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Lipids and stable isotopes in common eider, black-legged kittiwake and northern fulmar: a trophic study from an Arctic fjord

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ABSTRACT: Lipid class and fatty acid compositions were determined in common eider (*Somateria mollissima*), black-legged kittiwake (*Rissa tridactyla*) and northern fulmar (*Fulmarus glacialis*) from Kongsfjorden, Spitsbergen. Muscle and liver were sampled in all species, while fat tissue was sampled in eiders and fulmars. Triacylglycerols (TAG) dominated the lipid class compositions of all tissues, and the major fatty acids found in TAG were: 18:1n9, 16:0, 18:0, 20:5n3 and 16:1n7 for eider; 16:0, 18:1n9, 18:0, 20:1n9 and 16:1n7 for kittiwake; 18:1n9, 16:0, 20:1n9, 22:1n11, and 18:0 for fulmar. To attain information on prey composition, fatty acid signature analysis was performed on muscle fatty acid profiles of the bird species, together with fatty acid data from potential prey species. This study of lipids combined with stable isotopes supports the following findings: (1) Common eiders are strongly linked to the benthic food chain, through both fatty acid compositions (high levels of 20:4n6) and stable isotope values (high levels of $\delta^{13}C$). (2) Black-legged kittiwakes and northern fulmars are linked to the pelagic food chain, through both fatty acid compositions (high levels of 20:1n9 and 22:1n11) and stable isotope values (low levels of $\delta^{13}C$). The high level of 20:1 and 22:1 moieties also indicates the importance of *Calanus* in the Arctic pelagic food chain supporting fulmar and kittiwake. (3) The levels $\delta^{15}N$ show that of the 3 species, the fulmar occupies the highest trophic level, followed by kittiwake and common eider.

KEY WORDS: Lipids · Fatty acid signature · Stable isotopes · *Somateria mollissima* · *Rissa tridactyla* · *Fulmarus glacialis* · Arctic

INTRODUCTION

Nowhere among vertebrates does the capability for storing energy exceed the level found in the class Aves (Blem 1976). However, few organisms face energetic dilemmas as extreme as those of birds. They must be capable of maintaining energy reserves for reproduction, migration and other stressful events even though the storage abilities are limited by the constraints of flight and wing loading. At high latitudes, seabirds use body fat for insulation to decrease the cost of thermoregulation when exposed to low temperatures and as energy reserves during periods of restricted food supply (Gabrielsen 1994). The absorption of fat from the diet is extremely efficient (>80%) in birds (Place 1996) and they are capable of utilising large quantities of body fat and can adapt to an extremely wide range in levels of fat intake (Griminger 1986).

The depot of fat is mostly in the form of triacylglycerols (TAG), which often exceed by content 80% of the total fat (Johnston 1973). However, since many birds, especially seabirds and some passerines, have a high capacity for assimilating non-glyceride-based fats (e.g. wax esters, WE) (>90%, whereas mammals generally

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attain <50%), the TAG stored can be a result of assimilated TAG and/or converted WE (Place 1992).

During periods of fasting, the primary energy source is the adipose tissue (fat depot), followed by fat stored in the liver and muscle (Whittow 1986). A relation between fatty acid composition in birds and that in their respective prey has been established after repeated detections of seasonal variations in fatty acid composition in storage tissue corresponding to shifts in prey (Lovern 1938, Walker 1964, Tanhuanpää & Pulliainen 1969, Caldwell 1973). The importance of the composition of the diet upon the fatty acid composition of depot fat in birds has been determined experimentally (Donaldson 1968, Edwards et al. 1973, Johnston 1973).

The concept of using lipids as biomarkers in marine ecosystems has received considerable attention in the past few decades (e.g. Sargent & Falk-Petersen 1981, Sargent et al. 1988, Volkman et al. 1989, Falk-Petersen et al. 2002). Some of the first evidence for a conservative transfer of marker fatty acids in neutral lipids up the food chain came from experiments on phytoplankton and copepods (Lee et al. 1971). Biomarkers can be traced through several trophic levels, and thus they provide knowledge not only about potential prey but also about the base of the food web. Fatty acid profiles in predators show an integration of prey fatty acids within periods of weeks to months; comparison of a fatty acid profile (or signature) of a certain prey with that of its potential predator will reveal dietary information beyond what is possible from stomach-content data alone. Different multivariate statistical methods have been introduced to assist in studying this phenomenon (Grahl-Nielsen & Mjaavatten 1991, Iverson 1993, Smith et al. 1997, Raclot et al. 1998, Grahl-Nielsen 1999, Dahl et al. 2000, Budge et al. 2002). Such methods allow comparison of not just single fatty acids but all fatty acids derived from animal tissues simultaneously, and they aid in the detection of relationships and patterns within complex data as well as the communication of results to non-specialists (Birks 1987). However, there is an ongoing discussion about the significance of fatty acid signature analysis, concerning both the conservative transfer of fatty acids and which statistical method is most appropriate. It is a complex issue, and more questions need to be answered through research before we know the full potential of this approach (for discussion see Smith et al. 1997, Grahl-Nielsen 1999). While there have been several studies of the TAG fatty acid composition of wild birds (reviewed by Blem 1976), only 3 studies have investigated the relationships between fatty acids in the diets and adipose tissues of marine birds (Cheah & Hansen 1970, Bishop et al. 1983, Raclot et al. 1998). Only 1 study (Raclot et al. 1998) employed multivariate methods as a statistical tool for interpreting the results.

The stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) in consumer proteins reflect those in their prey in a predictable manner (DeNiro & Epstein 1978, 1981, Peterson & Fry 1987). Based on analytical determination of $\delta^{15}N$ and a predictable stepwise enrichment between trophic levels, it is possible to quantitatively describe the structure of, for example, Arctic marine food chains (Hobson & Welch 1992, Hobson et al. 1995, Fisk et al. 2001). $\delta^{13}C$ may also correlate with trophic levels (Rau et al. 1983, Fry & Sherr 1984), but it provides additional information about the source of carbon entering a food chain, e.g. marine versus freshwater input (Hobson & Sealy 1991, Smith et al. 1996) or inshore/benthic versus pelagic feeding (Hobson 1993, Hobson et al. 1994, Sydeman et al. 1997).

In the Kongsfjorden area (78° 57′ N, 11° 50′ E) located on the west coast of Spitsbergen (Fig. 1), the estimated stock of breeding seabirds is approximately 15 000 pairs comprising 9 species (Mehlum & Bakken 1994). Common eider (*Somateria mollissima*), black-legged kittiwake (*Rissa tridactyla*) and northern fulmar (*Fulmarus glacialis*) represent 3 of the largest species by biomass in the area (Hop et al. 2002) and are the species chosen in this study. The common eider is a benthic feeder that forages in shallow waters, usually down to a depth of 15 m (Frimer 1995). In the Svalbard area they feed on various benthic invertebrates, including molluscs (e.g. *Buccinum glacialis*, *Hiatella arctica*), barnacles (e.g. *Balanus balanus*), decapods (e.g. *Hyas araneus*) and amphipods (e.g. *Gamarellus homari*) (Ydenberg & Guillemette 1991, Weslawski et al. 1991, Guillemette et al. 1992). The fulmars and black-legged kittiwakes are surface feeders. Around Svalbard, the fulmars feed on cephalopods (*Gonatus fabricii*), polychaetes (*Nereis* sp.), small fishes (e.g. *Boreogdus saida*) and pelagic amphipods (*Parathemisto libellula*), whereas the kittiwakes feed on fish (*Boreogdus saida*, *Mallotus villosus*, *Liparis* sp., Stichaeidae), euphausiids (*Thysanoessa* sp.), pelagic amphipods (*Parathemisto* spp.), polychaetes (*Nereis* sp.) and pteropods (Gjertz & Gabrielsen 1985, Lydersen et al. 1989, Ydenberg & Guillemette 1991, Lønne & Gabrielsen 1992, Mehlum & Gabrielsen 1993).

The goal of this study is to utilise new techniques to (1) describe and compare the composition of lipids and fatty acids in the muscle, fat and liver in the common eider, black-legged kittiwake and northern fulmar; (2) study trophic linkages through lipid biomarkers (specific moieties of fatty acids/alcohols); (3) study predator–prey relationships through fatty acid profiles; and (4) study trophic level and feeding ground through stable isotopes.

MATERIALS AND METHODS

Sampling. The seabirds were shot in August–September 1997. The specimens were stored in a freezer at –20°C. Body weight and age group (based on plumage characteristics) were determined prior to autopsy (in March 1998). Pectoral muscle and liver were dissected from all collected individuals. Subcutaneous fat was only collected from fulmars and eiders, because kittiwakes were too lean to obtain fat samples for analysis. Sectional samples were collected from fat, muscle and liver. These samples were wrapped in aluminium foil and refrozen at –20°C until lipid analyses were undertaken.

Data on the lipid composition of potential prey species were available from samples of (1) the copepods *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*, (2) the pteropod *Limacina helicina* and (3) the euphausiid *Thysanoessa inermis*, all collected at the same time and the same location as the birds (Falk-Petersen et al. 2000, 2001, Scott et al. 2000); (4) polar cod (*Boreogadus saida*), capelin (*Mallotus villosus*), daubed shanny (*Leptoclinus maculatus*) and snake eelblenny (*Lumpenus lampretaeformis*), collected in Kongsfjorden in September 1999 (S.F.-P. unpubl. data); and (5) the amphipod *Parathemisto libellula*, collected to the north of Svalbard in September 1998 (S.F.-P. unpubl. data).

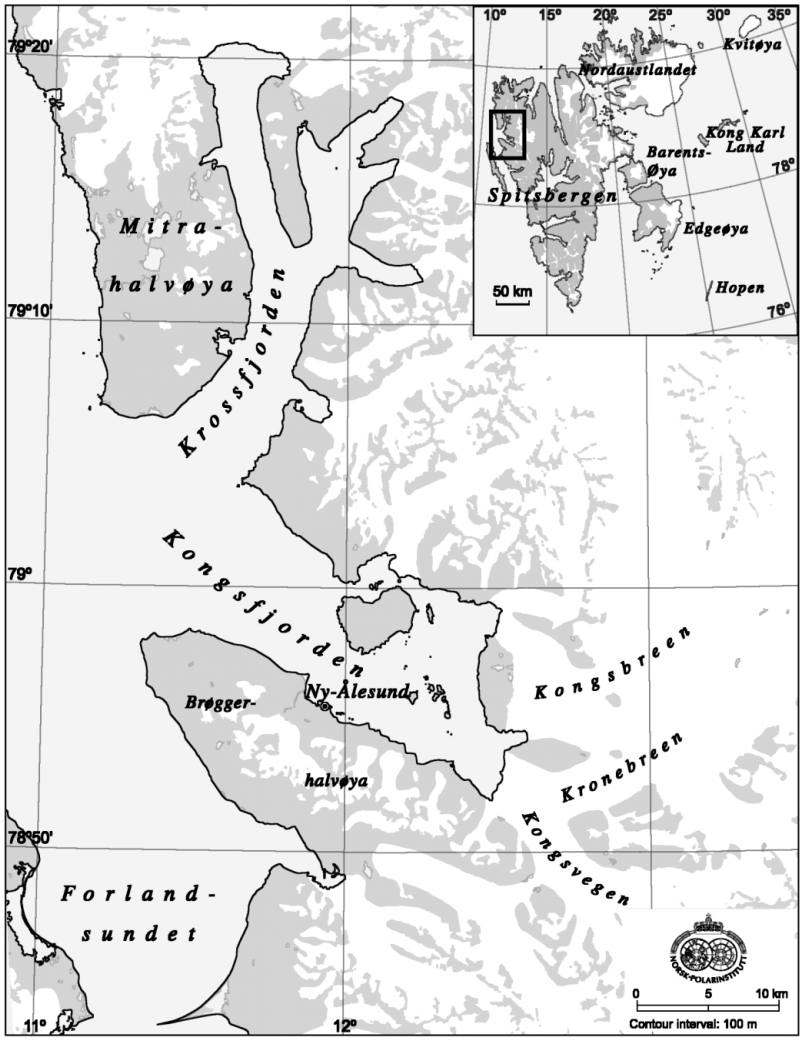


Fig. 1. Study area, Kongsfjorden, on the west coast of Spitsbergen, Svalbard

The eider is a benthic feeder, but only little lipid data for benthos exist from the Svalbard area. Most prey included in this study are associated with the pelagic ecosystem and are mostly applicable to the diet of fulmar and kittiwake. However, to determine whether this would be reflected in our study, we found it interesting to include an analysis of eider versus prey.

Lipid analysis. Total lipid was extracted from known wet masses in different bird tissues using the method described by Folch et al. (1957). The amount of lipid recovered was determined gravimetrically, after removal of the solvent by evaporation under a stream of nitrogen. Lipid class composition was measured by quantitative thin-layer chromatography (TLC) densitometry (Olsen & Henderson 1989). TAG were separated on TLC silica gel plates using hexane:diethyl ether:acetic acid (90:10:1, by volume). The samples were supplemented with a known amount of the fatty acid 21:0 as an internal standard and transmethylated in methanol containing 1% sulphuric acid with toluene for 16 h at 50°C. Fatty acid methyl esters (FAME) were purified by thin-layer chromatography (TLC), using hexane:diethyl ether:acetic acid (85:15:1, by volume) as the developing solvent. They were recovered from the absorbent by elution with hexane containing butylated hydroxytoluene (BHT). FAME were identified and quantified by gas chromatography. This was done by comparison with the internal standard and well-characterised marine fish oils, as described by Dahl et al. (2000).

Stable isotope analyses of $\delta^{15}N$ and $\delta^{13}C$. Samples of muscle tissues of seabirds were dried at 60 to 70°C to constant weight and then homogenised with a glass pestle and mortar. To reduce variability due to isotopically lighter lipids, which may influence the carbon

isotope ratio particularly (Attwood & Peterson 1989, Hobson & Welch 1992), lipids were removed by Soxhlet extraction for 2 h with a mixture of 93% dichloromethane (DCM) and 7% methanol. The samples were then dried at 80°C before they were rinsed with 2 N HCl for 5 min in order to remove traces of carbonates. All samples were thoroughly rinsed with distilled water and dried at 80°C before combustion in the elemental analyser.

For the determination of $\delta^{15}N$ and $\delta^{13}C$, about 1.0 mg of sample material was weighed and put into small Sn capsules. The samples were combusted with O_2 and Cr_2O_3 at about 1700°C in a Carlo Erba NCS Elemental Analyser. NO_x was reduced with Cu at 650°C. The combustion products N_2, CO_2 and H_2O were separated on a Poraplot Q column, and the $^{15}N/^{14}N$ and $^{13}C/^{12}C$ isotope ratios were determined on a Micromass Optima mass spectrometer. The laboratory (Institute for Energy Technology, Kjeller, Norway) applies international standards, generally run for each 10 samples, of Pee Dee Belemnite (PDB: USGS 24) for $\delta^{13}C$ and atmospheric air (IAEA-N-1 and 2) for $\delta^{15}N$. The 1 yr analytical record showed that the repeated analyses were within the range indicated for each standard. Stable isotope concentrations were expressed as: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X (‰) is $\delta^{13}C$ or $\delta^{15}N$ and R is the corresponding ratios of $^{13}C/^{12}C$ or $^{15}N/^{14}N$, related to the standard values.

Data processing. Animals preying on WE-rich prey convert both the WE fatty alkyl and acyl units to corresponding TAG fatty acyl units (Falk-Petersen et al. 2002). In order to compare the fatty acid signature of a predator storing fat as TAG with the WE-based signature found in different prey, TAG and WE need to be treated as one and the same. This is done by averaging (by molecular weights) given fatty alkyl and fatty acyl units of WE with the same chain lengths and numbers and positions of double bonds. We have used the term 'moiety' for all processed data (see Falk-Petersen et al. 2002 for details).

The species included in the analyses were the most important mass species that are potential foods for the pelagic feeding seabirds. Fatty acid analysis of prey species included samples of whole individuals, except for polar cod, capelin and snake eelblenny. Both muscle and liver were analysed in the fish. We chose to use muscle since it constitutes a larger part of the body mass than the liver and because there was not found significant individual differences in this tissue for polar cod and capelin (S.F.-P. unpubl. data). The data for wt % of TAG fatty acids in muscle of bird, polar cod, capelin, snake eelblenny and whole individuals of daubed shanny were processed. Because TAG constituted the main neutral lipid in all these species, it was the only lipid class considered during the data processing. The pteropod *Limacina helicina* had only 30% of its neutral lipid represented as TAG, but this was the only neutral lipid class analysed and processed. For the copepods *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*, WE constituted the main neutral lipid (83 to 88% of total neutral lipids) and was thereby the only class considered. Thus, both the fatty acid and alcohol part of WE was processed from these 3 species. Data of *Parathemisto libellula* and *Thysanoessa inermis* showed that both TAG and WE were main neutral lipids (62% TAG and 31% WE of neutrals in *P. libellula*; 39% TAG and 46% WE of neutrals in *T. inermis*), and therefore both these classes were considered in the data processing.

Statistical analyses. Calculations of wt % compositions in fatty acids and fatty alcohols were only performed for fatty acids and alcohols (14:0, 16:0, 18:1, 22:1, etc.) represented with at least 1 value above 0.5%. Variables with very low amounts in all samples were not included because the precision of their determination is low and they introduce more noise than real information to the results. Remaining percentage values were log-transformed and subjected to principal component analysis (PCA; Wold 1987), using the program package SIRIUS (Kvalheim & Kvarstang 1987). Firstly, PCA was used to explore relationships between the different bird species' tissues based on their TAG fatty acid compositions. One PCA was performed on eider and fulmar alone, from which fat, muscle and liver were sampled. Then, another PCA was performed on all 3 species, including only the tissues sampled in all, namely liver and muscle. Secondly, PCA was used to explore relationships between each of the bird species and the potential prey items based on their moiety compositions.

To analyse the effect of species and tissue on the moiety compositions, the samples' scores on the principal components (PCs) were used as response variables in analysis of variance (ANOVA, Type-III sum of squares; Sokal & Rohlf 1995), followed by Tukey's honestly significant difference (HSD; Day & Quinn 1989). The α-level was 0.05. The tests were performed using SAS 8.0 (SAS Institute).

Because of large size-correlated variations in TAG fatty acid compositions among the shannies and because this may be induced by different vertical occupation in the water-masses, the 3 individuals were separated into 2 size classes (large: n = 1, small: n = 2). Low sample sizes prevented the inclusion of these data in the ANOVA, and PCA were used to describe each bird species' relations to this fish.

Individual samples (n) were included in all analyses, but for simplicity, only mean values are presented (see Tables 2 & 3). Only components having eigenvalues >1 that accounted for at least 5% of the total variance

were considered significant and, hence, were retained for evaluation. One liver sample of eider that had a very different composition to all other liver samples, as well as samples of muscle and fat of the same individual, was eliminated from statistical treatment.

RESULTS

Bird lipid composition

All collected birds were juvenile. The mean body masses were 1504 ± 251 g (range 1086–1715 g), 389 ± 50 g (range 327–459 g) and 780 ± 102 g (range 698–942 g) for eider, kittiwake and fulmar, respectively. The analysis of lipid classes shows that fat, muscle and liver contained substantially more neutral (58–93%) than polar lipids (7–40%; Table 1). Amongst the neutral lipids, TAG constituted the largest lipid class for all birds and all tissues, except for the eider liver, in which sterols constituted the largest class. In fulmar and eider the subcutaneous fat contained the highest levels of TAG (87% in fulmar and 70% in eider). In kittiwake and fulmar, muscle contained relatively high levels of TAG, 53 and 59%, respectively, whereas muscle in eiders contained only 20%. Livers contained the lowest amounts of TAG in all species. Free fatty acids (FFA) were represented in moderate levels in both liver and muscles in all 3 species (9–17%). Interestingly, moderate levels of WE-CH were found in livers of all 3 species (10–16%) and in muscle of eider (12%). A total of 23 TAG fatty acids were found at levels above 0.5% in at least 1 of the samples analysed, and hence were included in the PCA (Table 2). These fatty acids constituted 96–99% of the total fatty acids detected.

The major TAG fatty acids in eider were 18:1n9 (27–30%), 16:0 (24–26%), 18:0 (7–12%), 20:5n3 (5–7%) and 16:1n7 (4–7%) (Table 2). The major TAG fatty acids found in kittiwake were consistently 16:0 (22–29%), 18:1n9 (18–25%), 18:0 (7–16%), 20:1n9 (5–11%) and 16:1n7 (5–9%), whereas those found in fulmar were 18:1n9 (20–23%), 16:0 (12–19%), 20:1n9 (10–18%), 22:1n11 (4–14%) and 18:0 (4–12%) (Table 2).

Differences in bird fatty acid compositions

The exploration of fat, muscle and liver tissue of eider and fulmar by PCA resulted in the extraction of 3 significant components (PCs). In combination these PCs explained 81% of the total variance (PC1: 61%; PC2: 12%; PC3: 9%). The samples' variation in scores on PC1 was explained by both species and tissue ($ANOVA_{species}$ $F_{1, 25}$ = 366.2, $p \leq 0.0001$, $ANOVA_{tissue}$ $F_{2, 25}$ = 15.7, $p \leq 0.0001$, adjusted $R^2 = 0.93$). The samples' variation in scores on PC2 was explained only by tissue ($ANOVA_{tissue}$ $F_{2, 26}$ = 23.8, $p \leq 0.0001$, adjusted $R^2 = 0.62$), whereas the samples' variation in scores on PC3 was explained by neither species nor tissue. No difference was found between fat and muscle, whereas both these tissues differed from liver (Tukey's HSD, $p < 0.05$). Based on the fatty acid loadings along the 3 PCs, the separation of species was mainly due to differences in levels of 22:1n11 and 20:1n9 (high in fulmar, very low in eider). Differences in levels of 20:4n6, 16:0 and 18:0 also contributed to the separation between species (higher in eider than in fulmar). The separation of liver samples from fat and muscle was mainly due to significantly higher levels of 18:0 in this tissue compared to fat and muscle in both species. The liver of fulmar was also distinguished because of high amounts of phytanic acid (PA).

The exploration of muscle and liver samples of eider, kittiwake and fulmar by PCA resulted in the extraction of 4 significant PCs, explaining 84% of the total variance. Only the 2 most important components are presented (Fig. 2). The samples' variation in scores on PC1

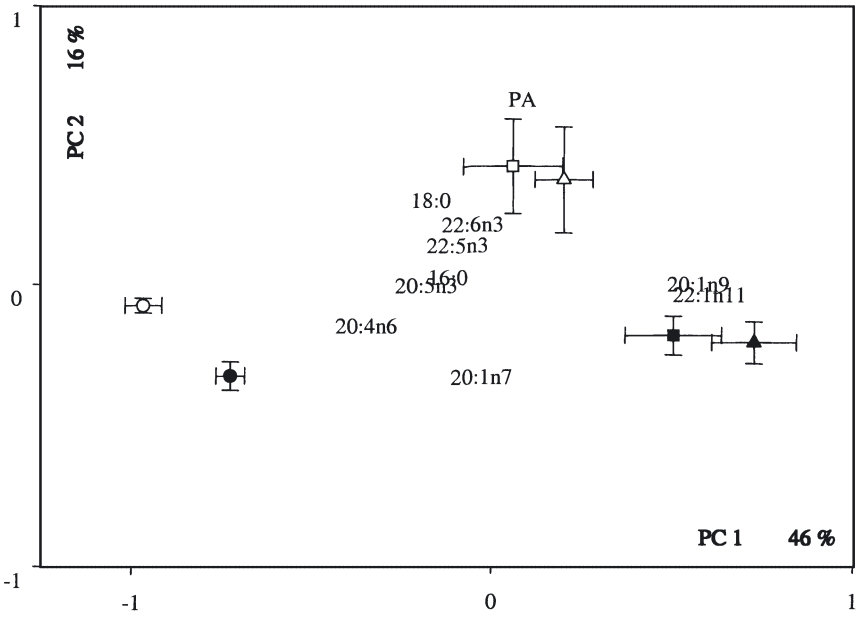
Table 1. *Somateria mollissima*, *Rissa tridactyla*, *Fulmarus glacialis*. Lipid class compositions of total lipid isolated from fat, muscle and liver from individual specimens of common eider, black-legged kittiwake (except fat) and northern fulmar. Values are mean percentage ± SD (in brackets) of 5 specimens. PL: polar lipids; NL: neutral lipids; FFA: free fatty acids; TAG: triacylglycerols; WE-CH: wax esters and/or cholesteryl esters

	Tissue	PL	NL	Sterols	FFA	TAG	WE-CE
Somateria mollissima (n = 5)	Fat	20.6 (7.3)	79.4 (7.3)	6.3 (2.5)	1.9 (1.0)	70.4 (10.6)	0.8 (0.5)
	Muscle	36.4 (4.7)	62.0 (4.5)	16.4 (5.0)	14.3 (3.1)	19.7 (12.6)	11.6 (10.1)
	Liver	40.1 (5.5)	58.1 (5.8)	19.5 (4.2)	15.6 (3.7)	13.5 (5.3)	9.5 (1.9)
Rissa tridactyla (n = 5)	Muscle	25.7 (3.9)	72.8 (4.0)	5.7 (1.1)	11.3 (1.9)	52.5 (6.4)	3.2 (0.9)
	Liver	24.9 (6.2)	73.3 (6.5)	10.9 (1.9)	16.6 (1.2)	28.1 (10.0)	16.0 (3.0)
Fulmarus glacialis (n = 5)	Fat	7.0 (5.2)	93.0 (5.2)	1.3 (0.9)	3.3 (1.8)	87.3 (6.3)	0.6 (0.7)
	Muscle	23.6 (4.1)	75.8 (4.4)	5.3 (1.3)	9.0 (2.9)	58.7 (7.6)	2.8 (1.0)
	Liver	28.2 (8.8)	70.9 (9.1)	11.9 (4.5)	16.5 (5.2)	26.7 (18.0)	15.2 (12.9)

Table 2. *Somateria mollissima*, *Rissa tridactyla*, *Fulmarus glacialis*. Fatty acid compositions (signatures) of TAG in fat, muscle and liver from common eider, black-legged kittiwake (except fat) and northern fulmar. Values are mean percentage ± SD (in brackets) of 5 specimens. Phytanic acid (PA) is a multimethyl branched fatty acid derived from phytol, a derivate of chlorophyll. SFA: saturated fatty acids; MUFA: mono-unsaturated fatty acids; PUFA: polyunsaturated fatty acids

Fatty acid	*Somateria mollissima*			*Rissa tridactyla*		*Fulmarus glacialis*		
	Fat	Muscle	Liver	Muscle	Liver	Fat	Muscle	Liver
14:0	2.2 (0.8)	0.9 (0.5)	1.3 (1.3)	4.3 (3.5)	2.1 (1.4)	2.4 (0.5)	2.8 (0.2)	1.2 (0.8)
15:0	0.5 (0.1)	0.4 (0.0)	0.2 (0.2)	0.4 (0.1)	0.2 (0.2)	0.2 (0.3)	0.2 (0.2)	0.2 (0.2)
16:0	24.7 (1.5)	23.6 (1.9)	25.9 (7.3)	21.7 (2.5)	28.5 (7.5)	11.8 (3.1)	14.2 (1.7)	19.4 (5.2)
16:1n7	6.9 (0.8)	6.1 (1.0)	3.5 (1.4)	9.0 (0.7)	4.5 (0.8)	7.1 (1.3)	7.7 (2.1)	4.3 (0.6)
C16 PUFAs	0.5 (0.3)	0.3 (0.3)	0.4 (0.4)	0.2 (0.2)	–	–	–	–
Phytanic acid	–	0.0 (0.0)	–	0.5 (0.5)	2.9 (2.1)	0.1 (0.2)	0.4 (0.4)	2.6 (2.7)
18:0	7.3 (0.7)	7.5 (0.7)	12.2 (5.6)	6.5 (1.4)	16.2 (6.3)	3.8 (1.0)	4.6 (0.7)	12.1 (5.8)
18:1n9	29.9 (2.9)	29.3 (3.8)	27.4 (4.8)	24.6 (4.4)	18.4 (1.2)	20.4 (6.4)	22.8 (4.5)	22.2 (5.2)
18:1n7	4.9 (1.3)	6.1 (2.3)	3.4 (2.0)	3.9 (2.2)	4.0 (0.3)	4.7 (1.2)	5.0 (1.0)	4.4 (2.6)
18:2n6	2.0 (0.9)	2.6 (1.0)	0.2 (0.2)	1.4 (0.2)	0.8 (0.2)	1.4 (0.3)	1.5 (0.2)	1.4 (0.4)
18:3n3	1.2 (0.7)	1.1 (0.3)	0.4 (0.4)	0.5 (0.4)	0.1 (0.1)	0.6 (0.3)	0.6 (0.3)	0.6 (0.4)
18:4n3	0.5 (0.5)	0.8 (0.5)	0.5 (0.8)	0.8 (0.5)	0.3 (0.3)	1.0 (0.5)	0.9 (0.4)	0.6 (0.6)
20:1n9	2.5 (1.4)	1.3 (0.5)	3.0 (4.9)	10.7 (4.2)	4.6 (3.1)	18.1 (8.6)	16.4 (5.9)	9.7 (5.1)
20:1n7	1.8 (0.4)	1.8 (0.8)	0.6 (0.3)	0.9 (0.3)	1.1 (2.0)	0.5 (0.4)	0.9 (0.4)	0.4 (0.2)
20:2n6	0.6 (0.1)	0.5 (0.3)	0.3 (0.1)	0.4 (0.2)	0.1 (0.1)	0.2 (0.2)	0.3 (0.0)	0.2 (0.2)
20:4n6	1.3 (0.2)	2.1 (0.5)	4.2 (2.1)	0.3 (0.2)	0.6 (0.4)	0.2 (0.2)	0.3 (0.1)	0.6 (0.6)
20:4n3	0.2 (0.1)	0.3 (0.2)	0.5 (0.4)	0.3 (0.1)	0.2 (0.2)	0.3 (0.2)	0.3 (0.1)	0.3 (0.2)
20:5n3	4.6 (2.4)	6.5 (2.7)	4.6 (2.4)	2.9 (1.9)	4.5 (4.8)	4.4 (2.0)	3.7 (2.2)	4.3 (1.9)
22:1n11	0.2 (0.3)	0.2 (0.2)	2.3 (5.0)	6.1 (2.8)	3.2 (3.1)	13.8 (6.5)	10.0 (3.2)	4.4 (1.2)
22:1n9	0.2 (0.1)	0.1 (0.1)	0.3 (0.6)	0.2 (0.5)	0.1 (0.2)	0.4 (0.6)	0.4 (0.5)	0.3 (0.4)
22:5n3	0.9 (0.4)	1.2 (0.3)	1.2 (0.5)	0.4 (0.3)	0.9 (0.7)	1.3 (0.3)	0.7 (0.3)	1.9 (1.0)
22:6n3	2.6 (1.5)	3.9 (1.4)	4.1 (2.4)	3.1 (2.2)	4.0 (2.8)	6.2 (1.6)	4.1 (2.6)	7.6 (1.0)
24:1	0.1 (0.1)	0.0 (0.1)	0.1 (0.3)	0.2 (0.2)	0.4 (0.4)	0.4 (0.4)	1.2 (1.8)	0.3 (0.3)
Total SFA	33.9 (2.5)	32.6 (1.5)	39.8 (11.6)	33.6 (5.2)	50.1 (12.3)	18.6 (4.4)	22.3 (2.0)	35.6 (10.5)
Total MUFA	50.3 (2.6)	47.1 (4.6)	41.8 (7.8)	56.1 (9.9)	36.9 (8.0)	65.8 (9.0)	65.2 (7.4)	46.8 (10.5)
Total PUFA	15.8 (4.0)	20.2 (4.6)	18.2 (5.4)	10.4 (5.6)	11.7 (9.1)	15.6 (4.7)	12.5 (5.6)	17.6 (3.2)

and PC2 was explained by both species and tissue (PC1: $ANOVA_{species}$ $F_{2,25} = 91.0$, $p \leq 0.0001$, $ANOVA_{tissue}$ $F_{1,25} = 23.3$, $p \leq 0.0001$, adjusted $R^2 = 0.88$; PC2: $ANOVA_{species}$ $F_{2,25} = 3.7$, $p = 0.0398$; $ANOVA_{tissue}$ $F_{1,25} = 24.6$, $p \leq 0.0001$, adjusted $R^2 = 0.52$). The samples' variation in scores on PC3 (15% of total explained) and PC4 (7% of total explained) was explained by neither species nor tissue variations. Kittiwake and fulmar differed from eider on PC1, whereas only kittiwake and eider differed in scores on PC2 (Tukey's HSD, $p <$



Somateria mollissima
● muscle
○ liver

Rissa tridactyla
■ muscle
□ liver

Fulmarus glacialis
▲ muscle
△ liver

Fig. 2. *Somateria mollissima*, *Rissa tridactyla*, *Fulmarus glacialis*. PCA plot based on TAG fatty acid compositions in muscle and liver of common eider, black-legged kittiwake and northern fulmar. Bird tissue samples are presented by their mean score value ± standard error on PC1 and PC2. Only fatty acids having high loadings on any of the significant extracted PCs are presented

0.05). Based on the fatty acid loadings along these 2 PCs (Fig. 2), the separation of eider from fulmar and kittiwake was mainly due to differences in levels of 22:1n11 and 20:1n9 (high in fulmar and kittiwake, very low in eider). Differences in levels of 20:4n6 also contributed to the separation of species (higher in eider than in kittiwake and fulmar). The liver samples of kittiwake also contained significantly higher levels of 18:0. This fatty acid was therefore involved in the separation of liver from other tissues in all species. As for fulmar, the presence of PA in relatively high amounts also contributed to the distinction of liver samples.

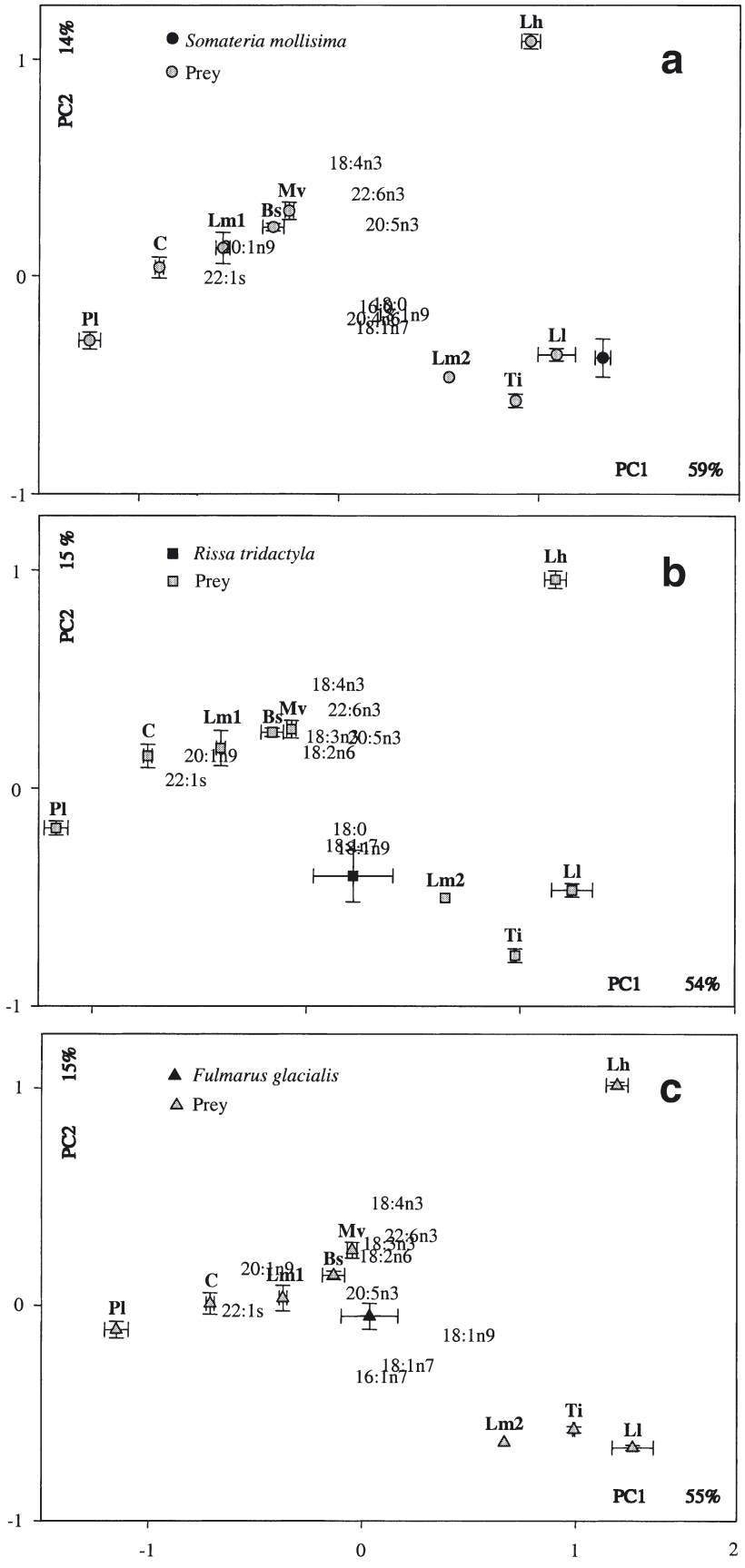
Birds and potential prey

In the analysis above we have shown that muscle is similar to fat tissue for both fulmar and eider. Both these tissues are well suited for further analysis together with their prey. We may assume that the same applies for kittiwake. Therefore, we chose to use the compositional data from muscle tissue for all bird species when making the comparison with potential prey. Compositional data for potential prey included a total of 32 moieties found in levels above 0.5% in at least 1 of the samples analysed (Table 3). These moieties constituted 97 to 100% of the total detected.

The exploration of eider and prey by PCA resulted in the extraction of 4 significant PCs, explaining 88% of the total variance. Only the 2 most important components are presented (Fig. 3a). The samples' variation in scores on all 4 PCs was explained by species ($ANOVA_{species}$ $F_{8,33} > 38.3$, $p \leq 0.0001$ for all 4 PCs). The eider's scores on PC1 did not differ from the prey *Thysanoessa inermis*, *Limacina helicina* and *Lumpenus lampretaeformis* (Tukey's HSD, $p > 0.05$). The eider's scores on PC2 differed from *L. helicina*, whereas the scores on PC3 (10% of total explained) and PC4 differed from *L. lampretaeformis* and *T. inermis*, respectively (Tukey's HSD, $p < 0.05$). The plot shows the clustering of eider with *T. inermis*, *L. lampretaeformis* and the large individual of daubed shanny along PC1 and the separation of *L. helicina* from all these species along PC2. All other prey species were very distinct and ac-

Table 3. Moiety compositions of potential prey organisms (see 'Materials and methods' for tissue specifications). Values are mean percentage ± SD (in brackets). PUFA: polyunsaturated fatty acids

Moiety	*Boreogadus saida* n = 5	*Mallotus villosus* n = 5	*Lumpenus lampretaeformis* n = 5	*Leptoclinus maculatus* (1) n = 2	*Leptoclinus maculatus* (2) n = 1	*Thysanoessa inermis* n = 2	*Parathemisto libellula* n = 7	*Calanus* spp. n = 6	*Limacina helicina* n = 4
14:0	2.7 (0.3)	6.0 (0.1)	3.1 (0.3)	3.5 (0.3)	2.1	8.9 (0.4)	2.6 (0.8)	4.3 (1.1)	2.9 (1.1)
15:0	0.3 (0.0)	0.4 (0.0)	0.9 (0.2)	0.3 (0.0)	0.7	0.5 (0.0)	0.2 (0.1)	0.4 (0.1)	0.6 (0.0)
16:0	8.2 (0.7)	12.9 (0.9)	11.5 (1.0)	7.0 (0.5)	14.2	29.9 (1.0)	8.2 (2.3)	6.7 (1.5)	14.2 (1.6)
16:1n9	0.1 (0.1)	0.1 (0.0)	0.4 (0.1)	0.1 (0.1)	0.3	–	–	–	0.6 (0.5)
16:1n7	11.9 (0.3)	9.2 (0.8)	20.1 (1.8)	15.3 (0.3)	15.0	16.5 (2.0)	7.4 (2.5)	12.7 (1.9)	5.6 (0.5)
Iso 17:0	0.2 (0.3)	0.1 (0.2)	1.2 (0.4)	–	–	–	–	–	0.6 (0.4)
17:0	–	–	–	–	–	–	–	–	1.2 (0.4)
Iso 17:1	0.2 (0.2)	0.2 (0.2)	1.2 (0.5)	–	–	–	–	–	–
17:1	0.0 (0.1)	0.1 (0.2)	0.8 (0.1)	–	–	–	–	–	–
C16 PUFAs	1.1 (0.2)	1.2 (0.1)	1.4 (0.4)	1.5 (0.3)	2.6	1.8 (0.3)	0.6 (0.1)	–	0.2 (0.4)
Iso 18:0	–	–	–	–	–	–	–	–	1.2 (0.4)
18:0	1.3 (0.3)	1.1 (0.1)	2.7 (0.4)	1.2 (0.3)	4.1	1.6 (0.3)	0.4 (0.2)	0.5 (0.1)	2.5 (0.6)
18:1n9	8.5 (1.0)	11.3 (0.8)	12.5 (3.5)	4.5 (1.5)	17.0	21.0 (2.6)	3.7 (1.7)	2.3 (0.8)	9.7 (2.1)
18:1n7	2.9 (0.5)	3.1 (0.6)	8.2 (0.8)	2.7 (0.6)	6.2	9.2 (0.1)	1.9 (0.2)	1.6 (0.4)	3.2 (0.4)
18:1n5	0.2 (0.3)	0.3 (0.4)	0.9 (0.5)	–	–	–	0.5 (0.1)	–	0.2 (0.4)
18:2n6	0.8 (0.0)	1.2 (0.4)	0.7 (0.0)	0.9 (0.0)	0.5	0.7 (0.2)	0.8 (0.3)	0.7 (0.2)	4.9 (0.7)
18:3n6	–	–	–	–	–	0.1 (0.1)	0.1 (0.0)	0.2 (0.3)	–
18:3n3	0.3 (0.2)	0.8 (0.1)	0.2 (0.1)	–	–	0.4 (0.1)	0.2 (0.1)	0.3 (0.1)	4.2 (0.3)
18:4n3	2.6 (0.3)	4.1 (0.5)	1.2 (0.3)	3.4 (1.6)	0.2	2.5 (0.4)	0.9 (0.4)	2.2 (0.9)	15.4 (2.7)
20:1n9	19.0 (1.8)	15.1 (0.9)	1.5 (1.0)	23.1 (1.1)	3.6	1.0 (0.2)	37.1 (3.5)	27.2 (5.1)	4.6 (1.0)
20:1n7	1.1 (0.2)	0.5 (0.1)	4.6 (0.8)	1.9 (0.2)	8.7	0.2 (0.0)	0.1 (0.0)	1.8 (0.9)	2.6 (1.9)
20:2n6	0.1 (0.1)	0.2 (0.0)	0.8 (0.1)	0.2 (0.0)	–	0.2 (0.0)	–	–	0.7 (0.1)
20:3n6	–	–	–	–	1.2	–	–	–	–
20:4n6	0.4 (0.2)	0.1 (0.1)	2.1 (0.5)	0.3 (0.4)	0.6	0.1 (0.0)	–	0.2 (0.1)	0.2 (0.2)
20:4n3	0.5 (0.0)	0.5 (0.0)	0.6 (0.1)	0.1 (0.2)	–	0.1 (0.0)	0.1 (0.1)	0.4 (0.1)	1.3 (0.1)
20:5n3	9.7 (1.2)	7.7 (0.4)	14.8 (4.8)	6.6 (0.6)	8.7	2.9 (0.6)	0.3 (0.1)	6.0 (0.4)	11.1 (1.8)
22:1s	18.8 (2.7)	16.1 (1.5)	1.3 (1.3)	22.3 (0.8)	6.6	–	33.0 (5.3)	28.2 (6.6)	0.8 (0.6)
22:4n6	–	–	0.6 (0.3)	–	–	–	–	–	–
22:5n3	1.0 (0.1)	0.5 (0.1)	1.8 (0.4)	1.0 (0.4)	3.1	–	–	0.4 (0.1)	0.5 (0.1)
22:6n3	7.5 (1.0)	6.4 (2.2)	3.1 (0.2)	3.8 (0.1)	4.7	0.5 (0.0)	0.6 (0.4)	1.0 (0.4)	9.8 (1.3)
24:0	–	–	–	–	–	–	0.6 (0.3)	0.1 (0.2)	–
24:1	0.5 (0.1)	0.8 (0.1)	0.1 (0.1)	0.3 (0.0)	–	0.1 (0.1)	0.4 (0.1)	0.1 (0.2)	–



cording to the moieties' loadings (Fig. 3a). This was mainly due to high levels of 22:1s and 20:1n9 in these compared to the eider and the prey more similar to eider. The latter two had higher amounts of 18:1n9 and 18:0. A score dendrogram (not shown) based on the individual samples' scores on all 4 PCs classified all eider samples as more similar to snake eelblenny and large daubed shanny than to krill.

The exploration of kittiwake and prey by PCA resulted in the extraction of 4 significant PCs, explaining 87% of the total variance. Only the 2 most important components are presented (Fig. 3b). The samples' variation in scores on all 4 PCs was explained by species variations ($ANOVA_{species}$ $F_{8,33} > 35.0$, $p \leq 0.0001$ for all 4 PCs). The kittiwakes' scores on PC1 did not differ from capelin and polar cod (Tukey's HSD, $p > 0.05$), whereas the kittiwake's scores on PC2 differed from both. The moieties' loadings (Fig. 3b) show that the position of samples along PC1 is steered by the variations 22:1s, 20:1n9, 20:5n3, 18:1n9, 18:1n7 and 18:0. The pattern of these moieties in kittiwake was most similar to large daubed shanny, polar cod and capelin. The main differences between the 2 latter species and kittiwake were mainly due to differences in the levels of 18:4n3, 20:5n3 and 22:6n3, which were higher in the fish than in the birds. On the other hand, the birds contained more 18:1n9, 18:0 and 16:0. Large daubed shanny contained less 20:1n9 and more 20:5n3. Neither PC3 (12% of total explained) nor PC4 (6% of total explained) added important information concerning the kittiwakes' relations to prey.

The exploration of fulmar and prey by PCA resulted in the extraction of 4 signifi-

Fig. 3. *Somateria mollissima*, *Rissa tridactyla*, *Fulmarus glacialis*. PCA plots of bird muscle samples against potential prey based on sample moiety compositions. Samples are presented by their mean score value ± SE on PC1 and PC2. Only moieties having high loadings on any of the significant extracted PCs are presented. Ll: *Lumpenus lampretaeformis*; Ti: *Thysanoessa inermis*; Lm1: *Leptoclinus maculatus* (small); Lm2: *Leptoclinus maculatus* (large); Lh: *Limacina helicina*; Mv: *Mallotus villosus*; Bs: *Boreogadus saida*; C: *Calanus* spp.; Pl: *Parathemisto libellula*

cant PCs, explaining 88% of the total variance. Only the 2 most important components are presented (Fig. 3c). The samples' variation in scores on all 4 PCs was explained by species variations ($ANOVA_{species}$ $F_{8,33} > 37.4$, $p \leq 0.0001$ for all 4 PCs). The fulmars' scores on PC1 did not differ from polar cod and capelin (Tukey's HSD, $p > 0.05$). The fulmars' scores on PC2 differed from capelin, whereas the scores on PC3 separated fulmar from polar cod (Tukey's HSD, $p < 0.05$). The moieties' loadings (Fig. 3c) show that the position of samples along PC1 was mainly steered by the variations in 22:1s, 20:1n9 and 20:5n3. The moieties 18:1n9, 22:6n3 and 18.1n7 also contributed to the spread of samples along PC1. The pattern of these moieties in fulmar was most similar to polar cod, capelin and small daubed shanny. Capelin differed from fulmar along PC2 due to higher levels of 18:4n3 and polar cod differed from fulmar along PC3 due to higher levels of 20:5n3 and 20:1n7. Neither PC3 (11% of total explained) nor PC4 (6% of explained) added important information concerning the fulmars' relations to prey.

Score dendrograms (not shown) based on the individual samples' scores on all 4 PCs confirmed that both kittiwake and fulmar were more similar to polar cod, capelin, small daubed shanny, *Calanus* spp. and *Parathemisto*, than to snake eelblenny, *Thysanoessa inermis* and *Limacina helicina*.

Stable isotope analyses of $\delta^{15}N$ and $\delta^{13}C$

Combined stable isotope signatures of the seabird specimens in this study exhibited significant interspecies variations both for $\delta^{13}C$ and $\delta^{15}N$ ($ANOVA_{species}$ $F_{2,12} > 21.91$, $p < 0.0006$; Fig. 4). Tukey's HSD, $p < 0.05$ showed that fulmar and kittiwake did not differ in $\delta^{13}C$ whereas eider differed from both. The same test also showed that kittiwake and eider did not differ in $\delta^{15}N$, whereas fulmar differed from both. The stable isotopes of nitrogen tended to be relatively enriched in fulmar (mean value 13.6‰), whereas kittiwake and eider had lower values (12.1 and 11.3‰, respectively). $\delta^{13}C$ values tended to be enriched in eider (–18.7‰) compared to kittiwake and fulmar (–20.5 and –20.7‰, respectively).

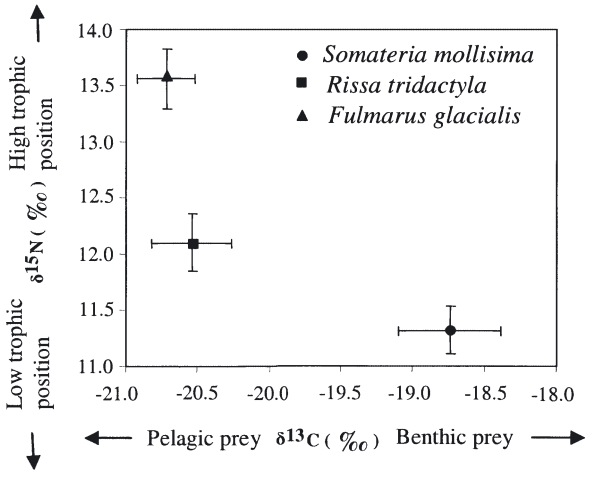


Fig. 4. *Somateria mollissima*, *Rissa tridactyla*, *Fulmarus glacialis*. Stable isotopes of nitrogen and carbon from the 15 seabird specimens from the Kongsfjorden area in Svalbard. Values are mean ± SE

DISCUSSION

Bird lipid composition

This is the first report on the lipid and fatty acid composition of body fat in common eider and black-legged kittiwake. In fulmar, the fatty acid composition was determined in an early study by Lovern (1938). However, that study only presented compositions extracted from the whole bird and not from different tissues.

The mean weights of juvenile eider, kittiwake and fulmar indicated that the seabirds were close to adult body mass and within normal condition at the time of sampling (Løvenskiold 1964). Our result that TAG is the most dominant lipid class is in agreement with the general storage pattern found in birds (Blem 1976). Not surprisingly, the depot fat, being the main storage tissue, contained the highest amounts. The content of TAG in bird adipose tissue (depot fat) often exceeds 80% (Johnston 1973), which is also the case for the fulmars in the present study (87% TAG). The lower amounts contained in muscle tissue of all these species support the idea that TAG is utilised directly after conversion to fatty acids as the major fuel for sustained muscular activity (George & Berger 1966).

The presence of moderate levels of FFAs in liver and muscle of all 3 species indicates that these tissues are involved in metabolising lipids. In muscles, FFAs are products of TAG breakdown, which further undergo β-oxidation to yield ATP for muscular activity. The liver is the main site of sterol synthesis (Lehninger et al. 1993), which is reflected by the relatively high levels of sterols in the livers samples of the 3 seabirds species.

The moderate levels of WE-CH found in the livers of the seabird species and in the muscles of eider are very interesting. Based on some earlier studies (Lovern 1938, Cheah & Hansen 1970, Bishop et al. 1983, Clarke 1989) it was concluded that even if the food consumed by seabirds is rich in WE, this lipid does not appear in the fat depots. The prevailing assumption of the lack of

WE in the fat storage depots of seabirds is that dietary WE are metabolised directly, converted to triacylglycerols for storage, or excreted. Thus the fate of these energy-rich lipids ingested by seabirds is of great interest and should be further investigated. However, since fatty alcohols have a higher energy density than triacylglycerols (Sargent & Whittle 1981), it would seem as an advantage, physiologically, to store energy in the first form.

Differences in bird fatty acid compositions

The comparison by PCA of the fatty acids contained in TAG of eider and fulmar fat depot, muscle and liver tissues showed clear-cut species differences within all tissues. The main fatty acids responsible for the separation were 22:1n11, 20:1n9 (both high in fulmar and kittiwake) and 20:4n6 (high in eider). This suggests that eider can be distinguished from fulmar irrespective of whether the tissue samples originate in the fat, muscle or liver. Both species shared the same pattern with respect to differences among their tissues, which were less than the difference between species. The muscle and fat tissue were very similar and could not be distinguished, which is most probably because circulating fatty acids originate mainly in the body fat (Blem 1990). The liver was different from these two, mainly due to higher level of 18:0. Cheah & Hansen (1970) also found a higher level of 18:0 in the liver of the petrels *Puffinus pacificus* and *Pterodroma macroptera* compared to that in adipose tissue.

The comparison, by PCA, of the fatty acids contained in TAG of eider, kittiwake and fulmar liver and muscle tissues showed clear-cut species differences only for eider. Also in this analysis, the main fatty acids responsible for the separation were 22:1n11, 20:1n9 (both high in fulmar and kittiwake) and 20:4n6 (high in eider). Kittiwake and fulmar could not be distinguished as stated, although different tissues had different compositions. As demonstrated for fulmar and eider, the liver of kittiwake could be distinguished from muscle due to higher levels of 18:0.

Birds and potential prey

Falk-Petersen et al. (1990) demonstrated the conservative transfer of fatty acids in neutral lipids from marine algae via zooplankton to higher-trophic-level animals. Of the important phytoplankton in polar waters, the diatoms tend to be rich in 20:5n3, 16:1n7 and C16 PUFA but deficient in C18 PUFA, whereas dinoflagellates tend to be rich in 16:0, 22:6n3, C18 PUFA and deficient in C16 PUFA and 20:5n3 (Falk-Petersen et al. 1998). *Phaeocystis pouchetii*, a species that often blooms in polar waters, tends to be characterised by C18 PUFAs (Sargent et al. 1985) and has 18:2n6 as a specific marker (Hamm et al. 2001), while benthic macro-algae contain high levels of 20:4n6. Oleic acid 18:1n9 is a major fatty acid of most marine animal lipids. The 18:1n7 moiety is also frequently found in large quantities, being derived from the elongation of 16:1n7 that is likely to originate mainly from phytoplankton. This means that 16:1n7 and 18:1n7 in animal lipids tend to reflect phytoplanktonic dietary input, whereas 18:1n9 reflects animal dietary input (Sargent & Falk-Petersen 1981). The 20:1n9 and 22:1n11 moieties, present in very large amounts in *Calanus*, are considered to be formed by de novo biosynthesis in these animals (Sargent & Whittle 1981, Kattner & Hagen 1995).

The high levels of 18:1n9 in tissues show that the 3 seabird species are feeding mainly on marine animals (Table 2). There is, however, a striking difference between kittiwake and fulmar on one side and eider on the other. The high level of the *Calanus* bioindicators 20:1 and 22:1 moieties in fulmar and kittiwake reveals the importance of *Calanus* in the Arctic pelagic food chain and indicates that these 2 species mainly feed on pelagic fish and zooplankton having *Calanus* as the basic food source. The even higher levels of 20:1 and 22:1 moieties in fulmar (total 26%) compared to these in kittiwake (total 17%) further indicate that fulmar is more strongly linked to the Arctic pelagic *Calanus*-based food chain than kittiwake. Eider on the other hand has very low levels of the 20:1 and 22:1 moieties, showing clearly that this bird does not rely on pelagic animals. The high levels of 20:4n6, originating from benthic algae, indicate a strong link to benthic food sources. There are also higher levels of the diatom indicator 20:5n3 and the *Phaeocystis pouchetii* indicator 18:2n6 in eider compared to fulmar and kittiwake. The comparison by PCA, of the fatty acids contained in TAG between the 3 seabird species (Fig. 2) showed clear-cut species differences only for eider. The main fatty acids responsible for the separation were 22:1n11, 20:1n9 (high in fulmar and kittiwake) and 20:4n6 (high in eider). However, as shown in Fig. 3, eider, kittiwake and fulmar share different relations to the prey species included in this study. There are numerous studies of the diets of common eider in the Barents Sea, showing that the eider is omnivorous and may eat most available benthic organisms, e.g. bivalves and polycheates (Bianki et al. 1979, Bustnes & Erikstad 1988, 1990, Lydersen et al. 1989). None of these studies have found fish to be of any great importance. By the aid of a score dendrogram, the eider fatty acid profiles were most similar to the benthic/demersal snake eelblenny

and the large individual (119 mm) of daubed shanny. Besides availability, the different energy content of the food (Goudie & Ankney 1986, Guillemette et al. 1992, Bustnes & Lønne 1995) also influences food selection (Anker-Nilssen et al. 2000), and juvenile daubed shanny has been found to be of high energetic quality (Falk-Petersen et al. 1986).

Both capelin and polar cod have often been found to dominate in the stomach content of kittiwakes (Belopolski 1957, Løvenskiold 1964), and it is most likely that capelin constitute important prey items for the kittiwakes when oceanographic conditions are favourable. Other than pelagic fishes, the amphipod *Parethemisto libellula*, euphausiids (mainly *Thysanoessa inermis*), and polychaetes (*Nereis* sp.) have also occurred frequently in stomach samples of kittiwakes from the Barents Sea and SW Spitsbergen (Løvenskiold 1964, Mehlum & Gabrielsen 1993). The PCA together with the score dendrogram demonstrated a higher relation to polar cod, capelin and small daubed shannies than to snake eelblennies, krill, large daubed shanny and pteropods. Pteropods have been found in stomachs examined from the Hornsund area (Lydersen et al. 1989). However, based on the results of the present of fatty acid signatures, only a very weak linkage exists between the kittiwake and the very abundant *Limacina helicina* in Kongsfjorden.

Previous food studies of fulmar around Svalbard present a very diverse dietary picture. Cephalopod beaks (mainly from *Gonatus fabricii*) and polychaete jaws (mainly from *Nereis irrorata*) have been found in large numbers in fulmar stomachs (de Korte 1972, Mehlum & Gjertz 1984, Gjertz & Gabrielsen 1985, Lydersen et al. 1989). The importance of these species is questionable since neither of these constitutes important parts of the permanent pelagic community, and prey with resistant hard parts tends to be over-represented in stomach analysis. Large crustaceans, such as the amphipods (*Parethemisto libellula*, *Parethemisto abyssorum*, *Gammarus* spp.) and krill (*Thysanoessa* spp.) have together with the pelagic fishes been found in large numbers in fulmar stomachs (Hartley & Fisher 1936, Mehlum & Gjertz 1984, Gjertz & Gabrielsen 1985, Lydersen et al. 1989, Camphysen 1993). The PCA together with the score dendrogram demonstrated, as for the kittiwakes, a closer relation to polar cod, capelin and small daubed shannies than to snake eelblennies, krill, large daubed shanny and pteropods. The relationship to the polar cod and capelin is much stronger for the fulmar than for the kittiwake. The fatty acid signature analysis results supports the importance of polar cod in the diet of fulmar. The polar cod is separated from fulmar by the third component, which also is the case for daubed shanny. Daubed shannies have not been reported as prey for fulmars around Svalbard, but the fatty acid signatures suggest that it is a potential prey. Juvenile (7 to 15 cm) daubed shannies are also a major component of the pelagic ecosystem and are frequently found caught in research trawls (S.F.-P. pers. obs.).

The results from the stable isotope analysis reveal that the trophic structure is different for the 3 seabird species investigated, suggesting dietary segregations. Fulmars occupied relatively high trophic positions, as indicated by relatively enriched $\delta^{15}N$ values, whereas kittiwake occupied a lower trophic position followed by eider at the lowest level. Additionally, relatively depleted $\delta^{13}C$ values indicate pelagic foraging, whereas relatively enriched $\delta^{13}C$ values indicate inshore or benthic feeding (Hobson 1993). We can thereby further confirm what was earlier known about the feeding behaviour of these seabird species: that fulmar and kittiwake depend more on pelagic prey than eider.

Based on our general knowledge of the Arctic marine ecosystem, lipid biomarkers, fatty acid signature analysis and results from stable isotope analysis, we can conclude the following:

- Common eider is strongly linked to the benthic food chain, which is reflected in its fatty acid composition (high levels of 20:4n6) and stable isotope values (high levels of $\delta^{13}C$). Low levels of $\delta^{15}N$ show that eider occupies the lowest trophic level of the 3 bird species, indicating a short food chain.
- Black-legged kittiwake and northern fulmar are linked to the pelagic food chain, both through fatty acid composition (high levels of 20:1n9 and 22:1n11) and stable isotope values (low levels of $\delta^{13}C$). The high levels of 20:1 and 22:1 moieties also indicate the importance of *Calanus* in the Arctic pelagic food chain supporting fulmar and kittiwake.
- High levels of $\delta^{15}N$ show that of the 3 species, the fulmar occupies the highest trophic level, followed by kittiwake and then eider.

Marine environments are often complex and gaining exact and well-defined information on trophic relations is in most cases a very comprehensive task. Today, no single method exists that manages a total breakdown of a predator's prey constituents both qualitatively and quantitatively. However, this study has shown that stronger tools can be provided by combining existing techniques with high potentials.

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