 et les années 1990, mais les amphipodes hypériidés (*Parathemisto* spp.) sont devenus les crustacés dominants en remplacement des euphausiacés (*Thysanoessa* spp.). Les changements dans le régime d'hiver des guillemots de Terre-Neuve corroborent d'autres sources d'information selon lesquelles des changements importants se sont produits dans la répartition et la biologie des organismes marins de l'Atlantique du Nord-Ouest au cours des années 1990.

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Introduction

Murres (*Uria* spp.) are the most numerous fish-eating seabirds of the continental-shelf waters off Newfoundland during winter, with about four million birds being present (Gaston 1980). During the past decade, this region has undergone massive ecological changes due to human overfishing and environmental shifts. Atlantic cod (*Gadus morhua*) stocks off the northeast coast have been fished to commercial extinction (Hutchings and Myers 1994; Hutchings 1996). Consequently, recent years have seen an increasing variety of intense fisheries directed toward organisms at lower trophic levels, such as the northern shrimp (*Pandalus borealis*) and snow crab (*Chionoecetes opilio*). Large-scale commercial fisheries for capelin (*Mallotus villosus*) continue, although at a lower level than prosecuted during the 1970s by offshore fleets. Seawater temperatures several degrees colder than those recorded in previous decades were measured in the northwest Atlantic during the 1990s (Colbourne et al. 1994). Coincident changes in the distribution patterns and biology of numerous organisms have been documented (e.g., several groundfish species, deYoung and Rose 1993; Rose et al. 1994; Gomes et al. 1995; capelin, Nakashima 1996; Carscadden and

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Nakashima 1997; humpback whales (*Megaptera novaeangliae*), J. Lien, personal communication).

Thick-billed Murres (*Uria lomvia*) that breed in the Canadian Arctic and Greenland move south in the autumn to winter off eastern and southern Newfoundland and the Grand Banks (Tuck 1961; Gaston 1980). These birds reach northern Newfoundland in mid-October and remain as far north as they can find large patches of open water. Smaller numbers of murres winter along the south coast of Newfoundland and in the Gulf of St. Lawrence (Gaston 1980). Both Thick-billed Murres and Common Murres (*Uria aalge*) are hunted legally in Newfoundland and Labrador in fall and winter, although most Common Murres winter farther south and offshore (Elliot 1991). About 50% of the murres taken in the hunt are juveniles (less than 1 year old) and Thick-billed Murres outnumber Common Murres by a factor of 10. The hunting season extends from September through March, although murres are usually only present and hunted for 1–3 months in any one location. Murres are normally shot from small open boats within 5–15 km of shore, when weather and ice conditions permit. The daily bag limit is currently 20/person. In addition to hunting pressure, the murres are subject to strong winds and rapidly changing ice conditions that determine distribution patterns and probably affect foraging efficiency and food requirements.

Elliot et al. (1990) conducted a major study of the diet of Thick-billed Murres wintering off Newfoundland by analyzing the stomach contents of birds shot by hunters in two winters: 1984–1985 (n = 660) and 1985–1986 (n = 550). In both years, fish, especially Arctic cod (*Boreogadus saida*), capelin, sand lance (*Ammodytes* spp.), and cod (*Gadus* spp.) predominated in samples from November to December, while crustaceans, particularly euphausiids (*Thysanoessa* spp.), predominated from January to March as murres moved south. In an earlier study from the late 1950s, capelin were dominant in the winter diet of murres (comprising 93% of the food items in 614 Thick-billed Murre stomachs and 92% of the food items in 44 Common Murre stomachs; Tuck 1961).

In this study, we investigated the winter diet of murres in coastal Newfoundland waters in the 1990s in relation to known environmental and ecological changes that have occurred since the 1980s. The objectives of our study were (*i*) to document the species and age composition of birds shot in the hunt, (*ii*) to quantify the winter diet and how this varied with location and time, and (*iii*) to compare the murre diet in the 1980s and 1990s.

Materials and methods

Field collections

The murres in this study were shot by hunters between October and March of 1996–1997 and 1997–1998. They were kept cool until cleaned by hunters, usually within a few hours of death. Together with other digestive organs, the stomachs (i.e., proventriculus and gizzard) were removed and frozen for later analysis in the laboratory. Heads were collected from all birds sampled, to identify species and age (first-year bird or older).

We could not control or record the time between death and the freezing of the stomach, during which time digestion could still occur. Although this affects the numbers of organisms that could be identified, we do not believe that there was a systematic bias in the distribution of these elapsed times.

We tried to obtain at least 20 stomachs for each collection date. Ten collections were made at nine locations around the coast of Newfoundland in 1996–1997 and two from two locations in 1997–1998 (Table 1). Samples were later grouped by time of season (early, October–December; late, January–March; see Elliot et al. 1990) and survey zone for analysis (Fig. 1).

Laboratory analysis

After thawing, the contents of the proventriculus and gizzard were sorted and identified. Individual food items were identified to genus or species where possible, using reference samples developed by Elliot et al. (1990) and standard keys. Identifications were confirmed by personnel from the Northwest Atlantic Fisheries Centre (Department of Fisheries and Oceans) and the Biology Department, Memorial University of Newfoundland. All fish material was well digested and was identified by the otoliths present. Owing to the difficulty associated with distinguishing between otoliths of Atlantic cod and Greenland cod (*Gadus ogac*), the two species were combined during analysis and subsequently referred to as "*Gadus* species." Arctic cod (*Boreogadus saida*) was easily distinguishable from the other cods (*Gadus* spp.) by otolith characteristics. The presence of pebbles and other nonfood items, such as plastic, was also recorded.

Data analysis and interpretation

The effects of differential digestive rates on the interpretation of murre stomach content data have been discussed by Bradstreet (1980) and Gaston and Noble (1985). With the exception of most bony or chitinous parts, prey tissue is digested very rapidly. Food remains from the main prey taxa encountered in our study were probably digested or evacuated in the following order: squid and fish flesh, crustaceans, fish otoliths, and squid beaks. Although otoliths and squid beaks may remain in the gizzard for several weeks, most other items probably disappear within 24 h (Bradstreet 1980; Gaston and Noble 1985).

We present our data in terms of (*i*) the proportion of stomachs containing food in which each major taxon was found (e.g., the proportion of stomachs with food that contained fish) and, (*ii*) for those stomachs containing fish and crustaceans, the proportion with particular prey taxa present (e.g., the proportion of stomachs with fish that contained capelin). We did not analyze the proportion of individual food items within individual stomachs.

The categories of "unidentified fish" and "unidentified crustaceans" include taxa that were too digested to identify. Some of these would be taxa identified and recorded from other stomachs, and some may never have been identified.

Samples were examined on the basis of murre species, bird age, survey zone, and time of season. The proportion of birds 4–8 months old was determined on the basis of interorbital distance (Gaston 1984). Individuals with an interorbital distance less than or equal to 12.7 mm were considered to be first-winter birds.

To contrast murre diet between 1984–1986 (Elliot et al. 1990) and 1996–1998, we looked for evidence of a diet shift between the autumn (October–December) and the winter (January–March), as previously documented by Elliot et al. (1990). We also used paired tests (to control for location and date) to compare the frequency of empty stomachs and the percent occurrence of the following diet categories in stomachs that had food: (*i*) all fish, (*ii*) all crustaceans, and (*iii*) squid. Frequencies of diet items were arcsine transformed to achieve normality. In addition, among the stomachs that contained fish, we used contingency table tests to compare the frequency of occurrence of particular species between 1984–1986 and 1996–1998. Elliot et al. (1990) reported little interannual variation in diet, so, to maximize our sample size and statistical power, samples collected between 1984 and 1986 were combined for analysis, as were those collected during 1996–1998.

Table 1. Murre stomach collections from the 1996–1997 and 1997–1998 hunting seasons.

Date	Location[a]	Survey zone[a]	No. of stomachs: Thick-billed Murres	Common Murres	Total
1996–1997					
1996					
October	Fischot Island	3	18	2	20
	Twillingate	6	20	0	20
October–November	Cape Bauld	3	20	0	20
	Fogo Island	6	68	4	72
November	Bay of Exploits	6	16	4	20
	Twillingate	6	72	1	73
1997					
January	St. Mary's Bay	10	8	4	12
January–February	Brunette Island	11	14	6	20
February	Belleoram	11	14	6	20
February–March	Grand Bank	11	31	29	60
1997–1998					
1997					
October	Hare Bay	3	13	1	14
November	Fogo Island	6	17	3	20
Totals			311	60	371

[a]See Fig. 1.

Results

General patterns

We analyzed the contents of 371 murre stomachs (311 from Thick-billed Murres and 60 from Common Murres). Thick-billed Murres predominated in samples from more northerly locations early in the season (October–December). Of the 311 Thick-billed Murres in our sample, 227 were aged and, of these, 148 (65%) were juveniles. Most of the Common Murres (45/60 = 75%) in our sample were obtained from the south coast in late winter. Nearly half (29/60 = 48%) of the Common Murres were obtained from the town of Grand Bank on the south coast of Newfoundland (survey zone 11) during February–March of 1997. Consequently, the interpretation of interspecific and age-related variation in the diet is confounded by differences in locations used and the timing of migration. Therefore, we did not quantify age-related differences in diet, as this was confounded by most immature birds being taken in the north and early in the season. In addition, Elliot et al. (1990) found no evidence that Thick-billed and Common murre diets were different, so we pooled the results for both murre species to maximize our sample size and simplify the analysis. Similarly, because the murre hunt (and thus our sampling) progressed from north to south during the winter season, we were not able to infer the relative importance of location and date in explaining murre diet.

Diet patterns during 1996–1998

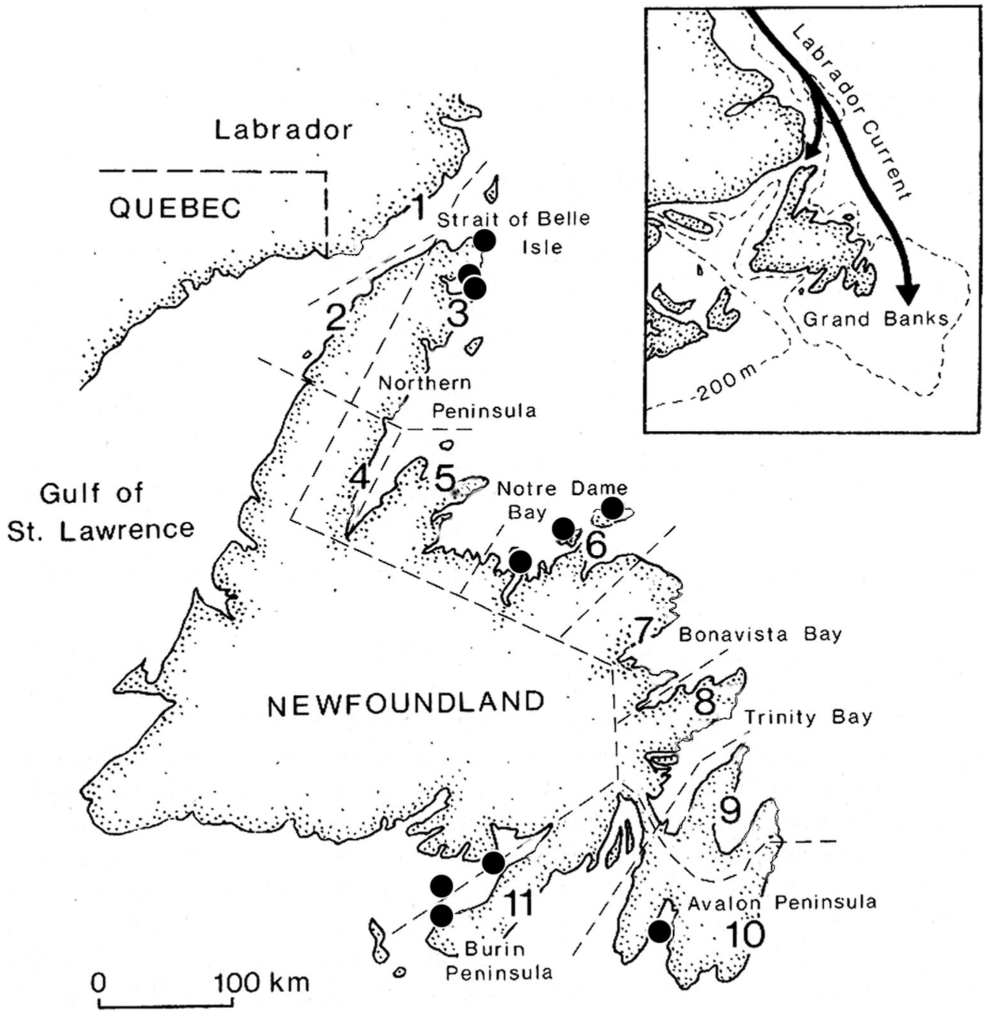
A total of 237 (64%) stomachs contained food items; the remaining 134 (36%) stomachs were empty. In our study, 65 stomachs contained fish, 170 contained crustaceans, and 55 contained Arctic squid (*Gonatus fabricii*) (Table 2). Cod (*Gadus* spp.) was the most abundant fish, and hyperiid amphipods dominated among the crustaceans. Some stomachs contained nonfood items, such as pebbles (61 stomachs), plastic (16 stomachs), and other debris (10 stomachs). Among the stomachs that contained food, we found no evidence that the diet differed between early and late in the season with respect to the proportion of fish (early, 41/162 or 25% of stomachs contained fish; late, 24/75 or 32% of stomachs contained fish; $G = 1.1$, df = 1, $p = 0.29$) or crustaceans (early, 118/162 or 73% of stomachs contained crustaceans; late, 52/75 or 69% of stomachs contained crustaceans; $G = 0.3$, df = 1, $p = 0.58$). However, we did find that squid were more abundant in the murre diet early in the season (early, 47/162 or 29% of stomachs contained squid; late, 8/75 or 11% of stomachs contained squid; $G = 10.7$, df = 1, $p = 0.001$).

Diet variation between the 1980s and 1990s

We tested the hypothesis that the frequency of empty stomachs would be greater in the 1990s (our study) than in the 1980s (Elliot et al. 1990) and found that this was indeed the case: relative frequencies (1984–1986/1996–1998) of empty stomachs in survey zones 3, 6, 10, and 11 were 0.02/0.13, 0.06/0.44, 0.03/0.08, and 0.15/0.36, respectively (paired $t = 2.6$, df = 3, one-tailed $p = 0.04$).

Among stomachs containing food, we found no evidence for a difference in the proportion of fish in the diet of murres between the 1980s and 1990s: relative frequencies (1984–1986/1996–1998) of stomachs containing fish in survey zones 3, 6, 10, and 11 were 0.51/0.51, 0.88/0.15, 0.40/0.36, and 0.12/0.31, respectively (paired $t = 0.76$, df = 3, two-tailed $p = 0.50$). However, we did find changes in the frequency of occurrence of some fish species between 1984–86 and 1996–98: Arctic cod (found in 305/558 or 55% of stomachs with fish in the 1980s; found in 8/65 or 12% of stomachs with fish in the 1990s; $G = 46.5$, df = 1, $p < 0.0001$)

Fig. 1. Map of the study area showing murre survey zones (1–11) and the locations (●) where stomach samples were collected in 1996–1998.



and capelin (found in 159/558 or 28% of stomachs with fish in the 1980s; found in 4/65 or 6% of stomachs with fish in the 1990s; $G = 19.2$, df = 1, $p < 0.0001$) decreased in frequency. Also, there was a nonsignificant increasing trend in the frequency of occurrence of *Gadus* species (found in 113/558 or 20% of stomachs with fish in the 1980s; found in 20/65 or 31% of stomachs with fish in the 1990s; $G = 3.5$, df = 1, $p = 0.06$).

Among stomachs containing food, we found no evidence for a difference in the proportion of crustaceans in the diet of murres between the 1980s and 1990s: relative frequencies (1984–1986/1996–1998) of stomachs containing crustaceans in survey zones 3, 6, 10, and 11 were 0.75/0.60, 0.04/0.78, 0.80/0.82, and 0.89/0.67, respectively (paired $t = 0.31$, df = 3, two-tailed $p = 0.78$). Elliot et al. (1990) found that euphausiids were the most common crustaceans in murre stomachs by mass, percent occurrence, and absolute number during 1984–1986. In contrast, we found that hyperiid amphipods (*Parathemisto* spp.) were most common during 1996–1998 (Table 2).

Among stomachs containing food, we found no evidence for a difference in the proportion of squid between the 1980s and 1990s: relative frequencies (1984–1986/1996–1998) of stomachs containing squid in survey zones 3, 6, 10, and 11 were 0.24/0.51, 0.40/0.20, 0.0/0.09, and 0.0/0.12, respectively (paired $t = 0.68$, df = 3, two-tailed $p = 0.55$).

Discussion

The species and age composition of birds shot in the Newfoundland murre hunt during 1996–1998 showed similar patterns to those recorded by Elliot et al. (1990). Thick-billed Murres predominated in samples taken early in the season and in northerly areas of Newfoundland, while Common Murres were taken mostly late in the season and along the south coast. As found in previous studies, most of the birds taken in the hunt were juveniles (although they are believed to represent about 16% of the murre population at sea; Elliot et al. 1990; Elliot 1991).

The winter diet that we observed during 1996–1998 was similar in its proportions of fish, crustaceans, and squid to that observed in 1984–1986 (Elliot et al. 1990), although empty stomachs occurred more frequently in our study, consistent with the idea that murres were having difficulty finding food during this period. As in the previous study, squid were more frequently taken in early winter and at more

Table 2. Frequency of major prey items in murre stomachs containing food during 1984–1986 and 1996–1998.

	No. of stomachs		Percent occurrence[a]	
	1984–1986[b]	1996–1998	1984–1986[b]	1996–1998
Cod (*Gadus* spp.)	113	20	10.2	8.4
Arctic cod (*B. saida*)	305	8	27.6	3.4
Capelin (*M. villosus*)	159	4	14.3	1.7
Unidentified fish	152	35	13.8	14.8
Any fish	558	65	50.4	27.4
Euphausiids	540	0	48.8	0
Hyperiid amphipods	196	56	17.7	23.6
Gammarid amphipods	24	0	2.2	0
Decapods	21	0	1.9	0
Unidentified crustaceans	42	119	3.8	50.2
Any crustacean	679	170	61.3	71.7
Polychaetes	4	0	0.4	0
Molluscs	11	0	1.0	0
Squid	152	55	13.7	23.2
Total no. of stomachs with food	1107	237		

[a]Among stomachs containing food.
[b]Data from Elliot et al. (1990).

northerly locations. However, unlike Elliot et al. (1990), we found no evidence for a seasonal shift from fish early in the season to crustaceans late in the winter. Elliot et al. (1990) invoked the seasonal decline of sea-surface temperatures to below 0°C as Arctic pack ice moved into Newfoundland waters to explain the shift from fish to crustaceans. Typically, fish are less available after December, because murres move south of the prey's range (e.g., Arctic cod) or because the fish move into deeper water (e.g., capelin and Atlantic cod). Conversely, crustacean prey may become more abundant late in the season, as euphausiids (*Thysanoessa* spp.) migrate inshore and to surface waters to spawn (Sameoto and Jaroszynski 1972) and hyperiid amphipods (*Parathemisto* spp.), which migrate vertically to surface waters each day, are locally abundant in more southerly locations (Shih et al. 1971). It is possible that the lack of an obvious seasonal diet shift during the late 1990s was due to less severe ice conditions (Drinkwater et al. 1998). Overall, our observed seasonal and geographic patterns in murre diet must be interpreted with caution, because these two factors are confounded.

Changes in the winter diet of murres off the coast of Newfoundland corroborate other sources of information regarding changes in the distribution and biology of organisms in the Northwest Atlantic during the 1990s. Although fish continue to be present in the murre winter diet, the formerly common fish species, Arctic cod and capelin, were much less prevalent during 1996–1998. This result parallels the decline in the frequency of capelin in the murre chick diet at the Gannet Islands, Labrador, between the early 1980s and the mid-1990s (Bryant et al. 1999). In our study of winter diet, we found that the previously abundant *Thysanoessa* euphausiids were inexplicably replaced in the 1990s by hyperiid amphipods. Unfortunately, there are no data available on the distribution or relative abundance of these crustaceans during this time period. However, the cause of this change is of considerable of interest. Despite drastic changes in the abundance of adult Atlantic cod during the past decade (Hutchings 1996), there was no difference in the frequency of *Gadus* species in the murre winter diet between the 1980s and the 1990s. However, because we were unable to distinguish between the otoliths of Atlantic cod and Greenland cod, we were unable to assess the relative importance of each of these species. Compared with the late 1950s, the frequency of capelin in the murre winter diet has radically declined and murres wintering off Newfoundland now rely much more on crustaceans (Tuck 1961). Taken together, these changes in winter diet raise the question of the energetic implications to wintering murres of such a drastic shift; from a pelagic schooling fish with high energy content to demersal gadids and crustaceans. The murre winter diet may provide useful indices of the abundance of several important but difficult to monitor fish and invertebrate species. Further study of the murre winter diet and foraging ecology is required if we are to understand the population dynamics of these species and the ever-changing nature of the Northwest Atlantic ecosystem.

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