

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

David R. Thompson*, Robert W. Furness, Sharon A. Lewis

Applied Ornithology Unit, IBLS, University of Glasgow, Glasgow G12 8QQ, United Kingdom

ABSTRACT: Stable isotope ratios of nitrogen ($^{15}\text{N}/^{14}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$) were determined in feather samples from northern fulmars *Fulmarus glacialis* sampled at around the turn of the century and in 1993 from 2 northeast Atlantic colonies. At both locations $\delta^{15}\text{N}$ values declined over time indicating a shift in fulmars to a lower trophic status. Similarly, $\delta^{13}\text{C}$ signatures declined over time. These findings are consistent with a change in diet from prey of relatively high trophic status, possibly involving the utilisation of offal from whaling activities around the turn of this century, to contemporary prey of lower trophic status. Contemporary dietary information from fulmars at both sites accords with feather isotopic signatures. Two prey species recorded in the diet of fulmars from St Kilda can be considered mesopelagic and have not been noted in seabird diets previously. This is the first study to show that stable isotopes in feathers can be used to determine long-term changes in bird diet.

KEY WORDS: Stable isotopes · Northern fulmar · Temporal trends · Diet · Mesopelagic prey

INTRODUCTION

The northern fulmar *Fulmarus glacialis* has shown a remarkable and dramatic expansion in population size and breeding range within the UK during this century (Lloyd et al. 1991). Prior to 1878, the only UK colony was at St Kilda, Outer Hebrides at which point Foula, Shetland became the second UK breeding site, possibly colonised by birds from Iceland or the Faeroe Islands (Fisher 1952). As well as being the two oldest UK colonies, St Kilda and Foula are also the largest fulmar colonies with ca 63000 and ca 47000 pairs, respectively (Tasker et al. 1988, Lloyd et al. 1991). Explanations for this marked expansion in this species have included the increased availability and utilisation of offal from whaling and fishing activities (Fisher 1952), a genetic or behavioural change (Wynne-Edwards 1962) and changes in oceanographic parameters (Salomonsen 1965, Brown 1970). It is difficult to differentiate between these alternatives; but, that northern fulmars made use of offal from commercial fisheries (including whaling) is supported, albeit indirectly, by

studies of heavy metal concentrations in this species. In a recent investigation into temporal trends in mercury burdens of a range of species of seabirds from the UK, Thompson et al. (1992) noted that virtually all species studied exhibited an increase in mercury concentrations from around the turn of the century to the present. The only species which fell outside this pattern, and which exhibited a significant decrease in mercury burdens over the same time period, from the same sites (St Kilda and Foula) at which other species had exhibited increases in mercury burdens, was the northern fulmar (Thompson et al. 1992). Since mercury, and more specifically methylmercury, accumulates up food chains (Bryan 1979), biota occupying relatively elevated trophic positions in a given system will exhibit correspondingly high mercury concentrations. It was suggested by Thompson et al. (1992) that one possible explanation for the decrease in mercury concentrations in northern fulmars from St Kilda and Foula could have been a change in diet to prey of lower trophic status, containing reduced mercury burdens. It is known that fulmars fed extensively on the offal from whaling activities around the turn of the century (Fisher 1952), including material from toothed whales (Odontoceti)

*E-mail: gbza67@vdcf.gla.ac.uk

which would have occupied relatively high trophic positions and exhibited relatively high mercury concentrations (Thompson 1990). Contemporary fulmars have been shown to feed mainly upon zooplankton at St Kilda and sandeels *Ammodytes marinus* and fish offal at Foula (Furness & Todd 1984), all of which occupy trophic positions below those of toothed whales and which are likely, therefore, to exhibit relatively low mercury burdens.

Stable isotope analysis has been used increasingly in recent years to elucidate trophic interactions and food web structure. The stepwise enrichment of ^{15}N at each trophic level within a food chain allows the status of any component within a system to be determined with respect to other components in that system (Minagawa & Wada 1984, Schoeninger & DeNiro 1984, Hobson & Welch 1992a, Hobson 1993, Hobson et al. 1994). Carbon stable isotope ratios have been used to indicate relative contributions of carbon from differing sources (terrestrial vs marine, for example) to the diet of particular species (Fry et al. 1983, Dunton & Schell 1987, Hobson 1987, 1990, Mizutani et al. 1990, Hobson & Sealy 1991). Additionally, the complementary analysis of both nitrogen and carbon stable isotope ratios affords greater species segregation on the basis of isotopic signature than if only one isotope ratio has been determined (Hobson 1991, 1993).

Stable isotope analysis has been used to reconstruct the diet or assess the trophic status of biota over long time scales. Preserved collagen from bones has proved particularly useful in this respect; ancient human diets and shifts in diet have been assessed from a range of sites (Van der Merwe & Vogel 1978, Van der Merwe et al. 1981, Chisholm et al. 1982, 1983, Ambrose 1986), whilst Hobson & Montevecchi (1991) investigated dietary and trophic characteristics of the extinct great auk *Pinguinus impennis* based on isotopic information from extracted bone collagen. Similarly, time-series of fish scales have been used to yield isotopic signatures and assess temporal trends in trophic status of a range of fish species (Wainright et al. 1993).

Potentially, long-term studies of diet and trophic status could be applied to birds, since large numbers of specimens have been preserved as study skins in museum collections. Feather samples from such collections have been used, for example, to investigate temporal patterns of mercury contamination over the last 150 yr at a number of locations (Thompson et al. 1992, 1993a, b). Whilst bone material, and hence collagen, exists in preserved bird collections, samples are difficult to procure. Feather samples are generally more readily obtained and, furthermore, keratin from which they are composed is chemically stable. However, feathers have been used relatively infrequently in isotopic studies, although recent work has indicated that

their isotopic signatures accurately reflect a bird's diet and trophic status. Mizutani et al. (1992) concluded that stable isotope information from feathers could be used to evaluate diet, based on a study of diet-feather isotopic enrichment in 11 species of birds. The $\delta^{13}\text{C}$ values of American crow *Corvus brachyrhynchos* feathers have been shown to track $\delta^{13}\text{C}$ values of the diet during feather growth (Hobson & Clark 1992) and, similarly, $\delta^{13}\text{C}$ values of cormorant *Phalacrocorax carbo* feathers have been shown to reveal the relative contributions of riverine and marine protein to that species' diet (Mizutani et al. 1990). Hence, feather samples from preserved study skins should permit an isotopic assessment of temporal patterns of the dietary preferences and trophic status of birds.

In this paper we present data from stable isotope analysis of feather samples from northern fulmars collected from study skins in British museums dating back to the middle of the last century. These data are contrasted with isotopic signatures of feather samples from contemporary fulmars in order to assess whether this species has undergone a change in diet and trophic status over this period, consistent with the decrease in mercury burdens reported by Thompson et al. (1992). Additionally, the contemporary diets of this species at St Kilda and Foula are contrasted and compared to corresponding isotopic information.

MATERIALS AND METHODS

Small body feathers (6 to 10 from each individual), plucked from the breast and back regions, were sampled from apparently healthy, breeding fulmars at St Kilda, Outer Hebrides (57° 49' N, 08° 35' W) and Foula, Shetland (60° 08' N, 02° 05' W) in 1993. Sampling was undertaken during July at both locations. A similar number of body feathers was also sampled from fulmars held as study skins in museum collections (see 'Acknowledgements' for museums visited). For comparative purposes, only skins labelled as being adults, collected during the breeding season prior to 1940 at St Kilda or from the northern isles (Shetland, Fair Isle and Orkney; for comparison with contemporary fulmars from Foula) were sampled. To test whether any change in $\delta^{15}\text{N}$ values (trophic status) over time was an artefact of the comparison between historical, museum-held samples and contemporary samples, body feathers were sampled from apparently healthy, breeding Manx shearwaters *Puffinus puffinus* at Rum, Inner Hebrides (56° 58' N, 06° 18' W). Contemporary samples were obtained in 1990 and historical samples from museum-held study skins dating from 1854 to 1935 from a range of northern and western British sites. For this species there was no *a priori* reason to suspect any

anthropogenic influence on diet and, hence, trophic status.

In all cases, feather samples were washed in an ultra-sonic bath to remove surface contamination using a chloroform/acetone washing regime (Muirhead 1986), and then dried in an oven at 50°C for at least 24 h. Dried feathers were chopped into very small pieces to produce a homogenous feather sample prior to isotope analysis.

Prey samples were obtained when handling adult fulmars during feather sampling or from chicks when approached. Both adults and chicks readily regurgitated food when handled or approached. Prey samples were placed in plastic vials and maintained deep-frozen (ca -20°C) prior to identification. On returning to the laboratory, prey samples were allowed to thaw and identified to the lowest possible taxon. Dietary items were treated on a presence/absence basis only. No attempt has been made to quantify the size (volume) of prey material regurgitated nor to record the numbers of particular prey species in regurgitations.

For isotope analysis, ca 20 mg of homogenised feather sample was combusted in an evacuated and sealed quartz tube containing excess copper (II) oxide (wire form) and silver wire. The furnace temperature was maintained at 850°C for 6 h, then allowed to cool to ambient laboratory temperature over a further 8 h. The resultant carbon dioxide and nitrogen were separated cryogenically and collected in individual ground glass-stoppered bottles, using a Toepler pump for nitrogen samples, to await analysis. Stable isotope ratios of carbon dioxide and nitrogen were analysed using VG SIRA10 triple collector and VG Micromass 602D double collector mass spectrometers, respectively. Stable isotope concentrations were expressed in conventional notation whereby:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. R_{standard} for ^{13}C and ^{15}N are PDB and atmospheric nitrogen from AIR, respectively. Analytical errors, based on replicate analyses of IAEA N-1, IAEA N-2 and NBS-21 standards, were $\pm 0.2\%$ for both carbon and nitrogen.

RESULTS

Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for fulmars sampled prior to 1940 and in 1993 from the northern isles and St Kilda are presented in Table 1. At both locations, significant

Table 1. *Fulmarus glacialis*. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (means \pm 1 SD with sample sizes in parentheses) of homogenised body feathers from adult fulmars sampled prior to 1940 and in 1993, change in isotope signature over this period and results of t -tests comparing the means of the 2 groups

Location	Isotope ratio	<1940	1993	Change (‰)	t -test
Northern Isles	$\delta^{15}\text{N}$	15.34 \pm 0.83 (30)	14.18 \pm 0.76 (30)	-1.16	$t = -5.62$ $p < 0.001$
	$\delta^{13}\text{C}$	-16.44 \pm 0.37 (30)	-17.39 \pm 0.55 (30)	-0.95	$t = -7.86$ $p < 0.001$
St Kilda	$\delta^{15}\text{N}$	14.39 \pm 0.96 (12)	13.65 \pm 0.75 (30)	-0.74	$t = -2.66$ $p = 0.011$
	$\delta^{13}\text{C}$	-16.81 \pm 0.50 (12)	-17.33 \pm 0.42 (30)	-0.52	$t = -3.45$ $p = 0.001$

decreases were measured in nitrogen and carbon isotope signatures (Table 1; Figs. 1 & 2). The decline in isotope signatures was greatest in fulmars from the northern isles: the mean $\delta^{15}\text{N}$ value fell by 1.16‰ from prior to 1940 to 1993, whilst the corresponding decline in $\delta^{13}\text{C}$ was 0.95‰ (Table 1).

The mean $\delta^{15}\text{N}$ value in contemporary fulmars from Foula was significantly higher than that in fulmars from St Kilda (Table 1; t -test: $t = 2.68$, $df = 58$, $p = 0.01$). There was no significant difference in the mean $\delta^{13}\text{C}$ value in contemporary fulmars from Foula and St Kilda (Table 1; t -test: $t = -0.45$, $df = 58$, $p = 0.66$). For contemporary fulmars at both sites, there was no significant correlation between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of feathers (St Kilda: $r = -0.09$, $n = 30$, $p = 0.63$; Foula: $r = -0.15$, $n = 30$, $p = 0.44$). There was no significant difference in the mean $\delta^{15}\text{N}$ values of Manx shearwaters sampled

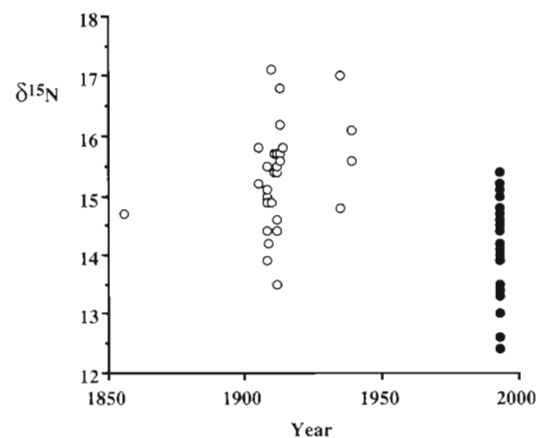


Fig. 1. *Fulmarus glacialis*. Changes in $\delta^{15}\text{N}$ signatures of homogenised body feather samples of northern fulmars over time at the northern isles (Shetland, Fair Isle and Orkney), UK. (●) Contemporary birds sampled in 1993. (○) Historical birds sampled prior to 1940. Each point represents an individual bird

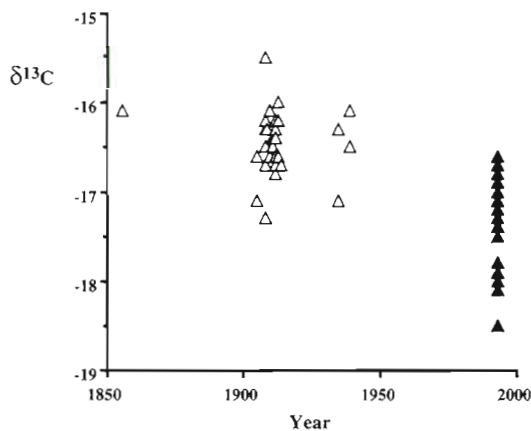


Fig. 2. *Fulmarus glacialis*. Changes in $\delta^{13}\text{C}$ signatures of homogenised body feather samples from northern fulmars over time. (\blacktriangle) Contemporary birds sampled in 1993. (\triangle) Historical birds sampled prior to 1940. Other details as for Fig. 1

prior to 1940 and in 1990 (pre-1940: mean = 17.63‰, SD = 1.3, n = 12; 1990: mean = 17.52‰, SD = 1.4, n = 12; *t*-test: *t* = -0.18, df = 22, *p* = 0.86).

The occurrence of particular prey species in the diet of fulmars at St Kilda and Foula is summarised in Table 2. Fish and/or fish offal occurred in virtually all (99%) regurgitations at Foula, with other prey types occurring relatively infrequently. Fish offal and unidentified whitefish both occurred in 30% of regurgitations, whilst sandeels were present in 24% (Table 2). The parasitic copepod *Caligus elongatus* occurred in 13 (35%) of a subset of 37 samples at Foula, always in association with whitefish. This species was absent from regurgitations at St Kilda. Although fish were present in 84% of all samples at St Kilda (Table 2), the whitefish species recorded were generally represented by small, juvenile individuals as determined from otolith size. All whiting *Merlangius merlangus*, for example, recorded at St Kilda were ca 5 cm in length (based on otolith size from whiting regurgitated whole). A total of 22 regurgitations (35% of samples) contained Crustacea and 5 (8%) contained squid. If *C. elongatus* is ignored, since this minute dietary item would have been ingested in conjunction with its fish host, Crustacea were present in only 3% of samples at Foula (Table 2). Two species regurgitated by fulmars at St Kilda can be considered mesopelagic: the decapod crustacean *Acantheephyra pelagica* and the melamphid fish *Scopelogadus beanii* (Foxton 1972, Mauchline & Gordon 1984).

DISCUSSION

The statistically significant decreases in mean $\delta^{15}\text{N}$ values of feather samples from northern fulmars between pre-1940 and 1993 are consistent with a shift to a lower trophic status in this species, at both St Kilda and, more dramatically, at the northern isles (Table 1; Fig. 1). However, the absolute decreases in mean $\delta^{15}\text{N}$ values at each location were not large, and were unlikely to represent a drop in trophic status corresponding to a whole trophic level in these respective food chains. From previous studies of marine food chain structure, trophic level enrichments of $\delta^{15}\text{N}$ have been determined as ranging from +3 to +4‰ (e.g. Schoeninger & DeNiro 1984, Wada et al. 1987, Hobson & Welch 1992, Hobson et al. 1994). Based on these data, the decrease in mean $\delta^{15}\text{N}$ signatures in northern fulmars between pre-1940 and 1993 at the northern isles (-1.16‰; Table 1, Fig. 1) and at St Kilda (-0.74‰; Table 1) represent reductions of ca one third and ca one quarter of a trophic level, respectively. Whilst

Table 2. *Fulmarus glacialis*. Prey of fulmars at St Kilda and Foula, determined from regurgitations. Values are numbers and percentage of samples containing a particular prey category

Species	St Kilda		Foula	
	No. of samples	% of samples	No. of samples	% of samples
Crustacea				
<i>Hyperia galba</i>	14	23	–	–
<i>Eurydice</i> sp.	1	2	1	1
<i>Acantheephyra pelagica</i>	13	21	–	–
Unidentified Crustacea	–	–	2	2
Total Crustacea	22	35	3	3
<i>Caligus elongatus</i>	–	–	13 ^a	35 ^a
Cephalopoda				
<i>Gonatus steenstrupi</i>	3	5	–	–
Unidentified squid	2	3	1	1
Total Cephalopoda	5	8	1	1
Pisces				
<i>Trisopterus luscus</i>	1	2	–	–
<i>Trisopterus esmarkii</i>	2	3	6	7
<i>Micromesistius poutassou</i>	–	–	1	1
<i>Melanogrammus aeglefinus</i>	1	2	1	1
<i>Merlangius merlangus</i>	10	16	–	–
<i>Callionymus lyra</i>	1	2	–	–
<i>Ammodytes marinus</i>	4	6	21	24
<i>Scopelogadus beanii</i>	7	11	–	–
Unidentified whitefish	26	42	27	31
Other unidentified fish	3	5	5	6
Fish offal	–	–	26	30
Total fish	52	84	85	99
Total no. of samples	62		86	

^aFrom a subset of 37 samples

modest, the reduction in $\delta^{15}\text{N}$ values in northern fulmars would appear to be a genuine effect. No such decline could be detected in Manx shearwater feather samples (see 'Results') collected over the same period as the fulmar samples. The reduction in $\delta^{15}\text{N}$ values in fulmars is consistent with the corresponding decline in mercury burdens (Thompson et al. 1992). Several possible hypotheses can be put forward to account for the observed trends in isotopic signatures.

Around the turn of this century, when nearly all of the historical fulmar feather samples were obtained, northern fulmars at St Kilda and the northern isles could feed, to some extent, upon offal and other waste products from the whaling industry. In Britain, whaling operations spanned 1903 to 1929 at Shetland and the Outer Hebrides with a smaller whaling industry at County Mayo, western Ireland, from 1908 to 1922 (Brown 1976). It is well documented that northern fulmars were attracted in large numbers to feed at whaling activities (see Fisher 1952). Whilst the majority of whales caught during this period were fin *Balaenoptera physalus* and sei *B. borealis* whales, smaller numbers of toothed whales were also caught, including sperm whales *Physeter macrocephalus* and bottlenose whales *Hyperoodon ampullatus* (Brown 1976).

Toothed whales feed largely on fish and squid, with baleen whales (Mysticeti) taking a greater proportion of zooplankton (see Evans 1987 for a review). Consistent with this dietary difference, $\delta^{15}\text{N}$ values in toothed whales have been found to range from +14.3 to +17.8‰ in collagen (Schoeninger & DeNiro 1984) and from +15.8 to +16.6‰ in muscle (Hobson & Welch 1992), with values in collagen of baleen whales generally lower, +11.7 to +15.8‰ (Schoeninger & DeNiro 1984). The relatively high $\delta^{15}\text{N}$ signatures in northern fulmars during the early part of this century (Table 1, Fig. 1) could, therefore, be due in part to the availability of offal from whaling, particularly from toothed whales which exhibit relatively high $\delta^{15}\text{N}$ values.

Concurrent with a reduction in $\delta^{15}\text{N}$ values, fulmars at both locations exhibited significant decreases in $\delta^{13}\text{C}$ signatures (Table 1, Fig. 2). Since there was no relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in feather samples from contemporary fulmars (see 'Results'), although $\delta^{15}\text{N}$ values spanned at least 3‰ (equivalent to a minimum of 1 trophic level) at both sites, it is unlikely that $\delta^{13}\text{C}$ signatures reflect trophic status. Other workers have concluded that, at higher levels within food chains, $\delta^{13}\text{C}$ signatures yield little information about trophic status (Wada et al. 1987, Fry 1988, Hobson & Welch 1992, Hobson et al. 1994). Nevertheless, the observed reduction in $\delta^{13}\text{C}$ values in fulmars may be linked to the disappearance of whale-derived carbon in their diet. The $\delta^{13}\text{C}$ signatures of plankton have been shown to vary with latitude (e.g. Rau et al.

1982, Dunton et al. 1989, Saupe et al. 1989), reflecting at least in part a positive correlation with sea surface temperature (Fontugne & Duplessy 1981, Rau et al. 1982). Whilst there is no evidence to indicate that any long-term change in sea surface temperatures has occurred to the northwest of the British Isles over the last 100 yr (Bottomley et al. 1990), latitudinal variation in $\delta^{13}\text{C}$ values at the base of marine food chains would lead to corresponding spatial variation in $\delta^{13}\text{C}$ signatures at other levels within those systems. The species of whales caught by Scottish and Irish whalers are migratory, spending winters at lower latitudes and moving northwards to higher latitudes during the summer (see Evans 1987). Whales which spent the winter at lower, warmer latitudes would have incorporated relatively ^{13}C -rich material. Fulmars feeding at higher, colder latitudes (St Kilda and the northern isles) would normally ingest material relatively depleted in ^{13}C . Material derived from whales and ingested by fulmars would be relatively ^{13}C -rich and may account for the elevated $\delta^{13}\text{C}$ signatures of fulmars at that time (Table 1). Schell et al. (1989) used $\delta^{13}\text{C}$ measurements in bowhead whale *Balaena mysticetus* baleen to indicate spatial variation in $\delta^{13}\text{C}$ values of prey as this species migrated through the Chukchi and Beaufort Seas, although this was not linked to latitudinal effects.

Whilst possible, the utilisation of whale offal by fulmars as an explanation for the decline in isotopic signatures has limitations. For the reduction in $\delta^{15}\text{N}$ signatures to be attributable to the availability of whale offal, a large proportion of the fulmar population would have to incorporate organic material from the relatively few toothed whales caught by the Scottish and Irish whalers. Fulmars can forage over large areas, yet offal from whaling would be concentrated at a relatively small number of coastal whaling stations.

Alternatively, long-term changes in the availability of fish and fish offal discarded by fishing boats may have influenced fulmar trophic status. In the northern North Sea, fishing activity has shifted from relatively large species and older age-classes to an increased proportion of smaller species and younger age-classes. Pope & Knights (1982) suggested that the greater proportion of smaller length-classes of groundfish in the northern North Sea compared to that recorded at the Faeroe Bank was the result of differences in fishing exploitation between these 2 sites, increased fishing pressure in the North Sea producing a fish community with relatively more smaller fish. Wainright et al. (1993) noted a decrease in trophic status of haddock *Melanogrammus aeglefinus* from the Georges Bank food web during this century, possibly linked to a reduction in the availability of fish prey. A relative increase in discarded material from fish of lower trophic status over time would result in a reduction in

the trophic status of fulmars scavenging on such fishery waste. Whilst such an explanation would be consistent with the observed decrease in $\delta^{15}\text{N}$ values in fulmars, it is difficult to see how the corresponding reduction in $\delta^{13}\text{C}$ signatures would be affected by a shift in fish and fish offal discards. Furthermore, any explanation based on temporal changes in fishing activity would be applicable largely to fulmars from the northern isles. The waters around St Kilda to the northwest of Scotland have not been as intensively fished as in the northern North Sea, yet fulmars at both locations show similar patterns of isotope decline (Table 1). Indeed, fish offal was only recorded in 0.8% of regurgitated food samples collected from fulmars at St Kilda by Furness & Todd (1984) and no fish offal was recorded from fulmar regurgitations at St Kilda in the present study (Table 2).

Any marked changes in the diet of fulmars from one year to the next would not be detected in the present study, where only one contemporary sample (from 1993) is compared to samples from several years prior to 1940. An eruption of medusae, for example, which are known to occur in the diet of fulmars (Harrison 1984), would lower the trophic status of fulmars. Although no mudusae were recorded in the present study, the presence of *Hyperia galba* in regurgitations from fulmars at St Kilda (Table 2) may indicate feeding on jellyfish, since this amphipod is known to associate with medusae (Harbison et al. 1977), and Leaper et al. (1988) noted fulmars feeding on jellyfish in waters around St Kilda in 1987. The significant decline in isotopic signatures of fulmars over time (Table 1) may be an artefact of a particular diet, comprising prey species of relatively low trophic status, in an exceptional single year, rather than a general long-term trend. Whilst possible, the same short-term change in diet would need to have occurred at both St Kilda and Foula in the same year. These 2 sites are about 450 km apart and occupy oceanographically distinct water masses (Bary 1963), so such an explanation is unlikely.

The significantly higher mean $\delta^{15}\text{N}$ signature in contemporary fulmars from Foula compared to that in fulmars from St Kilda, indicating a slightly higher trophic status of fulmars at Foula (see 'Results'; Table 1), is consistent with dietary differences between these 2 colonies. Based on the presence or absence of a particular prey type in regurgitations, fulmar diet at Foula consisted almost entirely of fish, whilst at St Kilda, although fish were present in over 80% of all regurgitations, a substantial proportion of regurgitations (35%) also contained crustacean prey (Table 2). The lack of any difference in $\delta^{13}\text{C}$ signatures of fulmars between these 2 locations (Table 1) probably reflects a pelagic feeding habit in this species. It has been suggested by several workers that $\delta^{13}\text{C}$ signatures in

seabirds and other marine biota reflected either benthic/pelagic or inshore/offshore feeding preferences (e.g. McConnaughey & McRoy 1979, Rau et al. 1983, Dunton et al. 1989, Hobson 1993, Hobson et al. 1994).

The diets of northern fulmars reported here are broadly similar to those described by Furness & Todd (1984). At Foula, sandeels, whitefish and fish offal are still the most important prey groups (Table 2), indicating a continued use of discarded material from whitefish trawler activities. Fulmars have been shown to consume most of the offal discarded by whitefish trawlers, aggressively excluding other seabird species from this food resource (Hudson & Furness 1989). The parasitic copepod *Caligus elongatus* was present in 35% of a sub-set of prey samples examined from Foula, always in association with whitefish; this species has been recorded in association with over 80 species of fish host (Kabata 1979). Interestingly, *C. elongatus* was absent from dietary samples from St Kilda despite a range of whitefish species being recorded (Table 2). However, since most of the fish species recorded in fulmar regurgitations from St Kilda were relatively small, juvenile individuals, it may be that insufficient exposure to this parasite had occurred.

Perhaps surprisingly, of 9 species of pelagic zooplankton and benthic invertebrates recorded in the diet of fulmars at St Kilda by Furness & Todd (1984) in 1981, only an unidentified species of *Acanthephyra* from that study was also recorded in the present study. We cannot explain why there should be such an apparent marked difference in species composition of the diet of fulmars at St Kilda over this period, since samples were collected at the same time of year in both studies and trawling activities, which bring benthic species to the surface as discards, are still in operation around St Kilda (as evidenced by the presence of a bottom-dwelling dragonet *Callionymus lyra*; Table 2). However, seabird diets have been shown to vary over relatively small spatial scales (Schneider & Hunt 1984), and it is likely that variation in diet would occur temporally.

Of the species recorded from fulmars at St Kilda in the present study, 2 can be considered as mesopelagic. The oplophorid *Acanthephyra pelagica* has been recorded at depths of 200 to 2000 m during the day, with highest densities mainly above 1000 m, migrating vertically to ca 500 m at night in the northeast Atlantic (Foxton 1972, Roe 1984). Similarly, the melamphid *Scopelogadus beanii*, whilst having been recorded from very close to St Kilda (Ebeling & Weed 1963), has not been recorded at the surface and rarely at depths less than 500 m, and evidence for a pronounced vertical migration is weak (Mauchline & Gordon 1984, Keene et al. 1987, Gartner & Musick 1989). That these species occur to an appreciable extent in fulmars' diets

at St Kilda (21% and 11% of samples contained *A. pelagica* and *S. beanii*, respectively; Table 2) raises the obvious question of how the birds obtain such prey items if they do not occur at or very near the sea surface, since fulmars have been shown to be able to dive to a maximum of only ca 3 m (Hobson & Welch 1992b).

Whilst bottom-dwelling or deep-water pelagic species may be brought to the surface and discarded by fishing activity (Hudson & Furness 1988), this would seem an unlikely explanation for the occurrence of *Acantheephyra pelagica* and *Scopelogadus beanii* in the diet of fulmars at St Kilda. Both these species are relatively small (total length of a few cm) and unlikely to be retained in nets. Furthermore, the diet of great skuas *Catharacta skua* at St Kilda includes several deep-water, bottom-dwelling species, presumably discarded from trawlers, but not the two in question (Thompson & Hamer unpubl. data). Predatory fish and mammals can force prey species to the surface and so make them available to seabirds (Martin 1986, Au & Pitman 1988, Grebmeier & Harrison 1992, Hamer et al. 1994). Such associations have not been recorded at St Kilda, nor does it seem likely that such deep-dwelling, and, in the case of *A. pelagica* in particular, slow-moving species could avoid a predatory fish or mammal and reach the surface. Ainley et al. (1986) reported deep-living prey species in the diet of seabirds from the Antarctic, whilst recently, Steele & Montevecchi (1994) hypothesised that crustacean prey recorded in the diet of Leach's storm-petrel *Oceanodroma leucorhoa* may migrate closer to the sea surface than previously thought. A similar explanation can be put forward to account for the presence of both *A. pelagica* and *S. beanii* in the diet of fulmars at St Kilda. It may well be, as suggested by Steele & Montevecchi (1994), that seabirds can act as independent samplers of marine fauna and complement information provided about the occurrence of mesopelagic organisms by conventional sampling techniques.

Acknowledgements. This work was supported by NERC grant GR3/8445 and the Shetland Oil Terminal Environmental Advisory Group. We thank Tony Fallick for the use of facilities at the SURRC, East Kilbride, Fred Cornwallis for building the vacuum line and Terry Donnelly and Susan Waldron for help and advice with isotope analysis. The Holbourn family kindly allowed us to conduct fieldwork on Foula and John Love facilitated access to St Kilda. We thank Ron Metcalfe and the Army Movement Control Detachment, Benbecula for help and assistance with travel to St Kilda and Jim Vaughan who helped with fieldwork on St Kilda and who made DRT's and SAL's stay there so enjoyable. We extend our thanks and appreciation to Werner Schwarzhans for identification of many of the fish otoliths, Mike Imber for squid beak identification, Karen Gresty for identification of copepods, Martin Attrill for help with identification of larger crustaceans and David Ellett for advice on sea temperatures. Historical feather

samples were obtained from the Royal Scottish Museum, Edinburgh, Liverpool Museum, the Hancock Museum, Newcastle upon Tyne, Bolton Museum and the British Museum (Natural History). Tring; we thank the staff of these institutions who allowed us access to their study skin collections. The manuscript was improved by the suggestions of 3 anonymous referees.

LITERATURE CITED

- Ainley DG, Fraser WR, Sullivan CW, Torres JJ, Hopkins TL, Smith WO (1986) Antarctic mesopelagic micronekton: evidence from seabirds that pack ice affects community structure. *Science* 232:847–849
- Ambrose SH (1986) Stable carbon and nitrogen isotope analysis of human and animal diet in Africa. *J Hum Evol* 15: 707–731
- Au DW, Pitman RL (1988) Seabird relationships with tropical tunas and dolphins. In: Burger J (ed) *Seabirds and other marine vertebrates*. Columbia University Press, New York, p 174–212
- Bary BM (1963) Temperature, salinity and plankton in the eastern north Atlantic and coastal water of Britain, 1957. I. The characterisation and distribution of surface waters. *J Fish Res Bd Can* 20:789–815
- Bottomley M, Folland CK, Hsiung J, Newell RE, Parker DE (eds) (1990) *Global ocean surface temperature atlas*. UK Meteorological Office and Massachusetts Institute of Technology, Meteorological Office, Bracknell
- Brown RGB (1970) Fulmar distribution; a Canadian perspective. *Ibis* 112:44–51
- Brown SG (1976) Modern whaling in Britain and the north-east Atlantic ocean. *Mamm Rev* 6:25–36
- Bryan G'W (1979) Bioaccumulation of marine pollutants. *Phil Trans R Soc Lond B* 286:483–505
- Chisholm BS, Nelson DE, Hobson KA, Schwarcz HP, Knyf M (1983) Carbon isotope measurement techniques for bone collagen: notes for the archaeologist. *J archaeol Sci* 10: 355–360
- Chisholm BS, Nelson DE, Schwarcz HP (1982) Stable-carbon isotope ratios as a measure of marine versus terrestrial protein in ancient diets. *Science* 216:1131–1132
- Dunton KH, Saupé SM, Golikov AN, Schell DM, Schonberg SV (1989) Trophic relationships and isotopic gradients among arctic and subarctic marine fauna. *Mar Ecol Prog Ser* 56:89–97
- Dunton KH, Schell DM (1987) Dependence of consumers on macroalgal (*Laminaria solidungula*) carbon in an arctic kelp community. *Mar Biol* 93:615–625
- Ebeling AW, Weed WH (1963) Melamphidae III. Systematics and distribution of the species in the bathypelagic fish genus *Scopelogadus* Vaillant. *Dana Report No. 60*, p 1–58
- Evans PGH (1987) *The natural history of whales and dolphins*. Christopher Helm, London
- Fisher J (1952) *The fulmar*. Collins, London
- Fontugne MR, Duplessy JC (1981) Organic carbon isotopic fractionation by marine plankton in the temperature range -1 to 31°C . *Oceanol Acta* 4:85–90
- Foxton P (1972) Observations on the vertical distribution of the genus *Acantheephyra* (Crustacea: Decapoda) in the eastern north Atlantic, with particular reference to species of the '*purpurea*' group. *Proc R Soc Edinb* 73(B):301–313
- Fry B (1988) Food web structure on Georges Bank from stable C, N and S isotopic compositions. *Limnol Oceanogr* 33: 1182–1190

- Fry B, Scanlan RS, Parker PL (1983) $^{13}\text{C}/^{12}\text{C}$ ratios in marine food webs of the Torres Strait, Queensland. *J Aust mar Freshw Res* 34:707–715
- Furness RW, Todd CM (1984) Diets and feeding of fulmars *Fulmarus glacialis* during the breeding season: a comparison between St Kilda and Shetland colonies. *Ibis* 126: 379–387
- Gartner JV, Musick JA (1989) Feeding habits of the deep-sea fish, *Scopelogadus beanii* (Pisces: Melamphidae), in the western north Atlantic. *Deep Sea Res* 36:1457–1469
- Grebmeier JM, Harrison NM (1992) Seabird feeding on benthic amphipods facilitated by gray whale activity in the northern Bering Sea. *Mar Ecol Prog Ser* 80:125–133
- Hamer KC, Thompson DR, Rundle AJ, Lewis SA, Stewart FM (1994) Mesopelagic fish eaten by yellow-legged herring gulls *Larus argentatus atlantis*. *Seabird* 16:30–33
- Harbison GR, Biggs DC, Madin LP (1977) The associations of Amphipoda Hyperiidæ with gelatinous zooplankton – II. Associations with Cnidaria, Ctenophora and Radiolaria. *Deep Sea Res* 24:465–488
- Hobson KA (1987) Use of stable-carbon isotope analysis to estimate marine and terrestrial protein content in gull diets. *Can J Zool* 65:1210–1213
- Hobson KA (1990) Stable isotope analysis of marbled murrelets: evidence for freshwater feeding and determination of trophic level. *Condor* 92:897–903
- Hobson KA (1991) Stable isotopic determinations of the trophic relationships of seabirds: preliminary investigations of alcids from coastal British Columbia. In: Montevecchi WA, Gaston AJ (eds) Studies of high-latitude seabirds. I. Behavioural, energetic and oceanographic aspects of seabird feeding ecology. *Can Wildl Serv Occas Pap* 68:16–20
- Hobson KA (1993) Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. *Mar Ecol Prog Ser* 95:7–18
- Hobson KA, Clark RG (1992) Assessing avian diets using stable isotopes I: turnover of $\delta^{13}\text{C}$ in tissues. *Condor* 94: 181–188
- Hobson KA, Montevecchi WA (1991) Stable isotopic determinations of trophic relationships of great auks. *Oecologia* 87:528–531
- Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. *J Anim Ecol* 63:786–798
- Hobson KA, Sealy SG (1991) Marine protein contributions to the diet of northern saw-whet owls on the Queen Charlotte Islands: a stable-isotope approach. *Auk* 108:437–440
- Hobson KA, Welch HE (1992a) Determinations of trophic relationships within a high Arctic marine food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar Ecol Prog Ser* 84:9–18
- Hobson KA, Welch HE (1992b) Observations of foraging northern fulmars (*Fulmarus glacialis*) in the Canadian high Arctic. *Arctic* 45:150–153
- Hudson AV, Furness RW (1988) Utilization of discarded fish by scavenging seabirds behind whitefish trawlers in Shetland. *J Zool, Lond* 215:151–166
- Hudson AV, Furness RW (1989) The behaviour of seabirds foraging at fishing boats around Shetland. *Ibis* 131:225–237
- Kabata Z (1979) Parasitic copepoda of British fishes. The Ray Society, London
- Keene MJ, Gibbs RH, Krueger WH (1987) Family Melamphidae, bigscales. In: Gibbs RH, Krueger WH (eds) Biology of midwater fishes of the Bermuda ocean acre. Smithsonian Contributions to Zoology 452. Smithsonian Institution Press, Washington, DC, p 169–185
- Leaper GM, Webb A, Benn S, Prendergast HDV, Tasker ML, Schofield R (1988) Seabird studies around St Kilda, June 1987. Nature Conservancy Council Chief Scientist Directorate Report 804, NCC, Aberdeen
- Lloyd C, Tasker ML, Partridge K (1991) The status of seabirds in Britain and Ireland. T & AD Poyser, London
- Martin AR (1986) Feeding association between dolphins and shearwaters around the Azores Islands. *Can J Zool* 64:1372–1374
- Mauchline J, Gordon JDM (1984) Occurrence and feeding of berycomorphid and percomorphid teleost fish in the Rockall Trough. *J Cons int Explor Mer* 41:239–247
- McConnaughey T, McRoy CP (1979) Food-web structure and the fractionation of carbon isotopes in the Bering Sea. *Mar Biol* 53:257–262
- Minagawa M, Wada E (1984) Stepwise enrichment of $\delta^{15}\text{N}$ along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim Cosmochim Acta* 48:1135–1140
- Mizutani H, Fukuda M, Kabaya Y (1992) ^{13}C and ^{15}N enrichment factors of feathers of 11 species of adult birds. *Ecology* 73:1391–1395
- Mizutani H, Fukuda M, Kabaya Y, Wada E (1990) Carbon isotope ratio of feathers reveals feeding behaviour of cormorants. *Auk* 107:400–403
- Muirhead SJ (1986) The accumulation, storage and elimination of metals and organochlorines in the great skua *Catharacta skua* and metal accumulation in Atlantic Procellariiformes. PhD thesis, University of Glasgow
- Pope JG, Knights BJ (1982) Simple models of prediction in multi-age fisheries for considering the estimation of fishing mortality and its effects. *Can Spec Publ Fish Aquat Sci* 59:64–69
- Rau GH, Mearns AJ, Young DR, Olson RJ, Schafer HA, Kaplan IR (1983) Animal $^{13}\text{C}/^{12}\text{C}$ correlates with trophic level in pelagic food webs. *Ecology* 64:1314–1318
- Rau GH, Sweeney RE, Kaplan IR (1982) Plankton $^{13}\text{C}/^{12}\text{C}$ ratio changes with latitude: differences between northern and southern oceans. *Deep Sea Res* 29:1035–1039
- Roe HSJ (1984) The diel migrations and distributions within a mesopelagic community in the north east Atlantic. 2. Vertical migrations and feeding of mysids and decapod Crustacea. *Prog Oceanogr* 13:269–318
- Salomonsen F (1965) Geographic variation of the fulmar (*Fulmarus glacialis*) and zones of the marine environment in the north Atlantic. *Auk* 85:327–355
- Saupe SM, Schell DM, Griffiths WB (1989) Carbon-isotope ratio gradients in western arctic zooplankton. *Mar Biol* 103:427–432
- Schell DM, Saupe SM, Haubenstock N (1989) Bowhead whale (*Balaena mysticetus*) growth and feeding as estimated by $\delta^{13}\text{C}$ techniques. *Mar Biol* 103:433–443
- Schneider DC, Hunt GL (1984) A comparison of seabird diets and foraging distribution around the Pribilof Islands, Alaska. In: Nettleship DN, Sanger GA, Springer PF (eds) Marine birds: their feeding ecology and commercial fisheries relationships. Supply and Services Canada, Ottawa, p 86–93
- Schoeninger MJ, DeNiro MJ (1984) Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. *Geochim Cosmochim Acta* 48:625–639
- Steele DH, Montevecchi WA (1994) Leach's storm-petrels prey on lower mesopelagic (Mysidacea and Decapoda) crustaceans: possible implications for crustacean and avian distributions. *Crustaceana* 66:212–218
- Tasker ML, Moore PR, Schofield RA (1988) The seabirds of St Kilda, 1987. *Scott Birds* 15:21–29
- Thompson DR (1990) Metal levels in marine vertebrates. In:

- Furness RW, Rainbow PS (eds) Heavy metals in the marine environment. CRC Press, Boca Raton, p 143–182
- Thompson DR, Becker PH, Furness RW (1993a) Long-term changes in mercury concentration in herring gulls *Larus argentatus* and common terns *Sterna hirundo* from the German North Sea coast. *J appl Ecol* 30:316–320
- Thompson DR, Furness RW, Lewis SA (1993b) Temporal and spatial variation in mercury concentrations in some albatrosses and petrels from the sub-Antarctic. *Polar Biol* 13: 239–244
- Thompson DR, Furness RW, Walsh PM (1992) Historical changes in mercury concentrations in the marine ecosystem of the north and north-east Atlantic ocean as indicated by seabird feathers. *J appl Ecol* 29:79–84
- Van der Merwe NJ, Roosevelt AC, Vogel JC (1981) Isotopic evidence for prehistoric subsistence change at Parmana, Venezuela. *Nature* 292:536–538
- Van der Merwe NJ, Vogel JC (1978) ^{13}C content of human collagen as a measure of prehistoric diet in woodland North America. *Nature* 276:815–816
- Wada E, Terazaki M, Kabaya Y, Nemoto T (1987) ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. *Deep Sea Res* 34:829–841
- Wainright SC, Fogerty MJ, Greenfield RC, Fry B (1993) Long-term changes in the Georges Bank food web: trends in stable isotopic compositions of fish scales. *Mar Biol* 115: 481–493
- Wynne-Edwards VC (1962) Animal dispersion in relation to social behaviour. Oliver & Boyd, Edinburgh

This article was submitted to the editor

Manuscript first received: January 30, 1995

Revised version accepted: March 27, 1995