Distribution of Puffins *Fratercula arctica* feeding off Røst, northern Norway, during the breeding season, in relation to chick growth, prey and oceanographical parameters

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In 1988, first-year Herring *Clupea harengus* were the dominant prey fed to Puffin chicks on Hernyken, Røst. Puffins carrying food loads were observed at least 137 km from the colonies in July. In early August, two major feeding areas were located about 20 and 85–105 km off Røst. These long foraging ranges and an insufficient availability of food are thought to be the main reasons for the poor chick growth this year. No relationships were found between the distribution of Puffins observed at sea and survey station data on prey distribution, sea temperature or salinity, but this may have been due to inadequate sampling of these parameters. A recorded seasonal change in flight direction of adults returning to colony is discussed in relation to food quality and chick growth.

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There have been few studies of the distribution of Puffins *Fratercula arctica* feeding around their colonies during the breeding season. Breeding Puffins feed their chicks mainly pelagic schooling fish, the most important being Herring *Clupea harengus*, Capelin *Mallotus villosus*, Sandeel *Ammodytes spp.* and Sprat *Sprattus sprattus* (Harris 1984). Schneider et al. (in press) found Puffins collecting chick food normally within 10 km of a colony in Newfoundland, but occasionally they flew up to 70 km offshore, which has been the maximum foraging range recorded for this species. Furness & Barrett (1985) suggested a short foraging range around Hornøy, NE Norway. Estimations based on flight speed and periods of time spent away on fishing trips have sometimes indicated maximum ranges of more than 100 km for some populations (Pearson 1968; Bradstreet & Brown 1985). However, in most areas Puffins forage relatively close to the colony (Harris 1984; Bradstreet & Brown 1985). Studies of fish net catches and dive times suggest that they normally do not dive below 30 m, and the maximum recorded diving depth of Puffins is less than 70 m (Bradstreet & Brown 1985; Piatt & Nettleship 1985; Burger & Simpson 1986).

Since 1969, Puffins breeding on Røst have experienced a shortage of food for chicks, and in most years virtually all young have died from starvation (Lid 1981; Anker-Nilssen 1987). Their breeding success at this site is strongly dependent on the occurrence of first-year Herring from the Atlanto-Scandian stock (Anker-Nilssen 1987; Barrett et al. 1987). The spawning stock of Atlanto-Scandian Herring collapsed following overfishing in the late 1960s (Jakobsson 1985; Røttingen 1985), and has only recovered slightly in more recent years (Hamre 1988; Anon. 1989).

Puffin numbers on Røst decreased dramatically following these breeding failures, and the population in 1988 was only 36% of that breeding in 1979 (Anker-Nilssen & Røstad unpublished). The availability of food, and especially of 0-group Herring during the breeding season, is thus probably the most important factor currently regulating the size of this population. It is therefore likely that the distribution of Puffins at sea off Røst in summer is primarily determined by the distribution of their most important prey.

Prior to 1988, the Puffins on Røst had only been studied at the colonies. In order to learn more about the feeding ecology of Røst Puffins, we investigated the relationships between Puffin distribution at sea and the distribution and abundance of their prey. We also examined foraging range, food quality and chick growth.

Methods and material

Studies in colony

We studied Puffins during the 1988 breeding season on Hernyken (67°26′N, 11°52′E, Fig. 1). With c. 43,000 occupied nest burrows in 1988, this island is one of the five major Puffin colonies in the Røst archipelago (Anker-Nilssen & Røstad unpublished).

The traffic of Puffins returning from feeding trips was studied on 24 occasions between 16 July and 16 August from a fixed observation site located 82 m above sea level, normally between 1300–1800 hours (1200–1700 GMT). With the exception of an obscured sector towards the NE of this point, the sea horizon was divided into 26 sectors, one for each 11.25°. In each sector the number of arriving groups of Puffins was counted for 2 minutes, using a telescope (20×) aligned on the midpoint of the sector with the horizon in centre of the view. Since birds tended to spread out when approaching the colony, only groups flying directly towards the observer and at distances beyond 3–4 km (well outside the outermost skerries) were counted.

Food loads intended for chicks were collected from adults caught in mist-nets placed in the colony. In each load, fish species were identified and weighed separately to the nearest 0.1 g, and their body lengths were measured to the nearest 1 mm. Occasionally, numerous small post-larvae of a single species were weighed collectively. In such cases, only the maximum and minimum length within the group were recorded. Altogether, 105 food loads (of which 93 were complete) containing a total of 1,072 individual prey items were collected during 21 days between 13 July and 19 August.

All the adult birds caught during the sampling of food loads were weighed to the nearest 5 g. Chick growth and fledging success were studied in 101 accessible nests containing an egg in mid June. All chicks found in these nests (n = 52) were weighed at 2–3 day intervals from 14 July to 24 August and on 1 September.

Studies at sea

The Institute of Marine Research (IMR) in Bergen conducted two ship surveys in July 1988 in order to map the distribution and abundance of first-year Herring off the central and northern coasts of Norway. The two research vessels, 'Håkon Mosby' and 'Sula', covered the sea areas off Røst from 16–20 July, and a seabird observer was present aboard 'Håkon Mosby'. Both ships sampled sea temperature and salinity at a depth of 20 m on fixed transect stations (Fig. 1), where they trawled for post-larvae and 0-group fish in the 0–60 m depth zone, cruising at a speed of 2–3 knots for 30 min. The distance between successive IMR stations within the transects varied between 24 and 56 km (13–30 nautical miles). IMR scientists identified and counted all fish in each trawl catch, and measured the body lengths of individuals in a random sample of each species.

On 3–4 August, the whaler 'Dag Senior' was chartered in order to locate major foraging areas of the Røst Puffins. The survey was directed towards the main incoming direction of birds registered on Hernyken on 2 August, but the ship's course was adjusted at sea to trace the incoming stream of Puffins (Fig. 1). A very short transect was run a few km NW of Røst on 5 August with the smaller vessel 'Falken', but the results are treated here as being part of the 'Dag Senior' cruise. Hydrography and fish were not sampled during the August surveys.

Seabirds at sea were counted in 10-minute periods, using standard procedures (Tasker et al. 1984). Transect width was normally 300 m to one side of the ship. The observation standpoints aboard 'Håkon Mosby' and 'Dag Senior' were 10 m and 6 m above sea level, respectively. Ship speed for the counts was from 8–12 knots, and was held constant on straight transects. Birds flying were counted separately from birds on surface, and the flight direction of Puffins was recorded. Whenever possible on the 'Dag Senior' cruise it was noted whether or not the Puffins were carrying food. Seabirds were counted for 485 km of the transects run by 'Håkon Mosby' between 66–69°N and for 322 km of the 'Dag Senior' cruise.

Statistical analyses and graph plots were made by using the SPSS (Statistical Package for Social Sciences) and CSS (Complete Statistical System) computer packages.

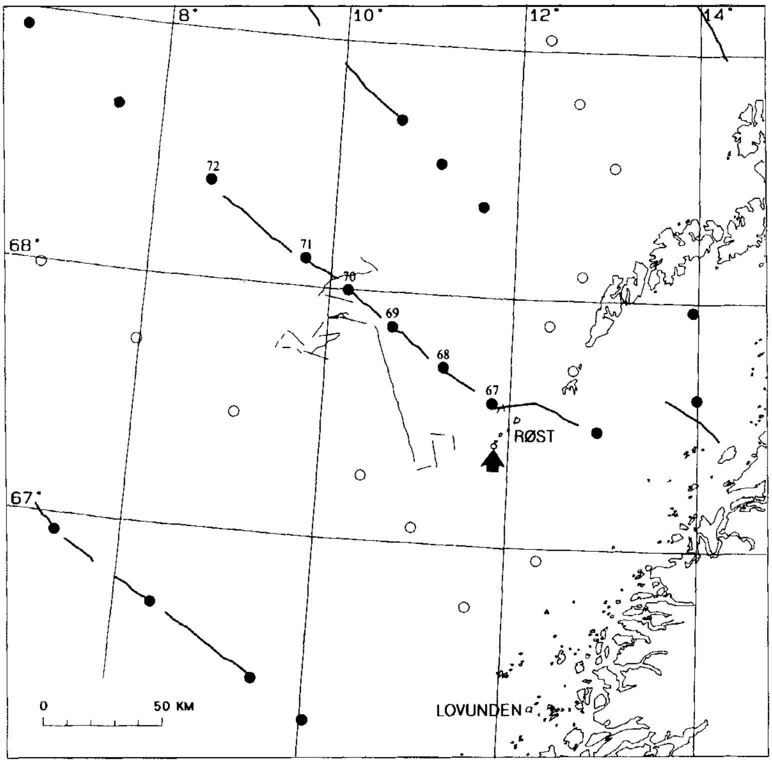

Fig. 1. Stations sampled by the research vessels 'Håkon Mosby' (filled circles) and 'Sula' (open circles) 16–20 July 1988. Seabird counts in transects were made from 'Håkon Mosby' (thick lines). Similar counts were done during the cruise with 'Dag Senior' on 3–4 August 1988 (thin lines). The location of Hernyken is indicated by the arrow. Station numbers refer to Table 2.

Results

Flight direction of Puffins returning to colony

The median direction towards groups of adults returning from the fishing grounds varied significantly throughout the season (Kruskal-Wallis $H = 183.9$, $df = 16$, $p < 0.001$). It was fairly constant about WSW during the second half of July, whereafter it turned gradually towards NW until mid August (Fig. 2). At the end of the season, there was a dramatic shift in direction, as most birds were returning from SW.

Foraging areas

During the 'Håkon Mosby' transects, the highest density of Puffins on surface was recorded 137 km NW of Røst, off the edge of the continental shelf (Figs. 3 and 4). This was primarily due to a single dense flock of about 300 birds foraging actively within the transect. Several flying birds were observed carrying food loads in this area, but poor light conditions made quantitative observations difficult. Within 110 km of Røst, the majority of the birds were flying, while birds on surface were predominant further out.

In the southernmost transect, Puffins were observed settled on surface as far as 208 km SW of Røst or 240 km from the next nearest Puffin colony, Lovunden (66°23'N, 12°20'E) (Fig. 3). However, we were unable to establish the origin and breeding status of these birds.

Puffin densities, particularly in flight, were generally higher on 3–4 August than those recorded two weeks earlier (Figs. 5 and 6). This was expected as the August survey aimed to find the major feeding areas, and transect routes therefore were chosen according to the traffic of Puffins to and from the colonies.

Two major foraging areas were found in early August, one c. 20 km W of the colonies and another 85–105 km to the NW. Between these two areas, as well as closer to Røst, there was a steady traffic of birds flying to and from the colonies (Fig. 6). The outer area was located over the continental slope, at its closest point of approach to Røst (Fig. 5). Here we observed the characteristic dense schools of 0-group Herring

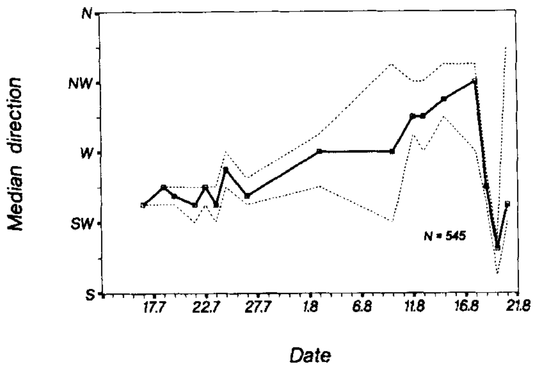

Fig. 2. Median direction (±1 quartile) from which groups of adult Puffins returned to Hernyken in 1988.

in the surface layer close to foraging Puffins. However, some Puffins were seen carrying food loads from beyond this distant feeding area.

Chick food, growth and fledging success

The composition of food brought to Puffin chicks on Hernyken varied throughout the season (Fig. 7), as did load weights and the number of prey items per load (Fig. 8). Generally, Herring was the most important food, although Saithe *Pollachius virens*, Haddock *Melanogrammus aeglefinus* and Rockling *Rhinonemus spp.* were important for shorter periods. The amount of Herring in the diet increased gradually in July, and was the only prey recorded between 30 July and 3 August, whereafter its importance decreased and accounted for c. 50% of the food weight in mid August.

Load weights varied significantly between 5-day periods (Kruskal-Wallis $H = 20.62$, $df = 8$, $p < 0.01$, Fig. 8), as did the number of preys per load (Kruskal-Wallis $H = 23.94$, $df = 8$, $p < 0.01$, Fig. 8). During July, median load weights were fairly stable between 8–10 g, but decreased rather suddenly in early August and remained low (5–6 g) during the rest of the sampling period. Most of the variation in median numbers per load was closely related to the corresponding shifts in weight dominance of preys (Fig. 7), being low (3–5) with Saithe and Haddock, medium (9–11) with Herring and high (20–24) when small Rockling was predominating.

Except for two short periods, the average chick

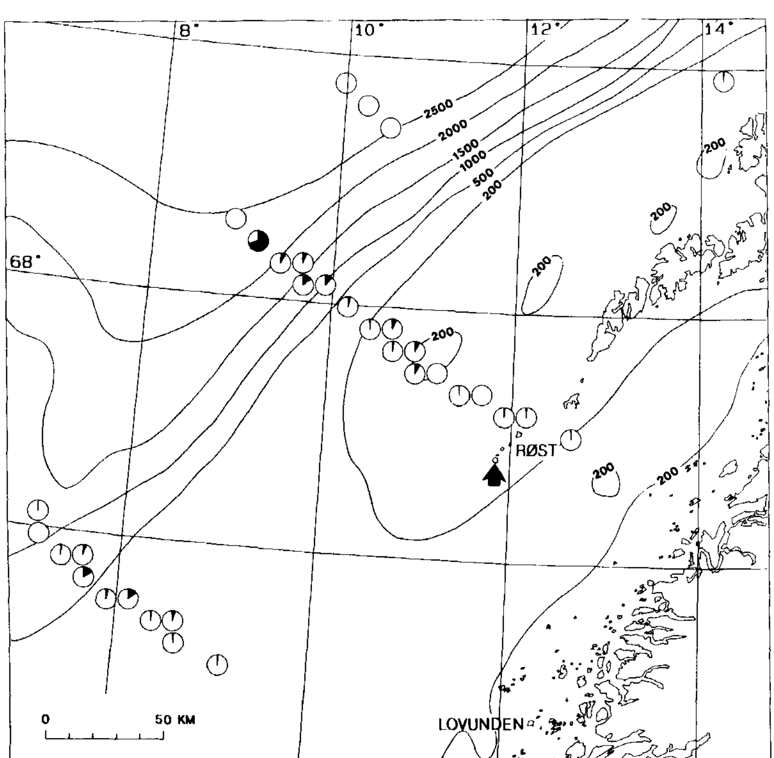

Fig. 3. Density of Puffins (birds/km^2) on the sea surface 16–20 July 1988. Data are aggregated to 10 × 10 km squares. A completely filled circle represents 50 birds/km^2. Depth contours are in metres.

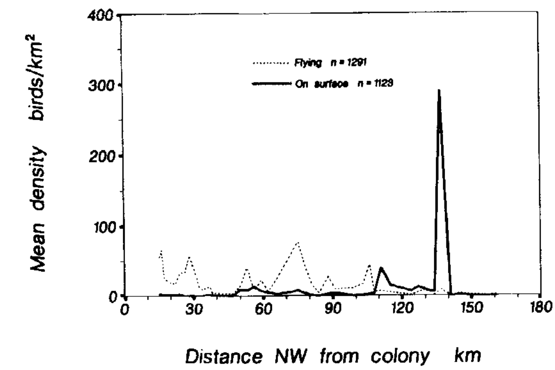

Fig. 4. Mean density of Puffins (birds/km^2) flying (dotted line) or on the sea surface (thick line) in relation to distance from colony, as observed in 10-minute intervals during the 'Håkon Mosby' transect directed NW from Røst 18 July 1988. The total number of Puffins observed within the transect area was 2,414.

weight increased by 2–6 g per day until early August, then growth retarded and chicks lost weight rapidly (Fig. 9). When the data were aggregated into 5-day periods, there was a significant relationship between the average weight change of chicks and the proportion of Herring in their diet between 15 July and 18 August (Spearman rank correlation, $r = 0.7857$, $df = 5$, $p < 0.05$).

The latest check (1 September) showed that only 2 study nests still contained a chick. At least 38 of 50 study chicks died in the nest and the maximum fledging success was estimated to 24%. Furthermore, those chicks that left the nest did so in a very poor condition, as the last recorded weight of the 12 study chicks that could have fledged averaged 197.3 g (SD = 29.5). The mean weight of 39 other fledglings checked on their way to the sea from 14–21 August was equally low (197.9 g, SD = 25.8). In late August and early September, several hundred dead chicks were seen floating on the sea near the colonies. Five of these chicks were dried, and their mean weight was only 133.4 g (SD = 6.1).

Adult body weight

Between 14 July and 20 August, 17 adult Puffins were weighed more than once. Nine of them were carrying food, while 5 of the others had been ringed as 'adults' (with ≥2 bill grooves) at exactly the same location between 1980 and 1983 (one

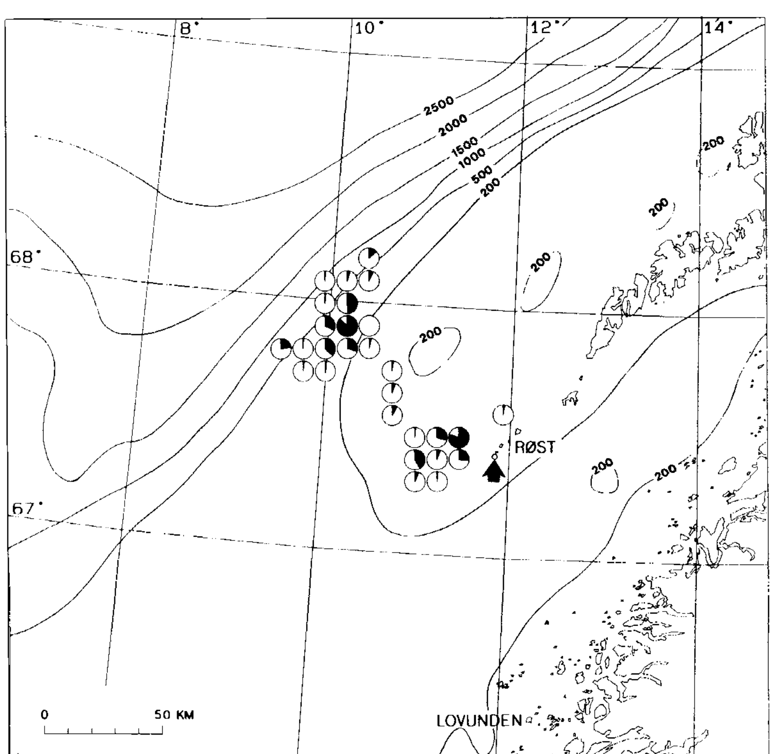

Fig. 5. Density of Puffins (birds/km^2) on the sea surface 3–4 August 1988. Data are aggregated to 10 × 10 km squares. A completely filled circle represents 50 birds/km^2. Depth contours are in metres.

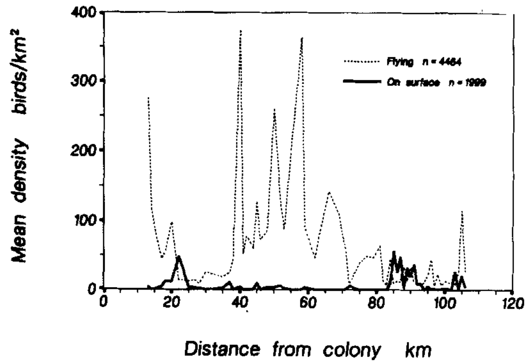

Fig. 6. Mean density of Puffins (birds/km²) flying (dotted line) or on the sea surface (thick line) in relation to distance from colony, as observed in 10-minute intervals during the 'Dag Senior' cruise NW of Røst 3–4 August 1988. The total number of Puffins observed within the transect area was 6,463.

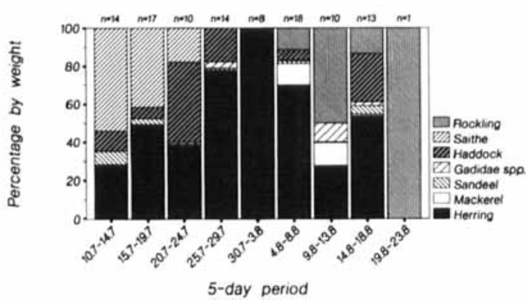

Fig. 7. Seasonal change in the composition of the principal prey species (percentage of diet by weight) brought to Puffin chicks on Hernyken during 5-day periods in 1988. The number of food loads examined in each period is indicated.

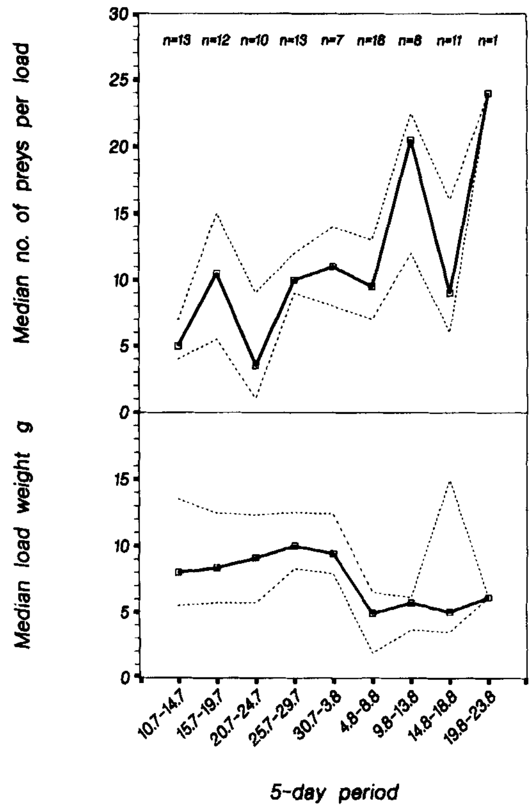

Fig. 8. Seasonal change in the median weight (lower) and median number of prey items (upper) in complete food loads brought to Puffin chicks on Hernyken during 5-day periods in 1988. Dotted lines show medians ±1 quartile. n = no. of complete loads examined in each period.

with food load in 1982). These 14 birds, which were considered to be breeders, lost weight at a mean rate of 0.70 g/day ($SD = 2.7$, $n = 17$) between successive retraps, but the decline was not statistically significant (ANOVA on regression, $F = 0.70$, $df = 1.15$, $p > 0.25$).

Comparisons with fisheries research data

Herring selected by Puffins were considerably larger than those sampled by IMR (Kolmogorov-Smirnov $D = 0.384$, $p < 0.001$, Table 1). This was also the case for Haddock (K-S $D = 0.749$, $p < 0.01$) but not for Saithe (K-S $D = 0.212$, $p > 0.05$). At this time, Haddock and Saithe in Puffin loads were of the same size (K-S $D = 0.25$, $p \approx 1$).

The catch of Herring in trawl samples varied greatly between stations, with respect both to the number of fish (1–12,000) and their median lengths (30.0–45.0 mm). This variation was also evident between the transect stations NW of Røst on 18 July (Kruskal-Wallis tests, $p < 0.001$), but could not be explained in relation to sampling hour or distance from the colonies (Table 2).

In order to test if the distribution of Puffins observed on surface during the 'Håkon Mosby' transects could be explained by the variation in Herring or oceanographical parameters sampled by IMR, the Puffin data were allocated to the nearest IMR sampling station (cf. Fig. 1). Herring biomass was estimated from the length measurements sampled by IMR, using a weight-length relationship derived from Herring brought to Puffin chicks on Hernyken from 13–23 July (Fig. 10).

No significant relationships were found between the surface density of Puffins and Herring biomass, Herring numbers, sea temperature

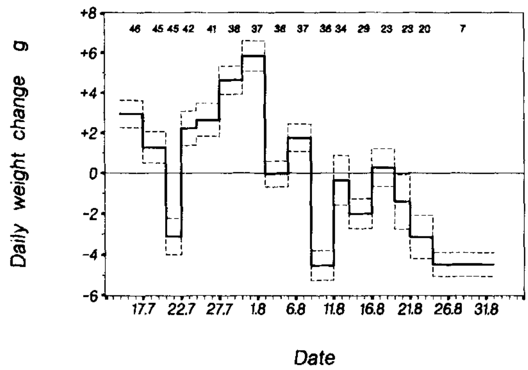

Fig. 9. Mean daily weight change (±1 SE) of individual study chicks on Røst in 1988. n values are shown in top line.

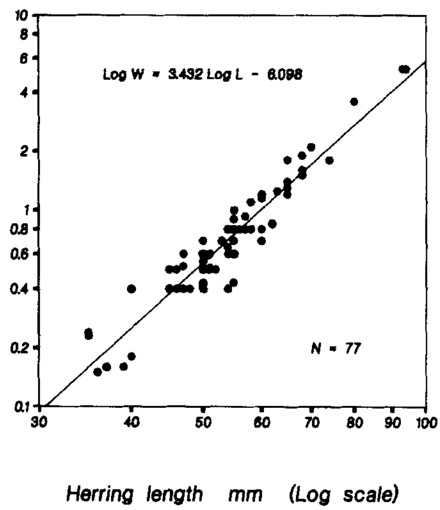

Fig. 10. Correlation between log length and log weight of Herring brought to Puffin chicks on Hernyken 13–23 July 1988 ($r = 0.9489$, $p < 0.001$). N = sample size.

or salinity at adjacent IMR stations from 16–20 July (Table 3). The correlations did not improve when only Herring of sizes taken by Puffins (>32 mm) were selected, nor when the Puffin data were weighted according to the linear distance from Røst, or when only Puffin densities within 5 km (2.7 nautical miles) of each station were used. The paucity of Puffin data did not permit much further reduction of the comparative scale, while comparisons on scales larger than the mean distance between successive stations (Table 3) were not made due to the low number of stations.

Discussion

First-year Herring was undoubtedly the most important prey fed to Puffin chicks on Røst in 1988. Judged on the flight direction of adults returning to colony when chick provisioning was significant, the main feeding grounds were located west of Røst, shifting gradually from WSW to NW through most of the nestling period. Late in the season, there was a sudden shift in the return direction. This event coincided with an evident decrease in food provisioning of chicks, causing most of the already starving nestlings to lose weight and die. In two years with good breeding success, 1983 and 1985, the average fledging weights of Puffin chicks on Røst were 301.5 g and 267.5 g, respectively (Anker-Nilssen 1987). Thus, the fledging weights of the few chicks that did survive the nestling period in 1988 confirm that they were severely undernourished.

The results show that significant numbers of Puffins were collecting food for their chick from a considerable distance. On 18 July, some were seen at least 137 km from the colony, which is

Table 1. Summary statistics for the length distribution (mm) of three major Puffin preys in 1988 sampled by adult Puffins breeding on Hernyken (13–23 July) and by IMR's research vessels off Røst (16–20 July). NW indicates data for the 6 innermost stations in the transect NW from Røst (18 July, cf. Fig. 1).

Species	Sample	Median	Mode	Range	Mean	SD	n
Herring	Puffins	41.0	35	33–94	45.02	11.08	264
	IMR	35.0	32	20–59	35.77	5.59	865
	IMR NW	32.0	32	22–54	33.68	5.47	197
Haddock	Puffins	102.5	100	85–120	104.67	13.28	6
	IMR	45.0	42	13–115	48.15	21.30	548
Saithe	Puffins	97.0	100	75–126	95.58	12.01	24
	IMR	93.0	88	32–117	93.03	14.42	39

Table 2. The median length, total number (N) and total biomass of Herring caught per half hour trawl periods in relation to time of day and distance from the colonies at the 6 innermost IMR transect stations NW of Røst 18 July 1988 (cf. Fig. 1). n = no. of Herring measured.

Station no.	Hour	Distance from colony km	Median length mm	n	N	Total biomass g
67	0800	17	36.5	10	11	2-74
68	1000	40	32.0	35	35	5.26
69	1200	68	32.0	53	165	17.27
70	1500	93	31.0	24	27	3.16
71	1700	117	32.5	26	27	5.25
72	2100	172	34.0	49	54	9.97

twice the maximum foraging range reported from other areas (70 km, Schneider et al. in press). Using the flight speed of 48 km/h recorded by Corkhill (1973), these birds spent a minimum of 5.7 hours flying in order to return with a load of 8–9 g. Observations made by local fishermen indicate that the foraging range of Røst Puffins has also been considerable in previous years (Anker-Nilssen 1987).

Unfortunately, feeding frequency was not studied on Røst in 1988, but chick growth was very poor from 17–20 July with only slightly increasing chick weights. Compared to Puffin chicks at Bleiksøy in 1982, which slowly gained weight with a food consumption of 23–32 g/day (Barrett et al. 1987), it is reasonable to believe that the chicks on Hernyken received no more than this in 1988. Nevertheless, each adult had to make 1–2 feeding trips per day, spending may be up to 50% of their time away from colony. In early August, the maximum recorded foraging range dropped by 25% compared to that of mid July, but then the median load weight was c. 40% lower.

These findings show that the maximum foraging ranges of more than 100 km estimated by Pearson (1968) and Bradstreet & Brown (1985) are within the capability of breeding Puffins. Furthermore, we have no indications that these long foraging ranges caused energy stress of adults on Røst in 1988. The recorded weight changes of individual birds represent an average loss of c. 4% of their prelaying body weight over one month, but this may be adaptive and is within the range of what has been recorded on Røst in previous breeding seasons (4–6% per month, Barrett et al. 1985).

At the peak of their growth, Puffin chicks require at least 50 g food per day to stay in good condition (Myrberget 1962; Harris 1976; Tschanz 1979; Barrett et al. 1987). If prey was easily caught in the distant foraging areas in 1988, the Puffins could, theoretically, have had just enough time in a day to provide their chicks with sufficient food. Consequently, the poor chick growth strongly suggests that prey was limited and/or that the adults did not devote all their time to feed the young. When compared to food loads collected on Røst in previous seasons (Anker-Nilssen 1987), load weights were very poor in August 1988, and indicated that prey was limited.

No significant relationships were found between Puffins at sea and the recorded distribution of Herring in July. Nevertheless, we believe that the steady shift in return direction to the colonies during the nestling season reflects the drift of Herring northwards to the nursery areas of immature Atlanto-Scandian Herring in the Barents Sea (e.g. Hamre 1988). The speeds of the collateral coastal and Atlantic ocean currents west of Røst may periodically be relatively fast (up to 2 knots, Sætre et al. 1979). However, the bottom topography causes frequent formation of eddies in the frontal system between the two

Table 3. Coefficients and p values (in parentheses) for Spearman rank correlations between the density of Puffins on surface and Herring biomass, Herring numbers, sea temperature and sea salinity 16–20 July 1988. Only data from IMR stations where adjacent Puffin data were available were used (cf. 'Håkon Mosby' survey, Fig. 1), either from all of these stations (n = 11), or only from those in the transect NW from Røst (n = 6). The spatial scale for the comparisons corresponds to the average distance between successive stations.

Data set	Spatial scale (km)	Herring biomass	Herring numbers	Sea temperature	Sea salinity
All stations	38.4	−0.1549	−0.2283	−0.2975	−0.0685
		(0.649)	(0.500)	(0.374)	(0.841)
NW transect	32.2	0.1429	0.0290	−0.6571	−0.4286
		(0.787)	(0.957)	(0.156)	(0.397)

water masses, which may lead to an increase in the retention time and density of young Herring in the area (Sundby 1984 pers. comm.).

The major aggregations of feeding Puffins were located over the continental slope in areas where a frontal system is especially pronounced (Sætre et al. 1979). Well developed frontal systems benefit primary production which in turn creates favourable conditions for schooling fish like the young Herring (e.g. Tait 1981). This, plus the retention of prey in occasional eddies off Røst, may well be a key factor explaining why Røst is the largest Puffin colony in Norway.

The rapid shift in return direction of Puffins observed late in the season, accompanied by a sudden retardation in chick growth, suggests that most Herring NW of Røst at this time had become unavailable for the Puffins. Possible causes are that the Herring had drifted too far away from Røst, that they were depleted by other predators (e.g. adult Herring, V. Øiestad pers. comm.), or that they went too deep for the Puffins to reach them. Our data suggest that distance from the colony was critical in 1988.

Although the IMR vessels and the Puffins apparently sampled fish from the same areas, the birds took significantly larger Herrings than those sampled by the IMR. This indicates that the Puffins actively selected the largest fish in the schools, and/or that most of these Herring were able to avoid the trawl.

However, the major bias in our study is undoubtedly the discontinuous sampling of fish and hydrographical parameters, and the fact that birds were not counted at IMR hydrography or trawl stations. Furthermore, through the 20 m sampling depth for sea temperature and salinity, local fronts in the surface layer may have been missed. The expected patchiness in the distribution of both Herring and Puffins was evident, and has likely severely reduced the probability of finding any significant relationships.

Scale-dependent patchiness is crucial and demands special attention (see Hunt & Schneider 1987 for a review), and only a few studies have succeeded in finding positive correlations between the distribution of seabirds and their prey. Schneider & Piatt (1986), Heinemann et al. (1989) and Erikstad et al. (1990) all found that the degree of correlation was higher at larger spatial scales, although Erikstad et al. (1990) suggested that the coefficients in their study reached an upper threshold around a scale of 40 nautical miles. The largest scale used in our study was only 38 km (21 nautical miles), but the low number of sampling stations would have made comparisons on larger scales unreliable.

This study documents the close relationship between the breeding success of Røst Puffins and the amount of Herring they fed their chicks in 1988. Although we were unable to find any relationships between the simultaneous occurrences of Puffins and first-year Herring, we cannot reject the theory that prey availability is the key factor determining the distribution of Puffins at sea off Røst during the breeding season. However, in order to fully understand the importance of this predator-prey relationship, it will be necessary to increase sampling and modify sampling procedures in future studies.

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