Recent responses to changes in stocks of prey species by seabirds breeding in the southern Barents Sea

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Seabirds breeding in the southern Barents Sea feed mainly on pelagic fishes – capelin *Mallotus villosus*, herring *Clupea harengus*, sand eels *Ammodytes* sp., and polar cod *Boreogadus saida*. This study shows how seabirds breeding in two colonies, one in northern Norway and one off the Kola Peninsula, Russia have responded to the recent huge changes in the capelin and herring stocks through changes in chick diet and breeding success. It seems that after recent collapses in the capelin stocks, the surface-feeding kittiwakes *Rissa tridactyla* are now having difficulty in finding enough food to maintain high breeding success and a positive population trend. While the pursuit diving common guillemots *Uria aalge* and puffins *Fratercula arctica* are faring better, there are signs that they too are having more difficulty in finding sufficient food despite the return of I-group herring to their foraging areas.

Key words: kittiwakes, puffins, guillemots, diet, trophic relationships.

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Introduction

The Barents Sea is one of the most productive seas in the world and a feeding ground for huge stocks of several commercial fish species and millions of seabirds (Loeng, 1989; Sakshaug *et al.*, 1994). Along the south coast are also some of the largest breeding colonies of seabirds in the North Atlantic (Norderhaug *et al.*, 1977).

Early studies in these colonies (Bepol'skii, 1957; Uspenskii, 1958; Norderhaug *et al.*, 1977) showed that these large seabird populations fed on relatively few fish species, the main ones being capelin *Mallotus villosus*, herring *Clupea harengus*, sand eels *Ammodytes* sp., and polar cod *Boreogadus saida*. In the early 1980s, capelin and sand eels were again the key species for seabirds breeding in East Finnmark (Furness and Barrett, 1985; Barrett and Furness, 1990).

The numbers of seabirds breeding along the southern coast of the Barents Sea have changed dramatically over the last 40 years. Large increases in numbers of several species were associated with a recovery from an excess harvest of eggs and adults in the first half of the century. A sudden collapse in the guillemot *Uria* spp. numbers in 1986/87 was probably due to a collapse in the capelin stocks in the same period (Vader *et al.*, 1990; Krasnov and Barrett, 1995). Similarly, a decline in the Brünnichs

guillemot *U. lomvia* population off the Kola Peninsula in the late 1970s was partly associated with a concurrent collapse in the polar cod stocks. Although capelin was a preferred prey, the only negative effect on seabird numbers registered in the region during the decline in the capelin stocks from 8.7 million tonnes in 1975 to 2.8 million tonnes in 1984 (Anon., 1995) was a temporary 50% drop in the number of kittiwakes *Rissa tridactyla* breeding on Kharlov between 1976 and 1977 (Krasnov and Barrett, 1995). Only in 1987, by which time capelin stocks collapsed to 100 000 tonnes (Fig. 1) were there clear signs of declines and breeding failures (Vader *et al.*, 1987, 1990). Since 1975, numbers of kittiwakes have actually increased on colonies off the Kola Peninsula. Kittiwakes and puffins *Fratercula arctica* have also increased in eastern Finnmark although the numbers of kittiwakes started to decrease again in the 1980s. Numbers of common guillemots *U. aalge* and Brünnich's guillemots have also increased in the region both before and after the sudden decline in 1986–1987 despite the second collapse in the capelin stock in 1991–1994 (Krasnov and Barrett, 1995).

This apparent lack of response illustrates how seabird populations, however easy they may be to census, are poor monitors of environmental changes due to the buffering effect of their low turnover rate through
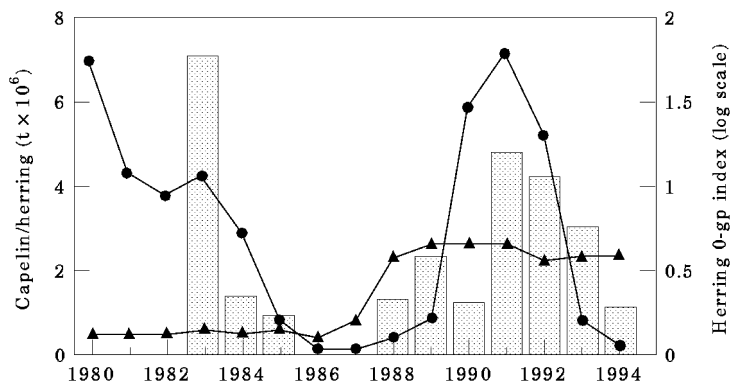
Figure 1. Estimated stock sizes of capelin and Atlanto-Scandic herring, and abundance indices for 0-group herring in the Barents Sea. (Source: Anon, 1995) ● =Capelin; ▲ =herring; bars represent 0-group index.

delayed maturity and low fecundity (reviewed in Montevecchi, 1993). Despite the large declines in primary prey fish stocks, no major negative tendencies were recorded in seabird numbers until the fish stocks were at an absolute minimum.

However, other parameters such as behavioural and reproductive responses have been recognised as giving much more useful information concerning the environment (Cairns, 1987; Baird, 1990; Montevecchi, 1993). Such parameters include the choice of food given to chicks, chick growth rate and reproductive success, all of which have the potential to respond more rapidly to changes in food availability (Cairns, 1987). Furthermore, they have been documented as good indicators and supplements to the traditional acoustic and trawl assessments of the state of some commercially important fish stocks, including the prediction of recruitment rates to these stocks (Barrett, 1991; Cairns, 1992; Montevecchi, 1993).

The Barents Sea capelin spawn along the coast of North Norway and Murmansk, with a more westerly spawning during cold-water years, in March–April. Some may spawn as late as June–July. The larvae drift north-eastwards and the maturing fish feed in the north of the Barents Sea. Although most of the Barents Sea capelin spawn in the early spring, there are nearly always some late (summer) spawners along the coast of Finnmark and Murmansk available to breeding seabirds. Capelin seldom grow longer than 15–20 cm in length, most mature at 12–15 cm, and most die after spawning (Jangaard, 1974; Winters, 1982; Forberg and Tjelmeland, 1984). Capelin are thus potential prey for seabirds throughout their life-cycle.

Herring, on the other hand, grow much larger than capelin and, due to a much greater height/length ratio, II-group fish (>15 cm long) are already much larger than those preferred as prey by auks and kittiwakes (Swennen and Duiven, 1977; Toresen,

1990). The Atlanto-Scandic herring spawn in southwestern Norway in February–April and after hatching ca. 2–3 weeks later, the larvae rise into the upper water layers (0–50 m) and are transported northwards, mainly in the Norwegian coastal current. The autumn distribution of the 0-group fish is widespread from the fjords of North Norway to offshore waters in the Norwegian and Barents Seas (Dragesund et al., 1980; Loeng, 1989). The following summer, the I-group fish in the Barents Sea move southwards and mix with those that have moved northwards from their wintering grounds in the fjords, forming open-sea concentrations in the south-western part of the Barents Sea (Dragesund et al., 1980). These I-group fish are periodically important prey for seabirds breeding in the region (Belopol'skii, 1957; Norderhaug et al., 1977, pers. obs.).

Despite the near complete collapse of the capelin stocks in the Barents Sea in 1986/87, Barrett and Furness (1990) failed to document a decrease in capelin levels in seabird diet or an increase in food partitioning on a colony in the region two years later. On the contrary, despite the still very low capelin stock, they found an increase in the amount of capelin fed to chicks in 1989 compared to a similar study in 1983. In other words, the chick diets did not reflect the availability of capelin which was apparent from the acoustic surveys. Their study was, however, limited only to a single colony and season. The present study encompasses a much larger set of dietary data gathered annually from kittiwakes, puffins and common guillemots since 1980 on the same colony. Hornoya (70°22′N, 31°10′E) in East Finnmark and on Kharlov (68°49′N, 37°20′E) off the Kola Peninsula (Fig. 2). It also encompasses a period during which large fluctuations in stocks of two of the major prey species, capelin and herring, have been documented (Fig. 1).
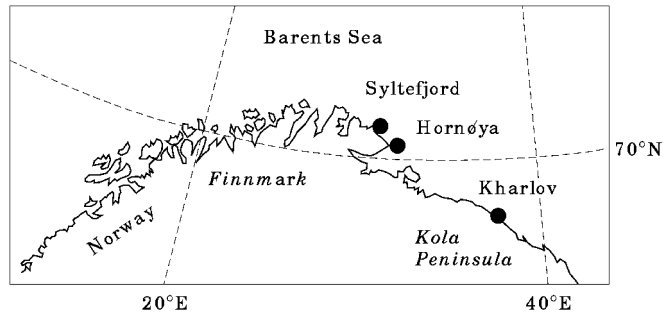
Figure 2. Map showing colonies and localities mentioned in the text.

Methods

Fish stock data were taken from the resource data published annually by the Norwegian Marine Research Institute, Bergen and the ICES Atlanto-Scandic herring and capelin working group (Anon., 1994, 1995). Capelin data are based on annual Norwegian–Russian acoustic surveys made in the Barents Sea in September–October. Because there is no relationship between herring stock size and that of the earliest cohorts due to an extreme variability in survival of the earliest life-stages (Dragesund *et al.*, 1980), an index of 0-group abundance was used as an indirect measure of the abundance of herring prey (I-group) for seabirds the following year. Estimates of such an index have been made annually from trawl surveys in the Barents Sea in August–September (Anon., 1995).

Seabird responses to changes in prey stocks were studied through changes in seabird diet and kittiwake breeding success. On Hornøya and Kharlov, kittiwake diet was sampled throughout the study period by collecting chick or adult regurgitations. Puffin food was collected on Hornøya in 1980–1983 by the retrieval of items carried by adults caught in mist nets while guillemot samples consisted mainly of fish collected on the breeding ledges. In 1985–1994, most puffin and guillemot data were collected by direct observation of food items carried by birds in the colony using 10×40 binoculars. Some additional samples were collected from adults caught using noose-poles. Supplementary to the Hornøya data were samples collected at Syltefjord, a large colony ca. 40 km to the west (70°35′N, 30°18′E) (Fig. 2).

The proportions of guillemot prey species were calculated numerically. For kittiwakes and puffins on Hornøya, the proportions were calculated by mass. For puffins (after 1985) these were based on an integration of the mass of the main prey items collected in the field into the direct observation samples. The degree of dietary overlap between species and between colonies was calculated using Horn's (1966) modification of Morista's (1959) index (see Diamond, 1983). This index is a

relative measure and varies between 0 (no overlap) and 1 (total overlap). The proportions of prey items in the diet of each species were correlated with prey stocks using arcsine-transformed diet data.

The total length (snout to end of tail) of the fish collected was measured directly to the nearest 1 mm. Lengths of fish in kittiwake regurgitations were calculated from the lengths of otoliths found. The relationships between otolith length (OL) and fish length (FL) were for capelin FL=25.8+48.0 OL (Barrett and Furness, 1990) and for herring FL=48.46 OL − 8.5 (Jobling and Breiby, 1986).

Two indices of kittiwake breeding success were considered. On Kharlov, annual counts of clutch size (no. eggs/nest) have been made since 1970, while on Hornøya the brood size (no. large chicks/nest) has been estimated annually through counts of chicks in the nests on the day the first chick in the colony was seen flying.

Results

Fish stocks

Since 1980, the capelin stocks have varied greatly (Fig. 1). They dropped steadily from 7 million tonnes in 1980 to 100 000 tonnes in 1987, increased suddenly between 1989 and 1991 to 7 million tonnes only to drop again to 199 000 tonnes in 1994. Within the same period, the herring stocks rose fairly steeply between 1986–1988 and in 1993 had reached 2.3 million tonnes (Fig. 1). As regards 0-group fish, there was a near total lack of recruitment of young herring into the Barents Sea in 1967–1982 but in 1983, a strong year class of 0-group fish was produced for the first time for many years. This resulted in concentrations of young herring over large areas of the Barents Sea in 1984 and 1985 (Loeng, 1989; Gjøsæter *et al.*, 1993). In 1984 and 1985, 0-group classes were also relatively strong but suffered a heavy mortality through predation by cod (Hamre, 1991). Very few 0-group herring were registered in 1986 and 1987 but, after a slight increase in the spawning stock in 1988,

Table 1. Frequency of occurrence (%) of diet items in kittiwake adult and chick regurgitates, Kharlov. n=no. of regurgitates. Note: 1981, 1985, and 1987 are very small samples. Figures in parentheses are comparable data from Hornøya.

Year	n	Clupea	Mallotus	Ammodytes	Crustacea	Other
1979	11	0	54	27	18	0
1980	50 (31)	0 (0)	64 (94)	6 (0)	30 (19)	0 (0)
1981	3	0	0	33	33	33[1]
1982	33	0	52	15	33	0
1983	24	0	38	29	29	4
1984	36	19	8	56	11	6
1985	5	60	0	40	0	0
1986	10	60	10	30	70	10
1987	6	0	0	17	83	0
1988	28 (80)	0 (0)	50 (80)	32 (0)	50 (19)	11 (20)
1989	49 (74)	6 (0)	88 (76)	47 (0)	6 (7)	12 (18)
1990	57 (67)	0 (37)	65 (54)	42 (9)	19 (7)	4 (0)
1991	42	5	36	43	12	5
1992	21 (61)	5 (37)	33 (69)	57 (4)	0 (0)	5 (3)
1993	53 (80)	9 (91)	81 (10)	13 (1)	0 (0)	2 (2)
1994	38 (81)	55 (88)	39 (2)	39 (0)	3 (0)	0 (17)

[1] Pholis gunnellus.

several good year classes of young fish have again been recorded in the Barents Sea (Fig. 1; Gjøsæter et al., 1993; Anon., 1995).

Seabird diet

Kittiwake. Although many birds were caught on Kharlov in 1981, 1985, and 1987, few regurgitated food and only 3–6 samples were collected. These samples are not further considered in the discussion concerning food choice. Although the remaining data from Kharlov is limited to frequency of occurrence (Table 1), it is apparent that capelin, sand eels, and crustaceans (mysids and euphausiids) constituted the main diet of kittiwakes. Herring were present in 1984–1986, 1989, and 1991–1994, and constituted >50% of the samples in 1986 and 1994.

On Hornøya and Syltefjord, capelin was the preferred food (54–93% by mass) of kittiwakes in eight of 10 years between 1980 and 1994 (Fig. 3). Crustaceans (euphausiids) were important (41%) in 1981 only. In 1993 and 1994, kittiwakes ate herring almost exclusively (>90% by mass).

Although direct comparisons of the kittiwake diets can only be made using frequency of occurrence tables, it is evident that herring was absent at both colonies before 1984 and in 1987 and 1988 (Table 1, Fig. 3). Furthermore, the proportions of the regurgitations containing herring were larger on Hornøya in 1990–1994 (Fig. 3). It is also apparent that a greater variety of prey items was taken on Kharlov with relatively larger proportions of the regurgitations containing capelin, sand eels, and crustaceans than on Hornøya (Table 1).

Common guillemot. Herring, capelin and sand eels have been the staple diet of guillemot chicks in the southern Barents Sea since 1980, but the proportions of each species varied greatly from year to year (Fig. 4).

On Hornøya (and Syltefjord in 1985), where samples have been collected in 11 seasons since 1980, capelin constituted >50% and sand eels almost the rest of the common guillemot chick diet in 1980–1983 and in 1989 and 1994. Small amounts of herring were present in 1980, 1985, and 1990–1994, making up 51% and 37% of the diet in 1992 and 1993, respectively (Fig. 4).

Samples of guillemot food have been collected on Kharlov every year since 1985 but the 1989 sample consisted of only seven fish and is not further considered. Sand eels made up >50% of the common guillemot diet in seven years since 1985, and capelin >50% in 1986 and 1991 (Fig. 4). Herring was present in seven years but in small amounts, at a maximum of 14% in 1986.

The degrees of overlap in the prey species taken by common guillemots at the two colonies varied considerably from year to year (0.27–0.99) and there was no temporal consistency in the variation between 1985–1994.

Puffin. Few data were collected systematically on Kharlov. However, incidental observations suggested that sand eels made up 100% of the diet in 1983–1986 and ca. 90% in 1989–1993. On Hornøya, the puffin diet was almost exclusively capelin and sand eels in 1980–1983 (Fig. 3). In 1989–1994, these items were still important but significant proportions of other prey items were also recorded. Gadoids made up 15% and
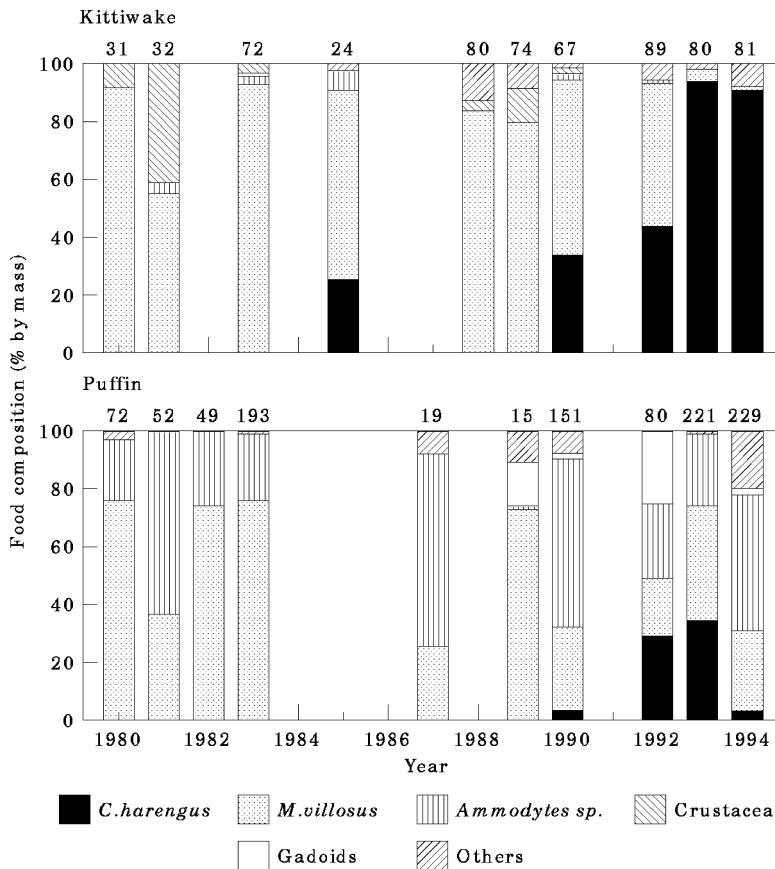
Figure 3. Species composition (% by mass) of food brought to kittiwake and puffin chicks on Hornøya, 1980–1994. Numbers above each column=no. of samples. Kittiwake data from 1985, 1988, and 1989 include samples from Syltefjord.

25% in 1989 and 1992, respectively, and herring made up 29% and 33% in 1992 and 1993, respectively. In 1994, small fry of wolffish *Anarhichas lupus* constituted ca. 16% of the diet (included in others in Fig. 3). The mean numbers of fish per load increased from a mean of 2.5 ± 1.8 (n=159 loads) in 1980–1982 to 5.8 ± 6.2 (n=497 loads) in 1992–1994 (two-sample t-test, t= -10.5, p<0.001). The numbers of prey species also increased in the same period (Fig. 3).

Diet overlap

There was a consistently higher diet overlap between the two auks than between each of the auks and kittiwakes on Hornøya throughout the period (Fig. 5). The overlap between the kittiwakes and auks was more variable than between the two auks with values approaching maximum overlap in 1980, 1983, and 1989, and a distinct minimum in 1994. For all case pairs there was a tendency for a higher variation and general decrease in overlap indices in 1990–1994 than in the preceding years.

Fish size

There was little variation in capelin size caught by all the species between 1980 and 1994, with guillemots and kittiwakes generally catching fish ca. 130–140 mm long. Only in 1981 and 1989 did kittiwakes catch capelin <120 mm $(88 \pm 23$ and 114 ± 40 mm, respectively). In 1987, guillemots caught capelin 106 ± 13 mm. Puffins caught consistently smaller capelin (ca. 90–110 mm).

The herring caught were slightly shorter than the capelin (kittiwakes: 131 ± 20 mm (1993), 115 ± 44 mm (1994); guillemots 128 ± 10 mm (1992), 127 ± 9 mm (1993)). All these are equivalent to I-group herring (Toresen, 1990). In 1992, the puffins caught two size classes of herring with means of 51 ± 4 mm and 115 ± 11 mm. These are equivalent to 0- and I-group fish, respectively (Toresen, 1990).

Responses to prey stocks

Despite the 70-fold variations in capelin stocks and large variations in the capelin content of the various diets
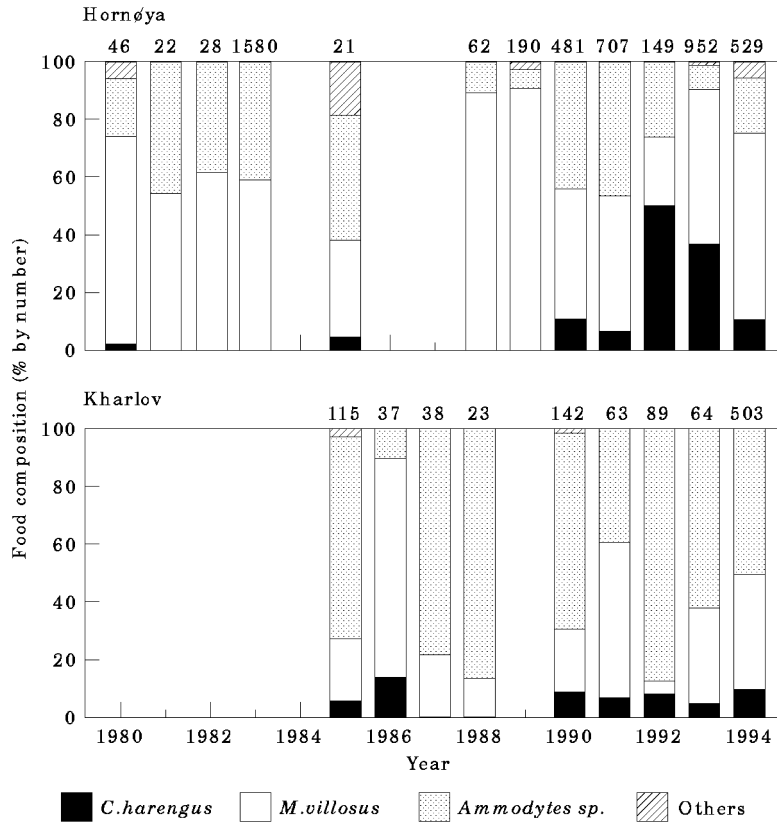
Figure 4. Species composition (% by number) of fish brought to common guillemot chicks on Hornøya (Syltefjord in 1985) and Kharlov, 1980–1994. Numbers above each column=no. of fish sampled.

studied since 1980, there was no correlation between the amount of capelin in the diets of kittiwakes, guillemots, and puffins on Hornøya and Kharlov and the fisheries scientists' estimates of the capelin stock sizes (r=0.04–0.41, df=7–10, p>0.05).

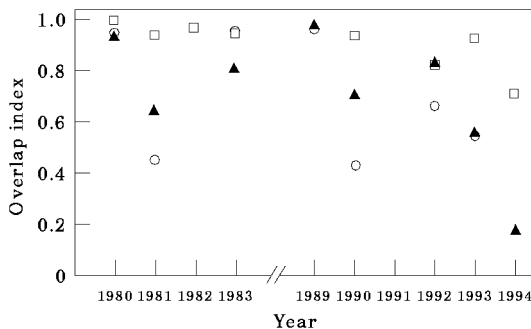

Figure 5. Morisita's indices of dietary overlap between kittiwakes, puffins, and guillemots on Hornøya, 1980–1994. ○=Puffin/kittiwake; □=puffin/guillemot; ▲=kittiwake/guillemot.

Herring first appeared in the diet samples in 1984, the year after the first strong 0-group year class was produced. The herring then disappeared from the diets, only to return in 1990, again a year after a strong 0-group year class was recorded. There were significant correlations between the % herring in the guillemot (r=0.92, df=10, p<0.01), kittiwake (r=0.79, df=8, p<0.01), and puffin (r=0.86, df=8, p<0.01) chick diets and the strength of the 0-group cohort (given as a log index, Anon., 1995) in the previous year (Fig. 6) on Hornøya. No such correlations existed for the kittiwakes (r=0.17, df=10, p>0.05) and guillemots (r=0.39, df=7, p<0.05) on Kharlov.

Although it was not possible to document a dietary response to the huge changes in capelin stocks, effects on other breeding parameters were detected. Along the Murmansk coast, capelin is the only species of shoaling pelagic fish available to kittiwakes as they prepare to breed in March–May (J. V. Krasnov, pers. obs.). As a result, the kittiwakes' body condition and initial clutch size are dependent on the amount of capelin available. For example, in 12 years when little or no capelin was observed along the Murmansk coast early in the
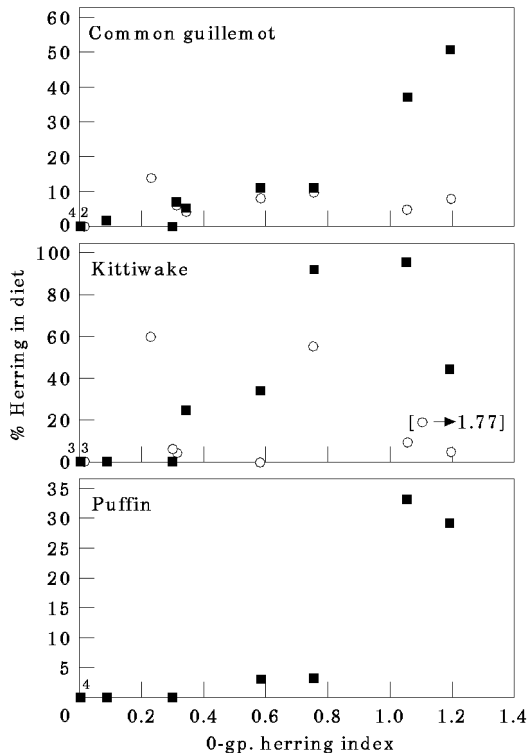
Figure 6. The relationship between the % herring in common guillemot (by number), kittiwake (by number on Hornøya, by frequency of occurrence on Kharlov), and puffin (by mass) chick diet on Hornøya and Kharlov, and the log index of 0-group herring abundance the previous year. Figures at the (0,0) intercept are numbers of points for Hornøya and Kharlov, respectively. ■=Hornøya; ○=Kharlov.

breeding season, the mean clutch size was 1.6 ± 0.2 eggs/nest. In the 12 years when capelin was present, it was 2.0 ± 0.2 eggs/nest. The difference is significant (two-sample t-test, $t=6.8$, $p<0.001$). Later in the summer, herring and sand eels also become available and their levels, plus those of the capelin, contribute to the final fledging success.

Furthermore, effects of the capelin content in the kittiwake diet were also detected. There was, for instance, a significant positive correlation between the brood size of kittiwakes on Hornøya recorded near the end of the fledging period (second half of July) and the % capelin in the chick diet in July (Fig. 7, $r=0.91$, $df=7$, $p<0.01$). Also on Kharlov, breeding success was poor or a total failure (and the food sample sizes were low) in the four years when capelin was absent or nearly so in the kittiwake diet (1981, 1985, 1986, 1987, J. V Krasnov, pers. obs.).

Discussion

The lack of correlation between the capelin content of seabird diets and the capelin stock is undoubtedly due to the huge difference in the spatial scales at which the two parameters were measured. Capelin stocks are estimated at the Barents Sea scale while seabirds forage within a few 10s of kilometres from the colony. Unfortunately, there are no independent estimations of capelin abundance at such a small scale. The lack of correlations are thus probably due to local, small-scale variations in capelin numbers within the foraging range which are independent of total stock size (Furness and Barrett, 1985). It is also possible that there are annual variations in the availability of capelin. Such variations may include changes in the vertical and horizontal distribution of capelin as a result of changes in sea temperature regimes.

Equally unfortunate is the total lack of fisheries estimates of the sand eel stock sizes near the colonies. Local populations do exist (R. T. Barrett, pers. obs.), but their sizes and movements are unknown. Around Kharlov the sand eel beds are distributed between the island and the mainland (Y. V. Krasnov, pers. obs.). The Kharlov stocks are probably larger than those around Hornøya and sustain a periodic local fishery. As a result, sand eels constitute a much larger and more stable part of the guillemot, puffin, and kittiwake diet on Kharlov than on Hornøya, where capelin and herring are more important (Figs 3, 4). The relative abundance of sand eels off the Kola Peninsula compared to off Finnmark is partly corroborated by the results of a minke whale *Balaenoptera acutorostrata* diet survey carried out in July and August 1992 (Haug *et al.*, 1995). Sand eels constituted ca. 30% of the diet (by mass) of 19 whales killed off Kola but <5% of the diet of 20 whales caught off Finnmark.

The herring stocks, on the other hand, are well documented. Not only is the distribution of the earliest life-stages restricted to relatively well-delimited coastal waters (Dragesund *et al.*, 1980), but there are also stock assessments which target the youngest fish (Anon., 1995). This allows a much finer tuning of the detection of any responses by seabirds to changes in herring availability.

The positive correlations between herring content of kittiwake, guillemot, and puffin diet and the strength of the previous year's 0-group cohort on Hornøya but not on Kharlov may be explained by the generally more westerly distribution of the youngest stages of the herring in the southern Barents Sea (Dragesund *et al.*, 1980). Kharlov is thus in a more marginal area where herring can be expected to appear more sporadically and unpredictably than off Hornøya. It is worth noting, however, that there was a relatively high frequency (46%, Kandalaksha Reserve archive) of herring in the diet of guillemot chicks on Kharlov in the late 1930s and herring was also common in the kittiwake diet up to ca. 1970, when it vanished and did not reappear until 1984 (Belopol'skii, 1957; Y. V. Krasnov, pers. obs.). This was
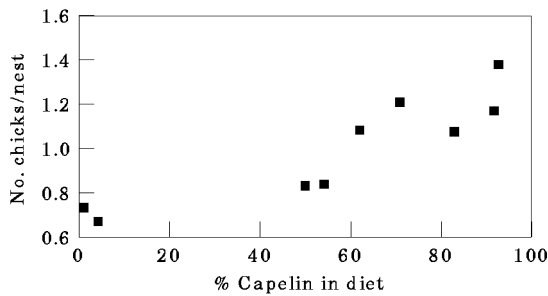
Figure 7. The relationship between the % capelin (by mass) in kittiwake chick diet and the breeding success of kittiwakes (chick/nest) on Hornøya.

a period when herring stocks were high and the youngest cohorts had a more easterly distribution (Dragesund *et al.*, 1980).

The positive correlation between kittiwake brood size and % capelin in chick diet in July (Fig. 7) suggests that kittiwake breeding success depends on the availability of capelin. This was especially evident in 1993 and 1994 when capelin stocks were low (Fig. 1) and capelin made up only 1–4% of the diet (and herring constituted >90%), resulting in two of the lowest breeding successes recorded on Hornøya since 1980 (0.67 and 0.73 chicks/nest, respectively, Erikstad *et al.*, 1995). The fact that capelin made up >50% of the guillemot diet suggests that, although capelin were also present off Hornøya, kittiwakes could catch herring only and in amounts too limited to ensure an otherwise high breeding success.

Furness and Barrett (1985) provided evidence that there was an abundance of capelin and sand eels around Hornøya and that the seabirds there had no difficulty in obtaining food in the early 1980s. This is corroborated in the high dietary overlap indices between kittiwakes, guillemots, and puffins in 1980, 1982, and 1983 (Fig. 5). In 1981, there was a larger segregation between the kittiwakes and the auks. This is also reflected in the mean size of capelin caught by the kittiwakes which, in 1981, was the lowest ever recorded on Hornøya. The 1981 season was further exceptional for kittiwakes in that there was also a 10 d delay in breeding (Barrett, 1983). Since the first collapse in the capelin stocks in 1987, the dietary overlap has been lower than in the early 1980s with the exception of 1989, the very year in which Barrett and Furness (1990) failed to document any negative effect of the stock collapse. Instead, they found either no change or an increase in the capelin content of the diet of five auk species breeding on Hornøya when compared to 1983. Only for the kittiwake was there a slight decrease. This study suggests that 1989 may have been an exceptional year in that there has since been a clearer dietary segregation among kittiwakes, guillemots, and puffins. That kittiwakes failed to find capelin larger than 120 mm in 1989 is

undoubtedly due to the lack of recruitment of mature capelin after the collapse in 1987. This is reflected in the capelin stock assessments which found only 181 000 tonnes of mature capelin in 1989, but over 2 million tonnes in 1990–1992 (Anon., 1995).

In 1993–1994, kittiwakes have fed almost exclusively on herring while the two auks have taken a wider and differing variety of prey. That the segregation between the kittiwakes and each of the auks was consistently higher than between the two auks presumably reflects their different foraging techniques. Kittiwakes are surface feeders and thus excluded from the choice of fish which is available to the auks deeper in the water column. One should note, however, that fish size was not considered in the calculation of the overlap indices and, because puffins took smaller fish than guillemots, the segregation between the two auks was larger than illustrated here.

Optimal foraging entails a maximisation of food intake rates. For multi-prey loaders such as the puffin, it is presumably more efficient to catch few large, good quality prey than many small prey. Assuming that they forage until an optimal prey load mass is reached (Harris and Hislop, 1978) suggests that the number of prey items carried will provide a crude index of prey availability (Montevecchi and Barrett, 1987; Montevecchi, 1993). The increase in the number of puffin prey/load and the diversity of the prey in the early 1990s, plus the decline in the dietary overlap between the three species, suggest a general decline in the feeding conditions around Hornøya.

Furness and Barrett (1985) suggested that, of the three avian species considered here, the kittiwakes were most dependent on capelin as a food source. This is further corroborated in this study with the clear correlation between clutch size and breeding success of kittiwakes on Kharlov and Hornøya and the capelin content of the diet. Krasnov and Barrett (1995) documented a general increase in kittiwake, guillemot, and puffin breeding populations in the southern Barents Sea after 1960, but with a recent decline in several kittiwake colonies since the early 1980s. They hypothesise that this may be due to the birds not only recovering from an earlier over-exploitation of eggs but also taking advantage of a general increase in the capelin stocks in the 1960s–1970s during the absence of the capelin's main competitor and serious predator, the herring (Hamre, 1991; Anon., 1994). The hypothesis that the kittiwakes have benefited from an abundance of capelin is strengthened by the present documentation of delayed breeding, reduced clutch size, and reduced breeding success in the years capelin was less available. It seems that, although herring is potentially a good alternative food and is returning to the Barents Sea, kittiwakes are unable to utilise this new resource to the same degree as the auks, the populations of which are currently increasing (Krasnov

and Barrett, 1995). The situation was similar in two multi-species studies in the British Isles where clupeids were taken more readily by auks than by kittiwakes. On Canna, western Scotland, Swann *et al.* (1991) did not register any clupeids in kittiwake regurgitations while 36% of the diet of common guillemots was made up of sprats (and herring) with a mean mass of ca. 11 g (i.e. I-group). In north-eastern England, Pearson (1968) documented clupeids not only in common guillemots but also kittiwakes, lesser black-backed gulls *L. fuscus*, and terns *Sterna* spp. (all surface feeders). However, while the guillemots fed on "immature" fish (presumably I-group), the gulls and terns took post-larval and juvenile (0-group) fish. It thus seems that kittiwakes can readily access 0-group herring (or, on Hornøya, capelin when it is available), but not I-group fish as easily. This is probably due to differences in the schooling or escape behaviour between the two year classes of herring and between the I-group herring and capelin.

This study is one of several that have demonstrated correlations between diet choice by seabirds and the availability of prey as measured by fisheries scientists. Hislop and Harris (1985) showed a strong positive correlation between the frequency of sprats *Sprattus sprattus* and herring fed to young puffins in Scotland and the sprat biomass and indices of herring larval abundance in the North Sea. Likewise, Montevecchi and Myers (1992) found a clear positive relationship between the harvest of mackerel *Scomber scombrus* by gannets *Sula bassana* and a fisheries estimate of mackerel abundance. Hatch and Sanger (1992) also found a strong correlation between the proportion of walleye pollock *Theragra chalcogramma* in tufted puffin *F. cirrhata* diet on the Aleutian Islands and independent estimates of cohort strength over a three year period.

This study also illustrates how seabird species react differently to changes in food availability according to their feeding strategy (surface feeders vs. pursuit divers) with kittiwakes being the most sensitive of the species studied. Furthermore, it shows how studies of seabirds at a colony near the periphery of a prey's distribution (Kharlov) are more sensitive to changes in prey availability than those at a colony where the prey occurs more regularly (Hornøya). Finally, it supports earlier evidence for the need for a closer collaboration between fisheries biologists and marine ornithologists in an assessment of how seabirds can be used to monitor fish stocks (Cairns, 1992; Montevecchi and Myers, 1995).

Acknowledgements

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