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THE WINTER DIET OF THICK-BILLED MURRES IN COASTAL NEWFOUNDLAND WATERS

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Abstract. The diets of Thick-billed Murres wintering off Newfoundland were sampled by analyzing stomach contents of birds shot by hunters in 1984–1985 (N = 660) and 1985–1986 (N = 550). Fish, especially arctic cod (*Boreogadus saida*) with fewer capelin (*Mallotus villosus*), sand lance (*Ammodytes* sp.) and Atlantic cod (*Gadus morhua*), predominated in samples from November to December in northern zones. Crustaceans, particularly the euphausiids (*Thysanoessa* spp.), predominated from January to March as the murres gradually moved south. This switch in diet corresponded to a drop in surface temperature below 0°C as arctic pack ice moved into Newfoundland waters. We conclude that fish descended in the water column to reach warmer layers at a time when *Thysanoessa* migrated into coastal areas and swarmed near the surface, thereby reversing the relative availability of these prey for murres.

Key Words: euphausiid; murre; Newfoundland; diet; sea-surface temperature; food.

The summer diets of young and adult Thick-billed Murres (*Uria lomvia*) have been well described at colonies in the Canadian arctic and Labrador (e.g., Gaston 1985, Gaston and Noble 1985, Birkhead and Nettleship 1987). However, only Tuck (1961) and Gaston et al. (1983) have considered the diet of this species in winter in Newfoundland waters, from examinations based on limited stomach samples obtained from hunters.

Thick-billed Murres that breed in the eastern Canadian arctic and western Greenland move south in the fall with the Labrador current, which carries arctic water from western Baffin Bay and Hudson Strait along the coasts of Labrador and eastern Newfoundland to the Grand Banks. These birds reach northern Newfoundland in mid-October (Gaston 1980, pers. obs.), about two months ahead of the pack-ice. The murres remain as far north as they can find large patches of open water, but by March extensive ice keeps most birds southeast of the Avalon Peninsula (Gaston 1980). Smaller numbers winter along the south coast of the island, with a few in the Gulf of St. Lawrence.

Gaston (1980) calculated that about four million Thick-billed Murres from the Canadian arctic and western Greenland winter off Newfoundland. Based on the size of the annual harvest, we assume that about half of these birds spend part of that time in sheltered bays and coastal waters where Newfoundlanders traditionally hunt "turrs," the local name for murres (R. D. Elliot, unpubl.). The recovery of many harvested murres that had been banded in arctic colonies (Gaston 1980, R. D. Elliot and P. C. Ryan, pers. obs.) confirms that these are the same populations for which there is extensive information on summer diet (e.g., Gaston and Noble 1985). In addition to hunting pressure and disturbance, these wintering murres are subjected to many storms and rapidly-changing ice conditions that limit their movements and likely affect their feeding efficiency and requirements.

Both Thick-billed and Common murres (*Uria aalge*) are hunted legally in Newfoundland and Labrador, although most Common Murres move south of the island to winter offshore (Brown 1986). Thus, they are mainly taken early in the season, or along the south coast, and probably make up less than 5% of the total annual harvest (R. D. Elliot, unpubl.). The hunting season extends from September through March, although murres are usually present for only 1–3 months in any location, with most birds taken after November (Wendt and Cooch 1984). Murres are shot from open boats about 5–7 m long within 5–15 km of shore, when weather and ice conditions permit; 20–40 murres is a typical day's take for a crew of 2–3 hunters. Most birds are plucked and cleaned the day they are shot, giving us opportunities to collect stomach contents and data on species, age, and condition of the murres.

The objectives of this study were to determine the diets of Thick-billed Murres through the winter, in relation to surface water temperature, ice cover and geographic location, which are likely to influence the availability of prey. We compare the murres' winter and summer diets and review winter diets of potential competitors in Newfoundland waters. We also consider possible changes in murres' winter diet since the 1950s (Tuck 1961). Our results contribute new information on the wintering distribution of several species of non-commercial prey. Limitations imposed by reliance on hunters to provide stomach samples, and the lack of information on prey availability, are offset by the large numbers of samples obtained over five months of the fall and winter, from 1100 km of coast in the wintering range of this species.

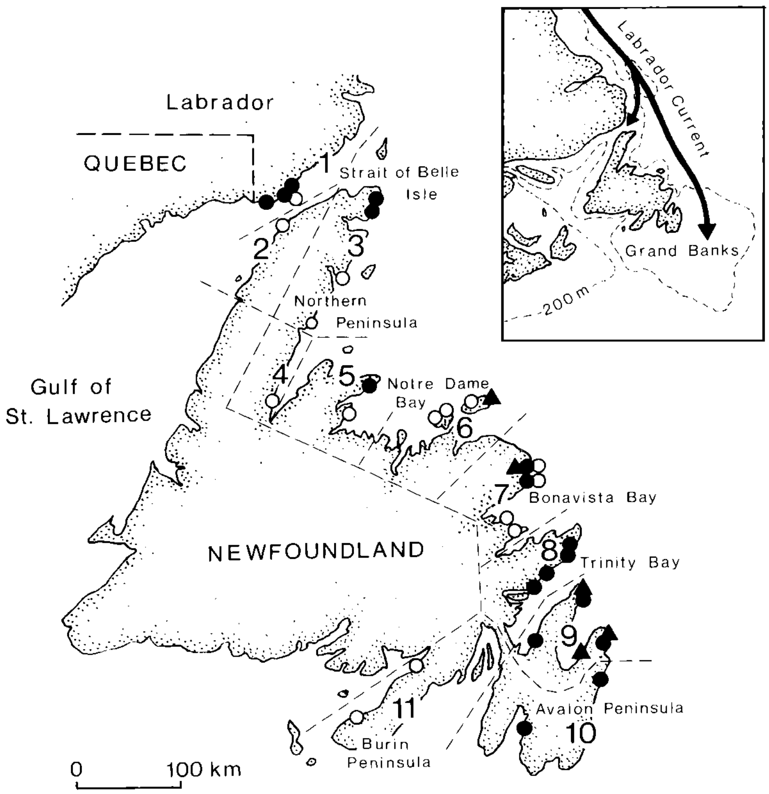

FIGURE 1. Map of the study area, showing murre survey zones and the locations where stomach samples were collected in early 1984 (▲), 1984–1985 (●), and 1985–1986 (O).

METHODS

Field Collections

Murres in this study were shot by hunters between 1 November and 31 March of 1984–1985 and 1985–1986, usually on the surface within 10 km of shore. It was not possible to collect foraging birds only, although most hunters believed that the birds were feeding when shot. Murres were kept cool until cleaned by hunters, usually within 6 h of shooting. For about half the samples we removed the stomachs (i.e., proventriculus and gizzard) and immediately froze them individually to avoid mixing or losing their contents. Stomachs from other samples were frozen by hunters for us, together with the other digestive organs, and were later thawed and separated in the lab.

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 and counted (see below), 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 on each collection date. Thirty-five collections were made from 17 locations in 1984–1985, and 26 from 15 locations in 1985–1986 (Fig. 1). Details of collecting dates and locations have been deposited in the Atlantic Regional Library, Canadian Wildlife Service (Box 1590, Sackville, New Brunswick E0A 3C0). Samples were later grouped by month and by survey zone (Fig. 1) for analysis. Samples were also collected at five locations in Zones 7 and 9 in early 1984 while we developed our techniques, and these were analyzed in less detail.

Heads were collected from almost all birds sampled to identify the species of murre involved, but were grouped for each sample, rather than being kept with the correct stomach. Stomachs from known Common Murres were excluded from analysis, although others were included in some samples kept for us by hunters. Based on the identification of the heads with the samples, we estimate that 2–3% of the stomachs considered here were from Common Murres. An exception is a sample of 61 murres from Zone 11 taken on 12–13 February 1986, of which 20% were Common Murres.

Laboratory Analysis

After thawing, the contents of the proventriculus and gizzard were weighed, sorted, identified, and counted separately. Contents were separated initially into fish, crustacean, and squid remains and wet weight was measured for each group. Pebbles and other non-food items such as plastic were also weighed and counted.

Individual food items were identified to genus or species where possible, using reference samples collected during the surveys and standard keys. All fish material was well digested, and was identified by the otoliths present. Identifications were confirmed by personnel from the Northwest Atlantic Fisheries Centre (Department of Fisheries and Oceans) and the Biology Department, Memorial University of Newfoundland. Crustacean remains were preserved in 40% isopropyl alcohol, and fish otoliths and cephalopod beaks were washed in water, dried, and stored on acetate sheets.

The higher number of left or right sagittal otoliths was taken as the minimum number of fish present for species such as capelin (*Mallotus villosus*), where left and right otoliths could be separated. For other species, otoliths paired by size and differing in length by less than 5% were considered to be from the same individual (Gaston and Noble 1985). The numbers of pairs of eyes were counted for euphausiids, and the number of complete telsons enumerated for other crustaceans. We used the numbers of jaws divided by two for polychaete worms, and the greater number of upper or lower beak halves for squid.

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). Prey tissue is digested very rapidly, with the exception of most bony or chitinous parts. Food remains from the main prey taxa encountered in our study are probably digested or evacuated in the following order: squid and fish flesh, crustaceans, fish otoliths, and squid beaks. Although the latter may remain in the gizzard for at least several weeks (Bradstreet 1980), most other items probably disappear within 24 hours (Uspenski 1956).

A crude estimate of the relative volumes of the major taxa consumed is given by the wet weight of the remains in the proventriculus. Gizzard contents were not included in these comparisons to reduce the error resulting from the more rapid digestion there of fish and squid. We presented our data in terms of: (1) the proportion by wet weight of fish, crustaceans and squid in the proventriculus; (2) the proportion of stomachs (proventriculus and gizzard) containing food in which each taxon was found; and (3) within fish and crustacea, the proportion of all individuals identified that were assigned to each taxon.

The categories of "other fish" and "other crustaceans" include taxa which were too digested to identify. Some of these would be taxa identified and recorded from other stomachs, and some may never have been identified. We assume that numbers involved were small enough to be of little consequence, with the possible exception of some unidentified gadoids (particularly *Gadus* and *Boreogadus*) grouped with "other fish."

Samples were compared on the basis of the murres' age composition, the proportion of ice cover, water temperature, survey zone and month. The proportion of birds 4–8 months old was calculated using a discriminant function based on four skull and bill measurements (Gaston 1984, Elliot and Gaston 1986). This proportion was derived from measurements of the overall sample of birds for which stomachs were analyzed. However, as the head and stomach from each individual were not usually kept together, we were unable to assign individual stomachs to a specific age category. Data for ice cover (expressed in tenths of the surface covered) were obtained from charts issued at 4-day intervals by the Atmospheric Environment Service, supplemented by hunter reports. Sea-surface temperatures were interpolated to the nearest 1°C from charts produced weekly by the Canadian Forces Meteorological Service.

RESULTS

Although a few stomachs from Common Murres were probably included in these analyses, their contents were generally similar to those from Thick-billed Murres. This similarity is apparent in the comparison of contents from the two species shot from the same flock in northern Bonavista Bay (Zone 7) on 12 December 1984 (Table 1).

TABLE 1. Comparison of Stomach Contents of Common and Thick-billed Murres from One Flock in North Bonavista Bay, 12 December 1984

	Proportion by wet weight in proventriculus		Percent occurrence of taxa in stomachs containing food	
Prey species	Common	Thick-billed	Common	Thick-billed
Atlantic cod			0	3.4
Arctic cod			14.3	37.9
Capelin			100.0	58.6
Other fish			0	20.7
All fish	1.000	0.997	100.0	100.0
Hyperiid amphipods			0	3.4
Gammarid amphipods			0	3.4
All crustaceans	0.000	0.003	0	6.8
No. of stomachs containing food			7	29
No. of empty stomachs			2	12

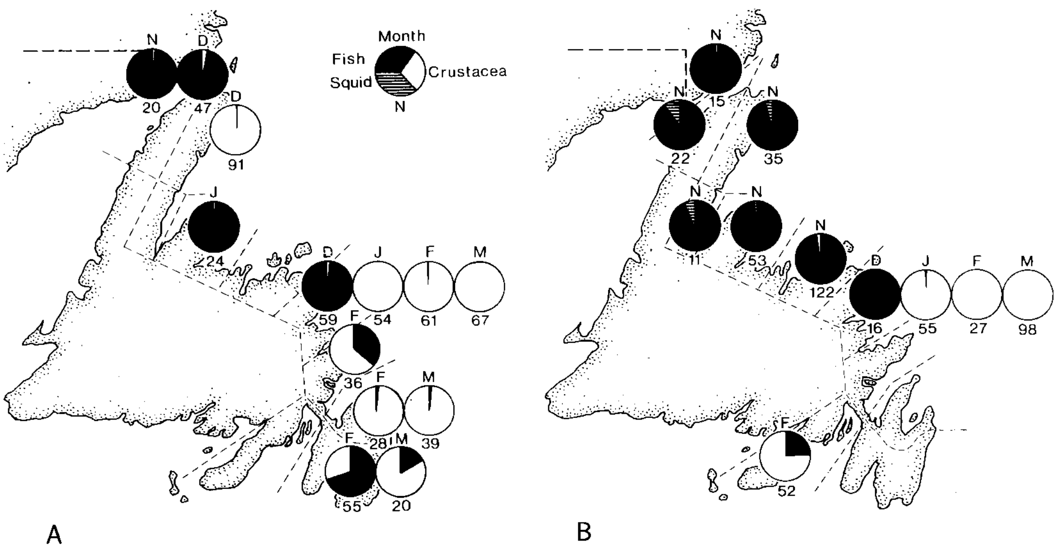

FIGURE 2. The proportions of major taxa in murre stomachs, by wet weight, month and survey zone. A, 1984–1985, and B, 1985–1986. The number of stomachs (N) is shown for each sample, and survey months are indicated as November (N), December (D), January (J), February (F), and March (M).

Overall Trends in Diet Composition

In 1984–1985 and 1985–1986 there was an overall trend for fish to predominate early in the season in samples in northern survey zones, when compared to the proportion of wet weight in the proventriculus (Figs. 2a,b). There was a marked shift to crustaceans after December in most southeastern zones in both years. Arctic squid (*Gonatus fabricii*) were only recorded regularly in northern survey zones early in 1985–1986 (Fig. 2b).

The increase in the proportion of crustaceans was related to increased ice cover and decreased surface water temperature. A step-wise multiple regression analysis of the factors in Tables 3 and 4, for both years considered together, showed that only the month of the sample and the amount of ice present significantly contributed to the regression relationship ($r^2 = 62.8\%$, $F = 20.40$, $P < 0.001$). The importance of sea-surface temperature is under-estimated in such a linear analysis, as it is related to the proportion of fish taken in a step function. Samples from water temperatures below and above 0°C have markedly different prey compositions (Fig. 3). Fish predominated in only two of the samples below 0°C, but in all from warmer surface waters.

All samples in north Bonavista Bay (Zone 7) included in Figures 2a,b were collected off the same 20-km stretch of coast near Wesleyville and Greenspond. In this zone, murres ate fish almost exclusively in December in both years, at sea-surface temperatures of about 2°C. They switched completely to crustaceans for the next three months when temperatures were below 0°C and pack-ice was usually present nearby (Tables 3, 4). Crustaceans also occurred in most stomachs there in January 1984 (Table 2) when surface temperatures were about −2°C. A similar difference between crustacea in December 1984, and fish in November 1985, off the eastern Northern Peninsula (Zone 3), again corresponded with lower water temperature and the presence of extensive ice in December (Tables 3, 4, Fig. 2). Similar trends were apparent when considering the percent occurrence of each prey taxon, or the proportion of stomachs from each sample con-

TABLE 2. Percent Occurrence of Major Taxa in Murre Stomachs Containing Food in Early 1984

	Month		
	January	February	March
Zone	7	9	9
Gadidae	8.9	64.9	3.7
Capelin	2.2	5.4	34.3
Other fish	20.0	21.6	29.6
All fish	31.1	70.3	67.6
All crustaceans	84.4	45.9	45.4
Arctic squid	2.2	0	0.9
No. of stomachs containing food	45	37	108
No. of empty stomachs	5	0	66

taining food in which that taxon occurred (Tables 5, 6).

Among the fish recorded, Atlantic cod (*Gadus morhua*), arctic cod (*Boreogadus saida*), capelin, and sand lance (*Ammodytes* sp.) each predominated in samples from different zones (Figs. 4a,b). Samples in which crustaceans predominated showed less variation, with euphausiids (*Thysanoessa* spp.) being the most common in all but those from the Burin Peninsula in February 1986 (Zone 11, Tables 5, 6).

COMPARISON OF FISH SPECIES IN THE DIET

Individuals of all the major fish species were of similar size (5 to 15 cm) based on the size of otoliths, which enabled us to compare the approximate proportion each species represented of the total numbers of fish present in each sample (Figs. 4a,b).

Arctic cod was the most common species, being numerically dominant in both years at most sites on the northeast coast (Zones 2–6) where fish were the major prey by weight. Capelin dominated in samples from northern Bonavista Bay (Zone 7) in December of both years, off the southern Avalon Peninsula (Zone 10) in February 1985, and in the small sample from White Bay (Zone 4) in November 1985. Sand lance was most plentiful off southern Labrador (Zone 1) in December 1985, and Atlantic cod was the major fish species in the only sample from the southern Strait of Belle Isle in November 1985 (Fig. 4, Tables 5, 6).

Small numbers of other species were identified in addition to those listed in Tables 5 and 6. We recorded 67 sand lance (N = 21 stomachs), 16 rock cod (*Gadus ogac*) (N = 9), 6 silver hake (*Merluccius bilinearis*) (N = 6), 3 Greenland halibut (*Reinhardtius hippoglossoides*) (N = 3), and 2 redfish (*Sebastes* sp.) (N = 2). Apart from sand lance, which were mostly from Labrador samples, individuals of these species occurred sparingly in most samples where fish predominated.

There was no apparent relationship between the number of pebbles in stomachs and the month or location, or with the presence of fish in the stomach (Tables 5, 6). Pebbles may have been retained from the previous summer, when murres had fed on bottom-dwelling fish such as blennies (e.g., Gaston and Noble 1985). Most pebbles were also small enough (ca. 2–5 mm across) to have been present in the stomachs of the fish eaten by murres.

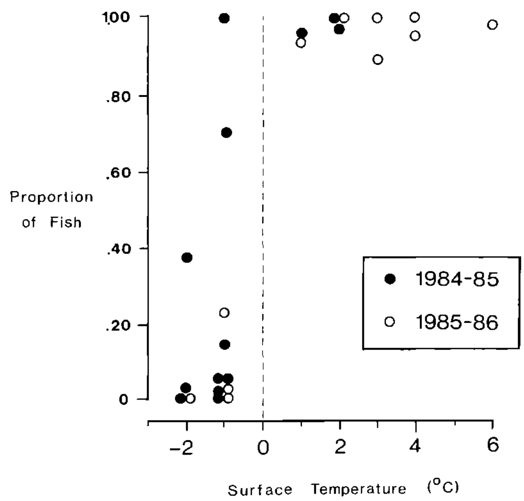

FIGURE 3. The relationship between sea-surface temperature and the proportion by wet weight of fish in the proventriculus.

TABLE 3. THE PROPORTION OF FISH AND CRUSTACEANS BY WET WEIGHT IN PROVENTRICULUS IN RELATION TO ZONE, MONTH, ICE COVER, TEMPERATURE AND PROPORTION OF FIRST-YEAR MURRES, IN 1984–1985

Survey zone	Month	Sample size	Proportion of fish	Proportion of crustaceans	Ice cover (tenths)	Surface temp. (°C)	Proportion of first-years
1	Nov.	20	0.996	0.004	0	2	0.92
1	Dec.	35	0.963	0.037	0	1	0.86
3	Dec.	91	0.007	0.993	10	−1	0.78
5	Jan.	25	0.995	0.005	10	−1	0.15
7	Dec.	73	0.973	0.027	0	2	0.33
7	Jan.	58	0	1.000	7	−1	0.29
7	Feb.	61	0.009	0.991	10	−2	0.30
7	Mar.	102	0	1.000	9	−2	0.49
8	Feb.	37	0.372	0.628	9	−2	0.20
9	Feb.	41	0.032	0.968	1	−1	0.29
9	Mar.	40	0.031	0.969	9	−1	0.29
10	Feb.	57	0.703	0.297	8	−1	0.29
10	Mar.	20	0.155	0.845	6	−1	0.29

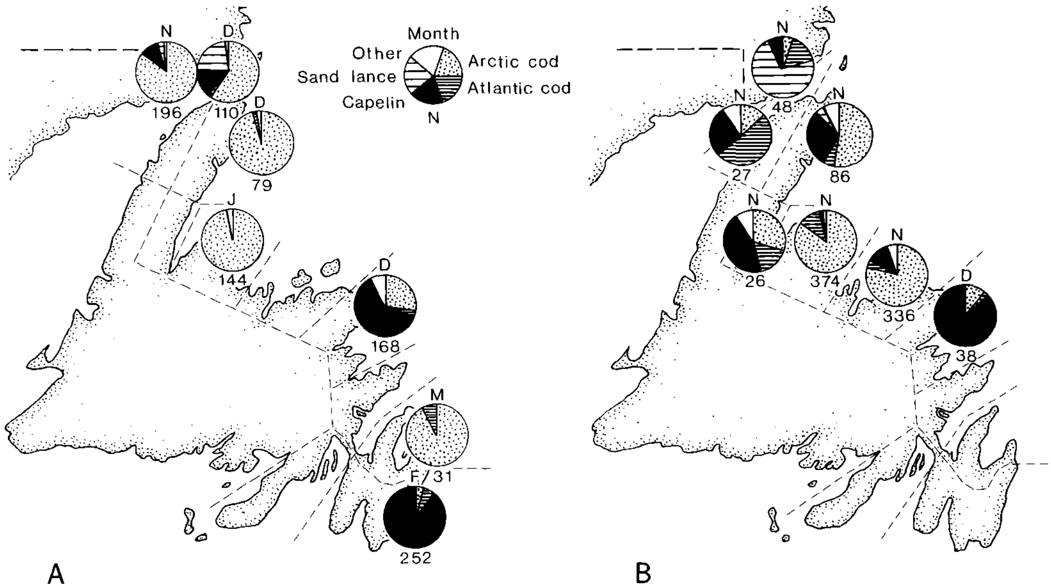

FIGURE 4. The proportion of all fish identified to species, by month and survey zone in (A) 1984–1985, and (B) 1985–1986, for samples in which at least 20 fish were identified. The number of fish (N) is shown for each sample, and survey months are indicated as November (N), December (D), January (J), February (F), and March (M).

COMPARISON OF CRUSTACEANS AND SQUID IN THE DIET

Comparisons of the relative importance of crustacean taxa by number are affected by differences in their biomass, ranging from relatively large shrimp such as *Pandalus borealis* to smaller euphausiids and amphipods such as *Parathemisto gaudichaudii.* However, this source of error is probably small, as euphausiids (*Thysanoessa* spp.) completely dominated all samples but one in which crustaceans predominated by weight, both by percent occurrence (Tables 5, 6) and by absolute number (Figs. 5a,b). The exception was the February sample from the south coast (Zone 11) where the hyperiid *P. gaudichaudii* predominated by weight and number.

Seven *Thysanoessa inermis,* 15 *T. raschii* and one *Meganyctiphanes norvegica* were positively identified to species in 1984–1985, and all of the several hundred euphausiids examined closely in 1985–1986 were *T. raschii.* The latter is assumed to have been the most abundant euphausiid taken in both years.

Of 1782 hyperiid amphipods identified to species, 1753 (98.4%) were *Parathemisto gaudi-*

TABLE 4. THE PROPORTION OF FISH, SQUID AND CRUSTACEANS BY WET WEIGHT IN PROVENTRICULUS IN RELATION TO ZONE, MONTH, ICE COVER, TEMPERATURE AND PROPORTION OF FIRST-YEAR MURRES, IN 1985–1986

Survey zone	Month	N	Fish[1]	Squid[1]	Crustaceans[1]	Ice cover (tenths)	Surface temp. (°C)	First-years[1]
1	Nov.	15	0.991	0	0.009	0	3	0.93
2	Nov.	22	0.889	0.111	0	0	3	0.91
3	Nov.	37	0.955	0.045	0	0	4	0.80
4	Nov.	12	0.941	0.051	0.008	0	1	0.89
5	Nov.	54	0.994	0.006	0	0	4	0.82
6	Nov.	130	0.980	0.001	0.019	0	6	0.95
7	Dec.	20	1.000	0	0	0	2	0.50
7	Jan.	58	0.012	0	0.988	8	−1	0.16
7	Feb.	27	0	0	1.000	9	−2	0.03
7	Mar.	115	0	0	1.000	9	−1	0.11
11	Feb.	60	0.238	0	0.762	0	−1	0.64

[1] Proportion.

TABLE 5. PERCENT OCCURRENCE OF MAJOR TAXA IN MURRE STOMACHS CONTAINING FOOD IN 1984–1985

	Month												
	Nov.	Dec.			Jan.		Feb.				Mar.		
Zone	1	1	3	7	5	7	7	8	9	10	7	9	10
Atlantic cod	0	3.7	1.1	10.2	0	0	1.6	0	0	9.1	0	5.1	5.0
Arctic cod	85.0	66.1	28.6	37.3	88.3	0	4.9	16.7	10.7	12.7	9.0	33.3	5.0
Capelin	65.0	29.6	0	59.3	0	0	0	8.3	3.6	43.6	0	0	10.0
Other fish	20.0	37.0	4.4	32.2	25.0	0	6.6	19.4	17.9	1.8	3.0	5.1	0
All fish	95.0	96.3	33.0	100.0	100.0	0	13.1	30.6	42.9	49.1	12.0	38.4	15.0
Euphausiids	5.0	14.8	96.7	1.7	4.2	100.0	100.0	80.6	39.3	69.1	85.1	92.3	80.0
Hyperiid amphipods	5.0	7.4	56.0	6.8	0	0	18.0	5.6	7.1	9.1	6.0	26.5	55.0
Gammarid amphipods	0	11.1	12.1	5.1	0	1.9	0	0	0	1.8	1.5	2.6	0
Decapods	10.0	3.7	4.4	0	0	0	0	5.6	7.1	1.8	0	0	5.0
Other crustaceans	0	7.4	0	0	4.2	0	0	2.6	3.6	0	0	0	15.0
All crustaceans	15.0	44.4	100.0	13.6	8.4	100.0	100.0	83.3	60.7	72.7	95.5	92.3	100.0
Polychaetes	0	0	2.2	0	0	0	0	0	0	0	1.5	0	0
Molluscs	0	3.7	1.1	0	0	0	1.6	2.8	7.1	0	1.5	0	0
Squid	0	7.4	4.4	1.7	4.2	0	0	5.6	0	0	0	0	0
No. of stomachs containing food	20	47	91	59	24	54	61	36	28	55	67	39	20
No. empty stomachs	0	8	0	14	1	4	0	1	13	2	35	1	0
% of stomachs containing pebbles	25.0	20.0	17.6	17.8	4.2	19.0	19.7	27.0	9.8	19.3	18.6	15.0	0

TABLE 6. PERCENT OCCURRENCE OF MAJOR TAXA IN MURRE STOMACHS CONTAINING FOOD IN 1985–1986

	Month										
	Nov.						Dec.	Jan.	Feb.		Mar.
Zone	1	2	3	4	5	6	7	7	7	11	7
Atlantic cod	26.7	45.5	0	18.2	50.9	9.0	6.3	29.1	3.7	7.7	10.2
Arctic cod	13.3	9.1	51.4	44.5	86.8	57.4	18.8	3.6	0	0	1.0
Capelin	20.0	18.2	31.4	54.5	9.4	18.0	87.5	3.6	0	0	0
Other fish	80.0	27.3	42.9	27.3	11.3	21.3	12.5	7.3	3.7	3.8	4.1
All fish	93.3	86.4	97.1	90.9	100.0	87.7	100.0	38.2	7.4	11.5	15.3
Euphausiids	6.7	0	0	0	0	0	0	32.7	92.6	1.9	96.9
Hyperiid amphipods	13.3	0	0	27.3	0	3.3	0	3.6	22.2	82.7	31.6
Gammarid amphipods	0	0	0	0	0	0	0	0	0	0	1.0
Decapods	0	0	2.9	0	0	0.8	0	3.6	0	3.8	1.0
Other crustaceans	6.7	4.5	5.7	0	0	0	0	41.8	0	11.5	0
All crustaceans	26.7	4.5	8.6	27.3	0	4.1	0	87.3	100.0	88.5	96.9
Polychaetes	0	0	0	0	0	0	0	0	0	1.9	0
Molluscs	0	4.5	0	0	0	0	0	0	0	0	2.0
Squid	13.3	77.3	74.3	72.7	64.2	40.2	25.0	0	0	0	0
No. of stomachs containing food	15	22	35	11	53	122	16	55	27	52	98
No. empty stomachs	0	0	2	1	1	8	4	3	0	8	17
% of stomachs containing pebbles	26.7	13.6	13.5	36.4	13.0	8.5	10.0	19.0	14.8	18.3	7.8

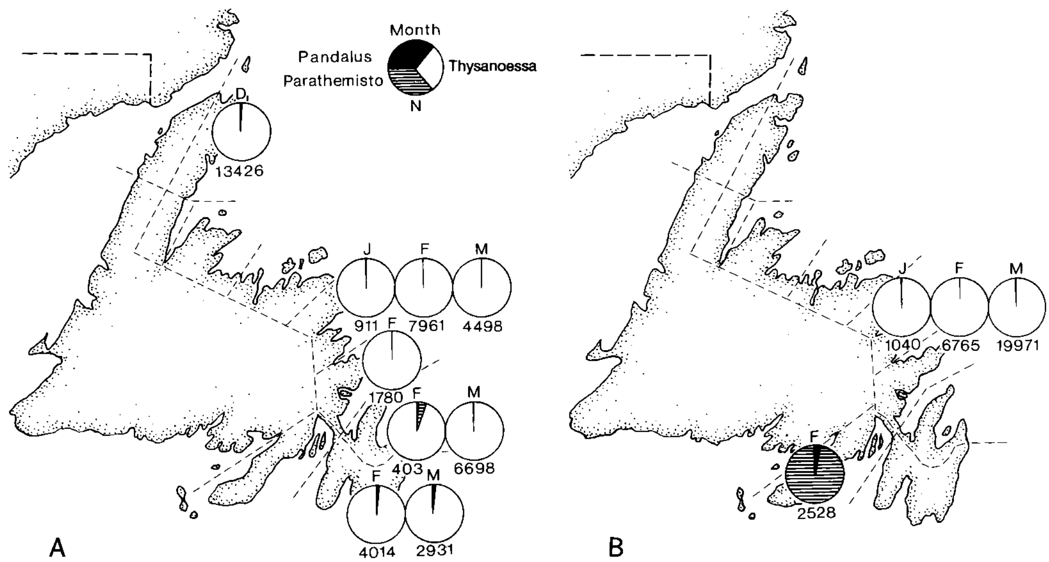

FIGURE 5. The proportion of all crustaceans identified to genus, by month and survey zone in (A) 1984–1985, and (B) 1985–1986, for samples in which at least 200 crustaceans were identified. The number of crustaceans (N) is shown for each sample, and survey months are indicated as December (D), January (J), February (F), and March (M).

chaudii (N = 15 stomachs) and 30 were *P. libellula* (N = 16). Twelve gammarid amphipods were keyed to species, including 2 *Gammarus wilkitzkii* (N = 1), 7 *G. locusta* (N = 7), 2 *Gammarellus angulosus* (N = 2) and 1 *Weyprechtia pinguis* (N = 1). Of 100 decapods identified, 94 were *Pandalus borealis* (N = 3), 5 were *P. montagui* (N = 3) and 1 was *Sabinea septemcarinata* (N = 1).

All of the 613 cephalopods identified by beaks in 149 stomachs were arctic squid. Most were recorded in 1985–1986 in November samples from southern Labrador and northern Newfoundland coasts (Zones 1–6, Tables 5, 6), at relatively warm surface temperatures of 1–6°C. Some beaks may have been retained in murres' stomachs for several weeks, and carried into these areas from farther north. The similar distribution of records of squid flesh in the proventriculus (Fig. 2), and the general absence of beaks from gizzards in samples collected farther south from January onwards in 1985–1986 (Tables 5, 6), suggest that retention times were short and that most squid were consumed in the zone in which they were recorded.

DISCUSSION

The diet of wintering Thick-billed Murres changed as they moved south along the Newfoundland coast ahead of advancing ice, and as water temperature decreased through the season at a single location. In both years, the diversity of the murres' diet declined markedly as surface temperatures dropped below 0°C, from a range of several important fish species to a single crustacean taxon, with a drop in the trophic level of their major prey. The records of Gaston et al. (1983) from the early 1980s fit well with the pattern recorded here; gadids, capelin and squid dominated the samples early in the winter, and euphausiids were most common later in the season.

The pattern of geographical and temporal change we recorded in coastal Newfoundland waters may not occur in murres wintering over the continental banks. Murres there concentrate at the shelf-breaks (Tuck 1961, Brown 1986), where upwelling conditions may make a different set of prey available (Ogi and Tsujita 1977).

Environmental Conditions and Prey Availability

The cold water and pack-ice carried south by the Labrador current influence the behavior and movements of the murres' winter prey as shown by differences in the birds' diet, both between years in one zone (e.g., Zone 2) and in one year through the season (e.g., Zone 6). The differing responses of prey to cold water and the presence of ice appear to be the main factors that affect their availability to murres.

Capelin

In summer capelin are the key forage fish for many vertebrate predators in Newfoundland waters, including fish (e.g., Reddin and Carscadden 1981, Akenhead et al. 1982), whales (Winters and Carscadden 1978), breeding alcids and visiting Greater Shearwaters (*Puffinus gravis*) (Brown and Nettleship 1984). Tuck (1961) also found that capelin predominated in winter murre diets in the early 1950s, occurring in over 90% of Thick-billed and Common murre stomach samples. Although the exact dates and locations of Tuck's samples are not known, it appears that capelin was a more important winter prey then, a conclusion also reached by Gaston et al. (1983) from fewer samples.

We doubt, however, that Tuck's (1961) samples were representative of the whole winter. Most capelin move well offshore as waters cool, or concentrate in deep inshore trenches in Trinity, Notre Dame and other bays (several of which were near some of our sampling sites), where they then occur in large inactive schools in cold water at depths of 140–200 m (Winters 1970). While these concentrations could be important prey for murres if within diving range, they were not heavily exploited during our study.

Capelin numbers vary markedly as a result of differential post-spawning survival of cohorts (Carscadden 1984, Leggett et al. 1984) and may be affected by commercial fishing. However, the commercial harvest has been low since 1979 (Carscadden 1984), and with high survival of the 1982 and 1983 cohorts (J. E. Carscadden, pers. comm.) appreciable numbers of 1½ to 3½ year-old capelin were probably available during our study. We conclude that capelin may be important prey early in the winter before they move to deeper water, and later in areas where birds are able to reach winter concentrations by diving deeply.

Arctic cod

The most important fish prey was the arctic cod, a small pelagic cold-water species often associated with near-shore environments and ice edges (Bradstreet 1982). It feeds on the same prey as the similarly-sized capelin (Lilly 1980) and is a major prey of breeding thick-bills in the arctic (e.g., Gaston et al. 1985); it also appears in the diet of Common Murre chicks in southern Labrador (Birkhead and Nettleship 1987). Tuck (1961) reported it as only an incidental prey item of murres wintering in Newfoundland waters. Gaston et al. (1983) found gadids, most of which were probably arctic cod, in 56% of stomachs from Twillingate (Zone 6) in November 1981, and 77% from Trinity Bay (Zone 9) in February 1983.

Arctic cod apparently spawn off Labrador in winter, with fry carried south in the Labrador Current, to remain in varying numbers off northern Newfoundland for one or more years. This probably reflects differences in year-class strength (W. H. Lear, pers. comm.). Arctic cod numbers appear to have increased in areas north of Bonavista Bay from the 1950s to the 1970s (Lear 1979), and were still quite high in late 1984 (Lear and Baird 1985). Most arctic cod have been recorded in concentrations at depths from 28–400 m, and at temperatures from -1.7 to 3.5°C (Lear 1979), although the murres we sampled fed on them in coastal waters at depths of less than 150 m.

Since arctic cod occasionally associate with ice in arctic waters, we doubt that their general absence from murre diets in late winter reflects a downward movement in the water column, out of the birds' diving range. Our small January 1985 sample in ice-covered Green Bay (Zone 5) was dominated by arctic cod, although this species is not common from Bonavista Bay (Zone 7) south (Lear and Baird 1985). The general lack of arctic cod in murre diets after January probably reflects the reduced overlap of areas occupied by the two species, as murres move south ahead of advancing ice.

Atlantic cod

Adult Atlantic cod are demersal fish that winter well offshore at depths of 200–600 m, at temperatures of 2–4°C (Lear 1984). However, many small cod of the size eaten by murres winter in coastal bays of eastern Newfoundland (Lear et al. 1980) frequented by murres. They may gradually become less available to murres as water temperatures drop through the winter, and they become less active and stay close to the bottom (Winters 1970). Atlantic cod was the dominant prey only in the southern Strait of Belle Isle (Zone 2) in November 1985, where surface temperatures were about 3°C, although they were still important later in the winter in southern zones at water temperatures close to 0°C.

Tuck (1961) reported Atlantic cod in about 4% of the stomachs of wintering Thick-billed and Common murres, similar to the overall proportion found in our study. Some of the gadids reported by Gaston et al. (1983) from Twillingate in November 1981, and Trinity Bay in February 1983, may have been Atlantic cod (see above).

Sand lance

Sand lance are important forage fish in areas where water is less than 90 m deep over a sandy bottom (Scott 1985). They are usually confined to cool waters in the range of -1 to 2°C (Winters 1983) and, unlike capelin, do not move to deeper water in winter. Spawning occurs from November to January (Winters 1983), and it seems likely that sand lance spend the winter in shallow water near, or buried in, the sandy bottom and are not available to murres in coastal areas after November.

Arctic squid

This pelagic species is widely distributed in arctic, low arctic and boreal waters (Wiborg 1979), and is a prey of minor importance for breeding Thick-billed Murres (e.g., Gaston 1985). It was found in low but regular numbers in coastal and offshore waters from southern Labrador to Bonavista Bay (Zones 1–6), by experimental trawls in November 1979, and November–December 1980 (E. G. Dawe, unpubl.). Arctic squid probably breed in April to June at one year of age (Wiborg 1979), so squid taken by murres in late fall were probably young-of-the-year about 2–5 cm in length.

All arctic squid that we recorded were from murres killed during November and December, in relatively warm waters above 0°C. This suggests that the availability of fish and squid, which often occurred together in murre stomachs, may both have been related to water temperature.

Like other squid species, numbers of arctic squid may vary from year to year, as they differed markedly between 1984–1985 and 1985–1986. We recorded very few in late 1984, although Gaston et al. (1983) found small squid, probably *Gonatus fabricii,* in all 16 murre stomachs from Zone 6 in November 1981. It was the most numerous item in their sample, but occurred in only 40% of stomachs we collected from Zone 6 in November 1985.

Euphausiids

The main euphausiids eaten by murres, *Thysanoessa raschii* and *T. inermis,* are abundant herbivorous crustaceans in arctic and northern boreal waters over the continental shelf of the North Atlantic. Surveys by Berkes (1976) and Sameoto (1976) over six years showed that both species were abundant in the Gulf of St. Lawrence most of the year, although they were not sampled when heavy ice was present from February to April. Both euphausiids were also found in fall and winter in the Bay of Fundy (Kulka et al. 1982), on the Scotian Shelf (Sameoto and Jaroszynski 1972), and off southeast Newfoundland (Lindley 1980). They normally descend to great depths each day; for example *T. raschii* usually concentrates in the upper 20 m at night, but reaches depths of 100–200 m by day (Berkes 1976).

In Nova Scotian waters, Sameoto and Jaroszynski (1972) found that *T. raschii* and *T. inermis* migrated from offshore areas farther than about 25 km from shore to within 3–5 km of the coast, in late winter and spring to spawn. *T. raschii* appeared inshore in large numbers in January and February, and *T. inermis* arrived about a month later. Many of these euphausiids did not undergo diel vertical migration, but remained near the surface during the day in pre-spawning swarming activities (D. D. Sameoto, pers. comm.).

We assume that similar pre-spawning movements take place off Newfoundland, where swarms of *Thysanoessa* in the upper layers of inshore waters during the day, beginning in January, would be particularly available to foraging murres. Fish are also probably 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, Atlantic cod), and euphausiids then become the murres' main prey.

Hyperiid amphipods

The only other numerically-important crustaceans were the carnivorous hyperiids, *Parathemisto* spp. *P. gaudichaudi* has a more southerly distribution than the larger *P. libellula* (Shih et al. 1971), and was the dominant prey in the sample from the ice-free waters of Fortune Bay (Zone 11) in February 1986. Fish may not have been available in the upper sub-zero waters then, causing murres to prey on this locally-abundant crustacean which also migrates vertically each day.

COMPARISON WITH OTHER AREAS AND SEASONS

The diets of Thick-billed Murres collected at sea in the North Pacific Ocean have been dominated variously by squid (Sanger 1986), fish such as walleye pollock (*Theragra chalcogramma*; Ogi and Tsujita 1977), and crustaceans such as euphausiids (Ogi and Tsujita 1977) and amphipods (Ogi and Hamanaka 1982), the latter taken especially in deeper waters. Squid dominated a small sample (N = 8) from the west Gulf of Alaska in one of the few winter studies (Sanger 1986).

In the eastern Arctic, Thick-billed Murres fed mainly on arctic cod and a gammarid amphipod (*Onisimus litoralis*) in the Barrow Strait in June (Bradstreet 1980). Both fish and crustaceans also are taken by adults near arctic colonies in summer, with arctic cod usually predominating; sand lance and capelin are also important prey at some locations (Bradstreet and Brown 1985, Bradstreet and Gaston 1990).

Fish are usually fed to murre chicks at Canadian arctic colonies (Gaston 1985), and include the species eaten by adults along with several species of sculpins (Cottidae) and blennies (Blennioidea). Arctic cod are again usually the most important species numerically and by volume

(Bradstreet and Brown 1985). Most murres in our November and December samples were first-year birds, and their main prey species then were the same fish they were likely fed as chicks 3–4 months earlier. Thus there is considerable overlap in the diet of Thick-billed Murres in summer and winter, with arctic cod of major importance year-round except when murres are south of that prey species' range.

Factors Affecting Prey Availability

Although arctic cod and euphausiids were the main prey items recorded, each of four fish species and two crustacean genera predominated in murre diets at different times in the two winters studied. These prey are all closely linked, either as potential competitors or predators, and declines in one species such as capelin may permit others such as sand lance to increase (Winters 1983).

Most pursuit-diving seabirds that may compete with murres for prey during the summer in Newfoundland (Winters and Carscadden 1978, Brown and Nettleship 1984) leave the area during the fall or occur in areas where competition with murres is minimal. For example, Black Guillemots (*Cepphus grylle*) winter in low numbers along the coast, and feed singly or in small groups much closer to shore, most likely on benthic fish (Bradstreet and Brown 1985). Dovekies (*Alle alle*), which probably feed on small crustaceans, including the euphausiids taken by murres (Bradstreet and Brown 1985), winter in high numbers well offshore (Brown 1986).

Harp seals are the only numerous marine mammals in coastal waters in late fall and winter. They reach Newfoundland waters later than Thick-billed Murres, with the arrival of pack ice in December and January, and remain until April or May.

Adult harp seals prey largely on arctic cod, capelin and shrimps (e.g., *Pandalus borealis*) (Sergeant 1973, 1976; Bowen 1985) in northern coastal areas (Zones 3–6) under the pack ice. These prey are inaccessible to murres that have moved farther south. Harp seal pups first feed independently in April on euphausiids *Thysanoessa* spp. and *P. borealis* (Sergeant 1976, Beddington and Williams 1980), while adults continue to eat fish with varying amounts of crustaceans (Bowen 1985). Thus, euphausiids are important to seals in early spring, when they may still be major prey of Thick-billed Murres.

The commercial fishery may have the greatest influence on numbers of prey such as shrimp, Atlantic cod and capelin. An intensive offshore capelin fishery in the 1970s was suspected of adversely affecting food availability and puffin chick survival (Brown and Nettleship 1984). The apparent shift away from capelin in the winter diet of murres since the 1950s (Tuck 1961), could also reflect effects of the fishery. However, the predator-prey dynamics of murre prey species are very complex, and capelin stocks may be as high now as they were 30 years ago (J. E. Carscadden, pers. comm.).

Prey populations may also be greatly affected by environmental variables, such as the effects of meteorological and hydrographic conditions on survival of larval capelin (Leggett et al. 1984), or the strength of the Labrador current on numbers of arctic cod. Because the availability of specific prey probably varies from year to year, we suspect that murres feed opportunistically on whichever of several prey taxa may be locally abundant in coastal waters. Variations in weather and ice conditions, and disturbance by hunters, which affect short-term feeding success, seem more likely to affect winter survival than more gradual changes in the abundance of specific prey.

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