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Spatial and temporal diet segregation in northern fulmars *Fulmarus glacialis* breeding in Alaska: insights from fatty acid signatures

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ABSTRACT: Northern fulmars *Fulmarus glacialis* in the North Pacific Ocean are opportunistic, generalist predators, yet their diets are poorly described; thus, relationships of fulmars to supporting food webs, their utility as indicators of variability in forage fish abundances, and their sensitivity to ecosystem change are not known. We employed fatty acid (FA) signature analysis of adipose tissue from adults (n = 235) and chicks (n = 33) to compare spatial, temporal, and age-related variation in diets of fulmars breeding at 3 colonies in Alaska. FA signatures of adult fulmars differed between colonies within years, and between seasons at individual colonies. Seasonal and spatial differences in signatures were greater than interannual differences at all colonies. Differences in FA signatures reflect differences in diets, probably because the breeding colonies are located in distinct ecoregions which create unique habitats for prey assemblages, and because interannual variation in the physical environment affects the availability of forage species. Differences between FA signatures of adults and chicks in 2003 and 2004 suggest that adults fed chicks different prey than they consumed themselves. Alternatively, if adults relied on the same prey as those fed to chicks, the differences in signatures could have resulted from partial digestion of prey items by adults before chicks were fed, or direct metabolism of FAs by chicks for tissue synthesis before FAs could be deposited into adipose tissue.

KEY WORDS: Fatty acids · Northern fulmar · *Fulmarus glacialis* · Alaska · Diet analysis

INTRODUCTION

Northern fulmars *Fulmarus glacialis* are abundant seabirds in the northern North Pacific Ocean and are opportunistic, generalist predators. They are generally known to feed on cephalopods, zooplankton, lantern fishes (Myctophidae), Scyphozoan jellyfish, juveniles of commercial fish species, e.g. walleye pollock *Theragra chalcogramma*, and other forage fishes that are critical to pelagic food webs and sensitive indicators of environmental change, e.g. capelin *Mallotus villosus* and Pacific sand lance *Ammodytes hexapterus* (Hatch & Nettleship 1998). Fulmars also follow fishing vessels for offal (Hatch & Nettleship 1998). Nevertheless, fulmars are effective samplers of prey populations and their diets can provide information about forage populations and ecosystem change. However, diets of fulmars at nesting colonies during the summer breeding season have not been quantified. Thus, possible long-term changes in fulmar diets, relationships of fulmars to supporting food webs, and the sensitivity of fulmars to ecosystem variability, such as that driven by a changing climate or by commercial fisheries, also are highly uncertain.

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The population of fulmars in the North Pacific is estimated at 2.1 million individuals, with 70% occurring in Alaska (Hatch & Nettleship 1998). Fulmars are monogamous and lay one egg during the breeding season. The adults share incubation almost equally and they both care for the chick — while one parent is brooding, the other is usually foraging, and both parents feed the chick (Hatch & Nettleship 1998). There are 4 major breeding colonies in Alaska: (1) Chagulak Island (52° 35′ N, 171° 10′ W), located in the central Aleutian Archipelago adjacent to the deep oceanic basin, has a population estimated at 500 000; (2) the Pribilof Islands (56° 35′ N, 170° 35′ W), located on the outer continental shelf near the shelf edge in the southeastern Bering Sea, have approximately 80 000 individuals; (3) St. Matthew and Hall Islands (60° 25′ N, 172° 45′ W), located in the middle of the broad continental shelf in the central Bering Sea, have approximately 450 000 individuals; and (4) the Semidi Islands (56° 05′ N, 156° 45′ W), located on the narrow shelf in the western Gulf of Alaska, where the local oceanography is primarily influenced by the Alaska Coastal Current and the Alaska Stream, have approximately 440 000 individuals (Hatch & Hatch 1983, Hatch 1993) (Fig. 1). Because the colonies are located in distinct oceanographic habitats or ecoregions (Piatt & Springer 2007), the birds nesting at them are likely supported by prey assemblages and food webs characteristic of each region. By understanding the foraging ecology and diets of fulmars and other marine birds in diverse habitats, predator–prey relationships and foraging patterns can be used in comparative ways to measure the impact of environmental variation on the birds and the ecosystem (Piatt et al. 2007).

Several well-known problems and biases associated with traditional methods of estimating seabird diets have been reviewed thoroughly (see Barrett et al. 2007). An alternative method that overcomes many of these problems is the use of fatty acid (FA) signatures to infer the diets of predators (Iverson 1993). In seabirds, the analysis of FAs in lipids from adipose tissue, stomach oil, and plasma has been used to infer trophic levels, spatial and temporal patterns in foraging behavior, and the relative importance of specific prey in their diets (Raclot et al. 1998, Dahl et al. 2003, Connan et al. 2005, Käkelä et al. 2005, 2006, 2007, Connan et al. 2007a,b, Iverson et al. 2007, Williams et al. 2008).

Knowledge of spatial, temporal, and age-related sources of variability in diet is essential for determining if fulmars can be used as indicator species in marine ecosystems. The objectives of the present study were to assess spatial (between colonies), temporal (seasonal and interannual), and age class (adult– chick) variability in the diets of fulmars at 3 of the 4 colonies in Alaska — Chowiet Island (Semidi Islands), St. George Island (Pribilof Islands), and Chagulak Island. We predicted that the diets would: (1) differ among colonies because they are located in distinct ecoregions with different prey assemblages; (2) differ interannually because of variability in the physical environment and the production and availability of prey; (3) differ seasonally due to availability of prey whose presence and abundance respond to seasonal physical and biological cycles; and (4) not differ between adults and chicks because previous studies showed similarities between adult and chick diets during the chick-rearing period (Hobson 1993, Hatch & Nettleship 1998). Our results are the first characterization of dietary variability of nesting fulmars in Alaska and provide a basis for using these generalist predators as indicators of environmental change in the North Pacific.

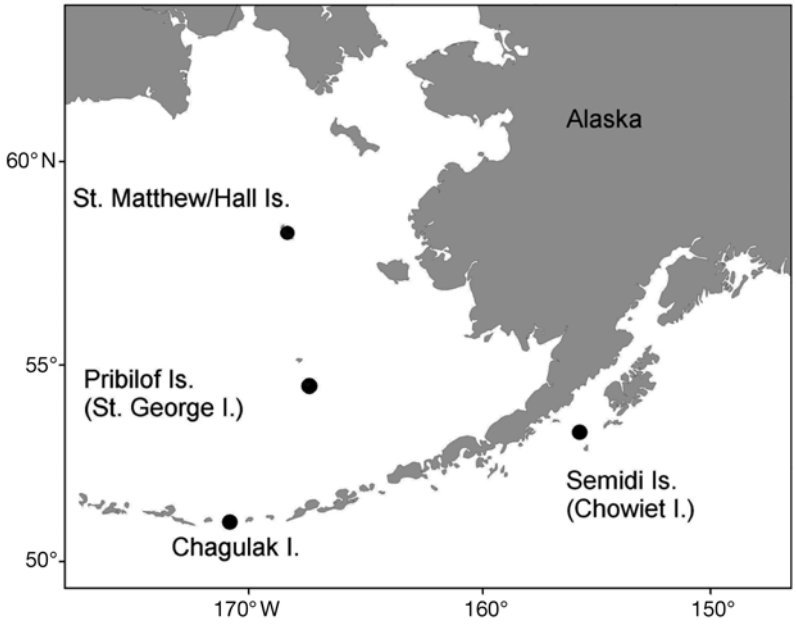

Fig. 1. *Fulmarus glacialis.* Locations of the 4 major colonies in Alaska. Semidi Islands (56° 05′ N, 156° 45′ W) in the western Gulf of Alaska; Chagulak Island (52° 35′ N, 171° 10′ W) in the eastern Aleutian Islands; Pribilof Islands (56° 35′N, 170° 35′ W) in the eastern Bering Sea; and St. Matthew and Hall Islands (60° 25′ N, 172° 45′ W) in the northern Bering Sea. Studies were not undertaken at the latter site

MATERIALS AND METHODS

Sample collection and analysis. Fulmars were captured either by using a modified dip net or a noose-pole, or by hand at their nests. Samples of synsacral adipose tissue were collected by live biopsy (Iverson et al. 2007) from

adult birds on Chowiet Island during the pre-incubation stage in May 2003 (n = 30) and 2004 (n = 25), and during the chick-rearing stage in August 2003 (n = 27) and 2004 (n = 31); on St. George Island during incubation in June 2003 (n = 29) and 2004 (n = 28), and during the chick-rearing stage in August 2003 (n = 9) and 2004 (n = 26); and on Chagulak Island during incubation in July 2004 (n = 30). Samples of adipose tissue were collected from chicks and one respective parent on Chowiet Island during August 2003 (n = 8 pairs) and 2004 (n = 25 pairs). Samples were not collected on the same dates at the 3 islands due to logistical constraints. Samples were stored frozen until analyzed for FA composition as described by Iverson et al. (2007) and Budge et al. (2006). Stomach oil samples were also taken from some birds in the present study to compare stomach oil and adipose tissue FAs; those results were reported in Wang et al. (2007).

Morphometric measurements were taken from all individuals. Wing length and mass were used to estimate the ages of chicks (Hatch 1979). All birds were released within 10 to 55 min after being captured and processed. It is unknown if nests were successful.

Lipids from adipose tissue samples were quantitatively extracted using a modified Folch technique (Folch et al. 1957, Iverson et al. 2001). FA methyl esters (FAMEs) were prepared from ≤100 mg of the lipid extracts using 3.0 ml Hilditch Reagent (0.5 N H_2SO_4 in methanol) in 1.5 ml methylene chloride with butylated hydroxytoluene, capped under nitrogen and heated at 100°C for 1 h (Budge et al. 2006). FAMEs were then extracted into hexane, concentrated, and brought up to volume (50 mg ml^{-1}) with high purity hexane. FAMEs were quantified using temperature-programmed gas liquid chromatography on a Perkin Elmer Autosystem II Capillary FID gas chromatograph fitted with a 30 m × 0.25 mm (inner diameter) column coated with 50% cyanopropyl-methylpolysiloxane (DB-23) and linked to a computerized integration system (Turbochrom 4 software, PE Nelson). All sample chromatograms and FA identifications were individually checked, corrected, and reintegrated as necessary.

Statistical analysis. Sixty-nine FAs were routinely identified in fulmar adipose tissue. In our data analyses, we used 18 FAs that had the largest overall variance, an overall mean of ≥0.2% by mass, and were known to reflect dietary intake (Iverson et al. 2004). Together these FAs accounted for 90.4% by mass of the total. Percentages of the 18 FAs were renormalized over 100% and then transformed into log ratios according to the following: $x_{trans} = \ln(x_i/c_r)$ where x_i is the percentage of a given FA, x_{trans} is the transformed FA, and c_r is 18:0, a reference FA (Budge et al. 2006). Transformation of raw percentages into log ratios was done to break the constraint that each observation must sum to a constant (Aitchison 1986).

The relationships between the FA signatures in different adipose tissue samples were analysed by principle components analysis (PCA). The relative positions of the samples or variables were plotted using 2 new coordinates, principal components PC1 and PC2, which represent the largest and second largest variance among the samples, respectively. To examine differences between individual FAs among groups, we conducted univariate analyses on the selected 18 FAs using analysis of variance (ANOVA) on ranked data followed by the Newman-Keuls test with alpha adjusted using Rice's sequential Bonferroni correction to correct for multiple tests of the same dataset ($p_1 \leq 0.05/18 = 0.0028$, Rice 1989). Chick age (d) was estimated from wing length (mm) using a logarithmic curve fitted to changes in length with age from a sample of known-age chicks (Hatch 1979). All statistical analyses were performed using SAS (SAS Institute).

RESULTS

Differences among adults

The most abundant FAs were generally similar across sampling groups, although levels of individual FAs varied greatly among colonies and over time (Table 1). All adults exhibited high levels of 20:1n-11 (9.4 to 29.6%) and 22:1n-11 (10.1 to 31.3%) (Table 1). Levels of 20:1n-9 (6.5 to 7.0%) in adults on Chowiet Island in May 2003 and 2004 were higher than the mean of all adults, and in May 2004 these birds were characterized by a unique signature, having levels of 20:5n-3 (0.2%) and 22:6n-3 (1.2%) significantly lower than the overall mean. FA 18:1n-9 (6.9 to 9.1%) was lowest in fulmars from Chowiet Island in August 2004 and St. George Island in June 2003 and 2004 (Table 1).

The PCA produced 4 eigenvalues >1.0. In combination, these PCs explained 84.1% of the variance (PC1: 40.0%; PC2: 20.2%; PC3: 14.2%; PC4: 9.7%). A plot of the mean scores ± SE on PC1 and PC2 shows separation between sampling groups, with PC1 separating all adults from Chowiet Island from adults on St. George and Chagulak Islands, and PC2 separating adults from Chowiet Island in August 2003 and 2004 and St. George Island in August 2003 from all other sampling groups (Fig. 2a). Overall, FA signatures from Chowiet Island were different than those on St. George Island (Fig. 2a). The PCA also demonstrated the interannual similarities in FA signatures among individuals from Chowiet Island in May and August 2003 and 2004, and individuals from St. George Island in June and August 2003 and 2004. FA signatures were similar among individuals from Chagulak Island in July and St. George Island in June 2004. Based on the FA loadings along

Table 1. *Fulmarus glacialis.* Fatty acid (FA) composition of adipose tissue of adult northern fulmars on Chowiet Island in May and August 2003 and 2004; St. George Island in June and August 2003, 2004; and Chagulak Island in July 2004. Values are mean (SD) weight percentage. Means with no common superscripted letter differ at $p < 0.0028$ (ANOVA on ranked data, Newman-Keuls test, Rice's sequential Bonferroni); [a]: largest mean. Only 18 of 69 FAs are shown

	Chowiet 2003		Chowiet 2004		St.George 2003		St.George 2004		Chagulak 2004
FA	May	August	May	August	June	August	June	August	July
14:0	1.83^{d} (0.43)	1.94^{cd} (0.84)	1.74^{d} (0.45)	2.52^{bc} (0.63)	5.69^{a} (1.94)	2.62^{bc} (0.94)	7.52^{a} (2.29)	3.40^{b} (1.08)	2.99^{b} (1.14)
16:0	5.81^{c} (1.66)	7.55^{bc} (3.68)	5.41^{c} (1.74)	7.32^{bc} (2.57)	8.74^{ab} (2.01)	11.45^{a} (2.43)	8.43^{ab} (1.61)	8.97^{ab} (2.11)	7.98^{b} (2.66)
16:1n-7	1.88^{c} (0.90)	2.31^{c} (1.56)	1.94^{c} (1.02)	2.11^{c} (0.86)	3.08^{bc} (1.55)	4.82^{a} (1.31)	2.81^{bc} (0.97)	3.87^{ab} (1.32)	3.08^{bc} (1.49)
17:0	0.31^{b} (0.18)	0.51^{a} (0.23)	0.16^{cd} (0.06)	0.43^{ab} (0.21)	0.21^{c} (0.11)	0.17^{cd} (0.13)	0.11^{de} (0.07)	0.14^{cd} (0.05)	0.09^{e} (0.04)
18:0	2.24^{de} (0.46)	2.90^{bcd} (0.85)	2.03^{e} (0.32)	3.67^{ab} (0.99)	2.77^{cd} (0.84)	4.48^{a} (1.00)	2.48^{de} (0.70)	3.25^{abc} (0.62)	2.70^{cd} (0.71)
18:1n-9	12.62^{bc} (3.82)	11.91^{bcd} (5.61)	13.19^{b} (2.94)	9.05^{cde} (5.44)	8.10^{de} (4.02)	19.19^{a} (4.23)	6.91^{e} (3.07)	12.65^{b} (3.32)	12.28^{bc} (4.37)
18:1n-7	1.55^{d} (0.65)	2.69^{bcd} (1.62)	1.41^{d} (0.35)	1.88^{cd} (0.98)	2.37^{cd} (1.58)	5.66^{a} (1.63)	1.60^{d} (0.92)	3.52^{ab} (1.12)	2.73^{bc} (1.21)
18:2n-6	1.01^{a} (0.13)	0.85^{b} (0.18)	0.97^{ab} (0.14)	1.04^{a} (0.28)	0.63^{c} (0.33)	0.88^{b} (0.05)	0.66^{c} (0.15)	0.95^{ab} (0.20)	0.94^{ab} (0.19)
18:4n-3	0.46^{b} (0.22)	0.76^{b} (0.53)	0.14^{c} (0.06)	0.89^{ab} (0.38)	0.79^{b} (0.57)	0.88^{ab} (0.55)	0.88^{ab} (0.53)	1.88^{a} (0.96)	1.14^{ab} (0.81)
20:1n-11	18.91^{cd} (3.39)	14.95^{de} (4.87)	23.63^{ab} (3.34)	18.42^{cd} (4.38)	26.00^{ab} (9.52)	9.44^{e} (4.80)	29.59^{a} (6.80)	17.67^{cd} (4.50)	20.37^{bc} (4.63)
20:1n-9	6.96^{a} (0.67)	5.26^{b} (1.91)	6.51^{a} (0.25)	4.03^{bc} (0.83)	4.09^{bc} (0.53)	4.48^{c} (3.07)	3.81^{c} (0.73)	3.58^{c} (0.74)	4.11^{bc} (0.76)
20:1n-7	0.55^{abc} (0.10)	0.65^{ab} (0.20)	0.42^{d} (0.06)	0.73^{a} (0.18)	0.52^{bcd} (0.22)	0.68^{ab} (0.25)	0.54^{bcd} (0.27)	0.47^{cd} (0.19)	0.47^{cd} (0.12)
20:4n-6	0.38^{ab} (0.08)	0.52^{a} (0.19)	0.27^{dc} (0.04)	0.61^{a} (0.27)	0.26^{d} (0.11)	0.52^{a} (0.13)	0.22^{d} (0.08)	0.33^{bc} (0.11)	0.25^{dc} (0.05)
20:5n-3	1.04^{d} (0.71)	3.02^{bc} (2.72)	0.21^{e} (0.13)	2.41^{bc} (1.38)	3.56^{abc} (2.45)	5.95^{a} (2.69)	1.92^{dc} (1.21)	4.71^{ab} (2.40)	2.33^{dc} (1.63)
22:1n-11	30.32^{ab} (5.36)	27.34^{abc} (10.75)	31.34^{a} (4.02)	26.52^{abc} (7.48)	19.99^{cd} (5.89)	10.05^{e} (6.12)	21.11^{cd} (3.94)	17.85^{de} (7.66)	25.03^{bcd} (9.43)
22:1n-9	2.76^{a} (0.41)	2.50^{a} (1.00)	2.43^{a} (0.27)	1.48^{bc} (0.41)	1.34^{bc} (0.31)	1.03^{c} (0.44)	1.21^{bc} (0.37)	1.16^{bc} (0.51)	1.63^{b} (0.60)
22:5n-3	1.15^{c} (0.49)	1.66^{bc} (0.68)	0.43^{d} (0.20)	2.55^{a} (0.76)	1.47^{c} (0.76)	1.95^{ab} (0.56)	1.34^{c} (0.60)	1.33^{c} (0.45)	1.18^{c} (0.36)
22:6n-3	2.85^{d} (1.52)	4.92^{bc} (2.12)	1.16^{e} (0.49)	5.68^{bc} (1.81)	3.93^{cd} (2.13)	8.60^{a} (1.97)	2.87^{d} (2.03)	6.53^{ab} (2.08)	3.79^{cd} (1.71)
n	30	27	25	31	29	9	28	26	30

PC1, the separation of sampling groups was due mainly to the combination of differences in levels of 18:4n-3, 20:1n-11, 20:1n-9, 20:1n-7, 20:5n-3, 22:1n-9, 22:1n-11, and 22:6n-3 (Fig. 2a,b). FA loadings along PC2 show that differences in levels of 14:0, 16:0, 16:1n-7, 17:0, 18:1n-9, 18:1n-7, 18:2n-6, and 22:5n3 also contributed to the separation among adults (Fig. 2a,b).

Differences between adult males and females

We found no differences in FAs between males and females on Chowiet Island in May and August, and St. George Island in June 2003 (ANOVA on ranked data, Newman-Keul's test, Rice's sequential Bonferroni, $p_1 > 0.05/18 = 0.0028$).

Differences between adults and chicks

The estimated ages of chicks sampled on Chowiet Island in 2003 and 2004 differed between years: 14 ± 5.8 d (range = 9 to 25) and 21 ± 5.9 d (range = 13 to 32), respectively (*t*-test, $p = 0.003$). FA composition varied between adults and chicks from Chowiet Island in both years (Table 2). For samples from

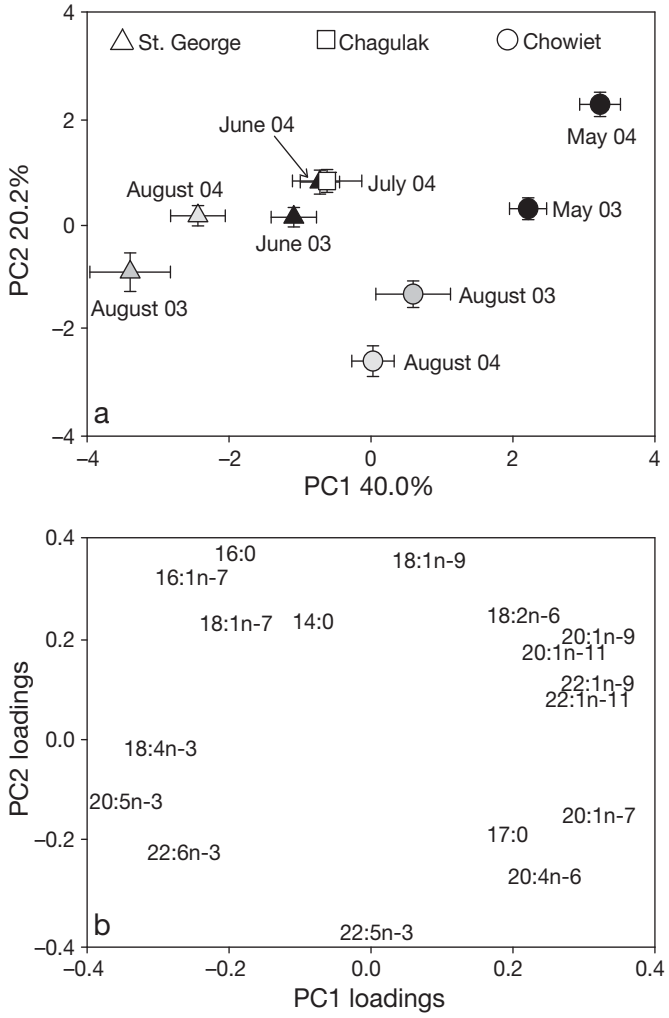

Fig. 2. *Fulmarus glacialis*. (a) Plots of mean (± 1 SE) scores for principle components analysis of northern fulmar adipose tissue samples for birds from Chowiet, Chagulak, and St. George Islands. Shading represents sampling groups (black: May/June; grey: August; no shade: July). (b) PC1 and PC2 loadings of 17 FAs used in analysis

2003, 6 FAs differed between adults and chicks: FAs 16:0, 16:1n-7, 18:1n-9, and 18:2n-6 were higher in chicks, while 22:1n-11 and 22:1n-9 were higher in adults (Table 2). In 2004, 10 FAs differed between adults and chicks: FAs 16:0, 16:1n-7, 18:1n-9, 18:1n-7, and 18:2n-6 were higher in chicks, while 17:0, 20:1n-7, 20:4n-6, 22:1n-11, and 22:5n-3 were higher in adults (Table 2). The PCA produced 4 eigenvalues >1.0, which in combination accounted for 85.7% of the variation (PC1: 33.7%; PC2: 31.9%; PC3: 13.7%; PC4: 6.4%). A plot of the mean scores ± SE on PC1 and PC2 showed a clean division between adults and chicks (Fig. 3a). Separation between adults and chicks along PC1 was mainly due to differences in levels of 16:0, 16:1n-7, 18:1n-9, 18:1n-7, 20:1n-7, 20:4n-6, 22:1n-11, and 22:5n-3 (Fig. 3a,b).

Table 2. *Fulmarus glacialis*. Fatty acid (FA) composition of adipose tissue of adult and chick northern fulmars on Chowiet Island in August 2003 and 2004. Values are mean (SD) weight percentage. Means with no common superscripted letter differ at $p < 0.0028$ (ANOVA on ranked data, Newman-Keuls test, Rice's sequential Bonferroni); [a]: largest mean. Only 18 of 69 FAs are shown

	2003		2004	
FA	Adult	Chick	Adult	Chick
14:0	1.81 (0.51)	2.40 (0.79)	2.50 (0.67)	2.41 (0.49)
16:0	6.77[b] (2.17)	10.65[a] (2.38)	7.12[b] (2.71)	9.54[a] (1.86)
16:1n-7	1.79[b] (0.59)	3.20[a] (0.94)	2.08[b] (0.86)	3.69[a] (0.93)
17:0	0.51[a] (0.19)	0.37[ab] (0.05)	0.46[a] (0.21)	0.29[b] (0.05)
18:0	2.94 (0.92)	3.63 (0.95)	3.60 (1.08)	2.92 (0.53)
18:1n-9	10.20[b] (4.15)	19.85[a] (2.63)	8.54[b] (5.43)	18.23[a] (3.09)
18:1n-7	2.17[ab] (0.83)	3.41[a] (1.21)	1.72[b] (0.83)	3.03[a] (0.96)
18:2n-6	0.91[b] (0.15)	1.29[a] (0.08)	1.05[b] (0.31)	1.30[a] (0.10)
18:4n-3	0.75 (0.38)	0.76 (0.55)	0.88 (0.40)	0.54 (0.29)
20:1n-11	15.58 (3.47)	13.13 (4.79)	18.86 (4.52)	17.39 (4.09)
20:1n-9	5.38[a] (0.96)	4.80[ab] (1.00)	3.95[b] (0.84)	5.09[ab] (0.71)
20:1n-7	0.70[ab] (0.21)	0.60[ab] (0.10)	0.73[a] (0.19)	0.51[b] (0.08)
20:4n-6	0.65[a] (0.24)	0.51[a] (0.20)	0.62[a] (0.29)	0.32[b] (0.13)
20:5n-3	2.45 (1.20)	2.95 (2.28)	2.36 (1.45)	1.75 (1.05)
22:1n-11	29.16[a] (7.28)	14.86[b] (4.76)	27.27[a] (7.64)	18.44[b] (4.18)
22:1n-9	2.60[a] (0.78)	1.43[b] (0.31)	1.48[b] (0.42)	1.37[b] (0.27)
22:5n-3	1.94[ab] (0.88)	1.54[ab] (0.41)	2.53[a] (0.81)	1.26[b] (0.48)
22:6n-3	5.42 (2.27)	6.95 (2.20)	5.53 (1.86)	4.61 (1.30)
n	8	8	25	25

DISCUSSION

Differences in FA signatures of adult fulmars at the 3 locations within years and between seasons at individual colonies strongly supported our predictions that fulmar diets would differ between colonies and diets would differ between seasons within colonies. However, results only weakly supported the prediction that diets would differ between years within colonies. Sig-

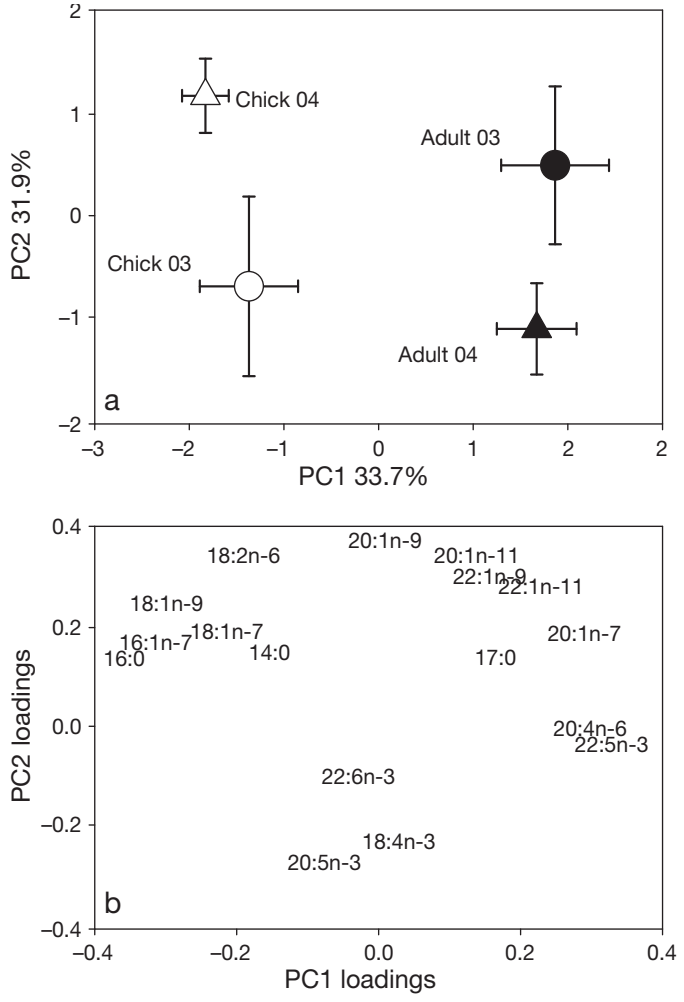

Fig. 3. *Fulmarus glacialis.* (a) Plots of mean (± 1 SE) scores for principle components analysis of adults (black symbols) and chicks (non-shaded symbols) on Chowiet Island in 2003 and 2004. (b) PC1 and PC2 loadings of 17 FAs used in analysis

natures of chicks differed significantly in both years from those of adults, which did not support prediction that diets of adult fulmars and their chicks would be similar. However, the comparison of adult and chick signatures is complex and is addressed further in the discussion.

Differences among adults

FA profiles of fulmars varied among the 3 colonies. Chowiet Island, on the narrow continental shelf of the western Gulf of Alaska, differed conspicuously from St. George Island near the edge of the broad shelf of the eastern Bering Sea. Chagulak Island, in the Aleutian Archipelago separating the basins of the Bering Sea and the Gulf of Alaska, lay midway between the other 2 sites. Seasonal differences were pronounced at both Chowiet and St. George Islands. We also found interannual differences at Chowiet and St. George Islands, but the variation was much less pronounced than the spatial differences between colonies or seasonal differences between the 2 islands.

Northern fulmars forage close to their breeding colonies compared to some other members of the family Procellariiformes. Observations on the daily activity of adults indicate that most foraging during the chick-rearing stage occurs within a radius of 100 km, whereas Atlantic fulmars are known to range as far as 1000 km before egg-laying and 40 to 200 km during incubation (Furness & Todd 1984, Hatch & Nettleship 1998). In Alaska, the greater the distances over which fulmars forage, the more ecoregions they would encounter, and thus the greater the array of prey. Because foraging ranges of fulmars may differ greatly between breeding stages, the suites of prey available to fulmars may differ accordingly.

Studies compiled by Hatch & Nettleship (1998) have shown seasonal and annual shifts, as well as longer-term variation, in the diets of northern fulmars in the Atlantic and Pacific. Those patterns are similar to the seasonal changes in FA signatures we found at Chowiet and St. George Islands. The differences we found in FAs, and thus implied differences in diets, are also consistent with variable assemblages of prey species in the Western Gulf of Alaska, Bering Sea, and Aleutian Islands and the trophic dependencies of seabirds in those regions. For example, squids are abundant and widespread throughout the North Pacific, and are known to be consumed by fulmars and many other species of seabirds that feed at the edge of and off the continental shelf; however, they are much less important for species and individuals foraging over the shelf (DeGange & Sanger 1986, Sanger 1987, Hills & Fiscus 1988, Hatch & Nettleship 1998). Capelin is a common and important forage species of piscivorous seabirds in the Gulf of Alaska, but is much less common at the Pribilof Islands and rare in the Aleutian Islands (Hunt et al. 1981, Sanger 1983, DeGange & Sanger 1986, Sanger 1987, Springer & Byrd 1989, Hatch & Sanger 1992, Springer et al. 1996). Similarly, most piscivorous seabirds at the Pribilof Islands consume large numbers of juvenile walleye pollock, the most abundant forage fish on the eastern Bering Sea shelf (Plan Team 2007). Additionally, fulmars are the most commonly observed species following longline vessels in the Bering Sea and the Aleutian Islands in which the offal discarded (mainly from pollock) is made available to scavenging seabirds (Furness et al. 2007). Diet studies of fulmars have also found a lower diversity of fish prey in high-arctic waters than in low-arctic or boreal zones, and higher diversity in the

northeast Pacific than elsewhere (Hatch & Nettleship 1998). This supports our finding of spatial differences in FA signatures at the 3 sampled Alaskan breeding colonies.

Additionally, the results from the present study are similar to those found by Dahl et al. (2003). Levels of total saturated, monounsaturated, and polyunsaturated FAs for fulmars in the present study were 14.2 ± 4.6, 68.7 ± 9.9, and 10.4 ± 5.8%, respectively. Dahl et al. (2003) reported similar amounts: 18.6 ± 4.4, 65.8 ± 9.0, and 15.6 ± 4.7%, respectively. However, the major FAs in fulmar adipose tissue in the present study differ from those in Dahl et al. (2003). The major FAs in fulmar adipose tissue in the present study were 22:1n-11 (24.4%), 20:1n-11 (20.7%), 18:1n-9 (11.1%) and 16:0 (7.7%); in Dahl et al. (2003) they were 18:1n-9 (20.4%), 20:1n-9 (18.1%), 22:1n-11 (13.8%), and 16:0 (11.8%). Overall, the level of 20:1n-9 (4.8%) in the present study was much lower than that found in Dahl et al. (2003). The present study was conducted in Alaska while Dahl et al. (2003) collected fulmars from Spitsbergen. We speculate that these differences in FAs are due to differences in fulmar diet in the 2 studies.

Differences between adults and chicks

FA signatures of adult fulmars differed from those of their chicks in both years. Two explanations for contrasting FA signatures in adults and chicks are possible: (1) adults fed their chicks a different diet than they relied on themselves, or (2) diets were the same, but FA signatures of ingested prey were altered by partial digestion before chicks were fed, and/or chicks differentially metabolized FAs directly from the diet to fuel non-adipose tissue synthesis, leaving an altered suite of FAs to be deposited into their adipose tissue.

Regarding the first possibility, Weimerskirch et al. (1994) suggested that adults of 4 species of Procellariiformes used short trips almost exclusively to gather prey for their chicks, while longer trips were used to replenish energy consumed during foraging for chick meals. If fulmars behave similarly, adults in the present study could have fed chicks different prey items than they consumed for themselves — there is evidence that this occurs in some seabird species, including other Procellariiformes (Hobson 1993, Hodum & Hobson 2000).

Regarding the second possibility, Hatch & Nettleship (1998) reported that adult and chick diets estimated from stomach contents and regurgitations were similar during the chick-rearing period. Hobson (1993) also reported no significant differences in trophic position between fulmar adults and chicks based on stable isotope analyses. Additionally, Bishop et al. (1983) reported that adult and chick diets of another Procellariiform, the short-tailed shearwater *Puffinus tenuirostris*, were the same despite large differences in 4 adipose tissue FAs (16:0, 18:1, 20:5, and 22:6). We found some similarities in our data, e.g. large differences in 16:0 and 18:1 isomers (data not shown); but no similarities with previous studies in terms of the levels of these 4 FAs. Bishop et al. (1983) considered a model, based on modes of existence, to explain how FAs in adults and chicks could differ even with the same diet. Adult shearwaters, for example, have a higher turnover rate of adipose tissue FAs: during chick-rearing they forage more or less continuously and dietary FAs are deposited into the adipose tissue to a limited extent. In contrast, growing chicks use essential and other FAs for tissue growth and accumulate large quantities of adipose tissue as an energy reserve and to fuel tissue synthesis. Differences in selective mobilization of adipose tissue FAs between adults and chicks could also affect FA compositions.

In addition, there is variability between stomach content, stomach oil, and adipose tissue signatures (Bishop et al. 1983, Wang et al. 2007). Bishop et al. (1983) suggested that the digestibility of prey, and the amount of time it remains in the stomach of the adult before it is fed to a chick, affects the lipid composition of the meal. That is, if adults collect food a considerable distance from the colony, some digestion will occur in the stomach prior to the chick being fed. Partial digestion of food items could explain the differences in signatures even if adults fed their chicks from the same meal they had consumed.

Finally, stomach oil is a source from which FAs can be mobilized directly. Storage of lipids in the proventriculus has energetic advantages for seabirds that frequently experience periods of fasting, because it reduces the need to synthesize fat reserves from assimilated FAs and later remobilize, at a metabolic cost, those stores during fasting (Roby et al. 1989, Roby et al. 1997). Chicks at the nest may preferentially use FAs from their stomach oil before accessing FAs stored in their adipose tissue, and that could influence which FAs are deposited into the adipose tissue. Because of this possibility, and partial digestion of prey by food-provisioning adults, the comparison of adult and chick FA signatures remains open to several interpretations.

We have demonstrated the potential of FA signatures as a useful technique in determining changes in fulmar diets and foraging patterns. Further work is being done to estimate quantities of prey species in fulmar diet using quantitative fatty acid signature analysis (Iverson et al. 2004, 2007). Such detailed information will provide more insight about fulmar diets and food webs in ecoregions that fulmars and other marine birds occupy.

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LITERATURE CITED

Aitchison J (1986) The statistical analysis of compositional data. Chapman & Hall, New York

Barrett RT, Camphuysen KCJ, Anker-Nilssen T, Chardine JW and others (2007) Diet studies of seabirds: a review and recommendations. ICES J Mar Sci 64:1675–1691

Bishop DG, Ritz DA, Hosie GW, Kenrick JR, Olley J (1983) Fatty acid composition of the lipids of *Puffinus Tenuirostris* (Temminck) in relation to its diet. J Exp Mar Biol Ecol 71: 17–26

Budge SM, Iverson DJ, Koopman HN (2006) Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. Mar Mamm Sci 22:759–801

Connan M, Mayzaud P, Boutoute M, Weimerskirch H, Cherel Y (2005) Lipid composition of stomach oil in a procellariiform seabird *Puffinus tenuirostris*: implications for food web studies. Mar Ecol Prog Ser 290:277–290

Connan M, Cherel Y, Mabille G, Mayzaud P (2007a) Trophic relationships of white-chinned petrels from Crozet Islands: combined stomach oil and conventional dietary analyses. Mar Biol 152:95–107

Connan M, Cherel Y, Mayzaud P (2007b) Lipids from stomach oil of procellariiform seabirds document the importance of myctophid fish in the Southern Ocean. Limnol Oceanogr 52:2445–2455

Dahl TM, Falk-Petersen S, Gabrielsen GW, Sargent JR, Hop H, Millar RM (2003) Lipids and stable isotopes in common eider, black-legged kittiwake and northern fulmar: a trophic study from an Arctic fjord. Mar Ecol Prog Ser 256:257–269

DeGange AR, Sanger GA (1986) Marine birds. In: Hood DW, Zimmerman ST (eds) The Gulf of Alaska physical environment and biological resources. NOAA Ocean Assessment Division, Alaska Office, Washington, DC, p 479–526

Folch J, Lees M, Sloane-Stanly GH (1957) A simple method for the isolation and purification of total lipids from animal tissues. J Biol Chem 226:497–509

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

Furness RW, Edwards AE, Oro D (2007) Influence of management practices and of scavenging seabirds on availability of fisheries discards to benthic scavengers. Mar Ecol Prog Ser 350:235–244

Hatch SA (1979) Breeding and population ecology of northern fulmars (*Fulmarus glacialis*) at Semidi Islands, Alaska. MS thesis, University of Alaska, Fairbanks, AK

Hatch SA (1993) Ecology and population status of Northern Fulmars *Fulmarus glacialis* of the North Pacific. In: Vermeer K, Briggs KT, Morgan KH, Siegel-Causey D (eds) The status, ecology, and conservation of marine birds of the North Pacific. Can Wildlife Service Special Publ, Ottawa, p 82–91

Hatch SA, Hatch MA (1983) Populations and habitat use of marine birds in the Semidi Islands, Alaska. Murrelet 64: 39–46

Hatch SA, Nettleship DN (1998) Northern Fulmar (*Fulmarus glacialis*). The birds of North America, Philadelphia, PA

Hatch SA, Sanger GA (1992) Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska. Mar Ecol Prog Ser 80:1–14

Hills S, Fiscus CH (1988) Cephalopod beaks from the stomachs of northern fulmars (*Fulmarus glacialis*) found dead on the Washington coast. Murrelet 69:15–20

Hobson KA (1993) Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. Mar Ecol Prog Ser 95:7–18

Hodum PJ, Hobson KA (2000) Trophic relationships among Antarctic fulmarine petrels: insights into dietary overlap and chick provisioning strategies inferred from stable isotope ($\delta^{15}N$ and $\delta^{13}C$) analyses. Mar Ecol Prog Ser 198: 273–281

Hunt GL Jr, Burgeson B, Sanger GA (1981) Feeding ecology of seabirds in the eastern Bering Sea. In: Hood DW, Calder JA (eds) The eastern Bering Sea shelf: oceanography and resources, Vol 2. University of Washington Press, Seattle, p 629–648

Iverson SJ (1993) Milk secretion in marine mammals in relation to foraging: Can milk fatty acids predict diet? Symp Zool Soc Lond 66:263–291

Iverson SJ, Lang SLC, Cooper MH (2001) Comparison of the Bligh and Dyer and Folch methods for total lipid determination in a broad range of marine tissue. Lipids 36: 1283–1287

Iverson SJ, Field C, Bowen WD, Blanchard W (2004) Quantitative fatty acid signature analysis: a new method of estimating predator diets. Ecol Monogr 74:211–235

Iverson SJ, Springer AM, Kitaysky AS (2007) Seabirds as indicators of food web structure and ecosystem variability: qualitative and quantitative diet analyses using fatty acids. Mar Ecol Prog Ser 352:235–244

Käkelä R, Käkelä A, Kahle S, Becker PH, Kelly A, Furness R (2005) Fatty acid signatures in plasma of captive herring gulls as indicators of demersal or pelagic fish diet. Mar Ecol Prog Ser 293:191–200

Käkelä A, Crane J, Votier SC, Furness RW, Käkelä R (2006) Fatty acid signatures as indicators of diet in great skuas *Stercorarius skua*, Shetland. Mar Ecol Prog Ser 319: 297–310

Käkelä A, Furness RW, Kelly A, Strandberg U, Waldron S, Käkelä R (2007) Fatty acid signatures and stable isotopes as dietary indicators in North Sea seabirds. Mar Ecol Prog Ser 342:291–301

Piatt JF, Springer AM (2007) Marine ecoregions in Alaska. In: Spies RB (ed) Long-term ecological change in the northern Gulf of Alaska. Elsevier, Amsterdam, p 522–526

Piatt JF, Sydeman WJ, Wiese F (2007) Introduction: seabirds as indicators of marine ecosystems. Mar Ecol Prog Ser 352: 199–204

Plan Team (2007) Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. 2007 Stock assessment and fishery evaluation report, Appendix A. North Pacific Fishery Management Council, Anchorage, p 1–40

Raclot T, Groscolas R, Cherel Y (1998) Fatty acid evidence for the importance of myctophid fishes in the diet of king penguins, *Aptenodytes patagonicus*. Mar Biol 132:523–533

Rice WR (1989) Analysing tables of statistical tests. Evolution 43:223–225

Roby DD, Brink KL, Place AR (1989) Relative passage rates of lipid and aqueous digesta in the formation of stomach oils. Auk 106:303–313

Roby DD, Taylor JRE, Place AR (1997) Significance of stomach oil for reproduction in seabirds: an interspecies cross-fostering experiment. Auk 114:725–736

Sanger GA (1983) Diets and food web relationships of seabirds in the Gulf of Alaska and adjacent marine regions. US Fish and Wildlife Service Report, Denver

Sanger GA (1987) Trophic levels and trophic relationships of seabirds in the Gulf of Alaska. In: Croxall JP (ed) Seabirds: feeding ecology and role in marine ecosystems. Cambridge University Press, Cambridge, p 229–257

Springer AM, Byrd GV (1989) Seabird dependence on walleye pollock in the southeastern Bering Sea. Proceedings of the International Symposium on the Biology and Management of Walleye Pollock, 14–16 November 1988. Sea Grant, University of Alaska, Fairbanks, p 667–677

Springer AM, Piatt JF, Van Vliet G (1996) Seabirds as proxies of marine habitats and food webs in the western Aleutian Arc. Fish Oceanogr 5:45–55

Wang SW, Iverson SJ, Springer AM, Hatch SA (2007) Fatty acid signatures of stomach oil and adipose tissue of northern fulmars (*Fulmarus glacialis*) in Alaska: implications for diet analysis of Procellariiform birds. J Comp Physiol [B] 177:893–903

Weimerskirch H, Chastel O, Ackerman L, Chaurand T, Cuenot-Chaillet F, Hindermeyer X, Judas J (1994) Alternate long and short foraging trips in pelagic seabird parents. Anim Behav 47:472–476

Williams CT, Iverson SJ, Buck CL (2008) Stable isotopes and fatty acid signatures reveal age- and stage-dependent foraging niches in tufted puffins. Mar Ecol Prog Ser 363: 287–298

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