

Capelin (*Mallotus villosus*) as an important food source for northern fulmars (*Fulmarus glacialis*) breeding at Bjørnøya (Bear Island), Barents Sea

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The food and feeding ecology of northern fulmars *Fulmarus glacialis* was investigated in July 1999 at Bjørnøya (Bear Island). Fulmars relied almost exclusively on fish during the brooding period. The main fish prey was capelin *Mallotus villosus* (87.0% by reconstituted mass), Atlantic cod *Gadus morhua* accounting for most of the remainder (9.7% by reconstituted mass). The estimated total length of capelin and Atlantic cod eaten averaged 15 and 17 cm, respectively. Adult fulmars performed short foraging trips averaging 8 hours when brooding chicks, and they foraged at a mean maximum distance of about 60 km, the birds being concentrated on the shelf surrounding the island. The study emphasizes the importance of capelin as a key link between zooplankton and top predators, including seabirds, in the pelagic ecosystem of the Barents Sea.

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Introduction

The seabird community in the Barents Sea is dominated by auks and includes only one procellariiform, the northern fulmar *Fulmarus glacialis* (Mehlum and Gabrielsen, 1995). The total breeding population of fulmars was recently estimated as 27 100 pairs (Mehlum and Gabrielsen, 1995), including about 15 000 pairs nesting at Bjørnøya (Bear Island). Bjørnøya is a remote island in the western margin of the Barents Sea and is located mid-way between northern Norway and southern Spitsbergen. Overall, the population of northern fulmars breeding there is poorly known, and little information is available on their food and feeding ecology (Duffey and Sergeant, 1950; Camphuysen and van Franeker, 1997).

The Barents Sea covers 1.4 million km² and is a high-latitude, shallow shelf area (Sakshaug *et al.*, 1994).

It is one of the most productive waters in the world and has large stocks of commercially important fish species such as Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*) and capelin (*Mallotus villosus*) (Bergstad *et al.*, 1987; Sakshaug *et al.*, 1994; Gjøsaeter, 1995; Krasnov and Barrett, 1995). Of special importance in the diets of seabirds are capelin, polar cod (*Boreogadus saida*) and, to a lesser extent, herring and sandeels (*Ammodytes* sp.) together with some crustacean species (Krasnov and Barrett, 1995; Barrett and Krasnov, 1996). The combined effects of environmental conditions and overfishing have led to dramatic fluctuations in pelagic fish stocks (Bergstad *et al.*, 1987; Sakshaug *et al.*, 1994; Gjøsaeter, 1995, 1998). These changes have, in turn, induced large decreases in some seabird populations (Krasnov and Barrett, 1995), with no information available for northern fulmars. For example, the collapse of

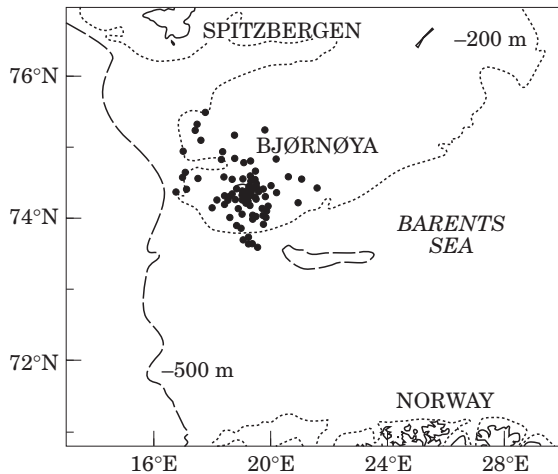


Figure 1. Distribution of satellite fixes of four northern fulmars during the brooding period in July 1999 at Bjørnøya, Barents Sea.

the capelin stock in the mid-1980s (Gjøsaeter, 1995, 1998) led to mass mortalities of common guillemots (*Uria aalge*) — an obligate capelin eater — at Bjørnøya (Vader et al., 1990).

The aim was to investigate the food and feeding ecology of the northern fulmar at Bjørnøya where more than half of the population of the Barents Sea breed. Prey identification allowed the determination of the trophic level at which fulmars forage in the pelagic ecosystem of the Barents Sea, and electronic devices attached to a few individuals provided preliminary information on the duration of feeding trips and the location of the foraging areas of a poorly studied seabird at Bjørnøya.

Materials and methods

The field study was carried out at Kapp Heer (74°22'N 19°10'E), Bjørnøya (Bear Island) (Figure 1). Fifty-eight regurgitations were collected from adults with small chicks between 9 and 24 July 1999. The brooding period was chosen because it is a period of high energy requirement for seabirds, both parents alternating in foraging at sea and in brooding their single chick (Ricklefs, 1983; Tveraa et al., 1998). Each bird was inverted over a plastic bag and its belly massaged in order to induce it to regurgitate food. Eleven additional samples came from unattended chicks (about 2–3 weeks old) at the end of the study period. Although samples provided reasonably unbiased data on recently-ingested prey, they were probably not the full contents of the proventriculus.

Food samples were frozen and stored at -20°C until analysis in France following the method described in Chérel and Ridoux (1992). Briefly, broad prey classes (fish, crustaceans and others) were weighed separately

and the number of all identifiable food items was noted. Due to the highly digested state of the samples, prey species were identified to the lowest possible taxonomic level using remaining hard parts (otoliths, vertebrae, caudal skeletons and jaw bones of fish, exoskeletons of crustaceans, and squid beaks) and standard guides (Clarke, 1986; Härkönen, 1986; Schneppenheim and Weigmann-Haass, 1986; Watt et al., 1997; Baker et al., 1990) and comparative reference material. Fish otoliths and euphausiid (krill) eyes were measured and converted to body length and fresh mass using allometric equations (Clarke, 1986; Härkönen, 1986; Dalpadado and Skjoldal, 1991; Lidster et al., 1994). The contribution by mass (reconstituted mass) of a prey taxon in a sample was then given by the number of individuals and the mean body mass of this taxon in the sample (Ridoux, 1994). Accumulated items (cephalopod beaks and polychaete jaws without flesh attached which accumulated in the birds' stomachs over time) were analyzed separately from the fresh items; they were not taken into account in the calculation of the reconstituted mass of the diet in order to avoid over-estimation of the importance of prey with slowly digestible hard parts.

Duration of foraging trips of adult fulmars was determined using a Pit Tag ID Logging System (Francis Scientific Instruments, Cambridge, UK). Each bird was fitted with a radio frequency transponder (Pit Tag, mass 0.35 g), which was taped on a plastic leg ring. The presence/absence of the birds carrying Pit Tags at their nest was then automatically recorded through the use of an annular antenna that circled the nest and which was connected to a data logger. Sixteen adult brooding birds (eight pairs) were monitored continuously between 16 and 24 July 1999. Four other adult birds were fitted with satellite transmitters (PTT 100, Microwave Telemetry Inc., Columbia, MD, USA). Tags (20–30 g) were attached directly to the back feathers using "Loctite 401" and a cable tie. Data were analysed using both ELSA (CLS Argos, Toulouse, France) and home-made software. Satellite locations in the present study corresponded to the tracking of birds during the period 16–24 July 1999 (see Weimerskirch et al., 2001, for more detailed information).

All values in the results section are means \pm s.d.

Results

The mass of food samples averaged 55.5 ± 27.1 g (range = 12.3–139.8 g). They included a few accumulated items (polychaete jaws and squid beaks), and mainly fresh material (54.7 ± 26.4 g). Stomach oil (food-derived oil held in the proventriculus of most procellariiform species) was found in 20 (34.5%) of the samples only. Fish occurred in all the 58 regurgitations and accounted for 98.5% of the diet by fresh mass. Crustaceans and

Table 1. Prey species found in 58 samples of regurgitated stomach contents of adult northern fulmars collected at Bjørnøya during the brooding period (9–24 July 1999).

Species	Occurrence		Number		Reconstituted mass	
	n	%	n	%	g	%
Fish						
Osmeridae						
<i>Mallotus villosus</i>	55	94.8	209	49.6	2 892.0	87.0
Paralepididae						
<i>Arctozenus risso</i>	1	1.7	1	0.2	29.2	0.9
Gadidae						
<i>Gadus morhua</i>	4	6.9	6	1.4	323.2	9.7
<i>Boreogadus saida</i>	1	1.7	1	0.2	3.1	<0.1
<i>Melanogrammus aeglefinus</i>	1	1.7	1	0.2	30.1	0.9
Unidentified fish	2	3.4	2	0.5	27.7	0.8
Crustaceans						
Euphausiacea						
<i>Thysanoessa inermis</i>	4	6.9	199	47.3	18.0	0.5
Natantia						
Natantia sp.	1	1.7	1	0.2	<0.1	<0.1
Copepoda						
Parasitic copepoda	1	1.7	1	0.2	<0.1	<0.1
(Secondary prey) ^a	(19)	(32.8)	(149)	—	—	—
Polychaetes						
(<i>Neanthes irrorata</i>) ^b	(3)	(5.2)	(4)	—	—	—
Cephalopods						
(<i>Gonatus fabricii</i>) ^b	(7)	(12.1)	(9)	—	—	—
Total	—	—	421	100.0	3 323.3	100.0

^aIncluding euphausiids, the amphipods *Themisto libellula* and *T. abyssorum*, and larval stages of crustaceans.

^bAccumulated items (polychaete jaws and squid beaks) only.

other items were minor components of the food, occurring in 8.6% (n=5) and 1.7% (n=1) of the samples, and accounting for 0.9% and 0.6% of the diet by fresh mass, respectively.

By number, the diet was dominated by capelin (49.6% of the total number of prey) and the krill *Thysanoessa inermis* (47.3%). However, capelin was found in most of the samples (94.8%) and, owing to its much larger size and weight than *T. inermis*, it was the dominant food source by reconstituted mass (87.0%), krill being negligible (0.5%) (Table 1). The only other significant food source was the Atlantic cod which occurred in four samples (6.9%) and accounted for 1.4% and 9.7% of the diet by number and reconstituted mass, respectively (Table 1). Other crustaceans including krill, amphipods and various larval stages were also identified, some of them being clearly associated with fish stomachs. They were fish prey secondarily ingested by the fulmars, and were not consequently furthermore considered in the present work. Finally, a few accumulated items also occurred in the stomach contents, jaws of the nereid polychaete (*Neanthes irrorata*) and eroded beaks of the gonatid squid (*Gonatus fabricii*). Most beaks were worn, thus precluding any measurements of all but the largest beak, whose lower rostral length (5.5 mm) indicated an

estimated mantle length and body mass of 194 mm and 154 g, respectively.

The average otolith length (OL) of capelin was 2.5 ± 0.2 mm (n=46, range=1.9–2.9 mm), giving a mean estimated total length and body mass amounting to 150 ± 15 mm (range=111–181 mm) and 13.8 ± 3.2 g (range=6.4–21.4 g), respectively. OL of the Atlantic cod averaged 7.5 ± 0.7 mm (n=3), individuals having an estimated mean fork length and mass of 167 ± 20 mm and 53.9 ± 22.3 g, respectively. The specimens of Arctic cod and haddock had a 3.0 and 8.1 mm OL, 80 and 157 mm fork length, and 3.1 and 30.1 g body mass, respectively. Eye diameter of the krill *T. inermis* was 2.9 ± 0.2 mm (n=11), indicating specimens of 22.9 ± 1.6 mm total length and weighing on average 90 ± 22 mg.

Oil, sometimes in large amounts (10–49 ml), was found in all but one chick regurgitation. Fish, mainly capelin and a few unidentified species occurred in the 11 samples.

When brooding chicks, adult birds were at sea for periods averaging 8.0 ± 4.5 h (range=0.2–20.3 h, n=146, all the data from the 16 birds pooled). Satellite tracking of four fulmars indicated short foraging trips in the vicinity of the island (Figure 1). Trips lasted on

average 10.2 ± 4.0 h (range=4.4–15.3 h, $n=16$) with a mean maximum foraging distance from the nest amounting to 61 ± 49 km (range=17–151 km).

Discussion

Northern fulmars from Bjørnøya ate mainly fish in July 1999. Fish was found in every sample and accounted for 99% of the fresh mass. Earlier studies at Bjørnøya had found that unidentified fish occurred in 35% of stomach contents (Duffey and Sergeant, 1950), or that fish occurred in 77–91% of the samples (Camphuysen and van Franeker, 1997). Fish (including offal) formed a major part of the diet in the United Kingdom (Furness and Todd, 1984; Fowler and Dye, 1987; Hamer et al., 1997), Iceland (Phillips et al., 1999), Greenland (Phillips et al., 1999), the Barents Sea (Erikstad, 1990; Weslawski et al., 1994) and the North Pacific (Bradstreet and Cross, 1982). The fish species varied from place to place. At ice-edges, polar cod was the major fish prey (Bradstreet and Cross, 1982; Mehlum and Gabrielsen, 1993; Weslawski et al., 1994), whilst the most common fish at high latitudes was the capelin (Camphuysen and van Franeker, 1997; Phillips et al., 1999). Our data fit well with this picture, but no other study has shown fulmars relying so heavily on only one prey species, capelin accounting for 87% by reconstituted mass of the diet at Bjørnøya in July 1999.

The size of fish prey eaten by fulmars was detailed in only a few dietary investigations. In Scotland, fulmars feed on sandeel *Ammodytes marinus* with a modal length of 72–94 mm (Fowler and Dye, 1987). In the Barents Sea in winter, they prey on fish with a median total length of 51 mm, including redfish (*Sebastes* spp.) (49 mm), Atlantic cod (58 mm) and polar cod (95 mm) (Erikstad, 1990). At Bjørnøya, they fed on larger fish, mainly capelin (150 mm) and, to a lesser extent, juvenile Atlantic cod (167 mm). Large capelin (120–160 mm) were also eaten by other capelin-eaters in northern Norway: herring gulls (*Larus argentatus*), kittiwakes (*Rissa tridactyla*) and guillemots (*Uria* spp.) (Furness and Barrett, 1985; Barrett and Furness, 1990).

Fulmars are well-known ship followers, and their dietary interactions with commercial fisheries have been recently critically evaluated (Camphuysen and Garthe, 1997; Phillips et al., 1999). The only common demersal species of fish occurring in the samples from Bjørnøya was Atlantic cod. There was an Atlantic cod fishery in the Barents Sea in July 1999, but it targeted larger fish than those eaten by the birds. In Scotland, juvenile gadids of various species are major prey for fulmars (Furness and Todd, 1984; Hamer et al., 1997). Some of them were presumably discarded from fishing vessels, but small juveniles could have been caught by the fulmars themselves (Phillips et al., 1999). No discarded

fish or offal were found in our samples, suggesting that fulmars were not dependent on fishery waste in July 1999. Natural prey also formed the bulk of the food at other high-latitude localities in summer (Phillips et al., 1999), although Erikstad (1990) suggested that discarded redfish may be an important item in the Barents Sea during the winter months.

Fulmars have a catholic diet, including not only fish but also zooplankton, squid and carrion (Cramp, 1977; Phillips et al., 1999). No carrion was found in food samples from Bjørnøya. Crustaceans were numerically important but were minor prey by mass, with only one main species involved, the krill *Thysanoessa inermis*. Krill is also a small part of the diet in Iceland (Phillips et al., 1999), but is the dominant prey at west Spitsbergen (Hartley and Fisher, 1936). In the Barents Sea, *T. inermis* is a major component of the macrozooplankton community (Dalpadado and Skjoldal, 1991; Sakshaug et al., 1994). Size (about 23 mm) indicates fulmars fed on adult krill, which is also a main target for seabirds from the Svalbard archipelago (Mehlum and Gabrielsen, 1993). Squid beaks and polychaete jaws are common accumulated items in fulmar stomachs (Hills and Fiscus, 1988; Bourne, 1997; Phillips et al., 1999). Jaws of *Neanthes* (= *Nereis*) *irrorata* were previously found from birds collected in the Barents Sea (Lydersen et al., 1989; Mehlum and Gabrielsen, 1993; Camphuysen and van Franeker, 1997), and squid beaks identified in the present study were all from *Gonatus fabricii*, a common squid in the area (Nesis, 1987; Dalpadado et al., 1998).

Short foraging ranges of fulmars during the brooding period were previously deduced from direct observations of nest attendance or the pattern of food provisioning (Furness and Todd, 1984; Hamer et al., 1997). However, direct evidence of the foraging range and feeding areas were lacking. Our data from satellite-tracked individuals showed that fulmars foraged in the waters surrounding Bjørnøya during the brooding period in July 1999 (Figure 1). This is in agreement with foraging trips of short duration (about 8 h) shown by parent birds fitted with Pit Tags. The scarcity of oil in food samples is also an indication of trips of short duration, because stomach oil in procellariiforms is associated with long foraging trips only (Weimerskirch and Cherel, 1998; Weimerskirch et al., 1999).

All the four tagged birds remained over the continental shelf, within the 200 m depth contour. Feeding in neritic waters was also indicated by the biogeography of the prey. Only one food sample contained an oceanic fish species, the paraplepidid *Arctozenus risso* (= *Notolepis rissoi*). *A. risso* is restricted to the warm Atlantic waters where it is a major component of the micronekton (Dalpadado et al., 1998). Feeding on *A. risso* therefore suggests that one individual fulmar may have foraged in oceanic waters west of Bjørnøya. All the other food

samples contained fish species which are known to be abundant on the shelf, with capelin and Arctic cod being major fish components of the pelagic ecosystem of the Barents Sea in open waters and ice-covered areas, respectively (Sakshaug *et al.*, 1994; Gjøsaeter, 1995). Thus, both satellite tracking and dietary analysis indicates that fulmars from Bjørnøya foraged almost exclusively over the continental shelf during the brooding period. They caught capelin at or near the surface, since two birds equipped with maximum depth gauges (Burger and Wilson, 1988) reached depths of 4.0 and 4.7 m during the study period (unpublished data). Such diving depths were higher than that (3.0 m) previously recorded experimentally on fulmars feeding on Arctic cod (Hobson and Welch, 1992).

The present work emphasizes the importance of capelin in the pelagic ecosystem of the southern and mid Barents Sea by adding a new species of seabird to the community of air-breathing vertebrates that prey on capelin. Among seabirds, capelin is a key food component for kittiwakes, gulls (*Larus argentatus*, *L. marinus* and *L. hyperboreus*), fulmars, puffins (*Fratercula arctica*), guillemots, and cormorants (*Phalacrocorax carbo*) (Furness and Barrett, 1985; Barrett *et al.*, 1990; Barrett and Krasnov, 1996; Barrett *et al.*, 1997; present study). Non-capelin eaters are restricted to dovekies (*Alle alle*) and shags (*P. aristotelis*) that feed upon crustaceans, and sandeels and young gadoids, respectively (Furness and Barrett, 1985; Barrett *et al.*, 1990; Weslawski *et al.*, 1999).

The apparent importance of capelin for fulmars during the critically important chick-rearing period is of particular interest in view of the large fluctuations of the capelin stock (Jangaard, 1974; Sakshaug *et al.*, 1994; Gjøsaeter, 1995, 1998; Barrett and Krasnov, 1996). Oceanographic surveys indicated that 1999 was a "medium" year, with the total capelin stock estimated to amount to 2.78 million tonnes in the Barents Sea, thus contrasting with lower stocks (0.10–0.91 million tonnes) in the periods 1985–1989 and 1993–1997 (Anonymous, 1999). Fulmars are surface feeders and are more vulnerable to food shortage than are underwater pursuit divers (Baird, 1990; Monaghan, 1996; Regehr and Rodway, 1999). They are thus potentially at risk to suffer high chick mortality in periods of low capelin stock. On the other hand, fulmars are capable of shifts in their diet in response to altering prey availability. For example, birds breeding in western Greenland feed mainly on capelin when the fish start to spawn, but they prey upon crustaceans before and after the fish reproductive season (Phillips *et al.*, 1999). In the same way, the breeding success of Shetland birds decreases by only 30% in years of drastically reduced sandeel abundance (Furness and Tasker, 2000), suggesting they may be able to compensate for decreased availability of their main prey. In the Barents Sea, fulmars fed on polar cod, Atlantic cod,

redfish and squid during the winter months following a crash in the capelin stock. However, no dietary data from a "normal" year were available for comparison (Erikstad, 1990), and more information is needed to investigate short- and long-term consequences of changes in capelin availability on the populations of fulmars in the Barents Sea.

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