The winter diet of thick-billed murres, *Uria lomvia*, in western Greenland, 1988–1989

KNUD FALK AND JAN DURINCK
Ornis Consult Ltd., Vesterbrogade 140, DK-1620 Copenhagen V, Denmark

Received September 23, 1991
Accepted August 12, 1992

FALK, K., and DURINCK, J. 1993. The winter diet of thick-billed murres, *Uria lomvia*, in western Greenland, 1988–1989. Can. J. Zool. **71**: 264–272.

The diet of thick-billed murres (*Uria lomvia*) wintering in coastal western Greenland was studied by analyzing the stomach contents of 202 birds supplied by local hunters in four regions, from October 1988 to March 1989. Fish and crustaceans were present in 68 and 71% (frequency of occurrence), respectively, of all stomachs containing prey remains (n = 195). Fish made up 81% wet weight, and crustaceans most of the remaining 19%, except for <1% squid (*Gonatus* sp.) and polychaetes (*Nereis* sp.). Capelin (*Mallotus villosus*) was the dominant prey species (61% wet weight), followed by *Thysanoessa* spp. (17%), *Parathemisto* spp. (1%), and *Meganyctiphanes norvegica* (1%). Euphausiids were the most abundant crustaceans (95% wet weight of all crustaceans), except in October, when hyperid amphipods were dominant (89%). Crustaceans were important in the murres' diet only in the northern part of the survey area; birds in the southern part preyed almost exclusively upon capelin. Most birds were in good body condition (based on the amount of body fat), but murres from the southern area had a slightly higher mean fat index than those from the northern area (7.19 vs. 5.35). We suggest that differences in body condition may be related to the higher proportion of fish, which is of higher caloric value, in the diet of murres in the southern area.

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Le régime alimentaire d'hiver de Marmettes de Brünnich (*Uria lomvia*) a été étudié chez des oiseaux de la côte ouest du Groenland, par l'analyse des contenus stomacaux de 202 oiseaux fournis par des chasseurs locaux en quatre régions, d'octobre 1988 à mars 1989. Les poissons représentaient 68% et les crustacés, 71% (fréquence en nombre), des aliments dans les estomacs qui contenaient de la nourriture (n = 195). Les poissons représentaient 81% de la masse fraîche et les crustacés, la plus grande partie du 19% restant, mais on trouvait aussi <1% de calmars (*Gonatus* sp.) et de polychètes (*Nereis* sp.). Le Capelan (*Mallotus villosus*) était la proie dominante (61% de la masse fraîche), suivi de *Thysanoessa* spp. (17%), de *Parathemisto* spp. (1%) et de *Meganyctiphanes norvegica* (1%). Les euphausiacés étaient les crustacés les plus abondants (95% de la masse fraîche totale de crustacés), sauf en octobre où les amphipodes hypéridés devenaient dominants (89%). Les crustacés n'étaient abondants dans le régime que dans la partie la plus boréale de l'aire étudiée; les oiseaux des régions sud consommaient presque exclusivement du capelan. La plupart des oiseaux étaient en bonne condition physique (d'après la masse de leurs graisses), mais les oiseaux du sud avaient un coefficient moyen de graisses légèrement plus élevé que les oiseaux du nord (7,19 vs. 5,35). Nous croyons que cette différence pourrait être attribuable à la proportion plus élevée de poisson, un aliment riche en calories, dans l'alimentation des oiseaux du sud.

[Traduit par la rédaction]

Introduction

The thick-billed murre, *Uria lomvia*, is an important part of the arctic marine ecosystem. It breeds in colonies, with especially large populations in the eastern Canadian Arctic, northwestern Greenland, Iceland, Jan Mayen, Svalbard, and Novaya Zemlya (Nettleship and Evans 1985). After the breeding season, huge numbers of wintering murres occur in the low-arctic waters along western Greenland and eastern Newfoundland. Most birds wintering in Canada originate from the eastern Canadian Arctic and Greenland (Gaston 1980; Brown 1985), whereas those wintering in western Greenland come from eastern Atlantic colonies (particularly Spitsbergen) and to a lesser extent from Greenland and Canada (Kampp 1988).

Residents of Newfoundland and western Greenland hunt murres during winter, and the birds constitute an important part of their diet. In Newfoundland, it is estimated that 0.7–1.5 million murres, mainly thick-billed murres but also common murres, *Uria aalge*, are shot each winter (Elliot *et al.* 1991); in western Greenland roughly 300 000 – 400 000 thick-billed murres are killed annually, most of them during the winter hunt (Falk and Durinck 1992). The magnitude of the hunt alone suggests the presence of very large wintering populations, and birds in the main eastern Atlantic 'source colonies' may number 2 million pairs (cf. data in Nettleship and Evans 1985), giving a potential autumn population of more than 3 million birds heading towards western Greenland.

But what food resources sustain such large seabird populations during the winter? Compared with our knowledge of seabird feeding ecology during the breeding season, where the birds are relatively easy to study, only very limited data exist on the winter diet of the birds (Bradstreet and Brown 1985). Detailed information is only available from Newfoundland (see Tuck 1961; Gaston *et al.* 1983; Elliot *et al.* 1990). In the 1960s, capelin, *Mallotus villosus*, was the dominant prey, present in 93.1% of all stomachs examined (n = 614), with other fish species forming the remainder (Tuck 1961). In samples from the 1980s, fish were dominant early in the winter (November to December), with a marked shift to crustaceans (mainly the euphausiids *Thysanoessa* spp.) when water temperatures dropped below 0°C in early January (Gaston *et al.* 1983; Elliot *et al.* 1990). Crustaceans (mainly *Thysanoessa* spp.) also contributed significantly to the diet of common murres wintering in Alaska (Sanger 1987).

There is only general information on the food habits of murres in Greenland, and no specific data on winter diet. Salomonsen (1950) states that the food consists mainly of *Parathemisto libellula*, *Thysanoessa inermis*, *Gammarus locusta*, and other crustaceans, but also to a large extent fishes

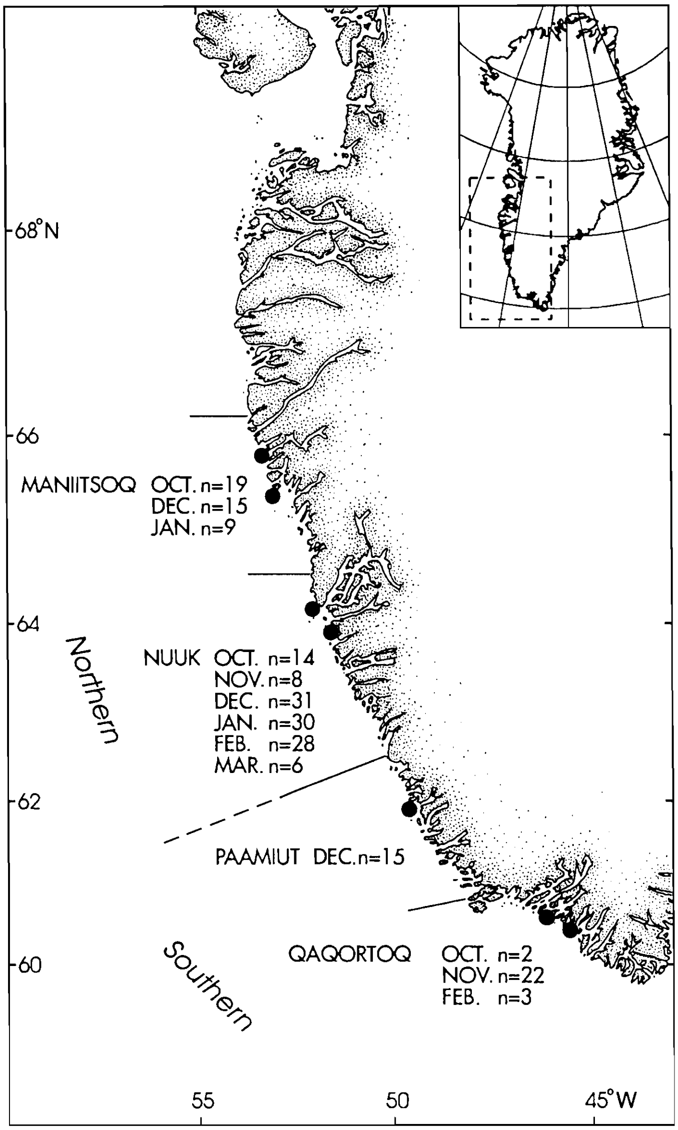

FIG. 1. Map of the study area, showing sampling districts, locations, and number of thick-billed murres sampled each month in each district. 'Northern' and 'southern' areas are indicated.

such as capelin and polar cod, *Arctogadus glacialis*, and occasionally nereids.

In this paper we give the results of the first analysis of the winter diet of thick-billed murres in the coastal waters of western Greenland. Stomach contents of birds shot by local hunters were examined to reveal differences in diet over time (from samples collected in the same district during a 6-month period) and variation between regions (by comparing samples taken in different regions) in western Greenland. Variation in diet in relation to age and physical condition of birds collected was also examined.

Methods

Sampling of birds

Fresh specimens of murres shot by Inuk hunters were bought at local markets (Falk and Durinck 1992). The largest regional sample (n = 117) came from Nuuk, the capital of Greenland, where 6–15 birds were collected at 2-week intervals from late October 1988 to early March 1989. Birds from other regions in western Greenland were obtained opportunistically in smaller numbers (for details of location and timing see Fig. 1).

Most murres were shot inshore before noon (Falk and Durinck 1992). As the birds were not sampled by us, we could not select actively feeding murres for examination. Stomach contents were not preserved, but outdoor temperatures were low (monthly average temperatures from October to March in Nuuk were between +2 and −11°C) and in winter most of the birds were frozen solid within 3–6 h of being killed.

Laboratory inspections

The birds were dissected following procedures outlined by Jones *et al.* (1982) and aged using criteria from Gaston (1984): 'adults' (>1 year) were birds with fully developed supra-orbital ridges and no cloacal bursae, and 'first-year' birds (<1 year) were those that had large bursae and only partly developed skulls and supra-orbital ridges. Birds showing intermediate characters (n = 14) were excluded from analyses correlating diet and (or) body condition with age. The amounts of subcutaneous and abdominal fat were scored (0–3; cf. Jones *et al.* 1982) at three locations on the bird (subcutaneous fat on breast and abdomen and fat deposited within the hind body cavity), and these values were added together to produce a fat index ranging from 0 (poor condition) to 9 (optimal condition).

Once the birds were obtained, the oesophagus, proventriculus, and gizzard were removed and kept frozen at −18°C until laboratory analysis. After it was thawed we opened each stomach and washed the contents carefully into a tray to ensure that no small objects such as fish otoliths remained in the gizzard. Stomach materials were sorted by taxon (using Enckell 1980; Breiby 1985; Härkönen 1986) and the length of whole food items was measured with calipers (to the nearest 1.0 mm); pebbles and plastic objects were also counted and measured. Fish were detected by the presence of otoliths, spines, bone fragments, and eye lenses; otoliths were measured to the nearest 0.1 mm. The length of amphipods was measured from the anterior part of the head to the telson without stretching the animal, whereas euphausiids were measured from the eyes to the tip of the telson. When stomachs contained large numbers (>100 individuals) of similar euphausiids (*Thysanoessa rascii* or *T. inermis*), a random sample comprising about 75 items was used for identification and measurements. Fragmented euphausiids and amphipods were counted by the number of pairs of eyes and by tail parts, respectively. Samples of whole individuals of each species were weighed individually to the nearest 0.002 g on a Mettler PM400 after excess water had been absorbed with tissue paper.

Data analysis

Length–weight regressions derived from the measurements of each crustacean species were used to estimate the weight of the remaining individuals of known length, whereas broken individuals were assigned the mean weight of all measured individuals of the species in question. The sizes of ingested fish were extrapolated from regressions of fish length and weight on otolith length (Table 1). Following Bradstreet (1980), we assumed that one fish had been eaten if the length of two otoliths differed by less than 0.2 mm; otherwise we assumed that the otoliths originated from two different fish. Fish bones and eye lenses found in stomachs without any otoliths were assumed to be from capelin, as the remains were virtually identical with those found in stomachs with otoliths from capelin only. We counted the squid as the number of upper or lower beaks, whichever was the greater, or by the number of pairs of eye lenses, and we used the number of paired jaws of similar size for polychaete worms. When estimating the wet weight of squid we used the weight of one intact specimen (0.8 g) that had beaks equal in size to most beaks found in other stomachs. Polychaete worms were assigned a weight of 0.5 g, as this was the approximate weight of *Nereis pelagica* with jaws of the same size as those identified in our samples (J. B. Kirkegaard, personal communication, 1990). Unidentified gadoids (detected by degraded otoliths) were assigned a weight of

TABLE 1. Regression equations for estimating lengths and weights of identified prey remains in the diet of thick-billed murres from western Greenland

	Equation	Source
Fish		
Capelin (*Mallotus villosus*)	FL = 24.02 + 44.31 × OL	Breiby 1985
	FW = $1.163 \times OL^{2.742}$	Härkönen 1986
Atlantic cod (*Gadus morhua*)	FL = −202.13 + 48.37 × OL	Härkönen 1986
	FW = $0.006855 \times OL^{4.435}$	Härkönen 1986
Polar cod (*Boreogadus saida*)	FL = −16.849 + 20.86 × OL	Härkönen 1986
	FW = $3.6 \times (10^{-6}) \times FL^{3.12}$	Härkönen 1986
Sand lance (*Ammodytes* sp.)[a]	FL = 8.776 + 51.906 × OL	Härkönen 1986
	FW = $0.61215 \times OL^{2.71}$	Härkönen 1986
Crustaceans		
Thysanoessa raschii	$W = 0.003176 \times L$ (n = 80)[b]	This study
T. inermis	$W = 0.004939 \times L$ (n = 53)[b]	This study
Meganyctiphanes norvegica	$W = 0.0042 \times L + 0.1771$ (n = 20)	This study
Parathemisto libellula	$W = 0.021938 \times L - 0.1781$ (n = 53)	This study
P. gaudichaudi	$W = 0.0079 \times L - 0.04173$ (n = 44)	This study
P. abyssorum	$W = 0.0078 \times L - 0.0256$ (n = 9)	This study

NOTE: FL, fish length; OL, otolith length; *L*, length; FW, fish weight; *W*, weight (wet weight).
[a]The equation for *Ammodytes marinus* was applied; the differences between *Amodytes* species are of negligible importance (Härkönen 1986).
[b]Forced through origin.

36 g, which was the average weight of the identified Atlantic cod, *Gadus morhua*, and arctic cod, *Boreogadus saida*.

Composition of the diet is presented in three ways: (*i*) frequency of occurrence in stomachs with identifiable items, (*ii*) numbers of individuals, and (*iii*) estimated wet weight (Duffy and Jackson 1986). Ninety-six percent of the 202 birds examined had identifiable prey remains in their stomachs; five stomachs were empty, while two contained non-food items only (plastic, pebbles, etc.). Only stomachs containing prey were used in the calculations of diet composition. When regional differences in diet are examined, Maniitsoq and Nuuk are referred to as the 'northern area' and Paamiut and Qaqortoq as the 'southern area' (Fig. 1).

Limitations of analysis

Analysis of the stomach contents gives only 'snapshot' impressions of food choice, and differential digestion rates for different taxa and sizes of prey items can bias the interpretation of bird diet composition (for details of these general limitations to dietary studies of seabirds see Bradstreet 1980, 1982; Blake 1984; Wilson *et al.* 1985; Springer *et al.* 1984; Duffy and Jackson 1986).

When estimating fish lengths and weights from otolith lengths we have adopted equations from studies carried out in non-Greenlandic waters, relationships that can vary between regions (Härkönen 1986) and times of the year (Blake 1984). We must therefore underline the fact that the fish lengths and weights calculated in this study provide only an index of prey size.

In addition to the general limitations that apply to any attempt to determine diet through analysis of stomach contents, the sampling procedure employed in this study introduces a unique bias: in mid-October, at the beginning of the winter hunting season in western Greenland, murres approach the coast and gradually enter the fjords (Falk and Durinck 1991). The birds are therefore collected in different parts of the archipelago or on the outer coast, and prey availability may vary locally. Thus, the results on diet presented here relate only to murres in coastal waters and may not be representative of birds wintering offshore and out of range of hunters. In February–March, ice conditions in some areas affected the birds' distribution and areas used by hunters. Therefore, the observed changes in diet during the winter may not exclusively reflect real changes in the birds' diet, but may also reflect differences in hunting areas.

Results

Overall trends in diet

In terms of frequency of occurrence, invertebrates and fish were roughly equally important, being present in 71 and 68%, respectively, of all stomachs containing prey remains (Table 2). Invertebrates were most important in terms of number of individuals, forming about 87% of all items, whereas by estimated wet weight the reverse was true, with fish species totalling 81% of the entire food mass.

Overall the capelin was the most important single prey species, accounting for 61% of the mass of the murres' diet. Among the invertebrates, crustaceans predominated, particularly the euphausiids *Thysanoessa raschii* and *T. inermis*, which formed 80% of all food items and made up 17% of the total diet by wet weight. Squid (*Gonatus fabricii*) and polychaete worms (*Nereis pelagica*) were rare, being found in only 6 and 7%, respectively, of all stomachs (Table 2).

Species composition

Apart from capelin and sand lance, *Ammodytes* spp., the murres had preyed upon a small number of gadoids of which Atlantic cod and arctic cod were identified; they are pooled under 'other fish' in Table 2.

In addition to the crustacean species mentioned in Table 2, we recorded 5 *P. abyssorum*, 4 *Hyperia galba* (associated with jellyfish tissue), 1 *Gammarus* sp., 1 *Orchomenella* sp., probably *O. pinguis*, 2 copepods (*Paracalanus parvus*), and 2 prawns (*Pandalus* sp.) of ca. 1 g, the largest crustaceans found.

Of non-food items, 23 pebbles and 23 pieces of plastic (all smaller than 10 mm) were found. Furthermore, we found 4 alga fragments. Endoparasites found comprised 8 flatworms (*Trematoda*), 1 tapeworm (*Cestoda*), and 92 nematodes (*Nematoda*).

Prey length

The length of individual fish consumed varied, with means for capelin and sand lance being 75.6 ± 22.7 (SD) mm (n =

TABLE 2. Occurrence of major food taxa[a] in the diet of thick-billed murres wintering in four districts in western Greenland, 1988–1989

	Northern area				Southern area					
	Maniitsoq		Nuuk		Paamiut		Qaqortoq		Total	
	n	%	*n*	%	*n*	%	*n*	%	*n*	%
Number of birds examined	43		117		15		27		202	
Number of stomachs empty	0		7	6	0		0		7	3
Frequency of occurrence of invertebrates	26	65	98	89	0	0	14	52	138	71
Frequency of occurrence of fish	40	93	53	48	15	100	24	89	132	68
Frequency of occurrence										
Capelin	39	91	35	31	15	100	24	89	113	57
Sand lance	9	21	3	3	0	0	1	4	13	7
Other fish	7	16	26	23	2	13	6	22	41	21
Parathemisto spp.	4	9	31	28	0	0	5	19	40	20
P. gaudichaudi	0	0	19	17	0	0	0	0	19	10
P. libellula	4	9	6	5	0	0	4	15	14	7
Meganyctiphanes norvegica	0	0	21	19	0	0	1	4	22	11
Thysanoessa spp.	14	33	81	72	0	0	6	22	101	51
T. inermis	5	12	49	44	0	0	0	0	54	27
T. raschii	9	21	55	49	0	0	4	15	68	35
Other crustaceans	5	12	3	3	0	0	0	0	8	4
Gonatus fabricii	4	9	7	6	0	0	1	4	12	6
Nereis pelagica	10	23	3	3	0	0	0	0	13	7
Number of individuals										
Capelin	447	30	249	3	105	85	251	48	1052	11
Sand lance	21	1	3	<1	0	0	1	<1	25	<1
Other fish	28	2	49	1	18	15	56	11	151	2
Parathemisto spp.	22	1	323	4	0	0	11	2	356	4
P. gaudichaudi	0	0	131	2	0	0	0	0	131	1
P. libellula	40	3	14	<1	0	0	24	5	78	1
Meganyctiphanes norvegica	0	0	79	<1	0	0	1	<1	80	1
Thysanoessa spp.	711	48	5745	74	0	0	120	23	6576	66
T. inermis	37	2	459	6	0	0	0	0	496	5
T. raschii	149	10	727	9	0	0	58	11	934	9
Other crustaceans	6	<1	3	<1	0	0	0	0	9	<1
Gonatus fabricii	4	<1	11	<1	0	0	1	<1	16	<1
Nereis pelagica	19	1	3	<1	0	0	0	0	22	<1
Estimated wet weight (g)										
Capelin	1170	75	553	38	241	82	434	70	2399	61
Sand lance	118	8	8	1	0	0	3	<1	129	3
Other fish	179	11	274	19	51	18	160	26	664	17
Parathemisto spp.	1	<1	17	1	0	0	1	<1	19	<1
P. gaudichaudi	0	0	3	<1	0	0	0	0	3	<1
P. libellula	8	1	2	<1	0	0	5	1	15	<1
Meganyctiphanes norvegica	0	0	20	1	0	0	0	0	20	1
Thysanoessa spp.	58	4	471	32	0	0	10	2	539	14
T. inermis	4	<1	44	3	0	0	0	0	48	1
T. raschii	11	1	51	4	0	0	4	1	66	2
Other crustaceans	3	<1	0	0	0	0	0	0	3	<1
Gonatus fabricii	3	<1	8	1	0	0	1	<1	12	<1
Nereis pelagica	9	1	2	<1	0	0	0	0	10	<1

[a]Among birds with identifiable prey remains.

993) and 91.1 ± 50.4 mm (n = 25), respectively. Mean lengths of the most common euphausiids were similar, although *T. inermis* (19.6 ± 65 mm (n = 305)) was significantly longer than *T. raschii* (18.6 ± 2.58 mm (n = 422); $t_{[725]} = 4.8038$, $P < 0.0001$).

Temporal and spatial variation in diet

Changes in diet during winter can only be assessed for birds that were collected near Nuuk. In October the murres fed almost exclusively on fish, but by March, the last month surveyed, crustaceans composed 88% of the diet by wet weight

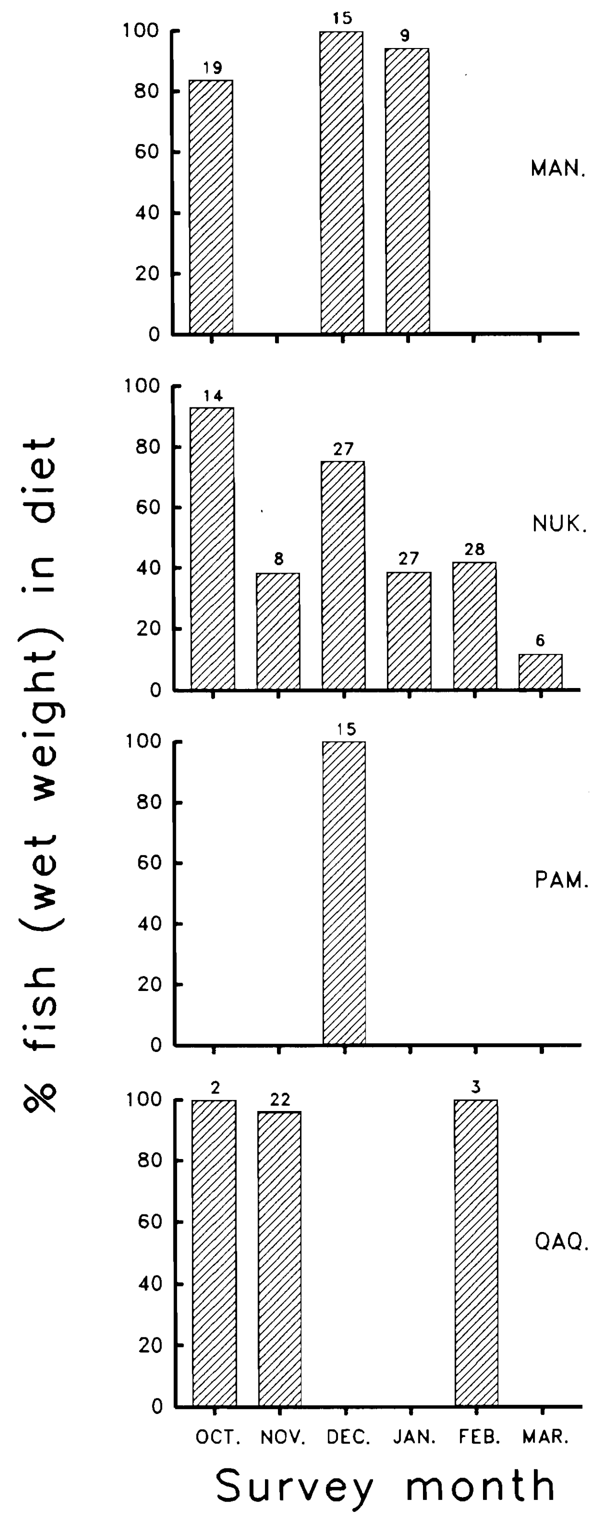

FIG. 2. Proportions of fish (by wet weight) in the winter diet of thick-billed murres in four areas of western Greenland. Numbers above the bars are sample sizes.

(Fig. 2), though the samples for both months were small (14 and 6 birds, respectively; see Fig. 1). From November to February the diet varied, with fish predominating in December and crustaceans in November, January, and February. Squid and polychaetes were present only until January, after which they disappeared from the diet (Table 3).

There was a marked shift in species composition among crustaceans (Table 3): amphipods, mainly *Parathemisto* spp., were dominant (89.4%) in October, when crustaceans were, on the whole, rare in the diet; from November onwards, euphausiids were the dominant invertebrates. *Thysanoessa raschii* made up approximately 75% of the identified euphausiids in November and December, after which *T. raschii* and *T. inermis* were of roughly equal importance. The largest euphausiid, *Meganyctiphanes norvegica*, was detected only from December to February and was most abundant in February, when it made up about 3% of the total food mass. The polychaete *Nereis pelagica* occurred only in samples from October (Table 3).

The gradual change in the diet from fish to crustaceans as the dominant group observed in Nuuk (northern area) was not recorded in the southern area of Greenland. Few crustaceans occurred in stomach samples from Paamiut and Qaqortoq (Table 2, Fig. 2), where they were found only in October and November. Any comparison between the two areas is invalid owing to the unequal sampling in each town during the winter (Fig. 1). However, a two-way ANOVA on the proportion of fish by wet weight (sampling unit: mean per district and month) in the diet revealed that 'sampling district' (town) as well as 'sampling month' contributed significantly to the total variation, with sampling district explaining more of the observed variation ($F_{[3,182]} = 21.28$, $P < 0.0001$) than sampling month ($F_{[5,182]} = 2.75$, $P < 0.0201$).

The only species found to be restricted to one area was the sand lance. Eighty-four percent of all sand lance recorded ($n = 25$) were from birds in Maniitsoq, where sand lance occurred in 21% of all stomachs (Table 2).

Diet in relation to age and physical condition

Murres from the southern area had a higher fat index, on average, than birds from the northern area (fat index ($\bar{x} \pm$ SD): south: 7.19 ± 1.85 ($n = 42$); north: 5.35 ± 2.58 ($n = 140$), a statistically significant difference ($z = 4.1329$, $P = 0.0001$, Wilcoxon's rank sum test). The difference between the two areas was significant for first-year birds as well as adults (Table 4; $z = 3.2671$ ($n = 96$), $P = 0.0011$ and $z = 2.3763$ ($n = 86$), $P = 0.02$, respectively).

Overall, there was no significant difference in fat index between adult and first-year birds in western Greenland (Table 4; $z = -0.8126$, $n = 182$, $P = 0.4165$). The same was true when birds from northern and southern areas were compared separately (north: $z = -0.2914$, $n = 140$, $P = 0.7707$; south: $z = 0.0787$, $n = 42$, $P = 0.9372$). As judged by the fat index, the murres' body condition showed a slight but insignificant positive trend during the winter (Spearman correlation, $r = 0.134$, $n = 188$, $P > 0.05$).

Discussion

Composition of diet of wintering murres

The results of this study indicate that thick-billed murres wintering in the southern area of western Greenland fed almost exclusively on fish, whereas farther north (Nuuk), crustaceans played a significant role in the diet and became increasingly important as winter progressed. Very few species accounted for most of the food consumed; capelin and the euphausiids *Thysanoessa raschii* and *T. inermis* made up nearly 80% of the food by wet weight. These findings, however, are based on samples that were taken irregularly and varied in size during a single winter. Consequently, a more thorough study would

TABLE 3. Monthly proportion (%) by estimated wet weight of different taxa in the diet of thick-billed murres in Nuuk, western Greenland, 1988–1989

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
n						
Fish						
Capelin	85.39	31.4	17.86	30.14	14.46	9.51
Unidentified sand lance	0.63	0	1.72	0	0.48	0
Other fish	6.83	6.85	55.54	8.34	26.52	2.12
Euphausiids						
Thysanoessa spp.	0.41	53.53	15.07	49.28	45.85	77.94
T. inermis	0.09	1.55	2.51	4.24	5.45	4.16
T. raschii	0.08	6.41	6.50	3.88	4.07	6.21
Meganyctiphanes norvegica	0	0	0.20	2.93	3.05	0
Amphipods						
Parathemisto spp.	3.81	0.13	0.16	0.33	0.05	0
P. libellula	0.41	0	0	0.23	0	0
P. gaudichaudii	0.67	0.10	0.05	0.06	0.06	0.03
Other amphipods	0	0	0	0	0	0
Other crustaceans	0	0	0	0	0.01	0.03
Squid (*Gonatus fabricii*)	1.34	0	0.39	0.58	0	0
Polychaete worms (*Nereis pelagica*)	0.36	0	0	0	0	0

TABLE 4. Mean fat indexes for thick-billed murres shot during the winter hunt in western Greenland, 1988–1989

	Mean fat index								
	'Old' birds			'First-year' birds			All birds		
Area and month	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*
Northern area									
Maniitsoq									
October	4.91	1.87	11	6.75	2.19	8	5.68	2.16	19
December	6.0	—	1	5.07	2.02	14	5.13	1.96	15
January	2.80	2.05	5	4.67	4.04	3	3.50	2.83	8
Nuuk									
October	5.69	2.14	13	5.0	—	1	5.64	2.06	14
November	8.0		1	7.71	1.25	7	7.75	1.17	8
December	5.50	3.08	14	4.50	2.54	12	5.04	2.84	26
January	5.85	2.79	13	3.58	2.47	12	4.76	2.83	25
February	5.06	2.14	16	4.75	3.86	4	5.00	2.45	20
March	9.00	0.00	3	9.00	0.00	2	9.00	—	5
Whole area	5.42	2.52	77	5.27	2.67	63	5.35	2.58	140
Southern area									
Paamiut									
December	6.50	0.71	2	7.15	2.12	13	7.07	1.98	15
Qaqortoq									
October	—	—	0	4.50	3.54	2	4.50	3.54	2
November	8.00	1.10	6	7.63	1.59	16	7.73	1.45	22
February	6.0	—	1	5.50	0.71	2	5.67	0.58	3
Whole area	7.44	1.24	9	7.12	2.00	33	7.19	1.85	42
Western Greenland	5.63	2.49	86	5.91	2.60	96	5.78	2.55	182

possibly reveal different patterns and annual differences in the murres' diet.

Although some prey species were present in very small numbers in the samples, they may be of local importance. Only one individual of *Orchomenella* sp., a gammarid amphipod, was found in the 202 stomachs examined, but one bird excluded from the analysis (collection date unknown) contained 560 *O. pinguis*, constituting a mass of 40 g (wet weight).

The murres' winter diet in western Greenland is similar to that known for birds in Newfoundland (Elliot *et al.* 1990). In both areas, crustaceans became increasingly important during winter, and among them, the euphausiids *Thysanoessa* spp. were predominant. However, there are major differences between areas too. The most important prey species in Greenland in 1988–1989 was the capelin, whereas in Newfoundland between 1984 and 1986, arctic cod was generally the most important prey, although this may be a recent phenomenon in Newfoundland (Gaston *et al.* 1983; Elliot *et al.* 1990).

In coastal Newfoundland waters, wintering murres appear to prey upon a wider diversity of fish and crustaceans than in western Greenland, but the difference could simply be an artifact due to the increased likelihood of detecting rare species in the larger sample (1200 murres; Elliot *et al.* 1990).

In Greenland, as well as in Newfoundland, local hunters supplied birds shot in coastal waters, so the food analyses have the same constraints. The only other study of the winter diet of thick-billed murres in the Atlantic was made by Erikstad (1990) in March 1987 in offshore waters in the Barents Sea. However, this study was made after a 'crash' in the capelin stock (Erikstad 1990 and references therein) in the area, and Atlantic cod (*Gadus morhua*), polar cod, and redfish (*Sebastes* spp.), which were the dominant fish in the diet, were probably serving as 'buffer' species in the absence of capelin. Crustaceans (unidentified) were also found to be important in the Barents Sea, where they were present in 23 of 24 murre stomachs examined (Erikstad 1990).

Diet in relation to physical condition

Judged by the amount of stored body fat, birds in the southern area of western Greenland were in better condition than those farther north, although mean fat scores were moderate to high in both areas. As stated above, there was also an obvious difference in the diet between the two areas: murres in the northern area were eating many more crustaceans than the birds in the southern area. Fish eaten by seabirds are known to have a higher caloric value than invertebrates (Bradstreet and Brown 1985). Among the fish species in the murres' prey, capelin has the highest energy content, 7.5 kJ/g (wet weight), followed by sand lance (6.8 kJ/g), arctic cod (5.9 kJ/g), and Atlantic cod (4.1 kJ/g; Birkhead and Nettleship 1987); in winter the energy content may be even higher, up to 9.4 kJ/g for capelin (see Montevecchi and Piatt 1984). Energy values increase with the size of fish (Harris 1984). In contrast, euphausiids and amphipods (*Parathemisto* spp.) contain only 3.5 and 3–5 kJ/g, respectively (Bradstreet 1976; Bradstreet and Brown 1985). Owing to the different caloric densities alone, the average diet of birds in Qaqortoq (Table 2) would contain roughly 26% more energy than that of birds in Nuuk. Therefore, the higher fat indices of murres collected in the southern area of western Greenland might be related to the greater proportion of fish in their diet: in this case the most energy-rich species, capelin. Such a correlation, however, was not confirmed by regression analysis of the fat index against the proportion of fish in the diet by wet weight (both values expressed as the monthly mean per sampling district; Spearman correlation $r = 0.049$, $n = 13$, $P > 0.1$). Erikstad (1990) also suggested that capelin was especially favored as a food by murres; in the absence of capelin, murres wintering in the Barents Sea had lower fat indices than prelaying murres that had been feeding on capelin.

Foraging patterns and prey availability

In western Greenland, the most important prey species for the wintering murres, the capelin, occurs in coastal areas and has not been recorded outside the banks along the coast. There are probably several local stocks, concentrated in the fjords in spring and summer, but in fall they disperse in the fjords and on the coastal banks, where some mixing between the stocks may occur (Sørensen 1985). Adult capelin often occur deeper in the water column than younger cohorts (Jangaard 1974), a pattern also noted in Greenlandic stocks (P. Kanneworf, personal communication, 1991). In western Greenland, capelin larvae are approximately 40 mm long by 1 January, but some may reach 70 mm, which is a considerable overlap with 1-year-old fish (Sørensen 1985; Kleist 1988; P. Kanneworf, personal communication, 1991). The length–frequency distribution of the capelin eaten by the murres wintering in western Greenland showed a bimodal distribution, with one peak in the 50- to 60-mm size interval and another peak in the 80- to 90- and 90- to 100-mm size intervals. The first group (50–60 mm) corresponds to larvae, and on the basis of growth curves for capelin sampled in Nuuk (Sørensen 1985), capelin measuring more than 80 mm are 2 years of age or older. Although mixed age groups of capelin occur together in coastal waters, small fish compose about 41% of the murres' diet.

In contrast to the capelin, the sand lance is most abundant on the banks off the coast (Andersen 1985). Young sand lance remain in the upper waters, body size and age increasing with sampling depth (Andersen 1985). One- and 2-year-old *Ammodytes dubis* caught off western Greenland had a mean length of less than 100 mm, whereas individuals aged 3 years and older were 110 mm or longer. Based on body length, about 65% of the small number of sand lance eaten by wintering murres were less than 2 years old.

The large proportion of young capelin and sand lance in the murres' diet probably indicates that by staying higher in the water the young of both species were more accessible to the foraging birds than the older cohorts.

Among the euphausiids, *T. raschii* has a more neritic distribution than *T. inermis* (Russell and Younge 1969; Einarsson 1945). This difference is reflected in the relative abundance of the euphausiid species in the diet of murres collected inshore in Nuuk (Table 3). *Meganyctiphanes norvegica* has a more pelagic distribution than *Thysanoessa* spp. (Russell and Younge 1969) and was the rarest euphausiid in the murres' winter diet; it does not spawn in western Greenland, but large numbers are carried there by currents from Icelandic waters (Hansen 1979).

Most prey species recorded from murre stomachs are known to perform daily vertical migrations, including euphausiids (Einarsson 1945; Russell and Younge 1969), capelin (Jangaard 1974; Sørensen 1985), and squid *G. fabricii* (Kristensen 1984), all of which move towards the sea surface after dark. Although thick-billed murres can dive to considerable depths (maximum 153 m; Burger 1991), most dives by alcids are relatively shallow (Barret and Furness 1990; Burger 1991; but see Piatt and Nettleship 1985 for the common murre). Therefore, nocturnal feeding may be an advantage to the murres, and even a prerequisite for wintering far north with very little light in midwinter. This is consistent with the very low proportion of empty stomachs (3%) in our survey, most birds having been shot in early morning hours, often around daybreak.

The few recent studies of winter diet, as well as studies of diet in the prebreeding and breeding seasons, portray the thick-billed murre as an opportunistic feeder prepared to switch to the locally most abundant and accessible prey such as schooling fish and swarming crustaceans (Gaston and Nettleship 1981; Bradstreet 1980; Elliot *et al.* 1990; Erikstad 1990). Nevertheless, in all studies fish are most important in the thick-billed murres' diet; the difference in caloric content probably accounts for the murres' preference for fish (Bradstreet and Brown 1985). By its general anatomy, in particular its bill size and shape, the thick-billed murre is better adapted to seize invertebrate prey than is the common murre (Spring 1971). Thus, the ability of the thick-billed murre to shift to less optimal but locally abundant prey probably accounts for its greater capability to live year-round in more extreme northern environments than its sibling species, as also noted by Spring (1971).

In conclusion, thick-billed murres wintering in coastal western Greenland rely heavily on the large local stocks of capelin. Few other fish species appear in the diet. When capelin are absent or rare, crustaceans (mainly small neritic euphausiids) become the dominant prey. Between October 1988 and March 1989 the southern part of western Greenland seemed to be a better feeding area for the murres, as the birds had heavier fat deposits, on average, than those farther north. We suggest that this may have been due to a greater availability of capelin, a forage fish with a higher caloric content than other available fish and invertebrates. The size distribution of fish and the occurrence of the most common taxa in the murres' diet in general reflected the expected relative availability of prey items to the birds.

Acknowledgements

We thank the Inuit Circumpolar Conference/Greenland for funding the analysis of winter diet. The murres were sampled during the study 'A quantitative description of the extent and effect of the winter hunting and gill-net fishery upon the thick-billed murre population of Greenland' funded by The Commission for Scientific Research in Greenland and initiated by the Zoological Museums Greenland Investigations, Copenhagen. Niels Odder Jensen kindly gave access to additional laboratory facilities and J. B. Kirkegaard, T. K. Kristensen, University of Copenhagen, and L. Thomas identified prey items. P. Kanneworf, Greenland Fisheries Research Institute, kindly provided unpublished information on the capelin in western Greenland. D. N. Nettleship and J. F. Piatt are thanked for giving precise and valuable suggestions, which improved this paper considerably.

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