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Diet of the northern fulmar *Fulmarus glacialis*: reliance on commercial fisheries?

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Abstract The massive expansion in breeding numbers and range of the northern fulmar *Fulmarus glacialis* over the last two centuries is generally attributed to an increased availability of fish offal and discarded fishes from commercial fisheries. This implies that discards should be a major component in fulmar diets in the more recently colonised areas in the south of their range. This paper examines the contemporary diet of the northern fulmar at three major breeding sites, Fair Isle (Shetland, UK), Iceland and Disko Fjord (western Greenland). At Fair Isle, 89% of regurgitates contained fishes, with sandeels (Ammodytidae) recorded in 37%; 32% contained crustaceans (mainly decapods); 8% contained squid. There was also a temporal trend; sandeels declining and crustaceans increasing in the diet from July to August. In Iceland, fishes were also the main prey (47 to 93% of wet mass), with sandeels common in the south and west, and capelin (*Mallotus villosus*) in the north and east. Other fish species were mainly discards, and together with discarded decapods and fish offal formed 5 to 72% of the diet, depending on the sector. Euphausiids, amphipods and copepods constituted 3 to 13% of the diet. At Disko, 39% of samples contained fishes, 64% contained crustaceans (mainly amphipods), 22% contained squid, and 16% contained pteropods. There was a clear temporal trend, with the bulk of the samples made up of crustaceans in mid-June, capelin from late June to late July, and crustaceans and pteropods from late July to late August. An extensive review of published studies was also carried out. The general pattern was for birds in more southerly populations to consume more discarded fishes, fish offal and benthic invertebrates. However, a considerable proportion of their diet also consisted of juvenile gadids, sandeels, capelin and pelagic zooplankton, which fulmars catch for themselves, and we suggest that breeding adults in the south are less dependent on fishing waste than is generally assumed.

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Introduction

The northern fulmar *Fulmarus glacialis* is a widespread and abundant seabird, with a world population of 15 to 20 million breeding pairs, of which 2 to 4 million breed in the western Palaearctic (Lloyd et al. 1991; Snow and Perrins 1998). Historically, its breeding distribution in the North Atlantic was restricted to Arctic regions, with the exception of a single colony located at St Kilda, Outer Hebrides, UK (Fisher 1952). During the mid-1700s, a gradual southward expansion is thought to have begun from Iceland through the Faroes, Shetland and Orkney, and down the British and Irish coasts to the Channel Islands and France (Snow and Perrins 1998). Fisher (1952) postulated that this expansion resulted from increased availability of offal from whaling, and latterly of fish offal and discarded fishes from commercial fisheries. This was disputed by Wynne-Edwards (1962) and Salomonsen (1965), who both argued that a behavioural or genetic transformation must have taken place and a colonising form have emerged amongst the boreal fulmar population which was able to spread into lower latitudes. In addition, Brown (1970) hypothesised that a gradual change in sea temperature or oceanographic conditions may have taken place.

Fulmars in the high Arctic appear not to rely on fisheries (Mehlum and Gabrielsen 1993; Weslawski et al. 1994). By contrast, the majority of offal or small fishes discarded by whitefish trawlers is eaten by fulmars in Shetland and the North Sea (Hudson and Furness 1989; Camphuysen and Garthe 1997), and it is generally assumed that fulmars rely heavily on discarding at southerly latitudes. However, the spatial overlap between fulmars and commercial fisheries is far from complete (Camphuysen et al. 1995), and while it is indisputable that northern fulmars are major consumers of fishery waste in the southern part of their range, the extent to which their distribution is or was, constrained by the availability of this resource is debatable.

This paper presents detailed information on the diet of the northern fulmar in three major areas: (i) Fair Isle (Shetland), the third largest colony in the UK with 43 000 pairs counted in 1996 (Riddington et al. 1997), (ii) Iceland, around which an estimated 4 350 000 birds are present during the breeding season (Lilliendahl and Solmundsson 1997), and (iii) Qeqertaq, Disko Fjord (western Greenland), the largest colony in Greenland, with ~85 000 birds present during the breeding season. Both Fair Isle and Iceland are located within regions of heavy commercial exploitation of fish stocks, and consequently discards could be expected to form a major portion of the diet. In contrast, there are few large-scale commercial fisheries and presumably limited discarding off western Greenland, and the diet of this colony would presumably be closest to that of ancestral, high-latitude fulmar populations, with little reliance on fishing waste. We also present an extensive review of previous diet studies for this species, and discuss spatial and seasonal patterns in the importance of different food resources. In addition, possible biases inherent in sampling methodologies are investigated using data from regurgitates and stomach contents of chicks collected during a single season on Fair Isle.

Materials and methods

Fair Isle, Shetland

Regurgitates were obtained from adult and chick *Fulmarus glacialis* on Fair Isle, Shetland (59°32′N; 1°38′W) in June to August 1997, with the great majority collected in July and August during chick-rearing. Regurgitation was not forced, and therefore although samples provided reasonably unbiased data on recently-ingested prey, they were unlikely to constitute the full contents of the proventriculus. In addition to the regurgitates, 23 fulmar chicks varying in age from 10 to 60 d (mean of 29 d) were collected under license from the same colony for a separate study on body composition. Chicks were later dissected, and the contents of the proventriculus and gizzard were removed for examination. Prey items were identified to the lowest possible taxonomic level using standard guides (Clarke 1986; Härkönen 1986; Watt et al. 1997) and comparative reference material.

Iceland

A total of 284 adult fulmars were shot at sea at 37 locations around Iceland between 31 May and 6 August in 1994 and 1995. Soon after collection, the stomachs were removed and preserved in alcohol until examination of their contents. Fresh prey items were found in the proventriculus of 164 birds. Prey were identified to species where possible; hard parts were measured and converted to fresh mass using length–mass formulae. Our own information on length–mass relationships were used (Lilliendahl and Solmundsson unpublished data), except in the case of squid (Clarke 1986) and hyperiids (Pakhomov and Perissinotto 1996). In order to avoid over-estimation of the importance of prey with slowly digestable hard parts, the analysis was based only on food items with flesh attached. Sampled birds were assigned to one of five marine sectors around Iceland (details in Lilliendahl and Solmundsson 1997).

Disko Fjord, Greenland

Regurgitations were obtained by water-offloading of adult fulmars caught on Qeqertaq in Disko Fjord (69°3′N; 54°4′W) in June to August 1992 and 1993. Prey items were identified using standard reference guides (Stephensen 1928, 1942; Clarke 1986; Härkönen 1986; Koszteyn et al. 1991). For temporal comparison, samples were split into three periods: Period 1, prior to ice break-up in Disko Fjord (11 to 14 June); Period 2, when capelin (*Mallotus villosus*) were spawning inside Disko Fjord (15 June to 27 July); Period 3, after capelin spawning had finished (28 July to 30 August).

Previous published studies of fulmar diet including quantitative data with reasonable sample sizes are also reviewed.

Results

Fair Isle, Shetland

Comparison between sample types

In total, 118 regurgitates plus 16 proventriculi and 10 gizzards from the dissected *Fulmarus glacialis* chicks contained identifiable prey items (Table 1). There was little variation between regurgitates collected from adults and chicks and proventricular contents of dissected chicks in the proportion containing fishes, crus-

Table 1 *Fulmarus glacialis*. Comparison (number and percentage containing different prey remains) between samples of diet at Fair Isle, 1997

Prey type	Adult and chick regurgitates (n = 118) n (%)	Chick Proventricular contents (n = 16) n (%)	Chick gizzard contents (n = 10) n (%)
Fishes	105 (89)	14 (88)	8 (80)
Sandeels	44 (37)	2 (13)	– (–)
Crustaceans	38 (32)	7 (44)	– (–)
Decapod crustaceans	31 (26)	5 (31)	– (–)
Squid	9 (8)	1 (6)	5 (50)

taceans or squid. However, chick gizzards were much more likely to contain squid and less likely to contain crustacean remains than the other two types of sample.

Prey species

Table 2 provides a detailed breakdown of prey items found in regurgitates. Fulmars at this colony consumed a diverse range of crustaceans and fish species. Although many fish otoliths and vertebrae were eroded and therefore of no use for determining species or exact fish size, it was clear from the otolith morphology that the gadid prey included many small juvenile fishes which, along with sandeels (Ammodytidae), were probably caught at the surface or by pursuit-diving. Many other samples comprised larger, older gadids (presumably the hosts for *Caligus elongatus*) obtained as discards. Very little fish offal was recorded (1% of samples only).

The crustaceans included the lobster *Nephrops norvegicus*; the hyperiid amphipod *Hyperia galba*, which may live in association with and be ingested along with medusae; the isopod *Eurydice pulchra*, which is common inter-tidally or inshore; the common, generally deep-sea, northern shrimp *Pandalus borealis*; and an unidentified euphausiid and an unidentified mysid. Another isopod, genus *Idotea*, was recorded in a chick proventriculus. In addition, a third of the regurgitates contained the small parasitic copepod *Caligus elongatus*, ingested along with its fish host. Two cephalopod species were identified in regurgitates: *Gonatus steenstrupii* (Gonatidae) and *Todarodes sagittatus* (Ommastrephidae). Beaks from a further nine *G. steenstrupii* were found in the gizzards of chicks aged 17 to 41 d.

Table 2 *Fulmarus glacialis*. Detailed breakdown of diet from regurgitates of adults and chicks at Fair Isle in 1997 ($n = 118$)

Species	n (%)
Fishes	
Trisopterus minutus	16 (14)
Unidentified *Trisopterus*	16 (14)
Micromesistius poutassou	3 (3)
Melanogrammus aeglefinus	7 (6)
Merlangius merlangus	3 (3)
Pollachius spp.	3[a] (3)
Clupeids	3[b] (3)
Sandeels	44 (37)
Hippoglossoides platessoides	1 (1)
Unidentified gadids	17 (14)
Unidentified fishes	20 (17)
Fish offal	1 (1)
Crustaceans	
Hyperia galba	5 (4)
Eurydice pulchra	4 (3)
Pandalus borealis	9 (8)
Nephrops norvegicus	5 (4)
Euphausiids	1 (1)
Mysids	1 (1)
Unidentified crustaceans	21[c] (18)
Caligus elongatus	39 (33)
Squid	
Gonatus steenstrupii	1 (1)
Todarodes sagittatus	1 (1)
Unidentified squid	7 (6)

[a] One *P. virens*, one *P. pollachius*, one unidentified sample
[b] One *Clupea harengus*, one *Sprattus sprattus*, one unidentified sample
[c] Mainly unidentified decapods

Temporal variation

Regurgitates collected on Fair Isle in August contained significantly more crustaceans and significantly less fishes, particularly sandeels, than regurgitates collected in July (Table 3). Few regurgitates were collected earlier in the season, so a comparison in diet between chick-rearing and incubation was not possible.

Iceland

Prey species

The prey species of adult fulmars around Iceland are listed in Table 4. The diet was extremely diverse, including a substantial proportion derived from commercial fishing activities as well as natural prey caught on, or just below, the surface. Sandeels and capelin were the most common fish species; both were apparently eaten as natural prey. Other fish species such as cod (*Gadus morhua*), blue whiting (*Micromesistius poutassou*), eelpouts (*Lycodes* spp.) and redfishes (*Sebastes* spp.), were more likely to have been discarded. Fish offal was also recorded in up to 11% of samples, depending on location. Many species of pelagic copepods, amphipods and euphausiids were consumed, as well as other crustaceans probably obtained from fishing vessels. Fresh remains of squid were very infrequent, although squid beaks were common in gizzards.

Spatial variation

The proportion of total wet mass of prey made up by fish offal, discarded fishes and discarded decapods varied greatly: 5% in the west, 36% in the south, 39% in the east, 49% in the north-west and 72% in the north-east. Although pelagic fishes, pelagic crustaceans or

Table 3 *Fulmarus glacialis*. Comparison (percentage containing different prey remains) between samples of regurgitates from adults and chicks on Fair Isle in July and August 1997

Prey type	July ($n = 89$)	August ($n = 27$)	Chi-square test	
			χ^2	P
Fishes	95	74	7.2	<0.01
Sandeels	47	4	15.0	<0.0002
Crustaceans	24	59	10.5	<0.002
Decapod crustaceans	21	41	3.1	0.08
Squid	9	4	0.2	0.63

Table 4 *Fulmarus glacialis*. Detailed breakdown of diets of adults in different Icelandic sectors in 1994 and 1995 (*PO* percentage of samples containing a particular item; *PWM* percentage of wet mass reconstructed from fresh remains; $*P < 0.5\%$)

	South ($n = 43$)		West ($n = 45$)		North-west ($n = 39$)		North-east ($n = 18$)		East ($n = 19$)	
	PO	PWM	PO	PWM	PO	PWM	PO	PWM	PO	PWM
Fishes										
Ammodytes marinus	49	59	38	42	5	3	–	–	–	–
Argentina silus	5	3	–	–	–	–	–	–	–	–
Gadus morhua	–	–	–	–	–	–	6	7	–	–
Micromesistius poutassou	23	23	–	–	–	–	–	–	–	–
Unidentified gadids	5	*	–	–	–	–	–	–	–	–
Mallotus villosus 0-group	–	–	–	–	3	*	–	–	–	–
Mallotus villosus 1+ group	2	*	2	2	26	29	28	15	37	48
Lycodes spp.	–	–	–	–	5	16	–	–	–	–
Myctophids	2	*	–	–	–	–	–	–	–	–
Sebastes marinus	2	3	–	–	3	9	11	26	5	13
Sebastes spp.	2	*	–	–	–	–	–	–	–	–
Unidentified fishes	12	1	4	1	3	1	6	*	11	*
Fish offal	7	3	2	2	5	5	11	9	11	5
Fish eggs	–	–	–	–	28	*	–	–	–	–
Crustaceans										
Nephrops norvegicus	2	2	–	–	–	–	–	–	–	–
Brachyurans	–	–	2	*	–	–	–	–	–	–
Pagurus spp.	–	–	2	*	–	–	–	–	–	–
Pandalus borealis	–	–	–	–	10	10	17	29	42	18
Hymenodora glacialis	–	–	–	–	13	6	6	2	5	*
Unidentified Natantia	–	–	2	1	5	2	–	–	5	1
Meganyctiphanes norvegica	23	4	–	–	3	*	50	11	5	*
Thysanoessa inermis	–	–	9	*	18	9	6	*	58	13
Unidentified euphausiids	2	*	–	–	–	–	–	–	–	–
Gammarus wilkitzki	–	–	2	*	–	–	–	–	–	–
Pseudalibrotes glacialis	–	–	2	*	–	–	–	–	–	–
Pseudalibrotes spp.	–	–	–	–	5	*	–	–	–	–
Unidentified lysianassids	–	–	7	*	–	–	–	–	–	–
Unidentified gammarids	–	–	24	3	15	*	–	–	–	–
Hyperia galba	–	–	2	*	–	–	–	–	–	–
Hyperoche medusarum	–	–	2	*	3	*	–	–	–	–
Themisto abyssorum	2	*	2	*	3	*	6	*	5	*
Themisto gaudichaudi	5	*	–	–	–	–	–	–	–	–
Themisto libelulla	–	–	11	*	21	1	17	1	21	*
Themisto spp.	7	*	7	*	8	*	17	1	5	*
Unidentified hyperiids	–	–	7	*	23	*	6	*	–	–
Cirripeds	–	–	–	–	3	*	–	–	–	–
Calanus finmarchicus	–	–	2	*	3	*	–	–	–	–
Calanus hyperboreus	–	–	–	–	3	*	6	*	–	–
Calanus spp.	–	–	4	*	–	–	–	–	–	–
Euchaeta glacialis	–	–	–	–	3	*	–	–	–	–
Euchaeta spp.	–	–	2	*	–	–	–	–	–	–
Chiridius armatus	–	–	–	–	3	*	–	–	–	–
Unidentified calanoids	–	–	2	*	–	–	–	–	–	–
Harpacticoids			–	–	15	*	–	–	–	–
Unidentified copepods	5	*	11	*	5	*	–	–	5	*
Ostracods	–	–	2	*	23	*	–	–	–	–
Unidentified crustaceans	–	–	4	*	41	8	–	–	–	–
Squid										
Gonatus fabricii	–	–	2	44	–	–	–	–	–	–
Hydrozoan polyps	–	–	–	–	3	*	–	–	–	–
Unidentified eggs	–	–	7	*	–	–	–	–	–	–
Organic particles	–	–	20	4	–	–	–	–	–	–

waste from commercial fisheries were eaten by fulmars in all sectors, species composition varied greatly among areas. Sandeels were frequent prey in the south and west, and capelin in the north and east of Iceland. In terms of wet mass, the remainder of the diet was made up mainly of blue whiting in the south, and of the squid *Gonatus fabricii* in the west, although in the latter case the importance of *G. fabricii* was elevated because of a single sample containing a large individual. Crustaceans were recorded in a large proportion of birds sampled in the south and west of Iceland, but made little contribution in terms of biomass. The fulmar diet was fairly similar in the north-west, north-east and east sectors of Iceland, generally consisting of capelin, northern shrimp, redfishes, euphausiids, and fish offal, and additionally some eelpouts in the north-west and cod in the north-east sector.

Disko Fjord, Greenland

Prey species

A total of 109 regurgitates contained identifiable prey items (Table 5). The most common fish species was capelin, and polar cod, *Boreogadus saida*, was recorded in one sample. The dominant crustacean in the diet was the amphipod *Parathemisto libellula*, which was very common in the area (Petersen personal observations). Several other crustaceans, including *Hyperia galba*, *Pandalus borealis*, *Calanus* sp. and a euphausiid, *Thysanoessa* sp., were also present in small numbers (3 to 8% of samples). Regurgitates also contained beaks from *Gonatus fabricii* and jaws from the polychaete *Nereis pelagica*, although no fresh parts were recorded.

Table 5 *Fulmarus glacialis*. Detailed breakdown of diet from regurgitates of adults at Disko Fjord, western Greenland, in 1992 and 1993

Species	1992 (n = 44) n (%)	1993 (n = 65) n (%)
Fishes		
Mallotus villosus	25 (57)	9 (14)
Boreogadus saida	– (–)	1 (2)
Unidentified fishes	4 (9)	3 (5)
Crustaceans		
Parathemisto libellula	13 (30)	26 (40)
Hyperia galba	1 (2)	5 (8)
Thysanoessa sp.	2 (5)	3 (5)
Pandalus borealis	2 (5)	2 (3)
Calanus sp.	– (–)	3 (5)
Unidentified crustaceans	2 (5)	29 (45)
Squid		
Gonatus fabricii	8 (18)	16 (25)
Polychaetes		
Nereis pelagica	6 (14)	11 (17)
Pteropods		
Limacina helicina	2 (5)	15 (23)

Temporal variation

Prior to ice break-up in Disko Fjord, fulmar regurgitates contained mainly crustaceans (Table 6). Capelin became the dominant prey item from mid-June, after the fish had started to spawn. Once spawning had ceased, fulmars switched to crustaceans and pteropods. During the summer, there were clear changes in flight directions of adults from the colony corresponding to the presence or absence of capelin in the Fjord.

Comparisons among all colonies

Comparable dietary data from regurgitates or stomach contents were available for breeding fulmars in previous years at Fair Isle, Foula (Shetland), St Kilda (Outer Hebrides, UK), a number of sites in the Barents Sea area, the Canadian high Arctic and the Bering Sea. It should be borne in mind that many of the latter were based on stomach contents of shot birds, sometimes including gizzard contents, and could be biased towards prey that leave hard remains.

Fishes

Within the UK, fishes or fish offal clearly formed much of the diet for most colonies in most years, with the exception of St Kilda in 1981 (Table 7). The importance of different fish species, however, varied greatly among years and among colonies (see Table 7 for references). Some or all of various gadid species including Norway pout (*Trisopterus esmarkii*), poor cod (*T. minutus*), whiting (*Merlangius merlangus*), blue whiting (*Micromesistius poutassou*) and haddock (*Melanogrammus aeglefinus*) were generally well represented in the samples (Tables 2 and 7). Many of these were presumably discarded from fishing vessels along with the variable fish offal component (0 to 30%) in the diet. However, depending on the colony, the diet also included a proportion of small juvenile fishes likely to have been caught by the fulmars themselves, particularly at St Kilda in 1993 and 1995 (Thompson et al. 1995), and some at Fair Isle in 1997 (see subsection "Fair Isle, Shetland – Prey species", above). If the presence of *Caligus elongatus* is an indicator of older fishes, then presumably much less of the diet at St Kilda in 1993 compared with 1995 was made up by discarded fishes. Sandeels were rare at St Kilda, but of variable and in some cases high importance in Shetland. One species of mesopelagic fish, *Scopelogadus beanii* (Melamphaidae), was recorded fairly frequently in the diet at St Kilda in 1993.

In Iceland, fishes formed the bulk of the diet in most sectors, although the dominant species changed dramatically from sandeels and discarded blue whiting and redfishes in the south, to sandeels in the west, capelin and discarded redfishes and eelpouts in the north-west,

Table 6 *Fulmarus glacialis*. Comparison (percentage containing different prey remains) between samples of regurgitates collected from adults at Disko Fjord in 1992 and 1993

Prey type	Period 1, 11 to 14 June (n = 10 samples) n (%)	Period 2, 15 June to 27 July (n = 58 samples) n (%)	Period 3, 28 July to 30 August (n = 41 samples) n (%)
Fishes	– (–)	40 (69)	2 (5)
Crustaceans	10 (100)	26 (45)	34 (83)
Decapod crustaceans	1 (10)	4 (7)	1 (2)
Squid	5 (50)	11 (19)	8 (20)
Polychaetes	2 (20)	6 (10)	4 (10)
Pteropods	– (–)	1 (2)	16 (39)

capelin, redfishes and discarded cod in the north-east, and capelin and discarded redfishes in the east (Tables 4 and 8). At Bear Island, capelin were important, along with polar cod (*Boreogadus saida*) and Norway haddock (*Sebastes viviparus*). In western Greenland, capelin was the dominant prey during the period when the fishes were spawning. Polar cod was a common prey item further north in the Bering Sea and west in the Canadian Arctic. In addition, a range of other fish species were consumed, varying with the colony (Table 8).

Crustaceans

The importance of crustaceans in the diet of the UK fulmar colonies was extremely variable, although it was generally lower in Shetland than at St Kilda (Table 7). Crustaceans formed the bulk of the diet at St Kilda in 1981, but were less common for this colony in later years. In terms of biomass, crustaceans were probably of less consequence in Shetland than the percentage occurrence data suggest as, for example, at Fair Isle in 1997 small numbers of individual amphipods or isopods were found in samples made up mostly of fishes. A diverse range of crustacean taxa were recorded, with, if anything, more consistency among colonies in the same year than among years at the same colony. The fulmar diet included pelagic zooplankton such as the decapods *Parapasiphaea sulcatifrons* and *Acanthephyra pelagica*, the euphausiid *Meganyctiphanes norvegica*, and the mysid *Gnathophausia zoea*, but also an isopod, *Idotea metallica*, which is common on drift weed. Several of these species are mesopelagic or bathypelagic, but they may migrate into surface waters at night (Thompson et al. 1995). A variety of benthic invertebrates, including *Nephrops norvegicus* and northern shrimp plus several other species recorded at Foula, would have been obtained as discards from fishing vessels.

Crustaceans were of variable importance outside the UK (Table 8). Discarded *Nephrops norvegicus* and northern shrimp formed a substantial portion of the diet in some, but not all, Icelandic sectors, amphipods were important in west Iceland, and euphausiids in most sectors. At Bear island, pelagic zooplankton (particularly euphausiids) were common in adult regurgitates in 1980. Their absence from stomach samples in 1980 emphasises the limitations of using the latter for quantitative diet analysis (see "Discussion-Biases in diet sample-collection"). Around Spitsbergen, fulmars consumed a diverse array of amphipods and, in some case, decapods. Amphipods also appeared in many samples from the Bering Sea and the Canadian Arctic, and were the dominant item in the fulmar diet at Disko Fjord during the time when capelin were unavailable. However, when the importance of crustaceans is considered in terms of biomass rather than percentage occurrence in the Canadian study, amphipod and copepod consumption would appear to make but a minor contribution to overall food intake.

Squid

Squid were comparatively uncommon in Shetland or at St Kilda during the breeding season, with a percentage occurrence of 0 to 8% in regurgitates, depending on colony and year (Table 7). Nor were squid important in Iceland, except perhaps in the west. Squid was more common at Disko Fjord, occurring in 22% of samples overall, although fresh remains were not recorded. In several higher-latitude colonies, percentage-occurrence values could be interpreted as indicating that squid features prominently in fulmar diet. However, most of these studies were based on the stomach contents of adults, and may have included beaks accumulated in the gizzard over a long period. Indeed, analysis of the diet at Bear island using regurgitates and of the percentage composition by mass (reconstructed using fresh remains only) at Pond Inlet in the Canadian Arctic suggested that squid were generally not important prey (Table 8).

Polychaetes and medusae

Polychaete worms (including *Nereis irrorata*) were consumed in very large numbers at Bear Island and at more northerly colonies, and in small numbers in the south-east Bering Sea. *N. pelagica* was found in 16% of samples at Disko Fjord. Nereids were absent from fulmars shot in March or April in the Barents Sea. This prey is presumably caught in surface waters during the summer, when the worms are in their epitokous (spawning) phase. Birds may retain polychaete jaws in their gizzards for a considerable period, over-emphasizising their importance.

Table 7 *Fulmarus glacialis*. Diet of breeding fulmars in UK colonies, determined from regurgitates. Data are percentage of samples containing any particular item; only dominant item is noted for samples from St Kilda in 1981 and Foula in 1978 to 1982 (+ prey present but no quantitative information available; – absent)

Dietary item	St Kilda, Outer Hebrides (adults/chicks)				Foula, Shetland (adults/chicks)			Fair Isle, Shetland (adults/chicks)				
	1981 (177 ad/ch)	1982 (12 ad)	1993 (62 ad/ch)	1995 (26 ad/ch)	1978–1982 (238 ad/ch)	1993 (86 ad/ch)	1995 (60 ad/ch)	1986 (24 ch)	1987 (14 ch)	1988 (37 ch)	1989 (23 ch)	1997 (118 ad/ch)
Total fishes (including offal)	8	50	84[a]	100[b]	86	99[c]	98[c]	100	94	97	100	89
Gadids	–	+	65	92	–	41	98	+	+	+	17	48
Fish offal	1	25	–	–	14	30	27	+	+	+	+	1
Sandeels	–	–	6	–	72	24	2	4	29	3	4	37
Clupeids	8	–	–	–	–	–	–	–	–	–	–	3
Total crustaceans	76	42	35	23	11	3	7	–	6	–	–	32
Amphipods	–	33[d]	23[d]	4[d]	–	–	–	–	–	–	–	4
Decapods	13[e]	8	21[f]	–	–	–	–	–	–	–	–	26
Euphausiids	34[g]	–	–	–	9[g]	–	–	–	–	–	–	1
Mysids	18[h]	–	–	–	1[h]	–	–	–	–	–	–	1
Isopods	11[i]	–	2[j]	4[j]	1[i]	1[j]	–	–	–	–	–	3
Caligus elongatus	–	–	–	27	–	35	+	–	–	–	–	33
Squid	–	–	8[k]	4[k]	1	1	–	–	–	–	–	8
Other prey	–	17[l]	–	–	–	–	–	–	–	3	–	–
Source	Furness and Todd (1984)	Camphuysen and van Franeker (1996)	Thompson et al. (1995)	Hamer et al. (1997), Thompson et al. (1995)	Furness and Todd (1984)	Thompson et al. (1995)	Hamer et al. (1997), Thompson et al. (1995)	Camphuysen and van Franeker (1996)	Harris and Riddiford (1989)	Harris and Riddiford (1989)	Jenks et al. (1993)	Present study[m]

[a] Species found in >5% of samples: *Merlangius merlangus* and *Scopelogadus beanii*
[b] Species found in >5% of samples: *Trisopterus esmarkii*, *T. minutus* and *Micromestius poutassou*
[c] Species found in >5% of samples: *Trisopterus esmarkii*
[d] *Hyperia galba*
[e] *Parapasiphaea sulcatifrons*, *Munida bamffica*, *Pagarus bernhardus*, *Nephrops norvegicus*, *Liocarcinus tuberculatus*, *Acanthephyra* sp.
[f] *Acanthephyra pelagica*
[g] *Megancytiphanes norvegica*
[h] *Gnathophausia zoea*
[i] *Idotea metallica*
[j] *Eurydice* sp.
[k] Includes *Gonatus steenstrupii*
[l] Hydrozoan medusa *Velella velella*
[m] See Table 2 for detailed breakdown

Table 8 *Fulmarus glacialis*. Diet of northern fulmars at high latitudes [*ad* adults; *R* regurgitates; *S* stomach contents; *PO* percentage of samples containing particular items; *PWM* percentage of wet mass reconstructed from fresh remains; *PDM* percentage of dry mass reconstructed from fresh remains, excluding offal for Pond Inlet samples; *IRI* index of relative importance [*PO* × (aggregate %vol + aggregate% nos); * percentage <0.5%]

Dietary item	Franz Josef Land		Hornsund (Spitsbergen)		Barents Sea		Bear Island			Disko Fjord
					Ice edge	Open sea				
	Aug 1991–1993 S (5 ad)		Sep/Oct 1984 S (17 ad),	Mar/Apr 1985 S (28 ad),	July/Aug 1982/1984 S (22 ad),	March 1987 S (30 ad),	July/Aug 1980 R (13 ad),	July/Aug 1980 S (22 ad),	July/Aug 1948 S (23 ad),	June–Aug 1992–1993 R (109 ad),
	PO	PWM	PO	PO	PO	PO	PO	PO	PO	PO
Total fishes	60	93	+	+	+	+	77	91	39	38
Unidentified fishes	20	7	53	18	27	83[a]	23	91	35	6
Polar cod	20	51	12	14	32	13	8	–	–	1
Sandeels	–	–	–	–	–	–	–	–	–	–
Capelin	–	–	–	–	–	–	31	–	–	31
Other fishes	20[b]	35	+[c]	32	5	+[d]	+[e]	–	–	–
Offal	–	–	–	–	–	–	8	–	4	–
Total crustaceans	–	–	+	+	+	–	46	5	–	63
Amphipods	–	–	+[h]	7	23[i]	–	15[j]	–	–	62
Decapods	–	–	–	29	14	–	8	–	–	4
Euphausiids	–	–	–	–	–	–	38[m]	–	–	5
Copepods	–	–	–	4	–	–	–	–	–	3
Squid	–	–	41[n]	75[n]	32[n]	57[o]	–	41	52	22
Polychaetes	60	4	82[p]	–	46[p]	–	–	82[p]	48	16
Other prey	20[q]	3	+[r]	–	–	–	–	–	–	16
Source	Weslawski et al. (1994)		Lydersen et al. (1989)	Mehlum and Gabrielsen (1993)	Mehlum and Gabrielsen (1993)	Erikstad (1990)	Camphuysen and van Franeker (1997)	Camphuysen and van Franeker (1997)	Duffey and Sergeant (1950)	Present study

Scyphozoan medusae were found in 41% of stomach samples from the south-east Bering Sea, and hydrozoan medusae were also recorded in regurgitates collected at St Kilda in 1982. Medusae are fragile and difficult to detect in diet samples, so their occurrence elsewhere may have been overlooked. Fulmars are assumed to eat medusae because of the presence of associated hyperiid amphipods (Harrison 1984).

Discussion

General pattern

Fulmarus glacialis has a very catholic diet, which exhibits much spatial and temporal variation (see Tables 7 and 8 for references). In the northern Barents Sea, at Franz Josef Land and Spitsbergen, fishes usually constituted a moderate to high proportion of the diet, although at some colonies during the summer, a diverse variety of amphipods and to a lesser extent various decapods and nereid worms were also of importance. This was not the case in an earlier study at west Spitsbergen, which found the euphausiid *Thysanoessa inermis* to be the dominant prey, with little emphasis on fish or squid consumption (Hartley and Fisher 1936). At Bear Island, fishes (capelin in particular), euphausiids and polychaetes formed the bulk of the diet. Fulmar diet in Iceland was very varied, with adults in different sectors feeding on combinations of sandeels, capelin, amphipods, euphausiids, and discarded fishes and decapods. At St Kilda and the Shetland colonies in most years, fishes were the dominant prey, although comprised of a wide variety of species. Crustaceans tended to be of less importance in the diet, except at St Kilda in 1981. Fulmars at Disko Fjord consumed mainly amphipods and capelin. In the Canadian high Arctic, polar cod, amphipods, copepods and pteropods were common prey, with some opportunistic feeding on marine mammal carcasses (see also Hobson and Welch 1992). In the south-east Bering Sea, northern fulmars consumed fishes, amphipods, medusae, and possibly squid (depending on whether gizzard contents were included in the samples).

Biases in diet sample-collection

Sampling biases associated with different collection methods have to be considered in any comparative diet analysis (see Duffy and Jackson 1986 for general review). Fishes are digested more rapidly than crustaceans or squid (Jackson and Ryan 1986), although the generally high incidence of fishes in the fulmar diet suggests that this was unlikely to be a major problem, at least in

Table 8 (Contd.)

Iceland										Pond Inlet, Canada		SE Bering Sea	Gulf of Alaska
South		West		North-west		North-east		East					
May–Aug 1994–1995 S (43 ad)		May–Aug 1994–1995 S (45 ad)		May–Aug 1994–1995 S (39 ad)		May–Aug 1994–1995 S (18 ad)		May–Aug 1994–1995 S (19 ad)		Summer 1979 S (31 ad)		Aug 1982 S (116 ad),	Various (no details) S (43 ad),
PO	PWM	PO	PWM	PO	PWM	PO	PWM	PO	PWM	PO	PDM	PO	IRI
95	93	42	47	64	64	50	57	63	67	19	97	+	4
12	1	4	1	3	1	6	*	11	*	–	–	28	–
–	–	–	–	–	–	–	–	–	–	19	97	–	–
49	59	38	42	5	3	–	–	–	–	–	–	–	–
2	*	2	2	26	29	28	15	37	48	–	–	–	1
51	31	4	1	8	26	22	33	16	14	–	–	+ [f]	3
7	3	2	2	5	5	11	9	11	5	32[g]	–	–	–
30	7	42	5	85	36	72	43	74	33	+	3	+	2
7	*	33	3	46	1	28	2	26	*	23[k]	2	37	–
2	2	7	2	18	18	22	31	47	20	6	1	6[l]	–
23	5	9	*	18	9	50	11	58	13	–	–	5	1
5	*	18	*	26	*	6	*	5	*	61	1	1	1
–	–	2	44	–	–	–	–	–	–	87	–	97	95
–	–	–	–	–	–	–	–	–	–	–	–	4	–
–	–	27	4	3	*	–	–	–	–	3[s]	*	41[t]	–
Present study		Present study		Present study		Present study		Present study		Bradstreet and Cross (1982)		Harrison (1984)	Sanger (1987)

[a] Cod *Gadus morhua* or polar cod *Boreogadus saida*
[b] Sculpin *Myoxocephalus scorpius*
[c] Saithe *Pollachius virens* and Arctic char *Salvelinus alpinus*, each in 6% of samples
[d] Redfishes *Sebastes marinus* or *S. mentella* in 63% of samples, cod *Gadus morhua* in 17% of samples
[e] Norway haddock *Sebastes viviparus* and saithe or pollack *Pollachius* sp., each in 8% of samples
[f] Gadids in 2% of samples, myctophids in 6% of samples
[g] Fat from marine mammal carcasses
[h] Unidentified hyperiid, *Hyperia galba*, *Parathemisto abyssorum*, *P. libellula*, *Onisimus littoralis* and *Gammarus oceanicus*, each in 6% of samples
[i] *Parathemisto libellula*
[j] One sample identified as *Parathemisto* sp.
[k] Hyperiids, lysianassids, calliopiids
[l] Crab larvae
[m] One sample identified as *Thysanoessa inermis*
[n] *Gonatus fabricii*
[o] *Gonatus* sp.
[p] *Nereis irrorata*
[q] Gastropod *Margarites* sp.
[r] Pteropods in 12% of samples, *Mysis oculata* in 6% of samples
[s] Mysids
[t] Scyphozoan medusae

studies using regurgitates or proventricular contents reviewed here. Harder, larger and less digestible parts of prey, particularly squid beaks, fish otoliths, and polychaete jaws, tend to accumulate in the gizzards of seabirds, often for weeks (Furness et al. 1984). The percentage occurrence of squid in the chick diet on Fair Isle or in adult diets in Iceland would have been greatly overestimated using whole-stomach or gizzard contents, and any study which analysed the stomach contents of shot or beached birds uncritically would suffer the same drawback. Unfortunately, although clearly aware of the problem, few researchers separate the two. Regurgitates collected at breeding colonies could be indicative mainly of prey fed to chicks if adults on long foraging trips feed on and digest other types of prey at sea. However, problems also arise in at-sea studies, where samples are far from random, and depend on the number of birds obtained from a feeding flock at a particular location or, as in some early studies, where collection was biased towards birds attracted to ships by fishing waste (Fisher 1952).

Seasonal variation in diet

There was strong evidence for seasonal changes in the prey of northern fulmars, although in many cases little information was available on wintering diets. In the Barents Sea, amphipods and swarming nereids were consumed in large numbers mainly during the summer, when the latter would be available in the upper water column in their epitokous phase (Table 8). In western Greenland during the breeding season, adults switched from feeding on crustaceans to capelin then back to crustaceans and pteropods (Table 6). At Fair Isle, sandeels declined and crustaceans increased in the diet during chick-rearing, from July to August (Table 3). This is consistent with the drop in the abundance of sandeels in the upper water column during the late summer when the fishes return to the substrate (Wright and Bailey 1993).

Several types of prey exploited during the summer, including sandeels, spawning capelin and euphausiids, are less likely to be available to surface-feeding fulmars during the non-breeding season. Consequently, fulmars might be expected to be more reliant on waste from commercial fisheries during the winter. However, in their analysis of fulmar distributions at sea, Camphuysen and Garthe (1997) concluded that fewer fulmars tend to exploit discards during the autumn and winter. Unfortunately, there is insufficient information on their winter diet to completely substantiate this hypothesis. However, several fulmars caught in November at North Berwick, south-east Scotland, regurgitated jaws and bodies of *Nereis virens* which were estimated to be up to 500 mm in length (Zonfrillo unpublished data); this suggests that feeding on polychaetes may be important for some UK fulmars during the non-breeding season. Circumstantial support for a reduced consumption of discards during the winter comes from the decline in $\delta^{15}N$ and $\delta^{13}C$ values in the primary feathers of adult fulmars collected at St Kilda, which indicates a probable switch in diet during the non-breeding season to prey of lower trophic status (Thompson and Furness 1995).

Reliance on squid

The squid exploited by northern fulmars in the eastern Atlantic, western Greenland, Barents Sea, and Canadian high Arctic were primarily *Gonatus steenstrupii* and *G. fabricii* (Table 8; and Hobson and Welch 1992), although beaks from various other squid, including mesopelagic and bathypelagic species have been found in gizzards of shot or beached birds elsewhere (Hills and Fiscus 1988; Bourne 1997). *G. fabricii*, and presumably the very similar, more southerly *G. steenstrupii*, are found throughout the water column, with mainly juvenile individuals occurring near the surface, and are likely to be caught by fulmars directly (Mehlum and Gabrielsen 1993). It has been suggested that the ability of the northern fulmar to feed on squid may have been a prerequisite for efficient exploitation of offal and discarded fishes, and hence was integral to their southerly expansion (Bourne 1997). In fact, squid are relatively infrequent in the fulmar diet, at least during the summer, certainly in the eastern Atlantic where studies have analysed regurgitates or proventricular contents (Tables 7 and 8). The presence of squid beaks in the gizzards of beached fulmars during the winter may mean that squid are important prey during the non-breeding season, but the absence of data from proventriculus contents makes this impossible to confirm.

Fish species consumed and reliance on commercial fisheries

Fisher (1952) considered that the expansion of the northern fulmar in the eastern Atlantic was facilitated by the provision of waste from fisheries, with Bourne (1966) speculating that the critical period would be the winter. In the latter case, possibly the availability of discards as a new food resource resulted in improved survival of first-year birds. We might therefore expect that southerly fulmar populations would still be more reliant on discards than would populations of the high or low Arctic during some part of the year.

The data presented here do confirm that fulmars in western Greenland and the Barents Sea are not generally dependent on discards, although Erikstad (1990) suggests that discarded cod and redfishes may be more important to birds in the open Barents Sea during the spring. The evidence that fulmars breeding further south are heavily reliant on fishery waste is more equivocal, particularly as regards winter diets. In Iceland, discarded fishes and decapods are certainly important to breeding birds. The bulk of the roundfish fisheries take place south, west and north-west of Iceland, in those areas where breeding fulmars are most numerous. Annual landings of fishes from Icelandic waters increased from 30–40 thousand tonnes in 1766–1777 to 1–2 million tonnes in the 1990s (Jonsson 1994; Anonymous 1998). The number of fulmars in Iceland has increased dramatically over the last few centuries. The explosion of fulmar populations in Iceland may therefore be linked to the increased availability of fish offal and discards which coincided with the expansion in the trawling fleet at the turn of this century. In fact, both fulmar numbers and fishing effort increased gradually in the 1700s and 1800s, and then expanded rapidly during the early 1900s. Increased survival of immature birds, particularly during the winter, might have facilitated the colonisation of new areas.

Alternatively, the increase in Icelandic fulmars could potentially be a consequence of some other major change in their biology or environment. Back-calculations from historical records indicate that air and sea temperatures were relatively low in the 18th century, with two warmer periods developing during the first half of the 19th century (Bergthorsson 1969). From a low in the 1860s, sea temperature slowly increased until the 1920s; a warmer period then followed which lasted into the late 1960s (Malmberg and Kristmannsson 1992). The gradual expansion of fulmars in Iceland in the 18th and 19th century therefore took place when the temperature was relatively low or fluctuating, yet most new sites were colonised during the first 40 yr of the 20th century when temperatures were higher (Fisher 1952). This pattern does not seem to fit particularly well with the climate data, and a link with changes in fisheries practices seems more likely.

While discarded fishes and, to a lesser extent, benthic invertebrates also featured prominently in the diet at more southerly colonies in some years, fulmars also eat many other types of prey which they catch for themselves, including sandeels, capelin and crustaceans (Tables 7 and 8). Indeed, if fulmar distribution is examined on a greater spatial scale, over the whole of the North Sea, their relative abundance seems not to conform to regional variation in the availability of fishery wastes, but to show a close relationship with hydrography (Camphuysen and Garthe 1997). This strongly suggests that the availability of natural prey is a more important determinant of the pelagic distribution of fulmars. Very large numbers of fulmars are often recorded at fishing vessels (Camphuysen et al. 1995), but a large proportion of these may be nonbreeders. Nonbreeders can account for between 50 and 80% of birds in attendance at colonies (Dunnet 1991), and in addition there will probably be yet more immature individuals wandering at sea. Breeding adults may therefore be less dependent on discards than has generally been assumed.

In addition, researchers sometimes assume that any gadids found in fulmar regurgitates must have been discarded. However, studies at both St Kilda and Fair Isle indicated that fulmars eat a large amount of juvenile gadids, although the exact proportion remained unquantified because of problems with otolith erosion in the gut (Thompson et al. 1995; and present study). Juvenile fishes can occur close to the sea surface, particularly at night (Conway 1973), and these would be well within the reach of fulmars, which have been shown experimentally to be capable of diving routinely to 3 m (Hobson and Welch 1992).

Furthermore, sandeels or capelin were recorded in very large numbers in the diet of northern fulmars in some years at Shetland, Iceland, Bear Island and western Greenland (Table 8; see also Fowler and Dye 1987). The abundance of sandeels, sprat (*Sprattus sprattus*) and Norway pout (another important prey of fulmars) increased markedly in the eastern Atlantic during the 1970s, possibly because of the depletion of herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) stocks, as a result of overfishing (Sherman et al. 1981). Presumably numbers of other fast-growing planktivorous fishes such as poor cod and capelin increased over the same period. By causing this dramatic change in marine ecosystem structure, commercial fishing may have benefited fulmars in recent years almost as much by this indirect means as by the direct provision of discards.

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