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Hydrographic Features, Cetaceans and the Foraging of Thick-Billed Murres and Other Marine Birds in the Northwestern Barents Sea

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ABSTRACT. The at-sea distribution of thick-billed murres (*Uria lomvia*) in southeastern Svalbard waters was studied during the summers of 1992, 1993, and 1996. The Storfjordrenna region south of Svalbard was confirmed as an important foraging area for thick-billed murres; murre aggregations were located at distances of 85 to 126 km from the closest breeding colonies. Fish, mainly polar cod (*Boreogadus saida*), but also capelin (*Mallotus villosus*), were the main prey found in 16 murres and 3 black-legged kittiwakes (*Rissa tridactyla*) collected from these aggregations. Murres were seen flying with fish in their beaks at four locations 78 to 102 km away from the colonies. Murre aggregations were associated with frontal zones between cold Arctic waters and warmer Atlantic water, and in areas with strong stratification in salinity at 15–30 m. A positive association was found between the abundance of murres and the occurrence of cetaceans. Murres and other marine birds were often seen near surfacing cetaceans. The most common cetaceans were minke whales (*Balaenoptera acutorostrata*) and white-beaked dolphins (*Lagenorhynchus albirostris*).

Key words: marine birds, thick-billed murre, *Uria lomvia*, foraging ecology, cetaceans, Barents Sea

RÉSUMÉ. Durant les étés de 1992, 1993 et 1996, on a étudié la distribution en mer de la marmette de Brünnich (*Uria lomvia*) dans les eaux du sud-est du Svalbard. La région Storfjordrenna au sud du Svalbard a été confirmée comme une zone importante de collecte pour la marmette de Brünnich; des concentrations de marmettes étaient situées à des distances allant de 85 à 126 km des colonies nicheuses les plus proches. Le poisson, en particulier la morue polaire (*Boreogadus saida*), mais aussi le capelan (*Mallotus villosus*), était la proie principale trouvée chez 16 marmettes et 3 mouettes tridactyles (*Rissa tridactyla*) prélevées dans ces concentrations. On a vu les marmettes voler avec du poisson dans leur bec à quatre endroits éloignés de 78 à 102 km des colonies. Les concentrations de marmettes étaient associées à des zones frontales entre les eaux froides de l’Arctique et l’eau plus chaude de l’Atlantique, et dans des régions ayant une forte stratification dans la salinité à une profondeur de 15 à 30 m. On a trouvé qu’il existait une association positive entre l’abondance des marmettes et la présence des cétacés. On voyait souvent les marmettes et d’autres oiseaux marins près des cétacés qui faisaient surface. Les cétacés les plus communs étaient les petits rorquals (*Balaenoptera acutorostrata*) et les dauphins à nez blanc (*Lagenorhynchus albirostris*).

Mots clés: oiseaux marins, marmette de Brünnich, *Uria lomvia*, écologie de collecte, cétacés, mer de Barents

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INTRODUCTION

Marine birds, such as alcids, sometimes travel considerable distances between their breeding colonies and foraging areas while provisioning chicks. Thick-billed murres (*Uria lomvia*) have been observed foraging up to 100 km from their colonies during the chick-rearing period (Gaston and Nettleship, 1981; Bradstreet and Brown, 1985). Similarly, near Bjørnøya in the Barents Sea, murres (*Uria* spp.) were seen carrying fish and flying towards the breeding colonies from up to 83 km (45 nautical miles) away (Mehlum et al., 1998).

Two large breeding colonies (Stellingfjellet and Kovalskifjellet) of thick-billed murres, comprising approximately 450 000 and 90 000 individuals, respectively (Mehlum and Bakken, 1994), are located on the southeastern coast of Spitsbergen (Fig. 1). During the breeding season, birds from these colonies forage, in part, in the adjacent waters of Storfjorden. Important foraging areas may also be located farther south (Mehlum et al., 1996). In 1989, one murre dyed with picric acid at Kovalskifjellet was resighted at 76˚ 40′ N near Sørkapp, 43 km south of the breeding colony (Mehlum, unpubl. data)

In years with adequate stocks of capelin (*Mallotus villosus*), an intensive fishery takes place in the Storfjordrenna region, i.e., the area between Bjørnøya and Spitsbergen. Several species of cetaceans, especially minke whale (*Balaenoptera acutorostrata*) and white-beaked dolphin (*Lagenorhynchus albirostris*), also gather there during summer and feed on fish

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and pelagic crustaceans (Christensen, 1977; Øien, 1990; Haug et al., 1995; Øien and Hartvedt, 1995; Øien, 1996). Marine mammals often associate with foraging marine birds (Pierotti, 1988). Thus birds may use the presence of the marine mammals as an indicator of dense prey aggregations.

In this study, we sought the main southern foraging habitats of thick-billed murres breeding in western Storfjorden. We also sought to determine if murres and other seabirds preferred to forage near surfacing cetaceans.

STUDY AREA

Storfjordrenna (Fig. 1) is a submarine canyon with depths reaching 300 m located south of the mouth of Storfjorden, which is a shallow fjord (depths < 180 m). To the south is a shallow bank, Spitsbergenbanken (or Svalbardbanken). Spitsbergenbanken extends southwest into Bjørnøybanken, which surrounds the island of Bjørnøya. The water masses in Storfjordrenna are dominated by warm Atlantic water transported by the North Atlantic Current (Fig. 1). To the south, at the slope of Spitsbergenbanken, these water masses meet colder, less saline, Spitsbergen Bank water in a more or less well defined frontal region (Loeng, 1991). At the eastern end of Storfjordrenna, the Atlantic water meets cold Arctic water from the East Spitsbergen Current (Fig. 1), which also enters Storfjorden. Cores of Atlantic water also penetrate northward from Storfjordrenna into Storfjorden. On the northern side of the mouth of Storfjordrenna, along the southern tip of Spitsbergen, cold water from the Sørkapp Current (Fig. 1) abuts the Atlantic water.

MATERIAL AND METHODS

Seabirds were recorded from the *R.V. Lance* using standardized strip transect methods (Tasker et al., 1984). One observer counted all birds within a 300 m transect width and classified their behavior as flying or sitting on water, while a second person entered the data directly into a field computer. On the few occasions when visibility was between 100 and 300 m, we made appropriate adjustments in calculations of bird densities. Ship followers were entered separately but not included in this analysis. Where appropriate, other behaviors, such as associations between species, feeding, and carrying fish, were noted. Individuals spaced less than 10 m from each other sitting on the water were treated as a group; others were considered to be single birds. Sightings of marine mammals also included individuals seen outside the strip transect. The computer's clock was synchronized with the ship's clock. The ship's geographical position (GPS-system) was entered into the field computer every 30 to 60 minutes during periods with steady course and speed, and otherwise when any changes in speed or direction occurred.

The abundance of birds observed on the sea surface was averaged over 0.2° north/south × 1° east/west blocks, corresponding to ca. 22×27 km blocks. Associations with cetaceans

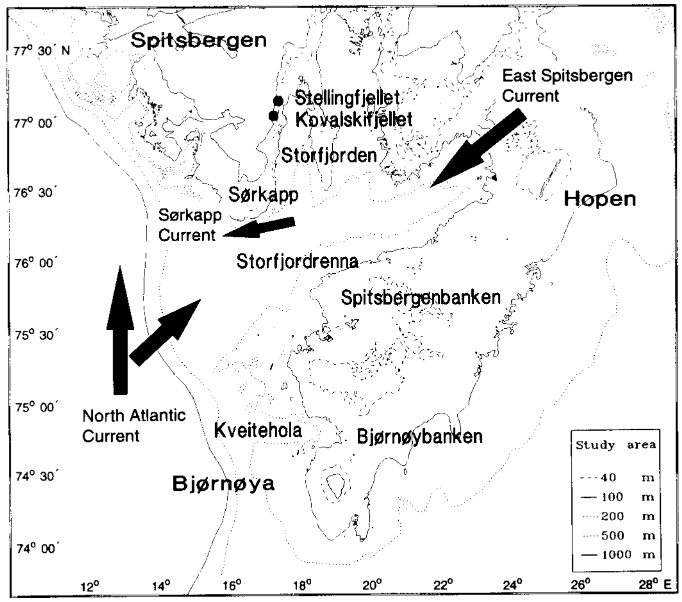

FIG. 1. Study area.

at the scale of these blocks were tested using a Wilcoxon-Mann-Whitney Test with exact probabilities (Mehta and Patel, 1995). On individual transects, observations of murres were divided into bins of six minutes, corresponding to one nautical mile (1.8 km) in length.

Foraging thick-billed murres were shot from a small boat in the period 13–15 August 1992 (6 birds at 76°12′N, 18°32′E; 2 birds at 76°09′N, 17°50′E; 3 birds at 76°11′N, 17°47′E; and 5 birds at 76°02′N, 17°21′E). Three black-legged kittiwakes (*Rissa tridactyla*) were also collected at 76°02′ N, 17°21′E.

Stomach and esophagus contents were stored in alcohol within one hour after collection. The food items were identified to the lowest taxon possible. Fish otoliths were measured to the nearest 0.5 mm. Two otoliths differing less than 0.5 mm in length were considered to be from the same fish. We assumed that unidentified, partly digested fish belonged to the same species as otoliths found in a bird, if the fish's length was similar to that estimated from otolith length.

The main study in Storfjordrenna was undertaken on 19 July, 27–30 July, and 13–15 August 1992. For the analyses of associations between murres and cetaceans, we also included ship transects conducted in Storfjorden and waters eastwards to Hopen Island on 20–26 July and 11–12 August 1992. The observation effort (km^2 covered) in each 0.2° north/south × 1° east/west block is shown in Fig. 2. Additional data were obtained along two continuous transects from Bjørnøya to Sørkapp conducted on 31 July 1993 and 6–7 July 1996, respectively (Fig. 3).

The distance between oceanographic stations varied between 5 and 10 nautical miles (9–18.5 km). In 1992, profiles of temperature and salinity as a function of water depth were obtained by using a ME-CTD probe (Meerestecknik Electronics - conductance, temperature, depth probe). The ME-CTD was equipped with a wire ca. 290 m long. At stations shallower than 290 m, data were collected down to about 5 m

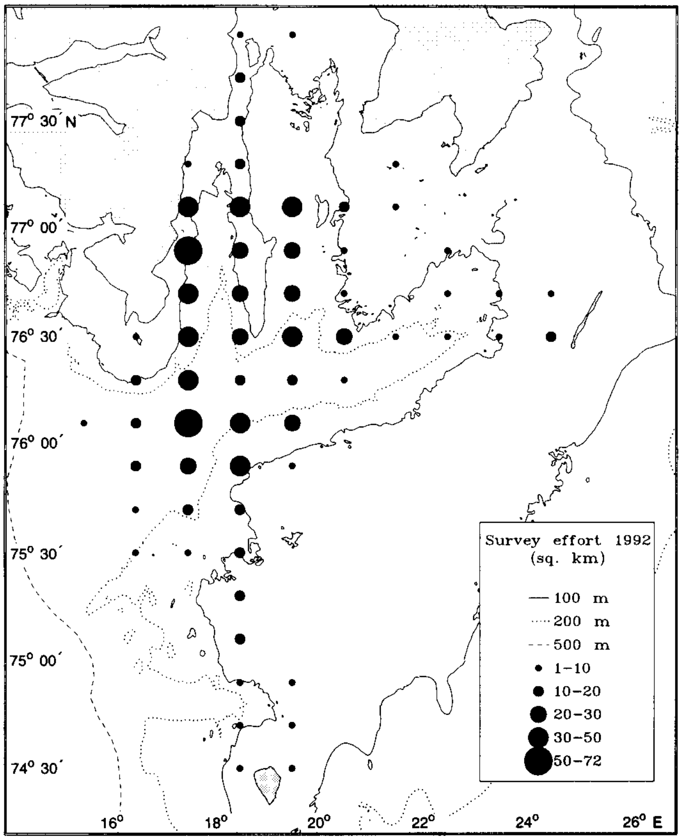

FIG. 2. Observation effort (km[2] covered) during seabird transects in 1992. The data are grouped in 0.2° north/south × 1° east/west blocks, each corresponding to ca. 22 × 27 km.

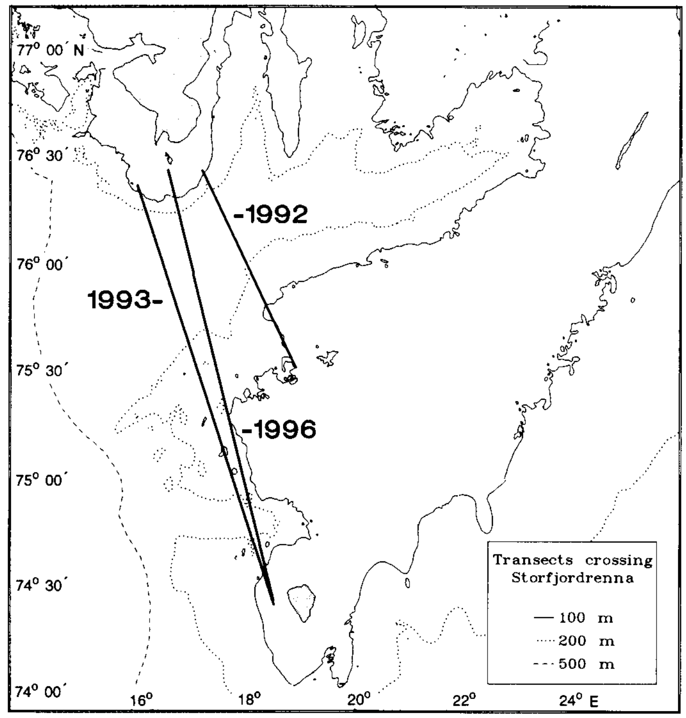

FIG. 3. Location of transects crossing Storfjordrenna in 1992, 1993, and 1996. All transects were made from south to north.

above the bottom; at the deeper stations, to the end of the wire. In 1993 and 1996, we used a Neil Brown Mark III CTD and collected data down to 5 m above the bottom. The distance between CTD stations was 10 NM; and in 1996, while the ship was cruising, we also conducted XBT (expendable bathythermograph, Tsurumi Seiki Co. Ltd., Japan) measurements midway between the CTD stations. For calibration of the conductivity cell, water samples were collected with a Niskin bottle attached to the wire above the CTD. All water samples were collected at the bottom of each station. Contour plots of temperature and salinity for different transects were made using SURFER (Golden Software).

RESULTS

Distribution and Grouping of Foraging Birds in 1992

Observations of flying murres and murres carrying fish indicated that large numbers of birds from colonies located in southwestern Storfjorden were foraging in Storfjordrenna and on the northern slope of Spitsbergenbanken. During an initial transect through the study area in Storfjordrenna (Fig. 4), we encountered large numbers (up to 127 birds per nautical mile transect length) of flying thick-billed murres. Most birds were observed in the central part of the transect. Many of them appeared to be flying in directions to and from the large breeding colonies in southwestern Storfjorden (39.6% toward NW, N, or NE; 60.4% toward SW, S, or SE; none toward W or E; n = 659 birds). Some aggregations of thick-billed murres on the sea surface were recorded on this transect, but the large flux of flying birds toward the south indicated that areas farther south were important foraging areas for birds breeding in Storfjorden. Later, during the survey in Storfjordrenna, we observed murres flying with fish in their beaks toward the breeding colonies in Storfjorden at four locations, at distances of 78 to 102 km from the nearest breeding colony, Kovalskifjellet. Murres flying with fish are usually carrying food to their young at the breeding colony.

Subsequent transects (Fig. 5) confirmed that murres on the sea surface occurred in large numbers farther south in Storfjordrenna. Most murres were observed toward the southern part of Storfjordrenna and the northwestern end of Spitsbergenbanken, and the highest murre densities were located between 75.4° and 76.2° N and between 16° and 18° E. Few murres were observed farther south towards Bjørnøya.

An analysis of murre distribution in Storfjordrenna at the scale of 300 m intervals along the ship transects showed that the birds sometimes were concentrated in large aggregations located 85 to 126 km from the closest breeding colonies at Kovalskifjellet in Storfjorden (Table 1). Individual thick-billed murre groups observed during the cruise comprised up to 250 birds. In one case, a large aggregation of thick-billed murres measuring ca. 2 km across comprised several groups which totaled 510 birds. A total of 19 groups with 30 or more thick-billed murres were recorded (Table 1), of which 16 groups were within the 300 m wide transects. Within the transects in Storfjordrenna, 16.8% of the murres

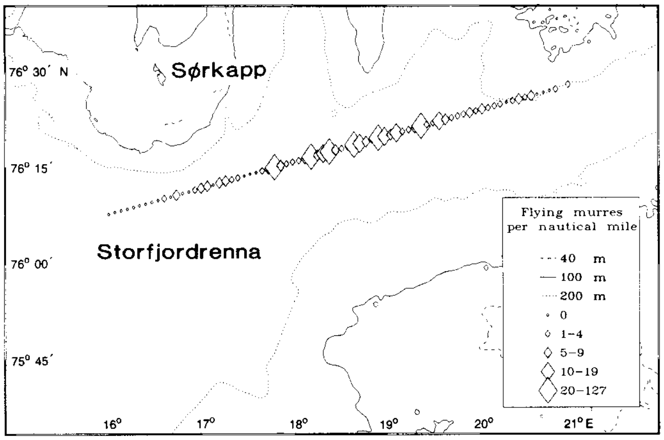

FIG. 4. Flying murres observed along a transect covering the central parts of the Storfjordrenna canyon.

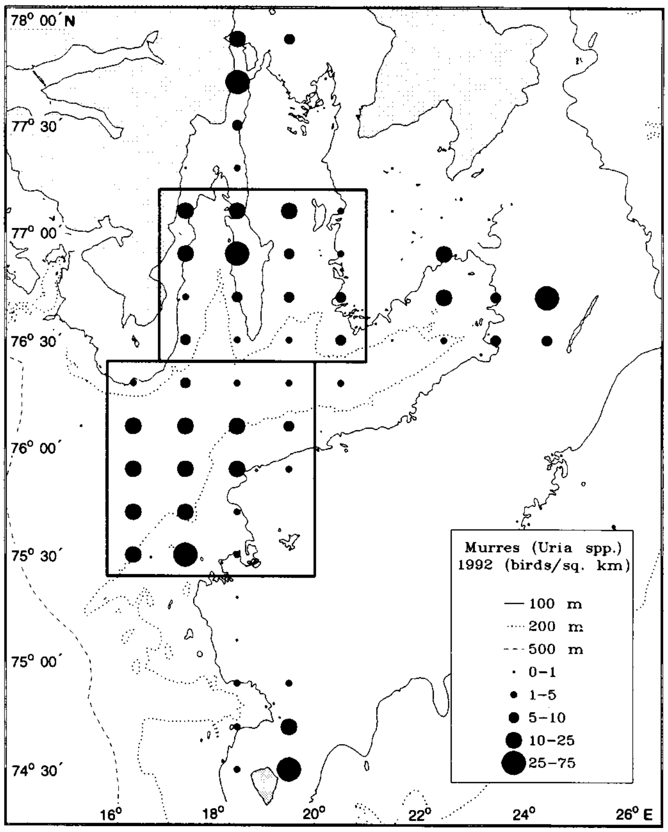

FIG. 5. Average densities of murres represented in blocks of 0.2° north/south × 1° east/west. The two rectangles represent areas in Storfjorden and Storfjordrenna for which the total murre abundance was estimated.

were observed as single individuals, whereas 49.7% of the birds were aggregated in groups of five or more birds.

All large aggregations of thick-billed murres (> 30 birds) were located in the central part of Storfjordrenna, where water depths exceed 200 m. The frontal zone between the cold water of the Sørkapp Current and the warm North Atlantic Current was located near the deepest part of the canyon, with depths of 200–300 m. The majority of murres were foraging in areas where there was a core of warm Atlantic water penetrating northeastward. Fig. 6 shows a typical cross-section in Storfjordrenna with a large aggregation of thick-billed murres (aggr. no. 3 in Table 1) in the Atlantic water south of the frontal zone. This aggregation was located over a strong halocline between 15 and 30 m in depth.

Within the block 75.4–76.4° N and 16.0–20.0° E (ca. 12 000 km^2) (Fig. 5), a total of 5138 murres were seen on the water during transects covering 389 km^2. Extrapolation of this number to the total block area yields an estimate of 158 000 murres. As a comparison, 4505 murres on the water were observed during 445 km^2 of transects in Storfjorden in the block 76.4–77.2° N and 17.0–21.0° E (ca. 8700 km^2), which may be extrapolated to 89 000 birds for the whole block. These estimates indicate that more murres are using the block in Storfjordrenna than the block in Storfjorden, which is located closer to the breeding colonies in Storfjorden.

Sections Crossing Storfjordrenna 1993 and 1996

During the 1993 transect from Bjørnøya to Sørkapp, thick-billed murres were concentrated in two regions: the southernmost was located over Kveitehola canyon (15–35 NM along the transect), and the northernmost over the deepest parts of Storfjordrenna (Fig. 7). At Kveitehola, there was a frontal zone between the cold water, from Spitsbergenbanken and Bjørnøya, and the warmer Atlantic water, which intrudes from the west. Similarly, in Storfjordrenna most murres were located on the warm side of a front between the cold water from the Sørkapp Current and the Atlantic water, characterized by a strong vertical salinity gradient. The maximum abundance of murres during this transect was 57 birds per NM.

Most of the birds in the southernmost concentration probably bred at Bjørnøya, which is located 40–50 km away. The birds in the northernmost concentrations are believed to originate from the colonies in Storfjorden because most flying birds followed northeast-southwest directions. In this area, one murre was observed flying with a fish in its beak at 76°08′ N, 16°20′ E and two birds at 76°17′ N, 16°05′ E (104 and 90 km from the nearest colony, Kovalskifjellet).

Oceanographic conditions observed during the 1996 transect (Fig. 8) were similar to those found in 1993, but the frontal zone between the Sørkapp Current and the North Atlantic Current was located closer to Sørkapp (the northern end point of the transect) than in 1993. Most thick-billed murres observed during this cruise were located in this frontal region, which was also characterized by a strong vertical salinity gradient. Two large aggregations were recorded, with 175 and 45 individuals per NM, respectively. No thick-billed murres were seen flying with fish in their beaks in the Storfjordrenna area during this cruise. Fewer murres were concentrated in the Kveitehola area than in 1993, but aggregations of up to 10 individuals were located in the frontal areas.

TABLE 1. Aggregations of thick-billed murres (individual groups ≥ 30 individuals) and distance to the closest thick-billed murre breeding colony.

Aggr. no.	Date	Time GMT	Position	Distance to Kovalskifjellet (km)	No. of thick-billed murres	Other species associated with the aggregation
1	19.07	11:42	76° 09′ N 16° 25′ E	102	50	30 kittiwakes, 2 minke whales, 1 white-beaked dolphin
2	19.07	11:46	76° 09′ N 16° 27′ E	101	50	125 kittiwakes, 2 minke whales, 1 white-beaked dolphin
3	29.07	04:02	76° 05′ N 17° 55′ E	108	120	
4	30.07	13:04	76° 08′ N 18° 11′ E	104	85	29 kittiwakes
5	30.07	13:06	76° 08′ N 18° 09′ E	103	35	
6	30.07	13:06	76° 08′ N 18° 09′ E	103	30	
7	30.07	13:08	76° 08′ N 18° 08′ E	103	40	
8	30.07	15:16	76° 08′ N 18° 48′ E	108	175	21 + 88 kittiwakes
9	13.08	19:47	76° 11′ N 17° 01′ E	96	33	Part of large aggregation (2 km across) incuding 510 thick-billed murres, 250 kittiwakes, 125 fulmars
10	14.08	14:26	76° 10′ N 17° 42′ E	98	120	165 kittiwakes, 15 glaucous gulls, 1 minke whale
11	14.08	14:29	76° 10′ N 17° 43′ E	98	60	
12	14.08*	16:50	76° 11′ N 17° 45′ E	96	250	100 kittiwakes, 32 fulmars, 11 glaucous gulls, 1 minke whale
13	14.08	23:22	75° 55′ N 16° 48′ E	126	70	60 kittiwakes
14	15.08	05:56	75° 55′ N 17° 31′ E	125	150	200 kittiwakes, 15 glaucous gulls
15	15.08*	07:47	76° 01′ N 17° 22′ E	114	120	270 kittiwakes, 3 humpback whales, 1 minke whale
16	15.08*	09:08	76° 01′ N 17° 24′ E	114	30	300 kittiwakes, 2 humpback whales, 3 white-beaked dolphins
17	15.08	10:05	76° 01′ N 17° 21′ E	114	70	90 kittiwakes
18	15.08	16:31	76° 17′ N 17° 25′ E	85	65	165 kittiwakes, 5 glaucous gulls, 1 minke whale
19	15.08	16:33	76° 17′ N 17° 26′ E	85	67	

* not included in ship transects

Association with Other Species

The large groups of murres observed during the 1992 cruise were often associated with other seabirds and cetaceans (Table 1). A total of 53 white-beaked dolphins, 29 minke whales, 6 killer whales (*Orcinus orca*), 5 humpback whales (*Megaptera novaeangliae*), 2 fin whales (*Balaenoptera physalus*), and 10 unidentified cetaceans were seen during the ship transects. All cetacean observations, except one minke whale seen in Storfjorden, were from Storfjordrenna (Fig. 9). In the 0.2° north/south × 1° east/west blocks in which cetaceans were present, thick-billed murres and black-legged kittiwakes were encountered in significantly higher densities than expected (Table 2). Neither northern fulmars (*Fulmarus glacialis*) nor dovekies (*Alle alle*) were significantly associated with the presence of cetaceans.

Seven of the thick-billed murre flocks in Table 1 were observed in the presence of minke whales, humpback whales and/or white-beaked dolphins. Flocks of other seabirds were also present in association with the thick-billed murre groups (Table 1). Black-legged kittiwakes were most frequently seen joining the aggregations, with group sizes of 29 to 300 individuals. Glaucous gulls (*Larus hyperboreus*) were seen at four aggregations (5 – 15 birds), whereas northern fulmars were part of two aggregations (32 and 125 birds, respectively). In several instances birds were feeding on prey forced to the surface by the cetaceans or on debris resulting from the foraging of the cetaceans.

In one case we observed an aggregation of cetaceans and seabirds where thick-billed murres were not a major component. This aggregation, located on 14 August 1992 at 76°12′ N, 18°28′ E, comprised 150 black-legged

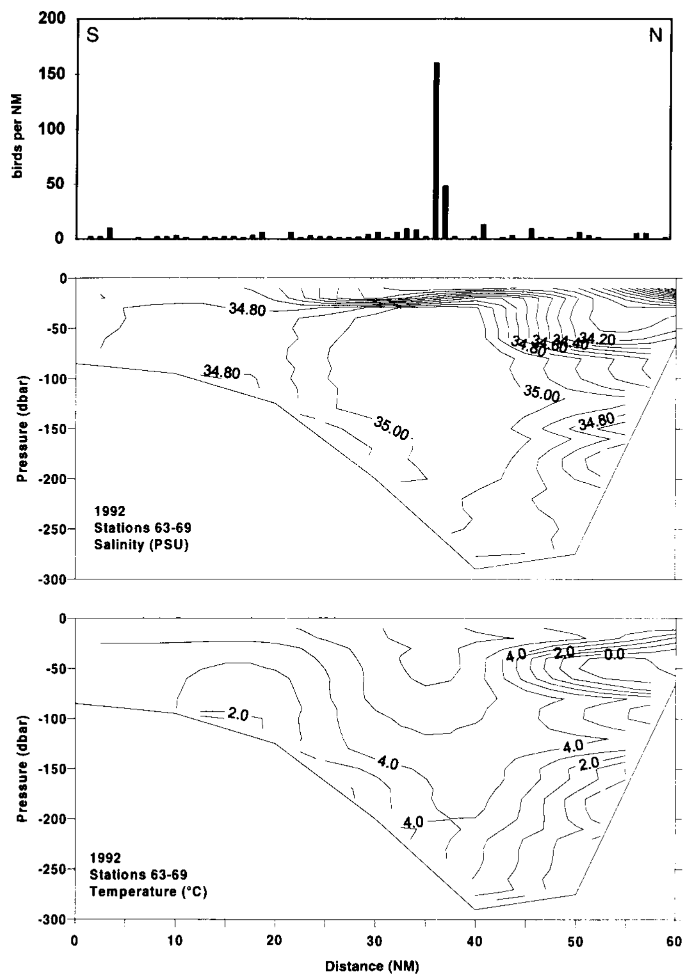

FIG. 6. Murre abundance, water temperature (°C), and water salinity (‰) along a transect crossing Storfjordrenna in 1992 (for location, see Fig. 3).

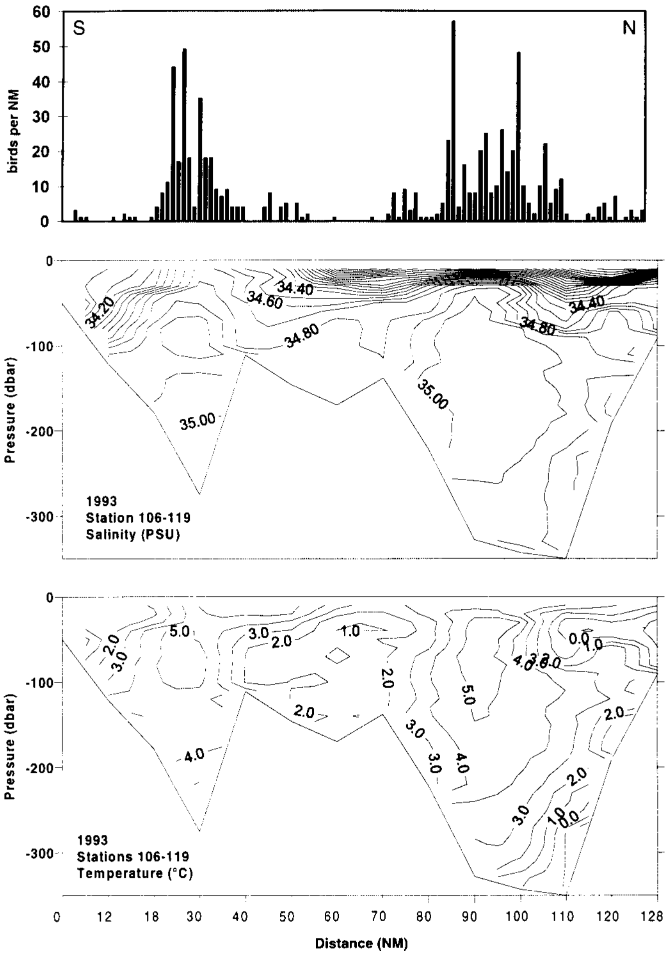

FIG. 7. Murre abundance, water temperature (°C), and water salinity (‰) along a transect crossing Storfjordrenna in 1993 (for location, see Fig. 3).

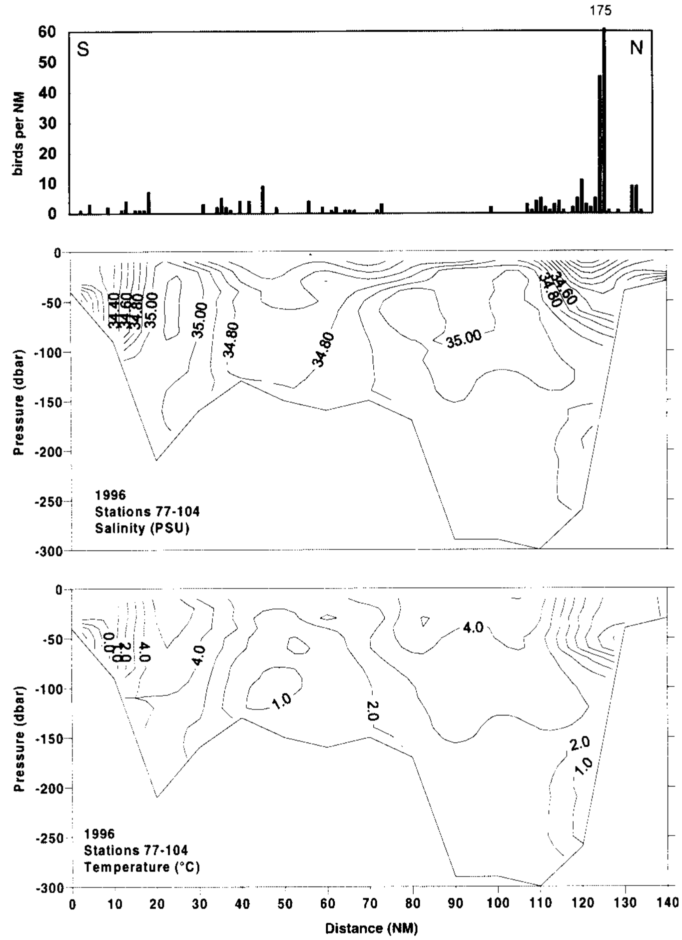

FIG. 8. Murre abundance, water temperature (°C), and water salinity (‰) along a transect crossing Storfjordrenna in 1996 (for location, see Fig. 3).

kittiwakes, 100 northern fulmars, and 30 white-beaked dolphins, but only 5 thick-billed murres.

Diet

Fish was the most frequently encountered prey in the stomachs of the thick-billed murres sampled in Storfjordrenna. Remains of polar cod were found in 11 of 16 (68.8%) of the birds, whereas capelin was found in three other murres (18.8%) shot in the same areas as those that contained polar cod. We did not identify any birds that contained both capelin and polar cod remains. Unidentified fish remains were recorded in seven of the birds (43.8%). Crustaceans were less common in the diet, but the euphausiid *Thysanoessa inermis* was found in three murres. The euphausiid in one of these birds consisted of fragments only, which probably originated from the gut of the fish also present in the murre stomach. Four additional taxa were recorded in one bird each. These were the pelagic amphipod *Parathemisto libellula*, an unidentified decapod, the squid *Gonatus fabricii*, and the pelagic polychaete *Nereis* sp. The three black-legged kittiwakes that were collected at aggregation no. 15 contained one, one, and two polar cod, respectively.

DISCUSSION

This study confirmed that the Storfjordrenna region is an important foraging area for thick-billed murres during the summer season. Large fluxes of birds flying in directions to and from the breeding colonies in Storfjorden, as well as sightings of birds flying towards the colonies with fish in their beaks, indicate that at least some of the foraging aggregations in Storfjordrenna originate from these breeding colonies. Large aggregations were located up to 126 km from the nearest colony (Kovalskifjellet) and 175 km from Bjørnøya. In a previous paper (Mehlum et al., 1996), we reported peaks in murre abundances on ship transects conducted closer to the breeding colonies in Storfjorden. The main aggregations in the Storfjorden area were located 19–56 km from the colonies (Mehlum, unpubl. data). The distances between the colonies in Storfjorden and the main thick-billed murre aggregations in both Storfjorden and Storfjordrenna are similar to distances reported for murres in Arctic Canada, where their mean foraging range was 56 km and the maximum range 112 km (Gaston and Nettleship, 1981).

Aggregations of murres observed in Storfjordrenna were larger than those reported from farther north in Storfjorden (Mehlum et al., 1996). In Storfjorden, no groups contained

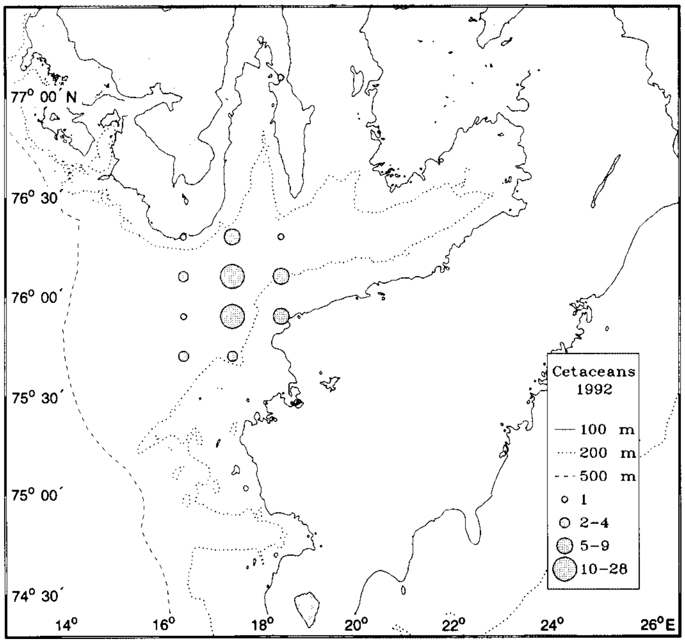

FIG. 9. Sightings of cetaceans during the 1992 cruise. Numbers indicate individuals.

TABLE 2. Densities (individuals per km^2) of different seabird species in blocks (0.2° N/S × 1° E/W) without (n = 42) and with (n = 12) observations of cetaceans.

Species	Without cetaceans		With cetaceans		Wilcoxon-Mann-Whitney Test	
	Mean	SD	Mean	SD	T	*p*
Northern fulmar *Fulmarus glacialis*	0.2	0.5	1.5	3.5	390	$p > 0.05$
Black-legged kittiwake *Rissa tridactyla*	0.8	1.9	2.4	3.3	477	$p < 0.01$
Thick-billed murre *Uria lomvia*	8.3	15.9	13.8	7.4	458	$p < 0.01$
Dovekie *Alle alle*	1.8	6.7	3.7	8.7	377	$p > 0.05$

more than 40 birds, whereas aggregations of up to 510 birds were seen in Storfjordrenna. Almost one-half of the murres in Storfjordrenna were aggregated in groups of more than five individuals. The proportion of single birds averaged 31.8% in the Storfjorden transects (Mehlum et al., 1996), but only 16.8% in Storfjordrenna.

Distances up to 126 km may seem to be long foraging distances for chick-rearing seabirds, but the murres are probably not time-constrained in connection with using foraging areas at such distances, because only a small fraction of the day is used for flying. Estimates of the daily number of feeding trips by thick-billed murres range from 3.5 to 8 (Gaston and Nettleship, 1981). With an estimated flight speed of 70 km/h, similar to that reported for common murres (*Uria aalge*) by Pennycuick (1987), the round-trip flight time between the colony and a foraging patch 126 km away would be 3.6 h. In order to provide food for its young, each parent would spend a total of 7.2 to 14.4 h flying per 24 h day. These values do not include additional time required to search for and capture prey or rest time at sea. Gaston and Nettleship (1981) estimated that a murre traveling 56 km to its foraging area used 3.4 hours per day traveling between the colony and the foraging area.

Some murre aggregations were associated with frontal areas between cold Arctic and warmer Atlantic water masses in Storfjordrenna, whereas other aggregations were found in areas with strong vertical stratification at 15–30 m depth, some of which were located in or near frontal regions. This stratification was caused by the presence of low-salinity water near the surface above the Atlantic water. Similarly, Mehlum et al. (1998) found aggregations of murres at the front around Bjørnøya and in the region of stratified water on the warmer side of the front. Aggregations of foraging murres have also been reported from a frontal zone near large colonies on Novaya Zemlya (Belopolskii, 1979) and at oceanographic fronts in the Bering Sea (Kinder et al., 1983; Schneider et al., 1990; Coyle et al., 1992; Decker and Hunt, 1996). Foraging aggregations above stratified water have also been reported in other arctic seabirds preying on copepods, such as dovekies (Mehlum, 1990) and least auklets (*Aethia pusilla*) (Hunt and Harrison, 1990; Hunt et al., 1990).

Physical forcing mechanisms and the behavior of marine planktonic organisms may result in the accumulation of biomass at oceanic fronts (Franks, 1992). When these aggregations include suitable prey, they can be exploited by predators, including fish, marine mammals, and seabirds (Haney, 1986; Fiedler and Bernard, 1987; Wishner et al., 1988; Hunt and Harrison, 1990; Schneider et al., 1990; Podestá et al., 1993; Decker, 1995).

Mammals might enhance seabird foraging success in three ways. First, some prey escape from the mammals and are thus available to surface-foraging birds (Obst and Hunt, 1990). Second, the mammals shape the fish schools (Parrish, 1992) and force the fish towards the sea surface, where they become accessible to diving and surface-feeding seabirds (Pierotti, 1988; Welch et al., 1993). It is documented that dolphins herd their fish prey into compact schools (Norris and Dohl, 1980; Wursig and Wursig, 1980), whereas humpback whales trap prey schools in “bubble-nets” and scare them towards the surface (Norris and Dohl, 1980). In one study, herring gulls (*Larus argentatus*) had higher rates of feeding success when foraging in assemblages with cetaceans, especially humpback whales (Pierotti, 1988). Third, surfacing and foraging marine mammals may act as a clue to seabirds for locating prey (Pierotti, 1988). Gulls are often the first birds to locate foraging cetaceans from the air and initiate a flock (Pierotti, 1988), while flocks of circling gulls may act as “catalyst” species and quickly attract other seabirds such as alcids (Hoffmann et al., 1981; Chilton and Sealy, 1987; Pierotti, 1988; Haney et al., 1992). The black-legged kittiwake probably acts as a “catalyst” species in the Barents Sea area, and the murres might be guided to the prey aggregations by the conspicuous flocks of foraging kittiwakes.

Recent studies have shown that the baleen whales tend to forage in regions with a high density of prey (Wishner et al., 1988; Piatt et al., 1989; Piatt and Methven, 1992; Macaulay et al., 1995). Piatt and Methven (1992) reported that baleen whales selected areas with capelin school densities above certain thresholds. These thresholds were higher for fin whale than for minke whale, the former requiring larger and more compact prey aggregations than the latter.

In minke whales, capelin constitutes an important part of the diet in the Bjørnøya region, but in years with low capelin abundance, other prey such as euphausiids predominate (Haug et al., 1995). Jonsgård (1982) reported that, in 1950, pelagic crustaceans, often mixed with capelin, were the main prey in the Bjørnøya area. Minke whale diet data from Storfjordrenna are scarce, but in August 1996, euphausiids and polar cod were found as major constituents (T. Haug, pers. comm. 1996). The other cetacean frequently seen in our study, the white-beaked dolphin, has not been thoroughly studied in the Barents Sea region (Øien, 1996). No data on its diet are available from the Barents Sea, but it is known from other regions that schooling fish are important prey species (Evans, 1987; Martin, 1990). In the Denmark Strait (southeast of Greenland), it was often seen feeding on capelin forced to the surface by fin whales (Jonsgård and Christensen, 1968).

Although the number of food samples in Storfjordrenna was low, it appeared that polar cod were more important than capelin in the stomachs of thick-billed murres. This fact, and the exclusive polar cod diet found in a small sample of surface feeding black-legged kittiwakes collected at one of the large foraging aggregations, support the assumption that polar cod constitute an important part of the fish schools in the area. The main prey item brought back to feed the thick-billed murre chicks at Kovalskifjellet in 1989 and 1992 was also polar cod (Mehlum and Gabrielsen, 1993; Mehlum et al., 1996).

The pelagic ecology, distribution, and aggregative behavior of polar cod in the Barents Sea are not well understood. The species is widely distributed in the northern Barents Sea during summer (Gjøsæter and Anthonypillai, 1995) and is an important element in the arctic marine food chains (Bradstreet and Cross, 1982; Welch et al., 1992; Mehlum and Gabrielsen, 1993). In Canadian coastal waters, this species may aggregate in dense schools from 3 to 5 m below the surface during late summer (Crawford and Jorgenson, 1993; Welch et al., 1993).

The schooling behavior of polar cod in the Barents Sea has to our knowledge not been investigated. Neither are we aware of any information about the co-occurrence of capelin and polar cod schools, which might explain the existence of both species in the diet of the murres examined in our study. We also lack information on how capelin and polar cod are influenced by oceanic fronts and vertical stratification in the water column. Further studies on the behavior of capelin and polar cod schools in the region would be needed to explain the aggregative foraging behavior of marine birds in Storfjordrenna and other parts of the Barents Sea.

Storfjordrenna and the northern edge of Spitsbergenbanken support a greater proportion of the thick-billed murres breeding along the western shore of Storfjorden than do the waters of Storfjorden, which are closer to the colonies. The waters of Storfjordrenna and the northern edge of Spitsbergenbanken are sites of major fisheries and an area known to support high numbers of cetaceans (Christensen, 1977; Øien, 1990; Haug et al., 1995; Øien and Hartvedt, 1995; Øien, 1996). We hypothesize, on the basis of our observations and the use of these waters by the fishery, that the waters of Storfjordrenna are richer in prey stocks than those of Storfjorden. A pronounced difference between the waters of Storfjorden and those farther south is the presence of predictably located, strong frontal systems and marine mammals in Storfjordrenna. These features, which indicate where aggregations of prey may be expected to occur, were lacking in Storfjorden. We hypothesize that thick-billed murres, like least auklets in Alaska (Obst et al., 1995), are willing to fly to more distant foraging grounds to obtain greater foraging success. This hypothesis has yet to be tested.

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