The diets of common and Brünnich's guillemots *Uria aalge* and *U. lomvia* in the Barents Sea region

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Guillemots *Uria* spp. account for ca. 70% of the total harvest of prey taken by seabirds breeding in the Barents Sea region. This paper presents guillemot chick diet data collected recently at four localities (Finnmark, Murman, Bjørnøya and Spitsbergen) and collates all the data found by the authors in the literature and in the archives of Tromsø Museum, the Norwegian Polar Institute and Kandalaksha State Nature Reserve. Guillemots consume a wide variety of prey and, in comparison to the harvest by predatory fish and marine mammals, their impact on the Barents Sea ecosystem is considered to be minimal. We point out the need for more systematic collection of data from different regions and at different times of the year before a final impact assessment can be made.

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Introduction

The Barents Sea is one of the most productive marine ecosystems in the world with vast stocks of commercially important fish, seabirds and sea mammals (Sakshaug et al. 1994). Of the ca. 3.7 million pairs of seabirds (with a biomass of ca. 4200 tonnes) that breed in the Barents Sea region (as defined by Mehlum & Gabrielsen 1995), Brünnich's guillemots *Uria lomvia* predominate both in numbers (ca. 1.6 million pairs = 43%) and biomass (ca. 2600 tonnes = 61%). They are in addition the major consumer among the Barents Sea seabirds, taking in the order of 60% of an estimated 2213 tonnes of food consumed daily by breeding seabirds during the summer (Mehlum & Gabrielsen 1995). When including the ca. 266,000 pairs of common guillemots *Uria aalge* which also breed in the Barents Sea, the total consumption by adults and chicks of both guillemot species has been estimated to be ca. 1500 tonnes/day or nearly 70% of the total seabird consumption by breeding seabirds (Mehlum & Gabrielsen 1995). However, guillemots are known to consume a wide variety of prey (Erikstad & Vader 1989; Vader et al. 1990; Barrett & Krasnov 1996), and this paper addresses the impact guillemots may have on the Barents Sea ecosystem. It first documents considerable diversity in prey use at four breeding colonies in the southern and western Barents Sea regions from 1980–1995 (Fig. 1) and evaluates data found in the literature and in the authors' respective institution's archives. Regional diet patterns are then presented, impact analyses are made and suggestions are given as to where effort should be made in future feeding studies. Little emphasis is, however, placed on temporal or inter-species statistical comparisons as these are dealt with in more detail by Barrett & Krasnov (1996) and Barrett et al. (1997), respectively.

Methods and material

Most of the recent data concerning the diet of both species during the breeding season were collected by the authors by direct observation of food items brought to the chick by the adults. Observations were made from 5–20 m using binoculars. In most cases the food items could be identified to species level. Identification controls were made by catching fish-carrying birds with a noose-pole and identifying the food item in the hand. Such studies have been carried out on Bjørnøya (Bear Island) (74°21′N, 19°06′E) nearly every year since 1988, on Hornøya, East Finnmark (70°22′N, 31°10′E) since 1980 and on Kharlov, off the Kola Peninsula (68°49′N, 37°20′E) since 1985 (Fig. 1).

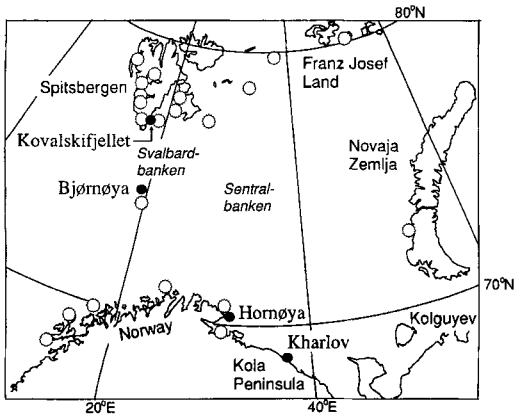

Fig. 1. Map of the Barents Sea showing the four colonies where guillemot diet data were collected by the authors (solid circles) and other localities mentioned in the text. Open circles indicate approximate positions of sampling sites listed in Tables 1 and 2.

Brünnich's guillemot chick diet was also studied on Kovalskifjellet, Spitsbergen (77°03'N, 17°17'E) in 1989 (Mehlum & Gabrielsen 1993) and 1992. In most years, observations were spread over two or three weeks during the main chick-feeding period (July) thereby reducing potential errors in shorter-term sampling due to seasonal changes in diet. More details are given by Barrett et al. (1997). Because Brünnich's guillemots generally land directly on their breeding site, conceal the prey by bowing their heads, and feed their chicks almost immediately on arrival, sample sizes for this species on Hornøya and Kharlov were often much smaller than for common guillemots which commonly hold the fish aloft before feeding the chicks. Some stomach samples from adults were also collected from both species on Kharlov in 1992 and from Brünnich's guillemots on Novaja Zemlja (1992) and Franz Josef Land (1993).

Comparisons of diets between colonies were made using χ^2 tests, and p-values <0.05 were considered to be significant. When numbers of food items from individual food categories were low in a sample, several categories were combined before testing.

Supplementary data gleaned from the literature and the Norwegian Polar Institute, Tromsø Museum and Kandalaksha State Nature Reserve archives differed so much in degree of quantification that they were impossible to compare directly. Furthermore, some of the data were based on observations of chick diet while other data were based on adult stomach samples. Because the relationship between chick and adult diet is unknown, chick and adult data are presented separately.

Results

Chick diet

Capelin *Mallotus villosus*, sand eels *Ammodytes* sp., and I-group herring *Clupea harengus* (Barrett & Krasnov 1996) constituted most of the diet of common guillemot chicks on Kharlov, Bjørnøya and Hornøya (Fig. 2). There were, however, clear differences among the colonies in the relative composition of the diets.

On Kharlov, sand eels were the most important prey items fed to common guillemot chicks. In some years, capelin was also important, and, in 1986, dominated the diet (Fig. 2). Herring

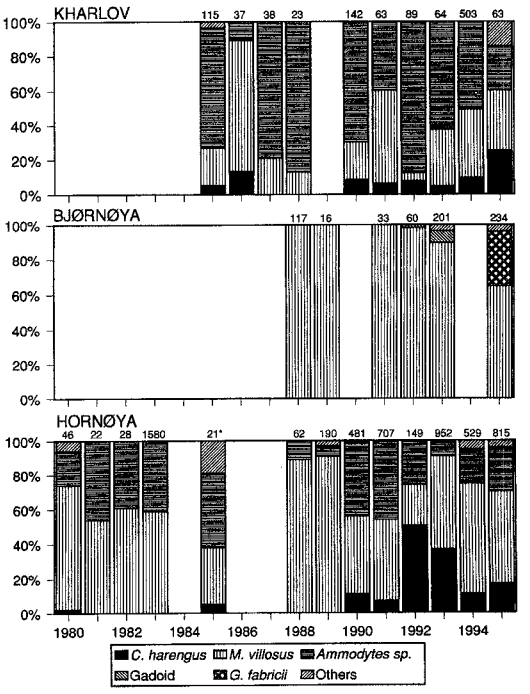

Fig. 2. Composition (% by number) of diet fed to chicks of common guillemots on Kharlov, Bjørnøya and Hornøya. Figures above columns = no. of fish counted. 21* indicates that the fish were collected on the neighbouring colony, Syltefjord. (See Fig. 3 text for English names of prey.)

occurred in some years but generally constituted <10% of the items recorded. In 1995, herring made up 25% of the fish recorded.

On Bjørnøya, capelin constituted 90% or more (by number) of the diet in five of the six seasons for which data exists. In the sixth year (1995), capelin made up >60% and the little squid *Gonatus fabricii* accounted for most of the rest (Fig. 2).

On Hornøya, capelin was again the most common prey item caught by common guillemots, while sand eels were regularly eaten but in lower proportions (Fig. 2). After 1990, herring was a periodically important constituent of the chick diet. In nearly all the years for which there is comparable data from Hornøya, Kharlov and Bjørnøya, there were significant differences in the diet composition among the colonies ($\chi^2 > 13$, df = 1–3, $p < 0.001$). The only insignificant differences found were between Hornøya and Kharlov in 1985 and 1991, but these may have been due as much to the small sample sizes as to the actual geographical differences.

While Brünnich's guillemots tended to feed their chicks a much more varied diet than did common guillemots on Bjørnøya, capelin, sand eels and I-group herring again made up the samples collected on Hornøya and Kharlov (Fig. 3).

On Bjørnøya, the Brünnich's guillemot samples contained six different prey items (capelin, squid, sculpins (Cottidae), polar cod *Boreogadus saida*, blennies *Lumpenus* sp. and eelpouts (Zoarcidae)) which occurred in varying proportions. Capelin were, however, the most common prey with squid constituting ca. 30% of the food items in three of the five years. There were significant differences between the prey compositions on Hornøya and Bjørnøya in the three years data were collected on both colonies (1989, 1991, 1993, $\chi^2 > 30$, df = 3, $p < 0.001$).

On Kovalskifjellet, Brünnich's guillemots fed their chicks almost entirely on polar cod in 1992. Two of the 148 food items observed were crustaceans, the only two specimens of this taxa observed fed to chicks in any of the colonies studied. On Kharlov, sand eels constituted 100% (in 1992) and 80% (in 1994) of the fish seen. The remaining fish recorded in 1994 were capelin (14%) and herring (5%).

Adult stomach samples

Of eight adult Brünnich's guillemot stomachs sampled on Kharlov in 1992, three contained capelin, two contained herring, two contained gadoids and one contained sand eels.

Data from the literature

Chick diet

Common guillemots on Hjelmsøy, West Finnmark, fed their chicks almost exclusively capelin in 1983, but in 1984 saithe *Pollachius virens* dominated their diet (Vader et al. 1990; Tromsø Museum unpubl.). On Røst, Lofoten, saithe, sand eels and occasionally butterfish *Pholis gunnellus*

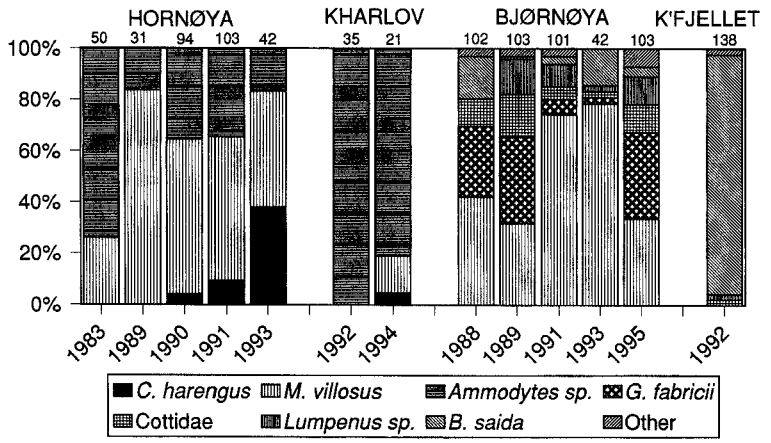

Fig. 3. Composition (% by number) of diet fed to chicks of Brünnich's guillemots on Hornøya, Kharlov, Bjørnøya and Kovalskifjellet, Spitsbergen. Numbers above columns = no. of fish counted. *C. harengus* = herring, *M. villosus* = capelin, *Ammodytes* sp. = sand eel, *G. fabricii* = squid, *Lumpenus* sp. = blenny, *B. saida* = polar cod.

Table 1. Food items in the diet of common guillemots in the Barents Sea recorded in the literature. N = numbers of adult stomachs (S) or chick food items (F) sampled. Number after a stomach food item = no. of stomachs containing that food item. ? = sample size not given.

During breeding season in or near colonies			
Date	*N*	*Food items*	*Source*
Novja Zemlja			
1947	13S	Polar cod 13, Atlantic cod 3.	Kandalaksha Reserve archives
1948–50	20S	Polar cod 8, Atlantic cod 2, sand eels 3, capelin 2, sculpin 2.	Uspenski 1956
Bjørnøya			
1948	?F	Mainly small gadoid fish.	Sergeant 1951
1996	?S	Mainly euphausiids	Mehlum et al. in press
Kola Peninsula (Kharlov)			
1935	46F	Atlantic cod, sand eel and herring, Fig. 4.	Belopol'skii 1957
1938	198F	Mainly sand eel, Fig. 4.	Kaftanovski 1938
1937–39	85F	Mainly capelin and sand eel, Fig. 4.	Kandalaksha Reserve archives
1947–49	24, 47 & 41S	Atlantic cod, sand eel and herring, Fig. 4.	Belopol'skii 1957
1960	21S	Gadoids 13, capelin 5, crustacea 3 and *Nereis* 1.	Gerasimova (in Krasnov et al. 1995)
1992	9S	Sand eels 5, herring 2, Atlantic cod 1, capelin 1.	Krasnov unpubl.
Norway			
1970s	?F	Vedøy, Røst. Mainly saithe and sand eels, occ. *Pholis gunnellus*	Tschanz & Barth 1978
1983	79F	Hjelmsøy. 99% capelin.	Vader et al. 1990
1984	24F	Hjelmsøy. Saithe 16, sand eel 3, *Anarhichas lupus* 3, squid 1.	Tromsø Museum unpubl.
1987	18S	Bleiksøy. Mostly squid beaks.	Barrett unpubl.
Outside breeding season in coastal waters			
Apr 1986	17S	East Finnmark. Exclusively capelin.	Erikstad & Vader 1989
Apr 1985	?	Tromsø. Mostly capelin.	Vader et al. 1990

were fed to chicks in the 1970s (Tschanz & Barth 1978).

In 1938, the only single year for which there is published data for the Brünnich's guillemots on Kharlov, sand eels constituted >80% of the diet of both species (Kaftanovski 1938). Of 20 fish observed in 1994 being fed to Brünnich's guillemot chicks on Novaja Zemlja by Strøm et al. (1994), seven were polar cod and four were capelin. On Bjørnøya, chicks of both guillemot species were fed mainly fish (Roi 1911; Duffey & Sergeant 1950; Sergeant 1951). These were identified as "mainly gadoids" and may well have been polar cod. On Kovalskifjellet in 1989, Brünnich's guillemot chick diet consisted almost entirely of polar cod (Mehlum & Gabrielsen 1993).

Adult stomach samples

Most of the data found in the literature were based on stomach samples from adult birds shot or otherwise collected on or near breeding colonies. Four other studies were of birds collected in ice-covered waters during the summer; another was from the central Barents Sea and five were from coastal waters during the autumn and spring (Tables 1 and 2). The methods of quantification varied considerably among the studies, from near anecdotal notes (e.g. the 19th century references) to detailed estimates of frequencies of occurrence of prey items (e.g. Lydersen et al. 1989; Erikstad 1990; Mehlum et al. 1996; in press) or percentage contribution by mass or energy (Weslawski et al. 1994). This prohibited any quantitative comparisons between sites. Certain patterns do, however, arise from the data.

There is little data on the common guillemot from Novaja Zemlja (in Bezymyannaya Bay), and the main food items documented in the late 1940s were polar cod and Atlantic cod *Gadus morhua* (Table 1). Further west, on Kharlov off the Kola Peninsula, common guillemot stomachs sampled in the late 1930s and 1940s again contained mainly fish (capelin, Atlantic cod, herring and sand eels, Table 1, Krasovskii 1937; Kaftanovski 1938; Belopol'skii 1957). These data are also summarised in Fig. 4. Of nine adult stomachs sampled on Kharlov in 1992, five contained sand eels, two contained herring, one contained Atlantic cod and one contained capelin (Table 1).

Polar cod and Atlantic cod constituted most of the Brünnich's guillemot diet on Novaja Zemlja in the late 1940s, but other fish such as sand eels, capelin, herring and sculpins were also eaten (Table 2, Fig. 4) (Krasowski 1937; Uspenski 1956; Belopol'skii 1957). In 1992, 10 of 31 Brünnich's guillemot stomachs sampled on Novaja Zemlja contained food (Table 2). Gadoids were found in four, snail fish *Liparis* sp. in two, and capelin, sand eels, sculpins, unidentified fish and crustaceans in one each. In 1993, 12 of 14 Brünnich's guillemot stomachs analysed in Franz Josef Land contained polar cod, four contained crustaceans, one contained polychaetes, and one contained unidentified fish.

Belopol'skii (1971) otherwise summarises the contents of 111 Brünnich's guillemot stomachs sampled on Kharlov in 1935, 1941 and 1947–49. Herring was found in 30, sand eels in 18, Atlantic

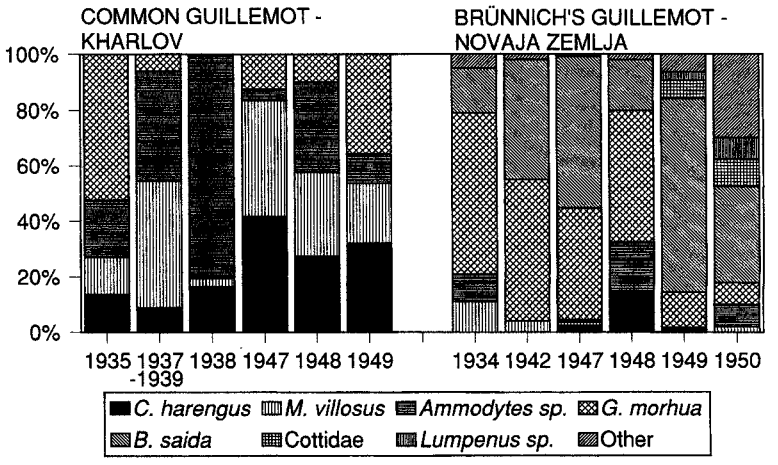

Fig. 4. Composition (%) of the diet of common guillemots at Seven Islands and of Brünnich's guillemots at Novaja Zemlja in the 1930s and 1940s. Data from Krasovskii (1937), Kaftanovski (1938), Uspenski (1956), Belopol'skii (1957) and Kandalaksha State Nature Reserve archive. Sample sizes are given in Table 1. (See Fig. 3 text for English names of prey.)

Table 2. Food items in the diet of Brünnich's Guillemot in the Barents Sea recorded in the literature. References marked with an asterisk (*) are quoted from Løvenskiold (1964). N = numbers of adult stomachs (S) or chick food items (F) sampled. Number after a stomach food item = no. of stomachs containing that food item. ? = sample size not given.

During breeding season in or near colonies

Date	*N*	*Food items*	*Source*
Novja Zemlja			
1925?	?F	Polar cod, gadoids, capelin.	Gorbunov 1925 in Uspenskii 1956
1934	62F	Mainly Atlantic cod, Fig. 4.	Krasovskii 1937
1942, 47	46, 292S	Mainly Atlantic and polar cod, Fig. 4.	Belopol'skii 1957
1948–50	44, 521, & 312S	Varied: Atlantic cod, polar cod, sand eels, Fig. 4.	Uspenski 1956
1992	31S	Gadoids 4, sculpins 2, Atlantic cod 1, capelin 1, s. eel 1, *Liparis* 1, crust. 1	Krasnov 1995
1994	20F	Polar cod 7, capelin 4, sand eels 2, blennies 2.	Strøm et al. 1994
Frans Josef Land			
1931	16S	Crustaceans 8, unid. fish 7, polychaetes 2.	Demme 1934
1991–93	11S	93% (by mass) polar cod, 6 spp. of crustacea, mainly *Parathemisto libellula*.	Weslawski et al. 1994
1993	14S	Polar cod 12, crustaceans 4, polychaetes 1 and unid. fish 1.	Krasnov 1995
Svalbard			
1889	?	Edgeøya. Amphipods, mainly *Gammarus locusta*.	Walter 1890*
1896	?F	Isfjorden, Polar cod.	Trevor-Battye 1897*
1898	?	Midterhuken, van Mijenfjorden. Polar cod.	Nathorst 1900
1898	?S	Amphipods and other crustacea, fish.	Römer & Schaudin 1900*
1898, 1900	?	Spitsbergen. Crustaceans, polar cod, *Lumpenus* sp.	Kolthoff 1903
?	?	Fish.	Birulja 1910*
1910	?S	Midterhuken, Bellsund. Mainly polar cod. Young fed on fish.	Munsterhjelm 1911
1924	?	Alkefjellet, Hinlopen. Adults and young fed exclusively on fish.	Montague 1926*
1933	4S	All contained *Thysanoessa inermis*.	Hartley & Fisher 1936
1967–69	1S	Edgeøya. Only gammarids.	de Korte 1972
1989	161F	84% polar cod, 10% Lumpenidae, 2% Cottidae, 4% unid. fish.	Mehlum & Gabrielsen 1993
1992	23S	Storfjorden. *Parathemisto* spp., *T. inermis*, *G. wilkitskii*, polar cod.	Mehlum et al. 1996

Bjørnøya			
1899	?	Adults ate crustacea, polychaetes and fish. Young fed on fish.	Swenander 1900
1908	?	Young fed on fish. Crustaceans in adult stomachs.	Roi 1911
1948	?	Young fed chiefly small (ca. 50 mm) gadoids. One stomach contained remains of gadoids & polychaetes.	Duffey & Sergeant 1950
1995, 1996	12, ?	Mainly euphausiids *T. inermis*.	Mehlum et al. in press
Kola Peninsula (Kharlov)			
1938	36F	86% sand eel, 8% herring, 3% gadoid, 3% "other".	Kaftanovski 1938
1935, 1940s	111S	Herring 30, sand eels 18, gadoid 16, capelin 14, crustaceans 5.	Belopol'skii 1971
1960	11S	Capelin 5, gadoid 5, *Sebastes* 1.	Gerasimova in Krasnov et al. 1995
Norway			
1983	49F	Hjelmsøy. 33% capelin, 24% squid, 22% sand eel.	Vader et al. 1990
During breeding season in open water/ice-covered waters			
Svalbard			
1985/86	18S	First year ice. Mainly *Pandalus borealis*, amphipods and polar cod.	Lønne & Gabrielsen 1992
1986	16S	Multi-year ice. 48% fish, mostly polar cod. 33% amphipods, most *G. wilkitskii*.	Lønne & Gabrielsen 1992
1982–87	13S	Pelagic, ice-covered waters. *Parathemisto libellula*, polar cod.	Mehlum & Gjertz 1984, Gjertz et al. 1985, Mehlum & Gabrielsen 1993
1984–85	12S	Kongsfjorden. Benthic amphipods, polar cod, unid. fish.	Mehlum & Gabrielsen 1993
Outside breeding season in coastal and open waters			
Sep 1984	21S	Hornsund. Polar cod dominated, followed by *P. libellula* and *Pollachius virens*	Lydersen et al. 1989
Spring 1985–87	76S	Marginal ice zone. *P. libellula*, polar cod, *T. inermis*, *Pandalus borealis*.	Mehlum & Gabrielsen 1993
Spring 1985	14S	Hornsund. *T. inermis*, gammarids, polar cod.	Mehlum & Gabrielsen 1993
Feb 1987	30S	Hopen. *P. libellula* and polar cod.	Bakken 1990
Mar 1987	24S	Sentralbanken. Atlantic cod, polar cod and crustaceans.	Erikstad 1990
Apr 1986	28S	East Finnmark. Exclusively capelin.	Erikstad & Vader 1989
Apr 1985	?S	Tromsø. Mostly capelin.	Vader et al. 1990

cod in 16, capelin in 14 and crustaceans in five (Table 2).

Very little data have been published from any of the huge Brünnich's guillemot colonies on Svalbard. Adult stomach samples and a few observations of food fed to chicks indicate that polar cod and crustaceans (mainly amphipods) are the most frequent items taken during the breeding season (Table 2). However, prior to and after breeding, the diet of Brünnich's guillemots shot in or near the ice edge consisted nearly solely of crustaceans dominated by amphipods *Parathemisto libellula* and *Gammarus* spp. and, in one study, the prawn *Pandalus borealis* (Table 2). Three studies of adult Brünnich's guillemots at and around Bjørnøya (Swenander 1900; Roi 1911; Mehlum et al. in press) recorded crustaceans, polychaetes and fish among stomach contents.

There are also little data from the coast of Norway, but it seems that fish again constituted the total diet of both species with capelin comprising 100% of the prey of both species when they gathered off the coast of Tromsø and Finnmark just before breeding in the mid-1980s (Tables 1 & 2). Squid beaks dominated the food remains found in 18 stomachs of adults sampled off Bleiksøya, Vesteraålen, in June and July 1987 (Barrett unpubl.).

The total number of prey taxa recorded in the Brünnich's guillemot diet in the Barents Sea region is at least 37, including 17 crustaceans, 16 fish, molluscs, polychaetes and squid. Thirteen taxa, mostly fish (capelin, herring, sand eel, Atlantic cod, polar cod, wolf fish *Anarhichas* sp., butterfish, sculpins (Cottidae), saithe and red fish *Sebastes* sp.) but also squid, polychaetes and molluscs have been documented in the common guillemot diet.

Discussion

General comparisons of Brünnich's and common guillemot diets in Canada are discussed by Tuck (1960) and Bradstreet & Brown (1985). This paper presents the first such comparison from the Barents Sea region. As in the Canadian studies, Brünnich's guillemots in the Barents Sea have a diet of fish and crustaceans, many of which are benthic or associated with ice. Their diet is also much more varied than that of common guillemots which catch mainly small pelagic, schooling fish. More details concerning the food differences between the two species at Hornøya and Bjørnøya are discussed by Barrett et al. (1997), while annual differences in chick diet at Hornøya and Kharlov are discussed in relation to prey availability by Barrett & Krasnov (1996).

It is, however, likely that adult birds consume food different from what they feed their chicks. This was found, for example, in gulls (Laridae) by Nogales et al. (1995) and partly shown for common guillemots on Kharlov in 1935 and 1992 by Belopol'skii (in Kandalaksha State Reserve archives) and JVK (Table 1), respectively. On Kharlov, chicks were fed mainly high energy, pelagic and schooling fish (capelin, herring and sand eel) while many adult stomachs also contained more benthic fish such as Atlantic cod and other gadoids. Similarly, Brünnich's guillemot chicks on Kovalskifjellet were mainly fed polar cod in 1992 (Fig. 3), while adults shot offshore, near the colony in the same season, had large proportions of amphipods and euphausiids in their stomachs (Mehlum et al. 1996). The same pattern was found at Bjørnøya in 1993 when stomachs of adults shot offshore contained predominantly euphausiids *Thysanoessa inermis* (Mehlum et al. in press), while chicks were fed mainly capelin and polar cod (Fig. 3). A study of both guillemot species in the same area in 1996 showed that euphausiids were also the dominant prey of common guillemots (Mehlum et al. in press). The potential for such differences between adult and chick diets, plus the paucity of data of either kind from all parts of the Barents Sea, seriously restricts the identification of definitive, broad-scale geographic trends.

Despite this, the data collected along the mainland coasts of Norway and Russia do suggest that capelin is especially important as guillemot prey in the early spring (March–April). This is the time when huge flocks of both guillemot species gather to feed on the mature, energy-rich capelin as it approaches the Finnmark coast to spawn (Barrett 1979; Erikstad & Vader 1989; Strann et al. 1991; Krasnov 1995; Nikolaeva et al. 1996). These flocks consist not only of birds which breed in the Barents Sea colonies but also of young common guillemots from, for example, British colonies (Strann et al. 1991). Furthermore, the distribution of guillemots out at sea early in the year (January–March) and in August–September also seems to coincide with the distribution of capelin (Fauchald & Erikstad 1995; Krasnov

unpubl.). This suggests that capelin is an important prey for both species in the central and southern Barents Sea for at least 4–6 months of the year.

Although the numbers of capelin along the coast drop after the spawning season, there are always some late spawners available to guillemots throughout the summer (Barrett & Furness 1990; Barrett & Krasnov 1996). At least half the numbers of capelin fed to common guillemot chicks on Hornøya during seven breeding seasons in the 1980s and 1990s were gravid females (Barrett unpubl.). That fewer capelin are taken at Kharlov reflects the fact that while capelin almost always occur and spawn in East Finnmark, their movements along the Kola Peninsula are limited to the years when large influxes of warm Atlantic water spread further east than normal (Ozhigin & Luka 1984; Gjøsæter et al. 1994). Similarly, when herring stocks are at their lowest (as was the case in the early 1980s), the youngest year classes of herring do not spread as far east along the coast as they do when the stocks are large (Dragesund et al. 1980). Such variations in stock levels explain the near absence of herring in the Hornøya samples before 1985 and the subsequent increase in the 1990s (Fig. 2) and the differences in the amount of herring caught by guillemots on Kharlov and Hornøya (Barrett & Krasnov 1996). Unfortunately little is known about the distribution of sand eels in the southern Barents Sea, but there are spawning grounds around Kharlov which are large enough to support a periodic local fishery (Krasnov & Barrett 1995) and hence contribute to the predominance of sand eels in the local guillemot chick diet (Figs. 2 and 3).

The data from the literature also document the importance of crustaceans in the diet of adult Brünnich's guillemots around Spitsbergen and Franz Josef Land. The dominance of crustaceans in the diet is especially true of birds sampled at sea around Spitsbergen during the late winter, spring and summer. Food samples in five of ten studies were dominated by the large hyperiid amphipod *Parathemisto libellula*, three by other crustaceans (amphipods or euphausiids) and only two by fish (polar cod). Among the 14 studies of birds collected in or near colonies around Spitsbergen and Franz Josef Land, seven recorded crustaceans as the main prey type (Table 2).

Among the crustaceans listed are the amphipods *P. libellula* and *Gammarus wilkitskii* which are often associated with waters near or covered by ice (Sakshaug et al. 1994) and which are much more abundant than, for example, polar cod. Although of poorer quality energetically (Gabrielsen et al. 1994; Gabrielsen pers. comm.), these amhipods are more widely spread, probably more accessible, and thus taken in preference to solitary fish hiding in the ice or on the sea bottom. However, because guillemots chicks are fed food items brought to them singly, the adults probably seek out the larger fish to make the transport into the colony energetically worthwhile. This would explain the high proportion of polar cod in the diet of chicks at Kovalskifjellet compared to the crustacean-rich diet of the adults collected offshore in 1992.

Despite the differences in chick and adult diets, geographical variation in the species of fish caught is apparent from our data and those found in the literature. Polar cod is an important prey in Svalbard, Franz Josef Land and Novaja Zemlja but not along the coasts of Norway and the Kola Peninsula where capelin, sand eel and herring dominate. The restriction of polar cod to the colder northern and eastern localities stems from the relatively limited distribution of the species' spawning grounds. The main spawning ground in the southeast corner of the Barents Sea, between Kolguyev and Novaja Zemlja, and a smaller one is located east of Spitsbergen (Gjøsæter et al. 1994). Adult polar cod are spread over much of the Barents Sea during the summer and are thus taken in very small proportions by guillemots on Bjørnøya where there are otherwise more accessible stocks of capelin. The main bulk of the polar cod population avoids the southwestern areas which is influenced by the inflow of warm Atlantic water (Gjøsæter et al. 1994). Other fish recorded in the literature and in our studies in the high arctic waters included benthic species of blennies (Lumpenidae or Stichaeidae), sculpins and eelpouts (Zoarcidae). The absence of these species in the more southern samples probably reflects the more northerly distribution of some of the species, e.g. *Lumpenus* sp., as much as the relative shallowness of the water (enabling the guillemots to reach the benthic species) in the northern areas where guillemots were sampled. The occurrence of the squid *Gonatus fabricii* in the diets of guillemots on Bjørnøya and Bleiksøy reflects the proximity of these colonies to the main flow of Atlantic water in the Norwegian and Barents seas with which this species is often associated (Wiborg 1979).

Ecosystem effects

Of the ca. 1.6 million pairs of Brünnich's guillemots which bred in the Barents Sea in 1986, ca. 405,000 pairs bred on the southeastern coasts of Svalbard (excluding Bjørnøya) and 1 million pairs on Novaja Zemlja. Furthermore, 245,000 of the total of 266,000 pairs of common guillemots bred on Bjørnøya together with ca. 100,000 pairs of Brünnich's guillemot (Mehlum & Gabrielsen 1995). In other words, ca. 25% of the guillemot food consumption during the breeding season in the Barents Sea in the mid 1980s took place around Svalbard, ca. 50% near Novaja Zemlja, ca. 20% around Bjørnøya and ca. 5% along the coast of North Norway and the Kola Peninsula.

The annual food requirements of both guillemot species in the Barents Sea is approximately 70% of the total seabird requirements: i.e., 70% × 3500 TJ (1 TJ = 10^{12} Joules) = 2450 TJ (Sakshaug et al. 1994; Mehlum & Gabrielsen 1995). If all the guillemots preyed on one or two fish species only, for example, capelin or polar cod, their annual harvest would have had a significant impact on these single prey populations, especially in years when the fish stocks were at a minimum. For example, when the capelin stocks plummeted to <0.5 million tonnes in 1986/87, their annual production was in the order of 1–2000 TJ only (Sakshaug et al. 1994). The same would have applied to the polar cod when stocks were at a minimum in e.g. the early 1970s and early 1980s (Gjøsæter 1995). However, this paper has shown that the guillemot diet constitutes many species and varies considerably both spatially (Svalbard; mainly crustaceans, Novaja Zemlja; polar and Atlantic cod, Bjørnøya; euphausiids, capelin and periodically squid, Norway and the Kola Peninsula; capelin, sand eels, herring and Atlantic cod) and temporally. Guillemots also take prey items from the lower trophic levels where annual production is an order of magnitude higher (Sakshaug et al. 1994). As a result, the overall impact of the guillemot population on the Barents Sea ecosystem is very slight compared to the annual production at the different trophic levels and of the different fish populations (Sakshaug et al. 1994). Furthermore, estimates of the annual food requirements of the top predators in the Barents Sea (Atlantic cod, seals, whales and seabirds) by Sakshaug et al. (1994) show that the total seabird harvest is equivalent to only ca. 7% of the total food requirements of higher predators in the Barents Sea, or to ca. 25% of the average annual capelin fishery outtake in the early 1980s (Sakshaug et al. 1994). On the other hand, the impact of the ecosystem on the guillemots can be great. This was illustrated in 1986/87 when the collapse in the capelin stocks resulted in huge declines in the breeding populations of common guillemots on Bjørnøya, in Finnmark, and on the Kola Peninsula (Vader et al. 1990; Krasnov & Barrett 1995).

More dietary data are needed before a full assessment can be made and a prey-consumption model for these species in the Barents Sea can be developed. This applies especially to the region around Novaja Zemlja where huge numbers of guillemots breed but where their diet is poorly documented. Further comparisons of chick and adult diets should also be made in the various regions to test if the documentation of chick diet (which involves a non-destructive method) can also be used to monitor adult food consumption during the breeding season. Finally, most data have, up to now, been collected during the summer and very little is known about the diet of guillemots at other times of the year. There is a need for systematic collection of birds from different parts of the Barents Sea and at different times of the year, especially from areas where large numbers are known to spend at least part of the autumn and winter (Fauchald & Erikstad 1995; Krasnov unpubl.).

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