

Spatial variation in the feeding ecology, foraging ranges, and breeding energetics of northern fulmars in the north-east Atlantic Ocean

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Northern fulmars (*Fulmarus glacialis*) are one of the most abundant birds in the North Atlantic Ocean and the two largest fulmar colonies in the UK are at St Kilda, Outer Hebrides and Foula, Shetland. These colonies are about 450 km apart and surrounded by waters that differ greatly in terms of potential food availability. Thus fish offal and whole fish discarded from whitefish trawlers are a major source of potential food in Shetland but not at St Kilda. Associated with this, previous studies have reported broad differences in diets and colony attendance patterns of adults at these two colonies, and have predicted better chick growth in Shetland than at St Kilda. More detailed information on differences between sites in the foraging behaviour and ranges of adults and the growth of chicks has not previously been available. This paper, therefore, presents detailed dietary analysis and uses land-based data to determine the durations and potential ranges of foraging trips by adults at the two colonies, feeding on different types of prey. Differences in the growth of nestlings at the two sites are described and explained, in terms of the body maintenance requirements of chicks, caloric density of food and variability in food provisioning rates by adults.

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Key words: procellariiform life histories, seabird-fishery interactions, strategic regulation of body mass.

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Introduction

The northern fulmar (*Fulmarus glacialis* L.) is one of the most numerous seabirds in the northern hemisphere, with a world population of 15–20 million breeding pairs (Lloyd *et al.*, 1991). For most of this millennium, fulmars bred within the UK only at St Kilda, Outer Hebrides. A southward colonization began from Iceland in the 18th century, reaching Shetland in 1878. Since then, fulmars have colonized most of the coasts of Britain and Ireland, and have spread as far south as France. However, the two largest concentrations of breeding fulmars in the UK are still in the Outer Hebrides and Shetland (120 000 and 240 000 pairs, respectively; Lloyd *et al.*, 1991). These two areas are about 450 km apart and lie in different oceanographic water masses that differ greatly in terms of potential availability of food to fulmars. Thus fish offal and whole

fish discarded from whitefish trawlers are major potential sources of food in Shetland (Hudson and Furness, 1989) but not at St Kilda, where comparatively few whitefish trawlers operate.

Associated with this difference in potential food supply, Furness and Todd (1984) reported broad differences in the diets of chicks and colony attendance patterns of adults at St Kilda and Shetland. Although the two areas were studied at different stages of the nestling period, adults in Shetland appeared to make shorter foraging trips on average, and the diet comprised a higher proportion of small fish and fish offal and a lower proportion of pelagic zooplankton in Shetland. However, meal sizes were not recorded, and so it was not possible to determine overall food provisioning rates of chicks. Nor has the growth of chicks been compared at the two sites, although Furness and Todd (1984) speculated that the additional food provided by

discards from trawlers may lead to better chick growth in Shetland.

This paper compares the diets, food provisioning rates and growth of nestling fulmars at St Kilda and Shetland. Food delivery is examined in terms of both feeding frequency and feed size (the amount of food received per chick per day); the term "meal size" is used to refer to food delivery by a single adult. We compare daily feeds in terms of both mass and caloric density of food, and we assess growth relationships for body weights of chicks in terms of both rate and elevation. Although restricted to the first half of the nestling period in a small number of years, to our knowledge this is one of the first papers to present a detailed quantitative analysis of spatial variation in provisioning and growth of chicks in a pelagic seabird.

Methods

Fieldwork was conducted during the first half of the chick-rearing period before chicks attained peak body weight, at Hirta, St Kilda (57°49'N 8°34'W) in 1994 and 1995 and at Foula, Shetland (60°08'N 2°05'W) in 1995. Food samples were collected from chicks in 1995 by inversion over a sealable polythene bag (chicks readily regurgitate in these circumstances) and stored frozen prior to analysis. In the laboratory, prey samples were allowed to thaw and were identified to the lowest possible taxon. Following [Thompson *et al.* \(1995\)](#), dietary items were treated on a presence/absence basis only, with no attempt made to quantify the size (volume) of prey material regurgitated nor to record the numbers of individuals of particular prey species. Fish and squid species were identified from sagittal otoliths and beaks, respectively. Samples varied from fresh to partly digested, and even those most digested allowed easy recognition of fish offal and contained enough hard material for identification of invertebrates. The water content and caloric density of a separate sample of regurgitates were determined by drying to constant mass followed by homogenization in an electric mill and direct combustion of weighed subsamples in a Gallenkamp ballistic bomb calorimeter calibrated with benzoic acid.

In order to examine provisioning and growth rates of chicks, in each case a sample of chicks not used for collection of food samples was measured (maximum flattened chord of right wing excluding down to the nearest millimetre with a stopped wing rule) within a few days of hatching in mid-July. The ages of chicks were not known precisely but were estimated from wing lengths calibrated against growth in birds of known age ([Hamer and Thompson, 1997](#)). Chicks generally receive small meals for the first few days post-hatching ([Warham, 1990](#)). The masses of food fed each day to chicks estimated to be over 5 d old were determined by

weighing them at 4 h intervals throughout the first 4 d of the study and at 8 h intervals (at 0700 h, 1500 h and 2300 h BST) for the following 10 d in each case. In addition, chicks at St Kilda were weighed at 4 h intervals over the final 2 d of the study in 1995. We were careful to approach chicks quickly and handle them gently, and none regurgitated food during handling. A few chicks ejected small quantities of stomach oil when being approached, but this was of negligible mass.

Increases in chick weight between weighings resulted from feeding by adults, and the weight of food delivered to chicks each day was calculated from the sum of positive weight increments between repeated weighings (referred to here as SUM). This under-estimated total food delivery by an amount equivalent to the weight lost by chicks through respiration and excretion between weighings. To account for this we examined rates of weight loss by chicks over 4 h intervals both prior to and after feeding, in relation to both body weight and body size (wing length). In all three groups the rate of weight loss (w , in g h^{-1}) prior to feeding was related to initial body weight but not to wing length ($p < 0.01$ in each case):

$$\text{St Kilda, 1994; } w = 0.01 \text{ (S.E. } \pm 0.003) \\ \text{(initial weight) + 0.05 (S.E. } \pm 1.0) \quad (1)$$

$$\text{St Kilda, 1995; } w = 0.01 \text{ (S.E. } \pm 0.003) \\ \text{(initial weight) + 0.96 (S.E. } \pm 1.4) \quad (2)$$

$$\text{Foula, 1995; } w = 0.02 \text{ (S.E. } \pm 0.006) \\ \text{(initial weight) - 1.16 (S.E. } \pm 1.03) \quad (3)$$

Following a feed, weight loss occurred at a higher rate and was similarly related to initial weight but not wing length ($p < 0.01$ in each case):

$$\text{St Kilda, 1994; } w = 0.01 \text{ (S.E. } \pm 0.003) \\ \text{(initial weight) + 2.24 (S.E. } \pm 1.0) \quad (4)$$

$$\text{St Kilda, 1995; } w = 0.01 \text{ (S.E. } \pm 0.004) \\ \text{(initial weight) + 2.59 (S.E. } \pm 1.3) \quad (5)$$

$$\text{Foula, 1995; } w = 0.02 \text{ (S.E. } \pm 0.006) \\ \text{(initial weight) + 0.14 (S.E. } \pm 1.24) \quad (6)$$

These regression equations were used to estimate weight loss over 4 h intervals, using the appropriate set of equations for each combination of year and site. Initially, each weight increment was corrected using Equations (1)–(3) (i.e. assuming an absence of feeding). Only if the corrected weight increment was greater than 10 g did we then recalculate the rate of weight loss using Equations (4)–(6). This might have excluded some small meals, but these would have been rare (assuming a normal distribution of meal size) and of little nutritional value to the chick.

In the absence of further feeding, weight loss by chicks is typically a negative exponential function of time over

prolonged periods. However, in the fulmar at least, average rates of weight loss following a feed are almost identical over periods of 4 h and 8 h, indicating a linear relationship for periods up to 8 h (Hamer and Thompson, 1997). Moreover, this relationship does not alter with chick age, at least up to about 35 d post-hatching (Hamer and Thompson, 1997). Equations (1)–(6) above were therefore used to adjust estimates of SUM obtained from weight increments over 8 h intervals.

Feeds result from delivery of food to the chick by either one or both parents. In order to examine meal size and feeding frequency separately, we used data collected at 4 h intervals to determine the masses of food delivered to chicks on each visit by one or other parent (hereafter termed meals). Direct observations of nest attendance by adult fulmars at St Kilda (Furness and Todd, 1984) indicated that at this colony each parent visited its chick every 29 h on average, and that individual birds were highly unlikely to return twice within 12 h. In this study, therefore, individual meal sizes at St Kilda were calculated from instances when chicks were fed on two occasions during a 12 h period. To avoid instances when chicks were weighed part-way through a meal, we used only those occasions when chicks were fed twice within 12 h separated by a period of at least 4 h with no feed.

On Foula, individual parents may return twice within 12 h (Furness and Todd, 1984) and so feeds received within 12 h of each other may in some cases result from feeding by both parents. To account for this, we used the method described by Ricklefs (1984) and Bolton (1995) to estimate the amount of food delivered by a single adult during a feeding visit. If the probability that an adult feeds its chick over a given 4 h interval is p , then the frequency of double feeds (p^2) can be calculated from the observed proportion of intervals when no food was received $[(1 - p)^2]$. This approach allowed division of recorded weight increases for chicks fed on two separate occasions over a period of 12 h. One division resulted from feeds by both parents; the other resulted from food delivery by a single parent, assuming that if both parents fed their chick during the same interval, the resulting increase in chick weight would be greater than that produced by a single feed. To ensure uniformity of methods between sites, this correction was also applied to data for St Kilda, although in practice it did not affect estimates of meal size at that site.

Results

Diets at the two colonies

The occurrence of particular prey species in the diets of fulmars at St Kilda and Foula is summarized in Table 1. Fish and/or fish offal occurred in virtually all samples at Foula, with other prey types occurring relatively

infrequently. Fish were also present in 90% of samples from St Kilda, but these were generally represented by small juvenile individuals, as determined from otolith size. In contrast to Foula, 32% of food samples from fulmars at St Kilda contained crustacean prey, mainly the amphipod *Hyperia galba* and the decapod *Acantheephyra pelagica*. The minute parasitic copepod *Caligus elongatus* occurred in only 8% of samples at St Kilda but in 35% of a subset of samples from Foula. Three species of mesopelagic fish (*Scopelogadus beanii*, *Lampadena speculigera* and *Benthosema glaciale*) were found in 10% of samples from St Kilda, whereas only one sample (1%) from Foula contained such prey.

Age-specific pattern of food delivery

The pattern of chick feeding at the two colonies was examined by dividing the data for each combination of site and year into 5 d age classes, with data aggregated to give mean values for each chick in each age class. Figure 1 shows the growth of chicks in terms of wing length at St Kilda in 1994 and 1995 and on Foula in 1995. An analysis of covariance for chicks aged 6–25 d post-hatching revealed no differences among groups in either slope ($F_{2,152}=1.0$, $p=0.4$) or elevation ($F_{2,154}=3.1$, $p=0.1$). We were confident, therefore, that wing length was a consistent index of chick age in all three groups.

Meal size

The mean sizes of individual meals recorded at 4 h intervals were 80.8 g ($n=34$, S.D. ± 21.0) at St Kilda in 1994, 84.4 g ($n=26$, S.D. ± 39.4) at St Kilda in 1995 and 42.1 g ($n=29$, S.D. ± 18.7) on Foula in 1995, with maximum values of 120 g, 130 g and 60 g, respectively. We used these maxima to estimate the number and sizes of meals received per chick per day (e.g. for St Kilda in 1994 we concluded that daily SUMs exceeding 120 g represented feeds by both parents, that SUMs exceeding 240 g resulted from receipt of at least three meals, etc.). This method tended to underestimate feeding frequency, although a detailed analysis of data for St Kilda in 1994 (Hamer and Thompson 1997) indicated that any bias was small.

Mean meal sizes estimated from daily SUMs (Table 2) were very similar to values recorded over 4 h intervals. Estimated meal size was significantly smaller on Foula in 1995 than at St Kilda in either year (two-way ANOVA followed by multiple range tests; $F_{2,146}=237.8$, $p<0.001$). Meal size also differed significantly among age classes ($F_{3,146}=4.7$, $p=0.01$) although the effect was slight and confined primarily to St Kilda in 1995, where estimated meal size increased from 83 g at age 5–10 d to 92 g at age 20–25 d.

Table 1. Prey of fulmars at St Kilda and Foula determined from regurgitations by chicks. Values are numbers and percentage of samples containing a particular prey category. Data are a combination of those from Thompson *et al.* (1995) and from the present study.

Species	St Kilda		Foula	
	n	%	n	%
Crustacea				
<i>Hyperia galba</i>	15	17	—	—
<i>Eurydice</i> sp.	2	2	1	1
<i>Acantheephyra pelagica</i>	13	15	—	—
Unidentified crustaceans	4	5	6	4
Total crustaceans	28	32	7	5
<i>Caligus elongatus</i>	7	8	13*	35
Cephalopoda				
<i>Gonatus steenstrupi</i>	4	5	—	—
Unidentified squid	2	2	1	1
Total cephalopods	6	7	1	1
Pisces				
<i>Trisopterus luscus</i>	1	1	—	—
<i>Trisopterus esmarkii</i>	4	5	16	11
<i>Trisopterus minutus</i>	2	2	—	—
<i>Micromesistius poutassou</i>	5	6	1	1
<i>Melanogrammus aeglefinus</i>	1	1	1	1
<i>Merlangius merlangus</i>	10	11	—	—
<i>Pollachius virens</i>	—	—	2	1
<i>Callionymus lyra</i>	1	1	—	—
<i>Ammodytes marinus</i>	4	5	22	15
<i>Gadiculus argenteus</i>	1	1	1	1
<i>Argentina sphyraena</i>	—	—	1	1
<i>Scopelogadus beanii</i>	7	8	—	—
<i>Lampadena speculigera</i>	1	1	—	—
<i>Benthosema glaciale</i>	1	1	1	1
Unidentified whitefish	40	46	74	51
Other unidentified fish	3	3	5	3
Fish offal	—	—	42	29
Total fish	78	90	144	99
Total number of samples	87		146	

*From a subset of 37 samples.

Feeding frequency, intervals between feeds and timing of feeds

The number of meals received per chick per day increased progressively with chick age (Table 3; two-way ANOVA for chicks up to 25 d post-hatching; $F_{3,146}=28.3$, $p<0.001$) and also differed significantly among groups ($F_{2,146}=243.1$, $p<0.001$). Multiple range tests indicated that at all ages studied, feeding frequency was consistently higher on Foula than at St Kilda, with no significant difference between years at St Kilda.

Feeding frequency gives little indication of the maximum intervals between feeding events for individual chicks. Figure 2 shows the frequency distribution of intervals between feeds, whether resulting from single or double meals, for each group of chicks. Long intervals were more likely to span the beginning or end of each recording period, and so would be under-represented. To overcome this problem, all intervals ending within

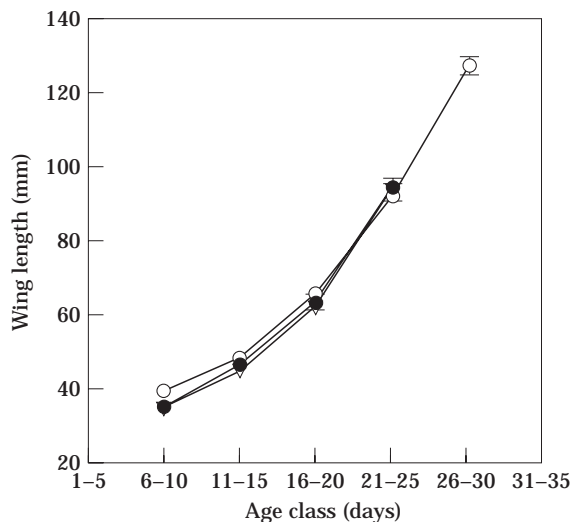


Figure 1. Growth in wing length of fulmar chicks at St Kilda in 1994 (open circles) and 1995 (closed circles) and on Foula in 1995 (open triangles). Error bars are ± 1 S.E.

the first 16 h or starting within the final 16 h of the recording period were excluded. The mean and maximum intervals between feeding events were, respectively, 16.2 h and 80 h at St Kilda in 1994; 12.3 h and 48 h at St Kilda in 1995; and 9.9 h and 32 h on Foula in 1995.

Table 4 shows the proportions of feeds at different times of day in each group. Feeding frequency differed significantly with time of day at St Kilda in 1994 ($\chi^2_5=26.0$, $p<0.001$) and 1995 ($\chi^2_5=24.1$, $p<0.001$), but not on Foula in 1995 ($\chi^2_5=6.9$, $p=0.2$). At St Kilda in both years the probability of feeding was highest between 0300 and 0700 h, and 1500 and 2300 h, and lowest between 1100 and 1500 h, and 2300 and 0300 h.

Provisioning and growth of chicks

There were significant differences among groups in the growth of chicks in terms of body weight (Fig. 3). Analysis of covariance followed by multiple pairwise comparisons indicated that chicks at St Kilda in either year were consistently heavier for their age than chicks on Foula in 1995 ($F_{2,245}=5.9$, $p=0.001$), although there was no difference among groups in the slope of this relationship ($F_{2,242}=0.3$, $p=0.8$), and there were no differences in slope or elevation between the 2 years at St Kilda. This difference in growth between sites could have resulted from differences in food provisioning rate, quality of food (mainly in terms of caloric density) and/or metabolic energy requirements of chicks.

Daily food provisioning

The total amount of food received per chick per day is the product of meal size (Table 2) and feeding frequency

Table 2. Age-specific variation in sizes of meals (g) delivered to fulmar chicks at St Kilda in 1994 and 1995 and on Foula, Shetland in 1995. n is the number of chicks in each age class.

Age class (d)	St Kilda 1994			St Kilda 1995			Foula 1995		
	n	Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.
6–10	6	83.1	19.2	12	83.0	16.6	20	47.0	5.0
11–15	10	73.2	10.8	17	85.6	15.2	17	50.3	2.5
16–20	17	81.6	7.1	15	91.4	9.1	17	51.6	2.1
21–25	16	85.5	5.6	5	91.6	6.1	6	53.4	2.7
26–30	10	88.0	9.8						

Table 3. Age-specific variation in frequency of meals delivered to fulmar chicks at St Kilda in 1994 and 1995 and on Foula, Shetland in 1995. Values are mean numbers of meals per chick per day. n is the number of chicks in each age class.

Age class (d)	St Kilda 1994			St Kilda 1995			Foula 1995		
	n	Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.
6–10	6	1.17	0.41	12	1.26	0.30	20	2.05	0.48
11–15	10	1.63	0.31	17	1.69	0.28	17	2.94	0.34
16–20	17	1.82	0.28	15	1.89	0.29	17	3.80	0.56
21–25	16	2.17	0.45	5	2.47	0.40	6	4.58	0.86
26–30	10	2.29	0.16						

(Table 3). Daily provisioning rate increased progressively with chick age in all three groups, from ca. 100 g d⁻¹ at age 6–10 d to ca. 240 g d⁻¹ at age 21–25 d (Fig. 4). An analysis of covariance followed by multiple pairwise comparisons indicated no difference in slope or elevation between the two sites in 1995, but a lower rate of increase in provisioning rate with chick age at St Kilda in 1994 ($F_{2,152}=5.9$, $p=0.03$), although the average daily rate of provisioning for chicks aged 6–25 d was very similar in the three groups (152 g d⁻¹, 153 g d⁻¹ and 156 g d⁻¹ for St Kilda in 1994 and 1995 and Foula in 1995 respectively).

Caloric density of food

There was no significant difference in the caloric density or water content of food delivered to chicks at the two sites in 1995 (Table 5; t-tests using pooled variance estimates for arcsine transformed data; for water content, $t_{53}=0.43$, $p=0.7$; for caloric density, $t_{53}=1.39$, $p=0.2$).

Chick maintenance requirements

Food requirements for body maintenance of chicks in each age class were calculated by regressing daily food delivery upon net change in body weight over 24 h, from 2300 h one day until 2300 h the next (referred to here as NET). The intercept on the y-axis (i.e. when NET=0) was taken as the food requirement for zero-growth, following Hamer (1994). This differed significantly among age classes (two-way ANOVA; $F_{3,40}=17.0$,

$p<0.001$) and at all ages was higher on Foula in 1995 than in either year at St Kilda (Fig. 4; $F_{2,40}=4.5$, $p=0.02$).

Discussion

The possibility that repeated weighing of chicks may reduce their feeding rates was raised by Payne and Prince (1979) but has seldom been tested, although Hamer and Hill (1993) and Hamer (1994) found no evidence of any adverse effects of weighing nestling Cory's shearwaters (*Calonectris diomedea* Scopoli) and little shearwaters (*Puffinus assimilis* Gould) at 4 h intervals overnight. In this study careful temporary removal of chicks from nests occupied by adults elicited little obvious response and the body condition of fulmar chicks after 14 d of repeated weighing was no different than that of chicks weighed for the first time on the same day (see Hamer and Thompson, 1997). In keeping with some other species of Procellariiformes, fulmar chicks tend to spit stomach oil at individuals of the same or other species approaching the nest (Warham, 1990). However, chicks quickly became used to handling and reductions in body-weight resulting from ejection of stomach oil were negligible.

Food supply and feeding rates of chicks

Diets of chicks at the two colonies indicated that fulmars made extensive use of discarded fish and fish offal from

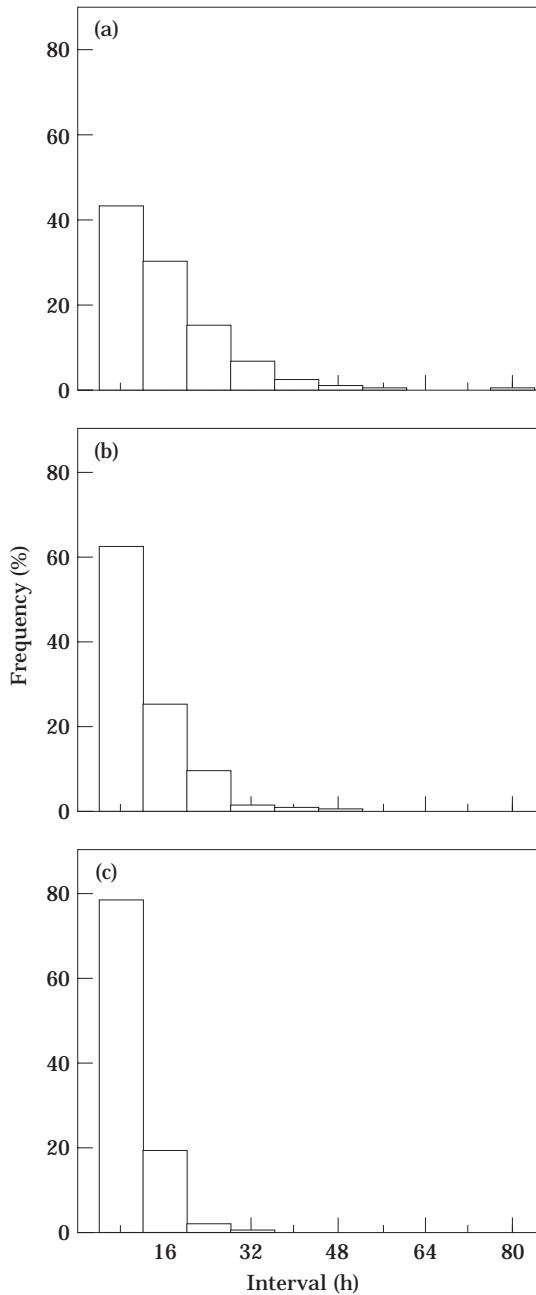


Figure 2. Frequency distribution of maximum intervals between feeds delivered to fulmar chicks at St Kilda in 1994 (top) and 1995 (middle) and on Foula in 1995 (bottom). $n=320$, 346 and 505 intervals, respectively. Feeds resulted from delivery of food by one or both parents.

whitefish trawlers in Shetland but not at St Kilda, where the diet comprised a high proportion of crustaceans and small, juvenile fish (Table 1). Furness and Todd (1984) found a similar difference between sites, although we found that the diets of chicks at both locations were

Table 4. Proportions of feeds delivered to fulmar chicks at different times of day at St Kilda in 1994 and 1995 and on Foula, Shetland in 1995. $n=119$ feeds on St Kilda in 1994, 76 feeds on St Kilda in 1995 and 93 feeds on Foula in 1995.

Time of day	Proportion of total feeds (%)		
	St Kilda 1994	St Kilda 1995	Foula 1995
2300–0300	6.7	5.3	12.9
0300–0700	25.2	29.0	15.1
0700–1100	21.0	14.5	21.5
1100–1500	8.4	11.8	17.2
1500–1900	12.6	21.1	20.4
1900–2300	26.1	18.4	12.9

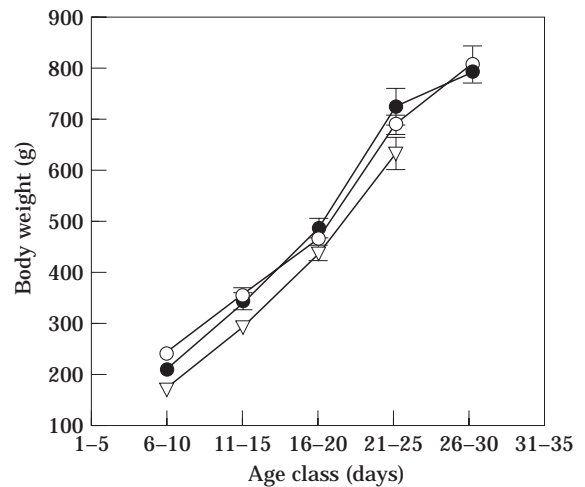


Figure 3. Growth in body weight of fulmar chicks at St Kilda in 1994 (open circles) and 1995 (closed circles) and on Foula in 1995 (open triangles). Error bars are ± 1 S.E.

considerably broader than previously reported. Mesopelagic crustaceans and fish were recorded in the diet at both sites but much more frequently at St Kilda than on Foula (Table 1). These items were unlikely to have been discarded by trawlers or forced to the surface by predatory fish or mammals (see Thompson *et al.*, 1995), but they may migrate vertically at night (Whitehead *et al.*, 1989). As noted by Steele and Montecvecchi (1994) and Thompson *et al.* (1995), seabirds may provide independent data about the distributions of such deep-dwelling species within the water column, and complement information obtained by conventional sampling techniques.

Coinciding with the use of discards by adults at Shetland, age-specific feeding frequencies of chicks were much higher here (Table 3) and maximum intervals between feeds for individual chicks were lower here (Fig. 2) than at St Kilda. This resulted in a lower coefficient of variation in feeding frequency at Foula (mean across all ages=17.1%) than at St Kilda (mean

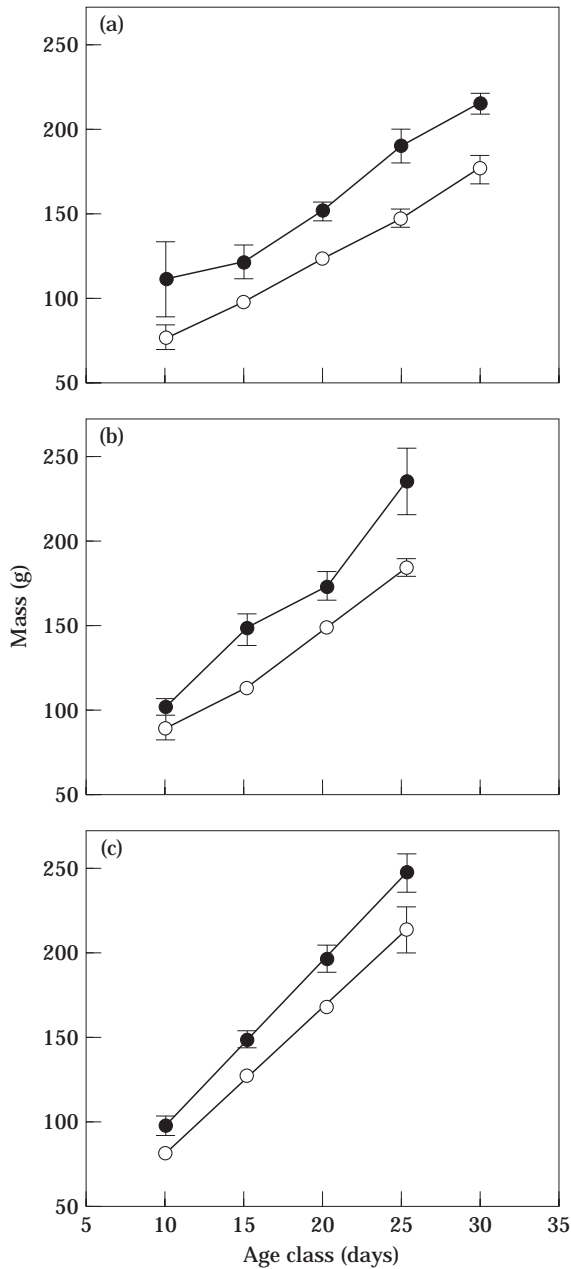


Figure 4. Variation in daily food delivery and food requirement for zero-growth in fulmar chicks at St Kilda in 1994 (top) and 1995 (middle) and on Foula in 1995 (bottom). Error bars are ± 1 S.E. Solid circles are mean mass of food delivered ($\text{g chick}^{-1} \text{d}^{-1}$); open circles are mean mass of food required for zero growth ($\text{g chick}^{-1} \text{d}^{-1}$).

across both years for chicks of comparable age, i.e. 6–25 days post-hatching = 20.3%; calculated from data in Table 3). In addition to differences in feeding frequency, meal sizes were about 40% smaller on Foula (Table 2), with much lower coefficients of variation (mean for chicks of comparable ages = 6.2% and 13.5% at Foula

Table 5. Water content and caloric density of food delivered to fulmar chicks at St Kilda and Foula in 1995. $n=25$ samples for St Kilda, 30 samples for Foula. Caloric density is expressed in terms of wet weight in each case.

Site	% Water		Caloric density (kJ g^{-1})	
	Mean	S.D.	Mean	S.D.
St Kilda	76.0	5.0	5.77	1.54
Foula	75.5	3.8	6.55	1.72

and St Kilda, respectively; calculated from data in Table 2). This resulted in similar age-specific provisioning rates at the two sites (Fig. 4), but with much lower variability on Foula than at St Kilda (mean coefficient of variation for chicks aged 6–25 days = 4.5% and 7.7%, respectively).

Although there were clear differences in feeding frequency between sites, chicks at both St Kilda and Foula were nonetheless fed more frequently than those of many other procellariiform species elsewhere (Ricklefs *et al.*, 1985; Hamer and Hill, 1993; Bolton, 1995; Lorentsen, 1996). This coincided with a comparatively high water content and low caloric density of food (Table 5), indicating that in contrast to some other species (Roby *et al.*, 1989) there was no substantial modification of prey before delivery to the chick. In this context, fulmars appear to be closer to diving petrels (Pelecanoididae), which also feed their chicks comparatively frequently (e.g. on 98% of chick-nights; Payne and Prince, 1979), than to species such as storm petrels that feed their chicks infrequently and rely on the formation of stomach oil from ingested prey in order to meet the energy requirements of the chick (Place *et al.*, 1989; Obst and Nagy, 1993).

Trip durations and foraging ranges of adults

At both sites, feeding frequencies of chicks were lowest at age 6–10 d post-hatching (Table 3), presumably reflecting the low food requirements of chicks at this age and the fact that chicks are brooded almost continuously by one or other parent until about 10 d post-hatching (Fisher, 1952; Furness and Bryant, 1996). Beyond this age adults spend little time at the colony (generally around 1 h d^{-1} ; Furness and Todd, 1984) and so feeding frequencies of chicks give a more direct indication of the durations of foraging trips by adults. For chicks aged 11–25 d post-hatching, the average intervals between individual meals (as opposed to feeds resulting from one or more meals) were 13.0 h and 12.2 h at St Kilda in 1994 and 1995, respectively, and 6.6 h on Foula in 1995. Assuming that each adult fed its chick independently of its partner and spent 1 h d^{-1} at

the nest, these data correspond to trip durations by individual adults of 25 h, 23 h, and 12 h, respectively. The two estimates for St Kilda are similar to the mean trip duration of 29 h obtained at this site by Furness and Todd (1984) from observations of adult attendance at the nest over a continuous period of 48 h. The estimate for Foula (12 h) is twice that obtained by Furness and Todd (1984) at a similar stage of the nestling period, presumably reflecting lower food availability on Foula during the present study. In both 1994 and 1995 at St Kilda, only around 5% of feeds were delivered during hours of darkness and there was a peak in feeding frequency during the early morning (Table 5), indicating possible nocturnal feeding by adults. This is also indicated by the presence in the diet of prey that migrate vertically at night (Table 1). By contrast, there was no diurnal pattern to food delivery on Foula.

Theoretically, the most energy efficient airspeed for fulmars is around 36 km h^{-1} , although in terms of ground speed this figure will be reduced by non-linear flight (Pennycuik *et al.*, 1984). In keeping with this, Falk and Møller (1995) recorded an average ground speed of 20.4 km h^{-1} for satellite-tagged adults during flights up to 100 km in length. Without allowing for time spent foraging, and assuming that adults make outward and return journeys at the same speed along the same track, estimated trip durations of 24 h and 12 h would give potential foraging ranges of 245 km and 122 km at St Kilda and Foula respectively. These data suggest that at least during the nestling period, breeding adults from the two colonies are unlikely to meet. A dual foraging strategy involving regular alternation of long and short foraging trips by individual birds (Weimerskirch *et al.*, 1994) would extend the potential maximum range of breeding adults considerably, although there is no evidence for such a strategy in fulmars.

Provisioning and growth of chicks

Coinciding with the availability of discards from trawlers in Shetland, fulmar chicks at Foula in 1995 maintained consistently lower body weights than those at St Kilda in both of the two years studied. Although further data are required for additional years to confirm this difference, it apparently does not support the prediction by Furness and Todd (1984) that chicks in Shetland should exhibit "better" growth than those elsewhere. There was no difference between sites in either overall provisioning rates of chicks (Fig. 4) or in the caloric density of the food provided by adults (Table 5). Rather, the lower body weights of chicks at Foula appeared to result from higher maintenance requirements (mean zero-growth requirement for chicks aged 6–25 d = 149 g and 118 g at Foula and St Kilda, respectively; Fig. 4), possibly due to higher costs of maintaining body temperature at Foula as a result of

differences in climate at the two sites. For instance the July mean daily temperature is ca. 3 deg C higher at St Kilda than at Foula (London Meteorological Office, 1952).

The fact that provisioning rates of chicks were similar at the two sites despite differences in body maintenance requirement suggests that adults may have been unresponsive to changes in nestlings' nutritional requirements, as is the case in some other species of Procellariiformes (Hamer and Hill, 1993; Hamer, 1994; Ricklefs and Schew, 1994). However, fulmars appear to be capable of modifying the rate of food delivery to the nest in response to short-term changes in a chick's nutritional status (Hamer and Thompson, 1997), and an alternative explanation is that the lower body weights of chicks at Foula resulted from adults adjusting the pattern of food delivery in response to the presence of a more reliable food supply at this site. In keeping with other procellariiforms, fulmars accumulate large quantities of lipid during the nestling period, much of which is subsequently shed prior to fledging (Warham, 1990). These reserves appear to serve, at least in part, as a buffer against highly variable food delivery resulting from stochastic variation in the foraging success of adults at sea (Ricklefs and Schew, 1994; Hamer and Hill, 1987). By utilizing fishery waste, fulmars in Shetland were able to increase feeding frequency (Table 3) and decrease meal size (Table 2), both of which acted to reduce the variability in overall food provisioning rate (see above). Chicks would not therefore require such large lipid reserves in order to reduce the impact of variable food provisioning by the parents, and so adults would not need to increase total food supply to the chick, despite higher body maintenance requirements in Shetland. Thus, inasmuch as they were fed less variably and may therefore have required smaller lipid reserves, chicks in Shetland in 1995 may in fact have been growing "better" than those elsewhere, as predicted by Furness and Todd (1984). This notion is supported to some extent by the fact that inexperienced Antarctic fulmars (*Fulmarus glacialis* Smith) fed their chicks larger meals less frequently than more experienced birds, and that chicks reared by inexperienced pairs had higher growth rates in terms of body weight (Weimerskirch, 1990). However, it is unclear to what extent differences in growth of body weight are due to differences in lipid accumulation, and further data are required to address this hypothesis.

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