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Diet and nest attendance of incubating and chick-rearing northern fulmars (*Fulmarus glacialis*) in Shetland

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Abstract We examined diets and nest attendance patterns of northern fulmars (*Fulmarus glacialis*) on Foula and Unst, Shetland, UK, during the breeding seasons of 1998 and 1999. Mean foraging trip duration, derived from nest attendance patterns, differed between incubation (32.5 h) and chick-rearing (early stage: 11.2 h, mid-stage: 20.4 h). It was influenced by chick age and obviously also by prey availability. The numbers of fulmars attending the colonies were influenced by wind direction, wind speed, time of day and state of reproduction. Diet samples were collected by regurgitations of adult and young fulmars. Diet was analysed by identifying prey items on the basis of otoliths, vertebrae, premaxillae (fish), cephalopod beaks and fragments of arthropod exoskeletons. Adult fulmars and chicks fed upon a wide range of prey types. Gadoid fish, including Norway pout (*Trisopterus esmarkii*), were the most common prey in the diet. Fish offal was found in 32% of regurgitates, clupeids in 15%. In contrast, the proportions of sandeels were very low (1%). This is different from previous studies where sandeels formed a large part of fulmar diet at Shetland in summer. Differences in food composition of incubating and chick-rearing fulmars were found for fish, but not for offal, crustaceans or squid. The percentage of non-discard fish (Clupeidae, Ammodytidae, Isospondylae) was significantly different between regurgitates from incubating and chick-rearing fulmars. Samples from chick-rearing adults contained non-discard items more frequently than regurgitates from

incubating birds. The results strongly indicate that fulmars select to feed their chicks on energy-rich clupeids.

Introduction

Seabirds are useful indicators of species composition and food availability within marine ecosystems (Furness and Camphuysen 1997). Indicators need to show rapid responses to changes of environmental conditions. In the Northeast Atlantic, northern fulmars (*Fulmarus glacialis*) might be suitable biomonitors because of their high abundance and widespread distribution. Population sizes of approximately 3.2 million individuals in summer and 1.9 million individuals in winter establish fulmars as the most numerous seabird species in the North Sea (Skov et al. 1995).

Changes in food supply affect immediately and markedly the reproductive success, diet composition and/or the activity budgets of breeding seabirds. Severe changes in staple foods are not uncommon in seabird populations and sudden changes are often linked with marked changes in food conditions or prey abundance (Tasker et al. 1999).

Recent studies have described the diet of fulmars in the North Sea and the Northeast Atlantic (Camphuysen and van Franeker 1996, 1997; Camphuysen and Garthe 1997; Hamer et al. 1997; Phillips et al. 1999). Within their habitats, fulmars are considered to be top-predators. Their main diet is fish, but squid and zooplankton were also frequently found in the regurgitations (Camphuysen and van Franeker 1996; Furness and Todd 1984; Hamer et al. 1997; Phillips et al. 1999; Thompson et al. 1995).

Seasonal variations in seabird diet have been described by several authors. For example, common guillemot (*Uria aalge*) diet changed between seasons (Blake et al. 1985). Variations on smaller temporal scales occur, e.g., within the reproductive period when parents change prey due to energy requirements of their growing

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chicks (Harris and Wanless 1986). Differences between chick and adult diet have been described by Harris and Wanless (1993) for European shags (*Phalacrocorax aristotelis*) on the Isle of May, Scotland. Phillips et al. (1999) highlight that data on diet composition of incubating fulmars are lacking, in contrast to several studies covering the chick-rearing period.

This paper describes the summer diet and nest attendance patterns of fulmars from two colonies on Shetland, UK, located within an area of intensive commercial demersal fishing. In order to compare the diet between incubation and chick-rearing, regurgitations were collected before and after hatching in 1999. Since fulmar foraging is known to be influenced by wind speed (Furness and Bryant 1996), we also related diet and feeding behaviour to local weather data.

Study area and methods

Field studies took place on Foula, Shetland (60°08'N, 2°05'W) in 1998 and on Unst, Shetland (60°45'N, 0°53'W) in 1999. Food samples (voluntary regurgitations) were obtained on Foula between 14 and 29 July 1998 and on Unst between 23 June and 8 July 1999. Adult birds were caught with a fishing-net at their nests and chicks were grabbed directly at the nests. Food samples were stored in alcohol (70%) until identification.

Dietary analysis

Samples were examined using a binocular microscope (Wild Herbrugg 60–500×). All diagnostic structures were stored dry or in 70% alcohol until identification. Prey species were identified to the lowest possible taxonomic level from otoliths and other hard parts such as vertebrae, premaxillae (fish), exoskeletons (crustacean) or beaks (squid) using available keys (Clarke 1986; Härkönen 1986; Hayward and Ryland 1995; Lincoln 1979; Watt et al. 1997) and reference collections.

Calculations on length-frequencies of Norway pout were made using regression equations given in Brown and Pierce (1998).

Fish of the families Gadidae, Scombridae, Gobiidae and Pleuronectidae were assumed to be taken from commercial fish trawlers and were hence classified as “discard”. These were fish of demersal habit that would not normally be available to surface-feeding seabirds such as fulmars. Fish such as Clupeidae, Ammodytidae and Isospondylae were assumed to be caught naturally and were hence defined as “non-discard”.

Patterns of nest attendance

A sample of 25 (Foula, 1998) and 24 (Unst, 1999) fulmar nests was randomly selected for studying nest attendance patterns. Fulmars were counted every 15 min during observation periods of 2×24 h each year. Between the counts, all activities (arrivals, departures) were noted. From these data, estimates of the time fulmars spent at sea or at the nest were calculated using the following formulae:

$$\bar{N}_{\text{arrivals/ind}} = \frac{N_{\text{arrivals}}}{n_{\text{ind}}} \quad (1)$$

where N_{arrivals} is the total number of arrivals observed, n_{ind} the total number of individuals, and $\bar{N}_{\text{arrivals/ind}}$ the mean arrivals/individual.

$$\bar{t}[\text{min}] = \frac{T[\text{min}]}{\bar{N}_{\text{arrivals/ind}}} \quad (2)$$

where T is the total time of observation [min], \bar{t} the mean time between two arrivals/ind [min].

$$T_{\text{nest}_i}[\text{min}] = T[\text{min}] * n_{\text{nest}} \quad (3)$$

where T_{nest_i} is the total time of nest observations [min], n_{nest} the total number of nests.

$$t_{\text{indatnest}}[\%] = \frac{\sum t_{\text{Fobsatnest}}[\%] + \sum t_{\text{FPobsatnest}}[\%]}{n_{\text{ind}}} \quad (4)$$

where $t_{\text{ind at nest}}$ is the time one individual spent at its nest, $t_{\text{F obs at nest}}$ is the total time single fulmars were observed at their nests, $t_{\text{FP obs at nest}}$ the total time pairs were observed at their nests.

$$t_{\text{indatsea}}[\%] = 100 - t_{\text{indatnest}}[\%] \quad (5)$$

where $t_{\text{ind at sea}}$ is the time one individual spent at sea (= foraging trip duration).

$$t_{\text{indatnest}}[\text{min}] = \frac{\bar{t}[\text{min}]}{100\%} * t_{\text{indatnest}}[\%] \quad (6)$$

$$t_{\text{indatsea}}[\text{min}] = \bar{t} - t_{\text{indatnest}}[\text{min}] \quad (7)$$

In addition, all resting fulmars on a certain cliff area were counted every 30 min to study colony attendance patterns in relation to weather effects.

Weather data from Foula and Unst were provided by the Meteorological Office, Glasgow, UK, for the field periods in 1998 and 1999.

In order to exclude bias due to autocorrelation of variates adjacent in time, tests for autocorrelation were carried out. On two days, data were autocorrelated. In these two cases, autocorrelation was circumvented by skipping every second value. Multiway ANOVAs (three-factor, Unst; four-factor, Foula) were used to examine the effect on colony abundance of adults (as dependent variable) of wind direction, wind force, time of day and period of breeding cycle (as independent variables). The parameters were grouped as follows:

- wind direction: 12 categories of 30° sectors (north: >345°–15°, north-northeast: >15–45°,....., north-northwest: >315–345°)
- wind speed: 3 categories (0–3.3 m/s, 3.4–6.2 m/s, 6.3–9.8 m/s)
- time of day: 4 categories (night=2100–0300 hours, dawn/dusk=0300–0600 and 1800–2100 hours, intermediate=0600–0900 and 1500–1800 hours, and day=0900–1500 hours)
- period of breeding cycle: 3 categories (incubation, early chick-rearing: chicks of age 5–7 days, mid chick-rearing: chicks of age 18–21 days)

Wind speeds were classified on the basis of data given by Furness and Bryant (1996) who found a linear relationship between wing beat frequency and mean wind speed <12 m/s for fulmars at Shetland.

Results

Mean foraging trip duration of breeding fulmars:

During incubation, mean foraging trip duration (= time spent at sea in one sequence) for an adult breeding bird was 32.5 h (Fig. 1). After returning from foraging, they spent on average 35.2 h at the nest. Overlapping time between adults of a pair was very small (2%). All nests under investigation were always attended by at least one adult during incubation.

During early chick-rearing, mean foraging trip duration was 11.2 h. A parent spent an average of 6.6 h at the nest before leaving the colony for a new foraging

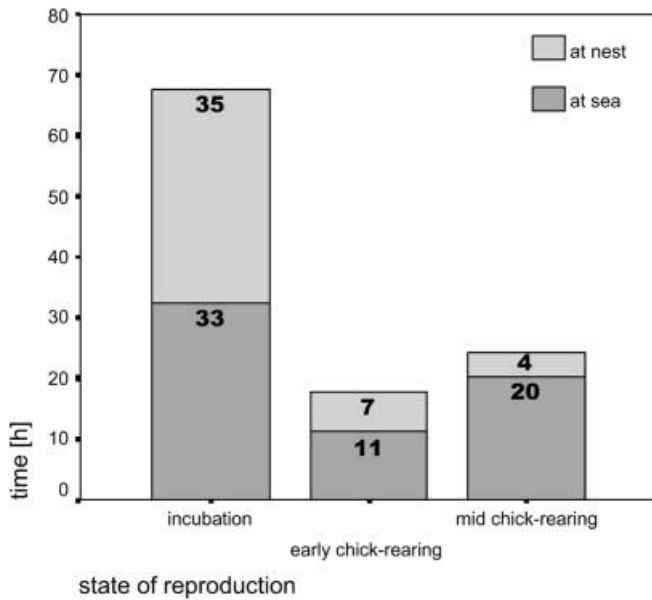


Fig. 1 Differences in foraging trip and nest attendance durations of northern fulmars (*Fulmarus glacialis*) during incubation ($n = 24$) and early/mid chick-rearing ($n = 25$)

trip. Both parents rarely stayed simultaneously with their chick (2%) and chicks were unattended 28% of the observation time.

Mean foraging trip duration during mid chick-rearing was 20.4 h. The average time parents spent resting at the colony or attending their chick was 3.8 h. The proportion of time chicks were not attended by adults increased to 69%.

Colony attendance of incubating fulmars

Wind direction had a significant effect on colony attendance of fulmars ($F = 11.176$, $df = 11$, $P < 0.001$). Highest numbers of birds were counted during winds from the north, north-west and west (Fig. 2), while with wind directions of east, south-east and south, lower numbers were found. The maximum of 119 fulmars occurred

when the wind came from the north ($> 345^\circ$ to 15°), the minimum of 76 individuals when the wind blew from the south-east.

Wind speed also had significant effects on colony attendance of birds (three-way ANOVA: $F = 5.392$, $df = 2$, $P = 0.013$). Up to 6.2 m s^{-1} , the mean number of observed fulmars was 109 birds. At stronger wind speeds ($\geq 6.3 \text{ m s}^{-1}$), a mean of 96 individuals was counted (Fig. 2).

Time of day also affected colony attendance (three-way ANOVA: $F = 3.615$, $df = 3$, $P = 0.036$). Between 1800 and 0600 hours (evening and night), more birds stayed in the colony than between 0600 and 1800 hours (morning until afternoon (Fig. 2).

Colony attendance of chick-rearing fulmars

During chick-rearing, colony attendance depended on state of reproduction ($F = 11.831$, $df = 1$, $P = 0.001$) as well as on daytime ($F = 8.361$, $df = 3$, $P = 0.002$). The average number of birds counted in the colony within early chick-rearing was significantly higher than that during mid chick-rearing. Between 2100 and 0300 hours, only a mean of 16 adults was present. The number of birds increased in the morning and reached a peak of 37 individuals during mid-day.

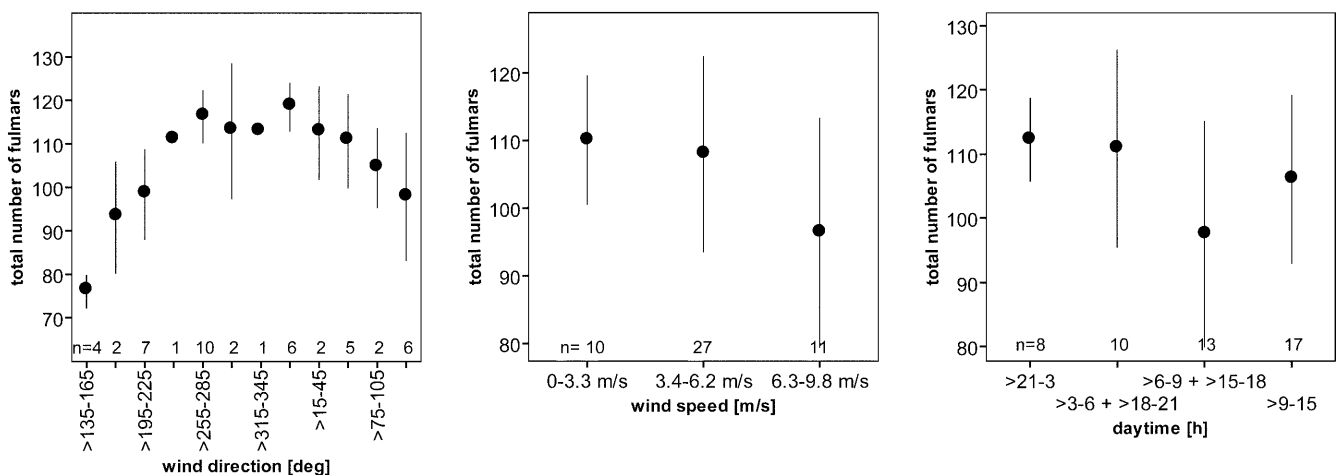
Wind direction and wind speed had no significant effects on colony attendance of fulmars ($F = 2.120$, $df = 8$, $P = 0.076$, and $F = 0.598$, $df = 2$, $P = 0.558$, respectively), although a tendency for lower individual numbers at higher wind speeds was suggested (Fig. 3).

Diet of adult and young fulmars in Shetland

Prey species

A total of 143 regurgitates of fulmars was collected in 1998 and 1999. A detailed breakdown of the prey items is given in Table 1.

Fig. 2 Colony attendance of incubating fulmars on Unst as a function of wind direction, wind speed and time of day in 1999



Gadidae were the most abundant prey found in regurgitates of fulmars, especially Norway pout (*Trisopterus esmarckii*) (18%), followed by Cod (*Gadus morhua*), Blue whiting (*Micromesistius poutassou*) and Poor-cod (*T. minutus*) (7–8%) (Table 1). Fish offal amounted to 32% by frequency of occurrence in the samples from Foula and Unst. Moreover, Clupeidae were frequently identified in the samples (15%). Sandeels (1%) were uncommon in the diet of fulmars at Shetland during the breeding seasons of 1998 and 1999.

Crustaceans were found in 31% of the regurgitates, squid in 6%. Unfortunately, remains of crustaceans and squid were often too fragmentary to allow further identification.

The length of Norway pout eaten by adult fulmars was unimodal (Fig. 4); the modal size was 12–15 cm. Modal size of herring (*Clupea harengus*) was 20–24 cm.

represented slightly more often in the samples from chick-rearing adults ($\chi^2 = 9.33, P < 0.01$).

Variations in diet of incubating and chick-rearing adults

Differences in food composition between incubating and chick-rearing fulmars were found for fish, but not for offal, crustaceans or squid (Table 3). Regurgitates from chick-rearing birds contained significantly more fish than regurgitates collected from incubating birds ($\chi^2 = 7.270, P = 0.007$).

Chick-rearing fulmars fed significantly more on non-discard fish than did incubating birds ($\chi^2 = 4.275, P = 0.039$) (Fig. 5). In contrast, the amount of discard fish did not differ between incubating and chick-rearing fulmars.

Variation in diet of adults and chicks

Food samples from Foula in 1998 scarcely showed differences in food composition between chick-rearing adults and chicks (Table 2). However, fish was

Discussion

Foraging trip duration and total distances travelled

In this study, mean foraging trip duration of fulmars differed between states of reproduction. Off-duty

Fig. 3 Colony attendance of chick-rearing fulmars on Foula as a function of wind direction, wind speed, state of reproduction and time of day in 1998

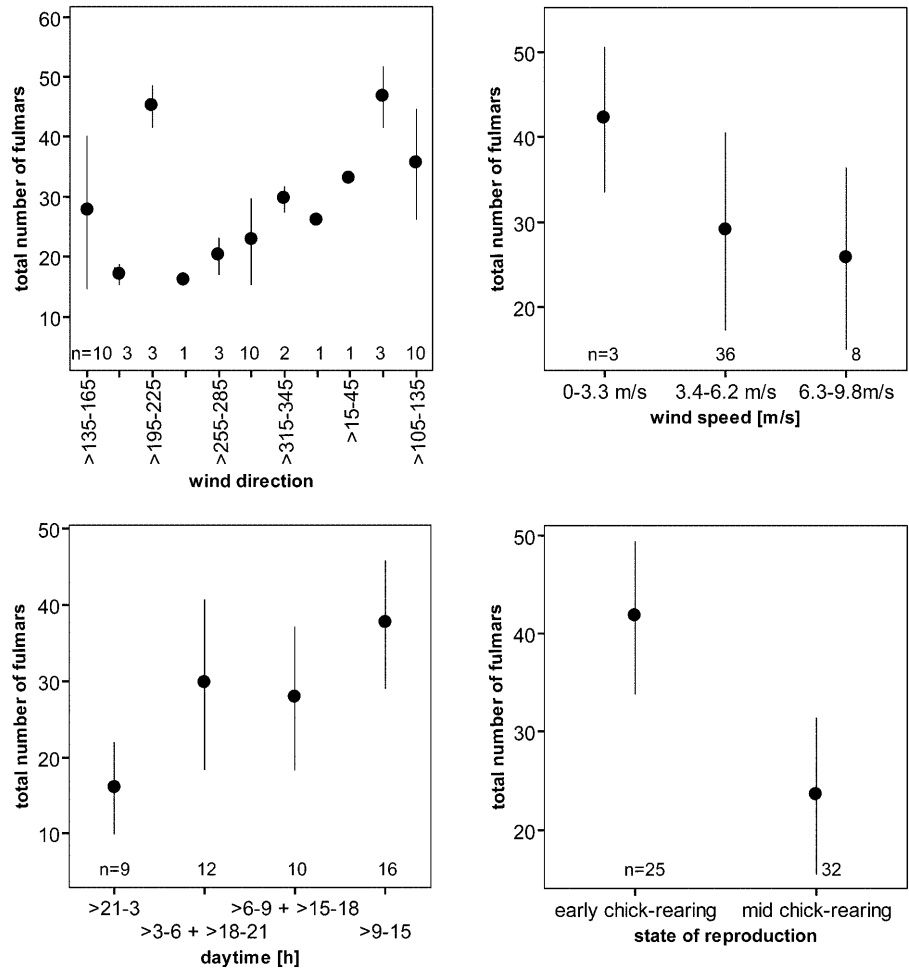


Table 1 Detailed breakdown of the diet of adult and young northern fulmars (*Fulmarus glacialis*) from Foula and Unst, Shetland, in the breeding seasons 1998 and 1999 ($n = 143$)

Species	<i>n</i>	%
Fish	117	82
Norway pout, <i>Trisopterus esmarckii</i>	26	18
Cod, <i>Gadus morhua</i>	12	8
Blue whiting, <i>Micromesistius poutassou</i>	11	8
Poor-cod, <i>Trisopterus minutus</i>	10	7
<i>Trisopterus</i> , unidentified	7	5
Haddock, <i>Melanogrammus aeglefinus</i>	4	3
Whiting, <i>Merlangius merlangus</i>	3	2
Silvery pout, <i>Gadiculus argenteus thori</i>	2	1
Four-bearded rockling, <i>Rhinonemus cimbricus</i>	2	1
Bib, <i>Trisopterus luscus</i>	1	1
Hake, <i>Merluccius merluccius</i>	1	1
Gadidae, unidentified	13	9
Herring, <i>Clupea harengus</i>	21	15
Clupeidae, unidentified	1	1
Mackerel, <i>Scomber scombrus</i>	4	3
Isospondylae	7	5
Sandeel, Ammodytidae	2	1
Gobiidae, unidentified	2	1
Dab, <i>Limanda limanda</i>	1	1
Fishes, unidentified	7	5
Fish offal	46	32
Crustaceans (excluding copepods)	31	22
Mysidacea/Euphausiacea	11	8
Isopoda sp.	5	4
<i>Eurydice pulchra</i>	3	2
<i>Hippomedon denticulatus</i>	1	1
<i>Orchestria gamarellus</i>	1	1
Crustacea, unidentified	15	10
Squid	8	6
<i>Gonatus fabricii</i>	1	1
<i>Todaropsis eblanae</i>	2	1
Squid, unidentified	5	3

incubating adults spent much longer spells at sea than chick-rearing birds. Calculated mean foraging trip duration of “early” and “mid-chick-rearing” fulmars on Foula in summer 1998 correspond to calculations made on Foula between 1978 and 1982 (10 h, 29 h) (Furness and Todd 1984). During incubation, birds seem to be able to extend the time spent foraging. Although both sexes are engaged at the nest site, incubation and protection of the egg from predators is managed by just one parent during an incubation shift.

Calculations on flight speed and trip duration lead to estimates of maximum foraging ranges of fulmars breeding on Shetland. Falk and Møller (1995) reported a

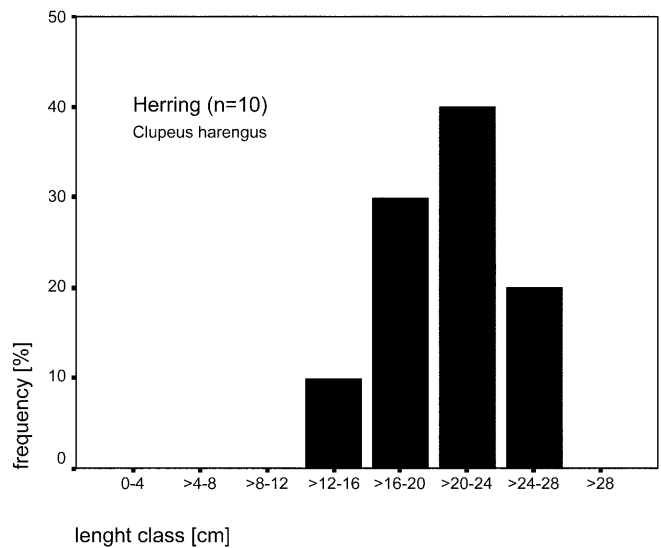
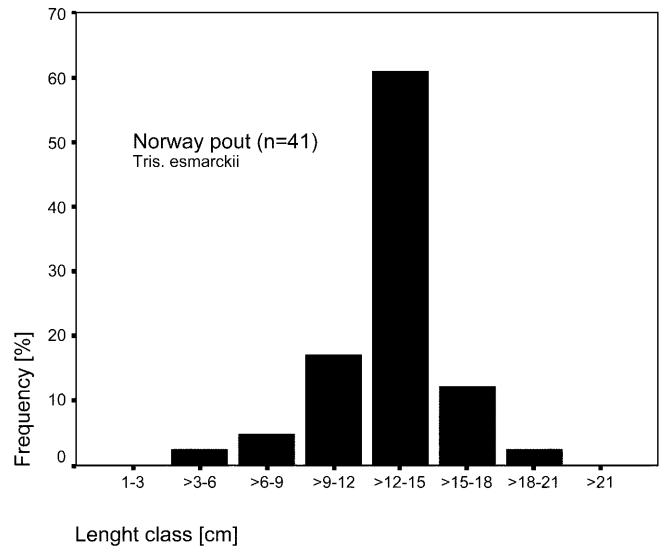


Fig. 4 Length distributions of Norway pout (*Trisopterus esmarckii*) and herring (*Clupea harengus*) consumed by fulmars from Foula and Unst, Shetland, () in the breeding seasons 1998 and 1999 (n for Norway pout = number of otoliths, n for herring = otoliths and vertebrae)

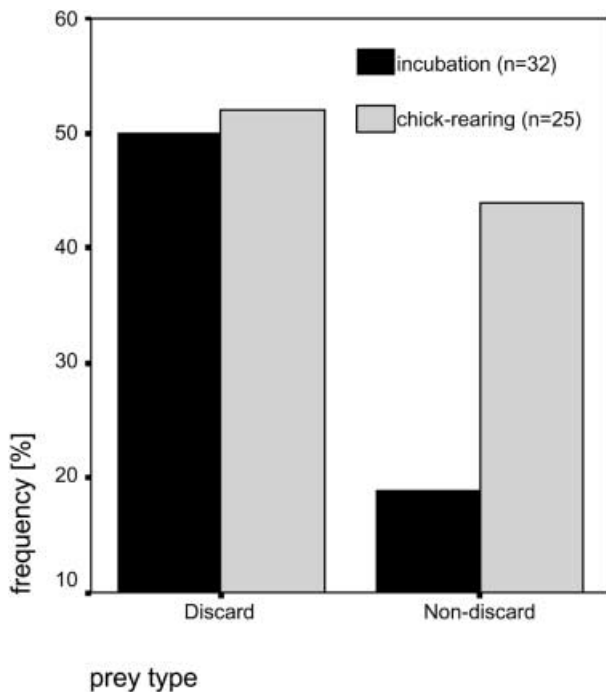
mean ground speed of 20.4 km h⁻¹ for satellite-tracked fulmars, with a range of ground speeds from 4.8 km h⁻¹ to 25.8 km h⁻¹. The potential distance covered by incubating birds in summer 1999 would have been between 156 and 839 km. This estimate of the average maximum range during foraging is very wide. Calculations of mean

Table 2 Comparison between samples of regurgitates from chick-rearing adult fulmars and chicks on Foula in July 1998. Comparison of frequencies of occurrence of prey types (%)

Prey type	Adults ($n = 59$)	Chicks ($n = 27$)	χ^2	<i>P</i>
Fish	88	59	9.33	< 0.01
Fish offal	31	30	0.01	n.s.
Crustaceans (excluding copepods)	3	15	0.75	n.s.
Squid	12	7	0.39	n.s.

Table 3 Samples of regurgitates from incubating and chick-rearing adult fulmars on Unst in June–July 1999. Comparison of frequencies of occurrence of prey types (%)

Prey type	Incubation (<i>n</i> = 32)	Chick-rearing (<i>n</i> = 25)	χ^2	<i>P</i>
Fish	75	100	7.270	0.007
Fish offal	31	40	0.472	n.s.
Crustaceans (excluding copepods)	47	32	1.290	n.s.
Squid	13	8	0.302	n.s.

**Fig. 5** Frequency of occurrence of discard (*Gadidae*, *Pleuronectidae*, *Gobiidae*) and non-discard items (*Clupeidae*, *Ammodytidae*, *Isospondylae*) within regurgitations from incubating and chick-rearing fulmars (Unst 1999)

ground speed of satellite-tracked birds include all activities between emitted signals, flying as well as resting, swimming or scavenging on the water surface, when the birds are not covering distances. Derived from counts of seabirds at sea, which were carried out near Shetland between May and August 1992–1994 (German Seabirds at Sea Database), we calculated that fulmars spent 81% of their time resting or swimming and only 19% flying. In combination with the knowledge that fulmars use gliding flight extensively during foraging (Pennycuick 1987) and that the most efficient airspeed for fulmars is

around 36 km h⁻¹ (Pennycuick et al. 1984), incubating birds had mean maximum foraging ranges of 222 km during our study (Table 4).

After hatching, foraging trip duration is shorter due to regular and frequent feeds of the chick. Moreover, chick age might affect foraging trip duration. Chicks aged 5–7 days are potentially not thermally emancipated like those investigated in the “mid-chick-rearing” stage; Mougin (1967) found that Fulmar chicks reach thermal emancipation some 3–6 days after hatching. During the first days after hatching (early chick-rearing), brooding and attending is thus necessary. Moreover, chicks are attended constantly by at least 1 adult for 10–16 days (Cramp and Simmons 1977; Hatch and Nettleship 1998). Therefore, the link of the parents to their nests is strong, adults not being able to spend as much time at sea as they do during the later chick-rearing stage and during incubation.

Colony attendance of fulmars

During incubation, colony attendance of fulmars was significantly affected by wind direction, wind speed and time of day on Unst in 1999. Clear variations in diurnal attendance were reported in several studies of breeding fulmars on St. Kilda, Scotland, and in Arctic areas (Camphuysen 1989; Cullen 1954; Furness and Todd 1984; Hamer et al. 1997; Hatch 1989; Moss 1965). In the cited studies, numbers of colony-attending birds decreased during the night, arrivals mostly occurring in the morning. A diurnal pattern is usually attributed to nocturnal feeding, because zooplankton and fish remain deeper in the water column at high light intensities (Furness and Burger 1988). In contrast, highest numbers of birds were found in the evening and night on Unst. These fulmars seemed not to leave the colony late in the day for nocturnal feeding. This is also indicated by the low percentage of prey species that migrate vertically at night, such as Mysidacea or Euphausiacea.

Table 4 Estimated foraging ranges of fulmars during incubation and chick-rearing at Shetland 1998 and 1999

State of reproduction	Mean foraging trip duration (h) (this study)	Average maximum range during foraging (km) (based on Falk and Møller 1995)	Average maximum range during foraging (km) (based on <i>Seabirds at sea</i> data, Pennycuick et al. 1984 and Pennycuick 1987; see text)
Incubation	32.5	156–839 (mean 663)	222
Early chick-rearing	11.2	54–289 (mean 228)	77
Mid chick-rearing	20.4	98–526 (mean 416)	140

Chick-rearing fulmars from Foula showed a reverse diurnal pattern of colony attendance. Many birds left the colony during the night while highest numbers were counted during mid-day. Nocturnal feeding by moving fulmars is conceivable, but that cannot be proved by the occurrence of pelagic prey.

In this study, colony attendance patterns corresponded well with wind parameters. Colony attendance of adults decreased with increasing wind speed. Flapping flight in calm conditions may influence patterns of colony attendance due to high energy costs (Furness and Bryant 1996). At high wind speeds ($> 12 \text{ m s}^{-1}$), wing beat frequencies tended to an asymptote close to zero. Energy demands are probably greatest during chick-rearing, when parents lose body mass after reaching their seasonal mass peak during incubation (Hatch 1990). Particularly during reproduction, adult birds should prefer energetically good weather conditions including high wind speeds while foraging.

Wind direction had a stronger effect than wind speed on Unst in 1999 (ANOVA: $F_{\text{wind direction}} 11,176$, $F_{\text{wind speed}} 5,392$). Similar results were reported by Hatch (1989). However, if fulmars had specific feeding grounds located at fixed distances from a particular colony, a relatively strong effect of wind direction on colony attendance would be expected (Hatch 1989). Observed breeding sites were on cliffs on the west side of Unst. A depressing effect on colony attendance of offshore wind (easterly direction) was found.

Diet of fulmars

Non-invasive methods such as spontaneous regurgitations may not empty the proventriculus or ventriculus entirely (Duffy and Jackson 1986), but regurgitates give information on the food recently consumed. Total numbers of prey caught cannot be estimated without biases, but frequency of occurrence of prey types gives reliable semi-quantitative data. However, the occurrence of otoliths in regurgitations could be the result of secondary consumption (Blackwell and Sinclair 1995).

The range of prey species found in this study was very similar to that reported from other studies (Furness and Todd 1984; Hamer et al. 1997; Phillips et al. 1999; Thompson et al. 1995). Differences in the diet of fulmars between studies is probably a reflection of the availability of food and shows the opportunistic feeding behaviour of the birds around Shetland.

Gadids, particularly of the genus *Trisopterus*, were the most important diet of fulmars during incubation and chick-rearing in 1998 and 1999. Dead fish taken as discards from commercial fisheries form an important part of the diet of fulmars (Garthe and Hüppop 1994; Garthe et al. 1996). Because of the demersal life habits of most gadids, it is most likely that fulmars scavenged on them after they had been discarded from fish trawlers. The difference between mean lengths of Norway pout ($> 12\text{--}15 \text{ cm}$) and herring ($> 20\text{--}24 \text{ cm}$) in the diet (this

study) seems to be a result of the specific morphologies of these fish species: Norway pouts have larger diameters than herrings of the same length so that birds cannot swallow them as easily (Swennen and Duiven 1977).

Offal was an important prey for fulmars in our study. Offal was produced by commercial fisheries in large quantities and fulmars particularly feed on offal when following fishing vessels (e.g., Cramp and Simmons 1980).

Previous studies of the diet of fulmars have shown a strong selection for sandeels during the breeding season around Shetland (Fowler and Dye 1987; Furness and Todd 1984; Hamer et al. 1997; Phillips et al. 1999; Thompson et al. 1995). Sandeels were the most common fish prey of fulmars recorded between 1978 and 1982 on Foula (Furness and Todd 1984), but sandeel consumption decreased significantly during the 1990s (Hamer et al. 1997; Thompson et al. 1995). In 1998 and 1999, the occurrence of sandeels in regurgitates from fulmars was negligible. An obvious increase of fish offal and discarded fish in the diet of fulmars on Foula until 1995 (Hamer et al. 1997) and the high proportion in 1998 and 1999 support the assumption that low sandeel availability probably led to higher amounts of discarded fish (gadoids) and fish offal in the diet of fulmars. Crustaceans and squids seem only to be of minor importance as food for fulmars at the present time on Foula and Unst.

Differences in the diet between incubation and chick-rearing: discard versus non-discard

Changes of diet in the course of the breeding season could be detected. In our study, clupeids were an important prey component during the chick-rearing period. This could be explained by different energy densities of fish. Gadids generally have a lower energy density ($< 5 \text{ kJ/g}$ wet mass) than clupeids ($\geq 10 \text{ kJ/g}$ wet mass for lengths of $> 20 \text{ cm}$; Hilton et al. 1998; Hislop et al. 1991). The energy content of offal is also high (10 kJ/g) (Tasker and Furness 1996). It can therefore be advantageous for fulmars to specialise on selecting energy-rich fish such as clupeids or fish offal during chick-rearing, the period of the breeding cycle with the highest energy demand.

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References

- Blackwell BF, Sinclair JA (1995) Evidence of secondary consumption of fish by Double-crested Cormorants. *Mar Ecol Prog Ser* 123:1-4

- Blake BF, Dixon TJ, Jones PH, Tasker ML (1985) Seasonal changes in the feeding ecology of Guillemots *Uria aalge* off north and east Scotland. *Estuar Coast Shelf Sci* 20:559–568
- Brown EG, Pierce GJ (1998) Monthly variation in the diet of harbour seals in inshore waters along the southeast Shetland (UK) coastline. *Mar Ecol Prog Ser* 167:275–289
- Camphuysen CJ (1989) Diurnal rhythm of the Fulmar *Fulmarus glacialis* in the arctic summer. *Dan Ornithol Foren Tidsskr* 83:85–86
- Camphuysen CJ, Garthe S (1997) An evaluation of the distribution and scavenging habits of northern fulmars (*Fulmarus glacialis*) in the North Sea. *ICES J Mar Sci* 54:654–683
- Camphuysen CJ, van Franeker JA (1996) Jellyfish and fishery waste as food sources of Northern fulmars *Fulmarus glacialis* feeding around St Kilda. *Sula* 10:143–150
- Camphuysen CJ, van Franeker JA (1997) Notes on the diet of Northern fulmars *Fulmarus glacialis* from Bjørnøya (Bear Island). *Sula* 11:1–10
- Clarke MR (1986) A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford
- Cramp S, Simmons KEL (1980) The birds of the western Palearctic, vol 1. Oxford University Press, Oxford
- Cullen JM (1954) The diurnal rhythm of birds in the arctic summer. *Ibis* 96:31–46
- Duffy DC, Jackson S (1986) Diet studies of seabirds: a review of methods. *Colon Waterbirds* 9:1–17
- Falk K, Møller S (1995) Satellite tracking of high-arctic northern fulmars. *Polar Biol* 15:495–502
- Fowler JA, Dye AP (1987) Sandeels *Ammodytes marinus* in the diet of the fulmar *Fulmarus glacialis* in Shetland, Scotland. *Seabird* 10:71–74
- Furness RW, Bryant DM (1996) Effect of wind on field metabolic rates of breeding Northern fulmars. *Ecology* 77:1181–1188
- Furness RW, Burger AE (1988) Effects of energy constraints on seabirds breeding at high latitudes. *Proc Int Orn Congr* 19:1205–1215
- Furness RW, Camphuysen CJ (1997) Seabirds as monitors of the marine environment. *ICES J Mar Sci* 54:726–737
- Furness RW, Todd CM (1984) Diets and feeding of Fulmars *Fulmarus glacialis* during the breeding seasons: a comparison between St Kilda and Shetland colonies. *Ibis* 126:379–387
- Garthe S, Hüppop O (1994) Distribution of ship-following seabirds and their utilization of discards in the North Sea in summer. *Mar Ecol Prog Ser* 106:1–9
- Garthe S, Camphuysen CJ, Furness RW (1996) Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. *Mar Ecol Prog Ser* 136:1–11
- Hamer KC, Thompson DR, Gray CM (1997) Spatial variation in the feeding ecology, foraging ranges, and breeding energetics of northern fulmars in the north-east Atlantic Ocean. *ICES J Mar Sci* 54:645–653
- Härkönen T (1986) Guide to the otoliths of the bony fishes of the northeast Atlantic. Danbiu, Hellerup
- Harris MP, Wanless S (1986) The food of young Razorbills on the Isle of May and a comparison with that of young Guillemots and Puffins. *Ornis Scand* 17:41–46
- Harris MP, Wanless S (1993) The diet of Shags *Phalacrocorax aristotelis* during the chick-rearing period assessed by three methods. *Bird Study* 40:135–139
- Hatch SA (1989) Diurnal and seasonal patterns of colony attendance in the Northern Fulmar, *Fulmarus glacialis*, in Alaska. *Can Field-Nat* 103: 248–260
- Hatch SA (1990) Time allocation by Northern Fulmars *Fulmarus glacialis* during the breeding season. *Ornis Scand* 21:89–98
- Hatch SA, Nettleship DN (1998) Northern Fulmar (*Fulmarus glacialis*). In: Poole A, Gill F (eds.) *The Birds of North America*:361. The Birds of North America, Philadelphia, Pa.
- Hayward PJ, Ryland JS (1995) Handbook of the marine fauna of north-west Europe. Oxford University Press, Oxford
- Hilton GM, Houston DC, Furness RW (1998) Which components of diet quality affect retention time of digesta in seabirds? *Funct Ecol* 12:929–939
- Hislop JRG, Harris MP, Smith JGM (1991) Variation in the calorific value and total energy content of lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. *J Zool (Lond)* 224:501–517
- Lincoln RJ (1979) British marine Amphipoda: Gammaridae. British Museum (Natural History), London
- Moss R (1965) Diurnal rhythms of fulmars *Fulmarus glacialis* in the arctic autumn. *Ibis* 107:533–535
- Mougin JL (1967) Etude ecologique des deux especes des fulmars: le fulmar atlantique (*Fulmarus glacialis*) et le fulmar antarctique (*Fulmarus glacialisoides*). *Oiseau* 37:57–103
- Pennycuik CJ (1987) Flight of auks (Alcidae) and other northern seabirds compared with southern Procellariiformes: ornithological observations. *J Exp Biol* 128:335–347
- Pennycuik CJ, Croxall JP, Prince PA (1984) Scaling of foraging radius and growth rate in petrels and albatrosses (Procellariiformes). *Ornis Scand* 15:145–154
- Phillips RA, Petersen MK, Lillendahl K, Solmundsson J, Hamer KC, Camphuysen CJ, Zonfrillo B (1999) The diet of the northern fulmar *Fulmarus glacialis*: reliance on commercial fisheries? *Mar Biol* 135:159–170
- Skov H, Durinck J, Leopold MF, Tasker ML (1995) Important bird areas for seabirds in the North Sea including the Channel and the Kattegat. BirdLife International, Cambridge
- Swennen C, Duiven P (1977) Size of food objects of three fish-eating seabird species: *Uria aalge*, *Alca torda*, *Fratercula artica* (Aves, Alcidae). *Neth J Sea Res* 11:92–98
- Tasker M, Furness RW (1996) Estimation of food consumption by seabirds in the North Sea. In: Hunt GL, Furness RW (eds) *Seabird/fish interactions, with particular reference to seabirds in the North Sea*. ICES Coop Res Rep 216
- Tasker ML, Camphuysen CJ, Fossum P 1999 Variation in prey taken by seabirds. *ICES Coop Res Rep* 232:18–28
- Thompson DR, Furness RW, Lewis SA (1995) Diets and long-term changes in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in northern fulmars *Fulmarus glacialis* from two northeast Atlantic colonies. *Mar Ecol Prog Ser* 125:3–11
- Watt J, Pierce GJ, Boyle PR (1997) Guide to the identification of North Sea fish using premaxillae and vertebrae. *ICES Coop Res Rep* 220