

Regional differences in fatty acid composition in common minke whales (*Balaenoptera acutorostrata*) from the North Atlantic

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ABSTRACT

Variation in fatty acid (FA) composition of blubber collected in 1998 from 170 common minke whales (*Balaenoptera acutorostrata*) was used to study population structure in the North Atlantic. Samples from seven IWC management units were analysed: West Greenland ('WG', $n=69$); East Greenland ('CG', $n=3$); Jan Mayen ('CM', $n=24$); Svalbard ('ES', $n=16$); the Barents Sea ('EB', $n=30$); Vestfjorden/Lofoten ('EC', $n=7$); and the North Sea ('EN', $n=21$). FA analyses were conducted on both deep and superficial blubber with a one-step extraction and esterification method followed by gas-chromatography. The 43 FAs identified comprised 93–99% of total FAs. CART and MANOVA analyses on FA signatures in both blubber sections suggested a '3-geographic Regions model' where the regions were Greenland (WG, CG), the Northeast Atlantic (CM, ES, EB, EC) and the North Sea (EN). This is in general agreement with a genetic study on the same samples and suggests that differences in FA signatures can be used for studying population structure in minke whales. Potential variation in FA signatures caused by internal and environmental factors needs to be better understood. It is recommended that future studies of blubber FA signatures in minke whales include samples from their entire North Atlantic range (including Canadian and Icelandic waters). Samples should be collected from a pre-specified body site to rule out possible internal variation and during a narrow time-window in the same year to rule out seasonal exchange between areas.

KEYWORDS: COMMON MINKE WHALE; STOCK STRUCTURE; POPULATION; FATTY ACIDS; GREENLAND; NORTH ATLANTIC; NORTH SEA

INTRODUCTION

The common minke whale (*Balaenoptera acutorostrata*) is the smallest and most abundant of the baleen whales in the North Atlantic (e.g. Stewart and Leatherwood, 1985; Donovan, 1991a; b). During summer, minke whales are distributed from the east coast of Canada to the North Sea, and as far northeast as the Svalbard-Barents Sea region (Fig. 1). This species is exploited by Greenlandic subsistence hunters in coastal Greenland waters (IWC, 2003, pp.68–70) and by Norwegian whalers along the Norwegian coast and offshore in the North East Atlantic region and the North Sea (e.g. Grønvik, 1998). Determining sustainable harvest levels for minke whales in these areas requires an understanding of the population structure and the ability to identify the exploited units demographically.

In 1977, the International Whaling Commission (IWC) divided the North Atlantic minke whale population into four management stocks: (1) West Greenland; (2) Central North Atlantic; (3) NE North Atlantic; and (4) Canadian East Coast (Donovan, 1991b). However, the evidence for some of these was 'somewhat scanty' and there have been a number of suggestions for changes and improvements (e.g. Larsen and Øien, 1988; Bakke *et al.*, 1996; Palsboll *et al.*, 1997). With the development of the Revised Management Procedure, the Committee re-evaluated the evidence and divided the North

Atlantic into 10 'Small Areas'¹ (IWC, 1993; 1994) (Fig. 1).

In the North Atlantic and elsewhere, genetic data have proved equivocal information on stock structure (e.g. IWC, 2004) and it is important that information from a variety of techniques is examined (e.g. Donovan, 1991b). Other studies have applied various techniques including comparison of catch composition (e.g. Larsen and Øien, 1988), morphological differences (Christensen *et al.*, 1990) and reproductive parameters (Olsen, 1997), but have not provided a definite answer to this question. However, new analytical tools that reflect changes over a shorter time-scale compared to genetics may assist in the understanding of the population structure of North Atlantic minke whales. One such tool is the composition of fatty acids (FAs) in depot fats such as the blubber of marine mammals. Examples where FAs have been used as a tool to discriminate between

¹The formal definition is that 'Small Areas are disjoint areas small enough to contain whales from only one biological stock, or be such that if whales from different biological stocks are present in the Small Area, catching operations would not be able to harvest them in proportions substantially different to their proportions in the Small Area'. They are thus management units and do not have to have boundaries that coincide with biological stocks. Medium Areas 'correspond to known or suspected ranges of distinct biological stocks'. (IWC, 1999).

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populations include: ringed seals, *Phoca hispida* (Käkelä *et al.*, 1993); harp seals, *Phoca groenlandica* (Grahl-Nielsen *et al.*, 1993); harbour seals, *Phoca vitulina* (Smith *et al.*, 1996; Iverson *et al.*, 1997); and harbour porpoises, *Phocoena phocoena* (Møller *et al.*, 2003). In addition, Olsen and Grahl-Nielsen (2002) were able to differentiate between minke whales from the Norwegian Sea and the North Sea using differences in FA signatures in blubber.

In marine mammals the dietary FAs are represented mainly by long chain mono-unsaturated (e.g. C18:1n-7/n-9, C20:1n-9/n-11, C22:1n-9/n-11) and poly-unsaturated fatty acids (e.g. C18:3n-3, 18:4n-3, 20:4n-6, C20:5n-3, C22:5n-3, 22:6n-3) (e.g. Ackman *et al.*, 1975; West *et al.*, 1979; Koopman *et al.*, 1996; Iverson *et al.*, 1997; Smith *et al.*, 1997; Walton *et al.*, 2000).

Previous genetic studies compared minke whales collected in different years, making it difficult to distinguish between spatial and potential temporal differentiation (IWC, 1998). To eliminate some of these uncertainties, this study used minke whales caught during a single whaling season in seven of 10 IWC 'Small Areas' in the North Atlantic. To date, the samples have been analysed for regional differences in signatures of elements and stable isotopes (Born *et al.*, 2003), organochlorines (Hobbs *et al.*, 2002), genetics (Andersen *et al.*, 2003) and caesium-137 (Born *et al.*, 2002).

This paper provides an analysis of the fatty acids in the deep and superficial blubber from 170 minke whales sampled in 1998 in West Greenland, the northeastern Atlantic and the North Sea with the objective of elucidating population structure. Information is presented on the FAs identified, and on the regional variation in the composition of the FAs in minke whales. Preliminary analyses were presented by Møller *et al.* (2000).

MATERIALS AND METHODS

Field sampling

Blubber samples were collected from 6 May until 31 October 1998 from 170 minke whales taken during directed catches by Greenlandic and Norwegian whalers in the North Atlantic region (Fig. 1): West Greenland ('WG', $n=37$); East Greenland ('CG' $n=3$); Jan Mayen ('CM', $n=24$); Svalbard ('ES', $n=16$); the Barents Sea ('EB', $n=30$); Vestfjorden/Lofoten ('EC', $n=7$); and the North Sea ('EN', $n=21$). Within the same period additional samples were collected in Greenland from 32 minke whales. These samples, for which exact information on site and date was not available, were grouped together with the three animals from CG to form a mixed CG and WG group, from here on referred to as 'GR' ($n=35$).

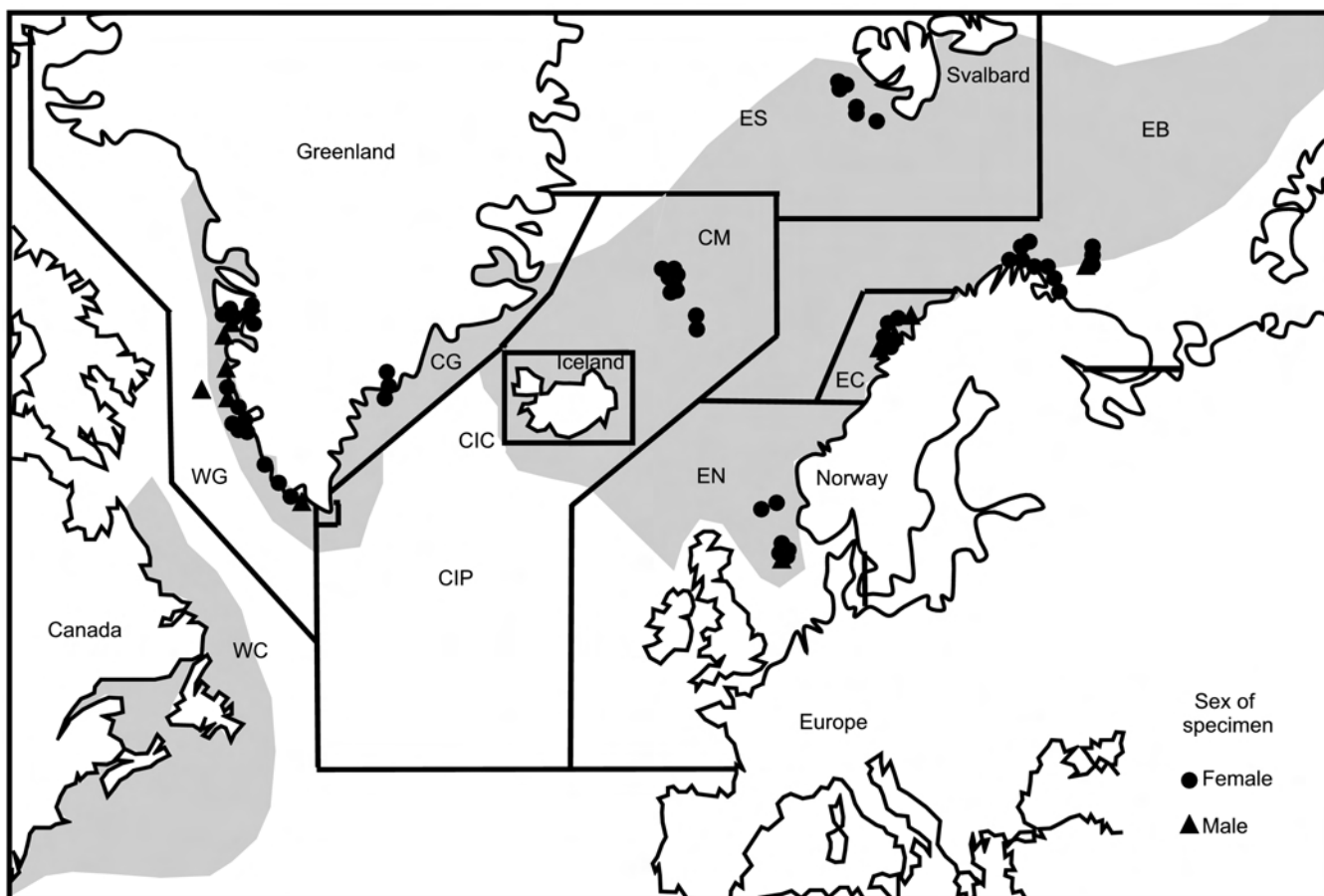


Fig. 1. Map showing the boundaries of the IWC 'Small Areas' and the location of sampling of tissues from a total of 170 minke whales in 1998. The approximate summer range of minke whales (Stewart and Leatherwood, 1985; Donovan, 1991a; b) is indicated in grey. The areas west of 57°W (i.e. the central parts of Davis Strait and the Canadian East Coast waters) have not been surveyed systematically and therefore it is not known whether or not the distribution of minke whales is continuous between western Greenland and Canada.] Key = WC (West Canada); WG (West Greenland); CG (Central Greenland); CIC (Central Island Coastal); CIP (Central Iceland Pelagic); CM (Central Jan Mayen); ES (East Svalbard); EB (East Barents Sea); EC (East Coastal); EN (East North Sea).

Samples for analyses were taken only if sub-samples included skin or muscle for correct orientation. This selection procedure resulted in deep blubber samples from 154 animals and superficial blubber samples from 164 animals representing 170 animals. Both the deep and superficial blubber were sampled from 148 minke whales.

A deep blubber core including skin and muscle was collected from each whale and stored at -20°C . The sex of each individual was determined genetically (Andersen *et al.*, 2003). The overall percentage of females in the samples was 79% ranging between 50% (EC) and 100% (CG).

Sample preparation and fatty acid methyl-esters

In September 1999, sub-samples representing the centre core of an entire blubber profile were transferred to polyethylene plastic bags where air was evacuated and samples stored at -80°C until analysis. For analysis, sub-samples were thawed and placed on oil-free paper where a 2–3mm thick blubber layer was dissected from (a) immediately under the skin, and (b) adjacent to the muscle core.

Following this procedure, the individual layers were transferred to thick-walled glass tubes to be sealed with screw-caps fitted with a silicone-PTFE cap-membrane. Lipids were extracted and FAs trans-esterified to produce FA methyl-esters (FAME) using a one-step method (Sukhija and Palmquist, 1988) as modified by Møller (1999). FAMES were stored in air-sealed GC-vials at -80°C until the identification-analysis could be performed (0–5 days). To avoid auto-oxidation of unsaturated FAs, all chemicals and headspace volumes were de-aerated using purified argon gas.

To avoid loss of particular volatile short-chained FAs (e.g. isovaleric acid) the use of FA butyl-esters (FABE) instead of the commonly used FAME has been recommended. However, analyses on blubber FABE in minke whales have shown no presence of such volatile FAs (P.M., unpublished data) and for convenience FAME (referred to as FAs in the following) were therefore chosen for this study.

FA analysis

The FAs were analysed and identified using a *Hewlett Packard* 5890 gas-chromatograph equipped with a split/splitless FID detector. A $30 \times 0.25\text{mm}$ internal diameter column coated with 50% cyanopropyl polysiloxane (0.247mm film thickness; J&W DB-23; Folsom California) was used. Helium was used as the inert carrier gas at a constant flow of 1.2ml/min. Injection- and detection-temperatures were set at 250°C and the initial column temperature at 65°C . Two minutes after sample injection the temperature was increased from 65°C to 165°C at $20^{\circ}\text{C}/\text{min}$ and held for 0.4min. The temperature was then increased to 210°C at $2^{\circ}\text{C}/\text{min}$, held for 1min, and then finally increased to 240°C at $30^{\circ}\text{C}/\text{min}$ and held for 1min. The entire program took 32.9min to complete. The Hewlett Packard ChemStation software (HP 3363 Series II ChemStation) performed integration of chromatograms. Identification of most individual FAs was performed using methyl-ester standard mixes FIM-FAME-7 and PUFA-3 (Matreya, Inc.). FAs of the n-11 and n-9 type were identified using an oil-extract from harbour porpoise blubber of known composition. The integrated area peaks were converted to FA percentage by weight (mass percentage of total FAs) using theoretical correction factors (Craske and Bannon, 1988; Møller, 1999). Standards were run before and after sample-sequences to calibrate the retention times and to monitor the condition of the column. Individual FAs have been named according to the short-hand IUPAC

nomenclature: C(#carbon):(double bonds)n-x, where x is the location of the double bond nearest the terminal methyl group.

Data analysis

Classification and Regression Tree analysis (CART), ANOVA and MANOVA available in *S-plus*[®] (version 4.5, Mathsoft, Inc.) were used to investigate patterns in the FA signatures among: (a) IWC 'Small Areas'; and (b) major regions i.e. Greenland (CG, WG), the NE Atlantic region (CM, ES, EB and EC pooled) and the North Sea (EN) (Fig. 1). In contrast to ANOVA and MANOVA, CART multivariate analysis (Clark and Pregibon, 1992; Venables and Ripley, 1994) is non-parametric and has no restriction as to the number of variables allowed in the model. Therefore the total array of FAs was tested when using CART. The CART technique has previously been applied to the analysis of FA signatures containing more than 60 variables (FAs) per observation (Iverson *et al.*, 1997; Smith *et al.*, 1997). An initial CART analysis revealed similar patterns for males and females and the two genders were therefore pooled in subsequent analyses of spatial differences. The deep blubber and the superficial blubber were analysed separately. Prior to analysis, the data were arcsin transformed to meet the assumption of normality and homoscedasticity. For construction of the classification trees, two stopping criteria were used to determine branches: (1) a change in deviation of less than 1% of the root node deviation; or (2) when the minimum number of observations at a node was less than 10.

A '3-Region model' and a '2-Region model' as suggested by the CART analysis was tested further by use of multivariable analyses of variance (MANOVA; Wilks λ) including a total of 18 FAs. Furthermore, analyses of variance (ANOVA) were conducted to indicate the probable importance of individual FAs included in the MANOVA. These 18 FAs were those responsible for the major splits picked up by the CART analyses and other FAs of dietary origin.

RESULTS

The 43 FAs identified in this study made up 93–99% of total FAs in the blubber of the minke whales. Of these FAs, the following 16 were generally represented by $> 1\%$ on weight basis: 14:0, 16:0, 16:1n-7, 18:0, 18:1n-11, 18:1n-9, 18:1n-7, 18:2n-6, 18:3n-3, 18:4n-3, 20:1n-11, 20:1n-9, 20:5n-3, 22:1n-11, 22:5n-3, 22:6n-3 (Table 1).

Regional differences based on CART analyses

Deep blubber signatures

Based on the FAs in the deep blubber, the overall percentage of misclassification of individuals to area was 17% (i.e. 26 misclassified of 154 analysed, 26/154). The model selected 19 of 43 FAs for the construction of a classification tree with 19 terminal nodes (Fig. 2). At the root C20:1n-7 formed an initial split into a NE Atlantic-North Sea group (3/69, 3 misclassified of 69 classified) and a NE Atlantic-Greenland group (0/85). Only 3 out of 64 Greenland animals were misclassified to the NE Atlantic-North Sea group. In addition, all 20 North Sea animals were found in this group where all but one could successfully be categorised in a clean terminal node (0/19). Within the NE Atlantic-Greenland group C18:4n-1 distinguished between NE Atlantic (9/32) and Greenland animals (1/53). In the Greenland group the one misclassified animal was from the neighbouring Jan Mayen area (CM). In both NE Atlantic sub-groups, Jan

Table 1
Fatty acid composition (average mass (%) \pm standard deviation) of the deep and the superficial blubber of minke whales representing the three regions, Greenland, the North Eastern Atlantic and the North Sea.

Fatty acid	Greenland		North Eastern Atlantic		North Sea	
	Deep	Superficial	Deep	Superficial	Deep	Superficial
C10:0	0.01 \pm 0.01	0.00 \pm 0.00	0.00 \pm 0.01	0.00 \pm 0.00	0.02 \pm 0.01	0.00 \pm 0.00
C12:0	0.14 \pm 0.05	0.09 \pm 0.03	0.08 \pm 0.03	0.07 \pm 0.01	0.12 \pm 0.02	0.07 \pm 0.01
C13:0	0.03 \pm 0.01	0.01 \pm 0.02	0.03 \pm 0.01	0.02 \pm 0.01	0.04 \pm 0.01	0.01 \pm 0.02
C14:0	4.80 \pm 0.56	4.21 \pm 0.45	5.54 \pm 0.74	4.15 \pm 0.37	4.99 \pm 0.54	4.37 \pm 0.51
C14:1n-7	0.22 \pm 0.10	0.08 \pm 0.02	0.22 \pm 0.15	0.06 \pm 0.02	0.14 \pm 0.05	0.09 \pm 0.04
C14:1n-5	0.22 \pm 0.05	0.72 \pm 0.30	0.17 \pm 0.05	0.92 \pm 0.19	0.17 \pm 0.01	0.99 \pm 0.38
C15:0	0.27 \pm 0.08	0.29 \pm 0.05	0.32 \pm 0.06	0.31 \pm 0.08	0.30 \pm 0.05	0.28 \pm 0.10
C15:1n-5	0.06 \pm 0.05	0.09 \pm 0.04	0.02 \pm 0.07	0.09 \pm 0.03	0.11 \pm 0.06	0.09 \pm 0.03
C16:0	10.73 \pm 2.18	8.71 \pm 2.18	14.46 \pm 2.45	8.49 \pm 1.34	10.32 \pm 2.12	7.28 \pm 1.34
C16:1n-7	7.78 \pm 2.46	13.45 \pm 2.63	6.88 \pm 2.51	13.06 \pm 2.21	5.61 \pm 2.33	10.66 \pm 1.79
C16:2n-4	0.44 \pm 0.13	0.54 \pm 0.10	0.38 \pm 0.11	0.36 \pm 0.10	0.34 \pm 0.09	0.35 \pm 0.08
C17:0	0.42 \pm 0.25	0.27 \pm 0.08	0.51 \pm 0.31	0.20 \pm 0.12	0.31 \pm 0.12	0.25 \pm 0.11
C16:3n-4	0.29 \pm 0.15	0.34 \pm 0.12	0.33 \pm 0.10	0.48 \pm 0.13	0.39 \pm 0.08	0.47 \pm 0.14
C17:1n-7	0.04 \pm 0.03	0.20 \pm 0.10	0.10 \pm 0.06	0.12 \pm 0.11	0.05 \pm 0.04	0.17 \pm 0.10
C16:4n-1	0.42 \pm 0.25	0.18 \pm 0.11	0.18 \pm 0.11	0.10 \pm 0.20	0.39 \pm 0.15	0.14 \pm 0.15
C18:0	2.45 \pm 0.68	1.84 \pm 0.44	2.54 \pm 0.77	1.77 \pm 0.33	2.75 \pm 0.59	1.84 \pm 0.46
C18:1n-11	1.54 \pm 0.74	2.60 \pm 0.94	0.82 \pm 0.64	2.15 \pm 0.61	1.61 \pm 0.63	2.70 \pm 0.83
C18:1n-9	13.80 \pm 3.44	18.31 \pm 2.84	21.35 \pm 4.44	22.16 \pm 2.23	11.22 \pm 2.73	18.63 \pm 2.03
C18:1n-7	3.71 \pm 1.14	4.52 \pm 0.95	5.19 \pm 1.76	4.86 \pm 0.99	1.84 \pm 0.23	2.93 \pm 0.63
C18:2n-6	1.33 \pm 0.28	1.64 \pm 0.25	1.28 \pm 0.35	1.93 \pm 0.20	2.16 \pm 0.43	2.34 \pm 0.35
C18:2n-4	0.12 \pm 0.04	0.09 \pm 0.05	0.07 \pm 0.04	0.08 \pm 0.05	0.09 \pm 0.04	0.05 \pm 0.05
C18:3n-6	0.10 \pm 0.03	0.02 \pm 0.05	0.12 \pm 0.04	0.10 \pm 0.09	0.10 \pm 0.07	0.06 \pm 0.07
C18:3n-4	0.14 \pm 0.04	0.65 \pm 0.16	0.10 \pm 0.05	0.95 \pm 0.21	0.12 \pm 0.03	1.40 \pm 0.24
C18:3n-3	0.52 \pm 0.14	0.95 \pm 0.38	0.66 \pm 0.21	1.03 \pm 0.20	1.11 \pm 0.39	1.47 \pm 0.28
C18:4n-3	1.60 \pm 0.58	0.33 \pm 0.13	1.81 \pm 0.67	0.22 \pm 0.18	2.32 \pm 0.69	0.18 \pm 0.07
C18:4n-1	0.24 \pm 0.11	0.00 \pm 0.00	0.10 \pm 0.06	0.01 \pm 0.03	0.20 \pm 0.07	0.00 \pm 0.00
C20:0	0.16 \pm 0.06	0.08 \pm 0.08	0.18 \pm 0.08	0.11 \pm 0.06	0.24 \pm 0.06	0.11 \pm 0.07
C20:1n-11	1.80 \pm 1.19	2.62 \pm 0.88	1.14 \pm 1.00	2.32 \pm 0.70	2.37 \pm 1.07	3.03 \pm 0.81
C20:1n-9	11.42 \pm 3.84	10.91 \pm 3.30	7.45 \pm 4.19	9.26 \pm 2.84	10.97 \pm 3.14	10.44 \pm 2.57
C20:1n-7	0.73 \pm 0.93	0.50 \pm 0.15	0.33 \pm 0.12	0.35 \pm 0.06	0.23 \pm 0.05	0.25 \pm 0.04
C20:2n-6	0.33 \pm 0.09	0.30 \pm 0.07	0.34 \pm 0.10	0.32 \pm 0.05	0.36 \pm 0.05	0.39 \pm 0.05
C20:3n-6	0.11 \pm 0.10	0.05 \pm 0.07	0.10 \pm 0.04	0.08 \pm 0.06	0.10 \pm 0.05	0.06 \pm 0.05
C20:4n-6	0.29 \pm 0.11	0.36 \pm 0.10	0.30 \pm 0.10	0.37 \pm 0.10	0.40 \pm 0.12	0.42 \pm 0.10
C20:3n-3	0.07 \pm 0.02	0.01 \pm 0.03	0.09 \pm 0.04	0.07 \pm 0.05	0.10 \pm 0.05	0.10 \pm 0.08
C20:4n-3	0.89 \pm 0.21	0.98 \pm 0.26	0.84 \pm 0.21	1.19 \pm 0.22	1.12 \pm 0.26	1.37 \pm 0.27
C20:5n-3	6.29 \pm 2.85	4.59 \pm 1.60	5.50 \pm 1.47	4.00 \pm 1.24	5.61 \pm 2.26	3.45 \pm 1.20
C22:0	0.04 \pm 0.02	0.00 \pm 0.01	0.02 \pm 0.03	0.01 \pm 0.01	0.02 \pm 0.03	0.01 \pm 0.01
C22:1n-11	9.08 \pm 3.47	7.37 \pm 3.04	7.30 \pm 4.39	6.20 \pm 2.43	12.72 \pm 3.64	10.18 \pm 3.47
C22:1n-9	1.01 \pm 0.35	0.90 \pm 1.00	0.56 \pm 0.37	0.58 \pm 0.16	0.83 \pm 0.19	0.60 \pm 0.12
C22:2n-6	0.40 \pm 0.16	0.24 \pm 0.10	0.40 \pm 0.17	0.26 \pm 0.08	0.54 \pm 0.14	0.27 \pm 0.11
C22:5n-3	2.82 \pm 0.65	2.64 \pm 0.62	2.30 \pm 0.65	2.55 \pm 0.61	2.68 \pm 0.46	2.38 \pm 0.74
C22:6n-3	6.75 \pm 1.59	5.01 \pm 2.00	5.37 \pm 2.03	4.79 \pm 1.88	8.06 \pm 2.45	5.79 \pm 2.25
C24:1n-9	0.41 \pm 0.18	0.19 \pm 0.10	0.31 \pm 0.21	0.17 \pm 0.08	0.79 \pm 0.15	0.20 \pm 0.12
Ident. FA	93.97 \pm 0.95	96.87 \pm 0.60	95.80 \pm 1.15	96.34 \pm 0.97	93.94 \pm 1.06	95.90 \pm 1.10
Not ident. FA	6.03 \pm 0.95	3.13 \pm 0.60	4.20 \pm 1.15	3.66 \pm 0.97	6.06 \pm 1.06	4.10 \pm 1.10
Sample size	64	71	70	74	20	19

Mayen and Greenland animals (GR and WG) intermingled while a lumping of Vestfjorden/Lofoten (EC) and Svalbard (ES) was apparent. The whales from the Barents Sea (EB) showed a more pronounced isolation from the rest of the NE Atlantic (i.e. 0/16 and 1/7). Approximately half of the Jan Mayen animals were isolated from the rest of the NE Atlantic and lumped together with the North Sea animals.

Superficial blubber signatures

The CART analysis based on FAs in the superficial blubber resulted in a slightly higher rate of misclassifications (22.0%, 36 misclassified of 164) (Fig. 3) than found for the deep blubber. The model selected 19 FAs to produce a total of 20 terminal nodes. At the root node, C18:3n-4 distinguished between animals from Greenland and the NE

Atlantic-North Sea with a misclassification rate of 12.2% (20/164). All of the 19 North Sea animals were along the NE Atlantic-North Sea branch where 17 were categorised correctly into a terminal North Sea (EN) node. The only misclassification at this node represented an animal from the neighbouring Vestfjorden/Lofoten (EC) area. Similarities between Jan Mayen (CM) and Greenland animals were observed as indicated by a general intermingling between animals from these two areas (Fig. 3).

Conclusion

The FA signatures of both the deep and the superficial blubber indicated: (1) that North Sea minke whales differed from those sampled in the northeastern Atlantic (i.e. Jan Mayen, Svalbard, Barents Sea and Vestfjorden/Lofoten) and

Greenland; and (2) that animals from Greenland waters differed from NE Atlantic minke whales; (3) a similarity between CM and Greenland; and (4) minke whales from the Barents Sea appeared to be somewhat different from the rest of the NE Atlantic. Although the FAs responsible for the tree construction differed between blubber layers, the complexity and overall topography of the trees did not.

Regional differences based on MANOVA and ANOVA

Eighteen principal FAs were included in the analyses of regional differences using MANOVA (Fig. 4). The FA composition of both the deep and the superficial blubber layers differed significantly among (a) IWC 'Small Areas'; and (b) among three regions in a '3-Region model' (i.e. all-Greenland versus NE Atlantic versus Eastern North Sea) ($p < 0.0001$, Table 2). However, the largest F -value resulted from the analysis of the '3-Region model'. Furthermore, a MANOVA on Eastern North Sea versus NE Atlantic supported the 3-Region model ($p < 0.0001$) (Table 2). The ANOVAs performed on the 18 individual FAs that were included in the MANOVA test of the '3-Region model' showed that six FAs in the deep blubber and seven in the superficial blubber were responsible for the significant differences in FA signatures among areas (Fig. 4). In three cases, the same FAs found both in the outer and inner blubber were involved in these differences.

DISCUSSION

Location of the tissue samples

In no instances, except for the North Sea, were the same FAs picked up by the tree functions from both the deep and the superficial blubber layer. This emphasises that the two layers likely represent different metabolic histories. The blubber layer of the North Atlantic minke whale is stratified in such a way that the FA composition in the superficial layer differs from that in the deep blubber (Fehn, 1996; Møller *et al.*, 2000; Olsen and Grahl-Nielsen, 2002). A similar stratification has been described for several other marine mammals (West *et al.*, 1979; Lockyer *et al.*, 1984; Fredheim *et al.*, 1995; Käckelä and Hyvärinen, 1996; Koopman *et al.*, 1996; Møller *et al.*, 2002). These studies suggest that the superficial blubber layer is a region for storage of relatively endogenous FAs with its main function being insulation. In contrast, the deep blubber layer has a higher degree of unsaturation and is thought to be metabolically more active.

The attempts to distinguish among all IWC 'Small Areas' resulted in relatively high percentages of misclassification both for the deep and the superficial blubber layer (17% and 22%, respectively). However, included in these percentages are misclassified animals from the mixed Greenland group (GR) representing 3 East Greenland animals and 32 Greenland animals with no exact information on sampling area (i.e. CG or WG). Animals from this group could in fact represent 'false' misclassifications. Consequently, a clear distinction between samples from the different IWC 'Small Areas' was not possible, although given that 'Small Areas' are not intended to correspond to separate biological stocks, this is not surprising. However, the classification trees constructed on the deep and the superficial blubber both indicated that whales sampled in Greenland differed from those from the NE Atlantic-North Sea region (Figs 2 and 3). In addition, CART analyses indicated that minke whales from the North Sea area (EN) differed from the NE-Atlantic minke whales. The MANOVA supported the existence of both a '2-Region model' (Greenland versus NE

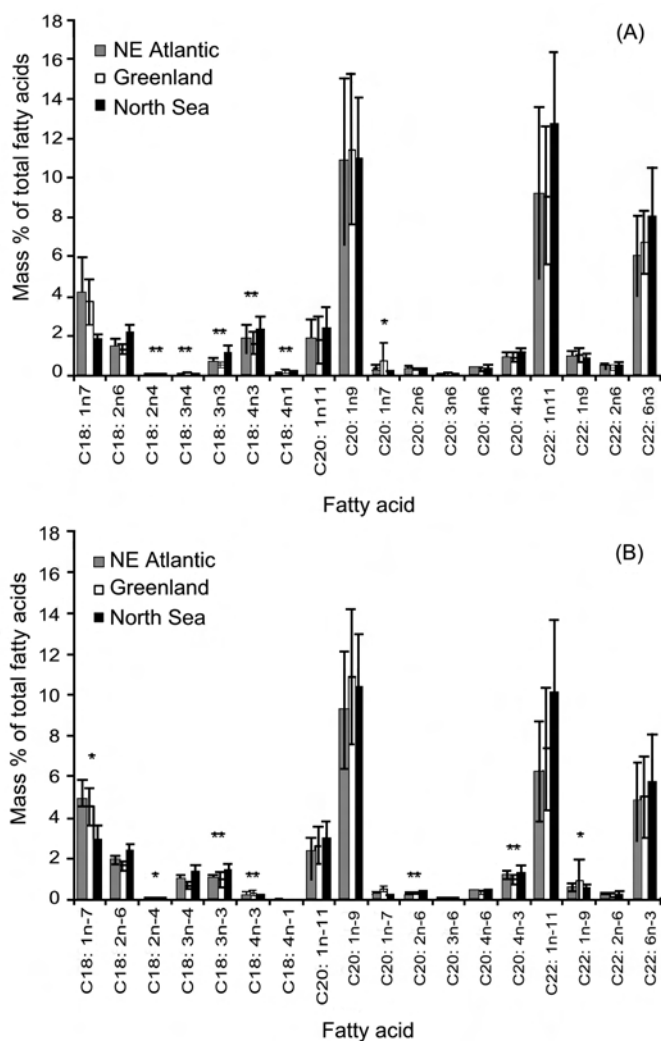


Fig. 4. Results of ANOVAs performed on 18 fatty acids in blubber of minke whales that were sampled in the North Atlantic region during 1998. Bars and lines represent the mean and standard deviation, respectively, by major region (NE Atlantic, Greenland, North Sea) as identified from the CART analyses. (A) deep blubber; (B) superficial blubber (* = $p < 0.01$, ** = $p < 0.001$).

Table 2

MANOVA analysis for the effect of areas on the concentration of 18 fatty acids in the blubber of minke whales from the North Atlantic (1998). (A) = deep blubber and (B) = superficial blubber.

Variable	Df	Pillai	Approx F	Num df	Denom df	P-value
(A)						
IWC small areas*	1	0.534	8.589	18	135	< 0.0001
3 areas**	1	0.731	20.373	18	135	< 0.0001
Residuals	152					
Eastern North Sea vs NE Atlantic	1	0.702	9.27	18	71	< 0.0001
Residuals	88					
(B)						
IWC small areas*	1	0.418	5.716	18	143	< 0.0001
3 areas**	1	0.699	18.438	18	143	< 0.0001
Residuals	160					
Eastern North Sea vs NE Atlantic	1	0.683	8.731	18	73	< 0.0001
Residuals	90					

*Six groups representing IWC small areas and one which represents animals from two IWC small areas (i.e. West and East Greenland). **Greenland vs North East Atlantic vs Eastern North Sea.

Atlantic-North Sea) and a '3-Region model' (Greenland vs. NE Atlantic vs the North Sea) model. However, larger *F*-values were obtained from testing the '3-Region model' for both blubber layers thereby favouring this model over the '2-Region model'. This effectively is in accord with IWC 'Medium Area' assumptions of three biological stocks (IWC, 2004). The MANOVA also indicated that there were significant differences among some IWC 'Small Areas'. However, because a total of 43 FAs were included in the construction of classification trees, the CART analyses are thought to be relatively more powerful than the MANOVA in separating among whales sampled in different areas. Differences in FA signatures in this study may have been influenced by the fact that samples may have been taken from different parts of the body of the whale. Differences in blubber FA composition between two dorsal sites (30cm in front of and 30cm behind the dorsal fin) have been reported for North Atlantic minke whales (Olsen and Grahl-Nielsen, 2002). However, this difference was much smaller than the difference in FA signatures between the deep and superficial layer (Olsen and Grahl-Nielsen, 2002). No information is available about the exact sites from where the samples were taken and therefore the potential influence of the uncertainty associated with the sampling method is difficult to assess. There is no indication that large (>7m) and small (<7m) whales feed on different food items (Haug *et al.*, 2002), but differences according to sexual maturity have been identified in harbour porpoise (Møller, 1999) and may also influence the results of this study to some degree. However, the fact that the findings in this study resemble those obtained in a genetic study using the same samples (Anderson *et al.*, 2002) indicates that the FA technique is useful irrespective of sexual status and the location of the blubber sample on the whale.

Animal movements

The lack of clear differences among regions could to some extent be explained by some animals moving rapidly among feeding grounds. Minke whales are capable of relatively high swimming speeds (i.e. 7-12km/h, Blix and Folkow, 1995; Folkow, in litt., 27 April 2000). Therefore, a directed movement between even distant areas within the range of this study may take a minke whale only a few weeks. Hence, a whale may have fed in one area to be sampled not much later in another area. Furthermore, the actual lag-time between the dietary intake of the FAs and their deposition as a signal in the blubber is not known.

Despite the fact that the composition of FAs in the depot fats of marine mammals is influenced by the composition of the diet (e.g. Ackman, 1980), finding a FA composition in a predator identical to that of its diet is unusual (Iverson *et al.*, 1995). This can be explained by an animal's ability to *de novo* synthesise and selectively metabolise, absorb and deposit FAs (Enser, 1984; Sargeant *et al.*, 1988). It is a combination of dietary fats and endogenous synthesis that influences the blubber FA signature. Even though the diet of North Atlantic minke whales has been shown to vary considerably between geographic regions and periods (e.g. Haug *et al.*, 2002; Sigurjónsson and Galan, 1990; Lydersen *et al.*, 1991), it is a combination of internal and environmental factors that influences the composition of the blubber.

Additional sampling areas

Ideally, samples of minke whales from neighbouring Canadian (WC) and Icelandic (CIP and CIC, *cf.* Fig. 1) waters should have been included in this study. However,

minke whales are currently not harvested by Canada or Iceland. Further work on differences in FA signatures to incorporate minke whales from the entire North Atlantic range of this species is recommended. Samples from areas where minke whales are not harvested may in the future be obtained from biopsies taken from free-roaming whales. Knowledge of the metabolism of the blubber, the turnover rate of FAs, and the effect of e.g. physiological state and reproductive status of the individual may significantly advance the feasible use of FA signatures as a tool in population studies.

The influence of foraging

Blubber FA signatures may reflect major and sometimes even minor differences in the diet (e.g. Iverson *et al.*, 1997; Møller *et al.*, 2003). Within the range covered by this study, there are major differences in food available to and consequently eaten by minke whales. Minke whales concentrate on traditional summer feeding grounds (Solvik, 1976; Harwood, 1990) where they feed in shallow shelf areas in association with highly productive frontal regimes (Mann and Lazier, 1991). In the Northern Hemisphere no single organism forms a predominant food supply in the minke whale diet. The complex oceanography and bathymetry of the North Atlantic (Mackintosh, 1965) can in part explain this heterogeneity. Minke whales differ markedly among the regions within the range of this study with respect to diet (Folkow *et al.*, 2000; Neve, 2000; Olsen and Holst, 2001; Haug *et al.*, 2002). Capelin (*Mallotus villosus*) is an important food for minke whales in West Greenland waters whereas polar cod (*Boreogadus saida*) seems to be of relatively greater importance in eastern Greenland (Neve, 2000). Generally, the minke whale food composition in Greenland waters resembles that reported for Icelandic nearshore waters where capelin and sand eel (*Ammodytes* sp.) made up ca 56% and krill (mainly *Thysanoessa* sp.) ca 35% of the food on weighted frequency basis (Sigurjónsson *et al.*, 2000).

Studies of minke whale diet in the Northeast Atlantic over the period 1992-1999 showed that the food comprised of relatively few species and that the dietary composition varied considerably both in space and time, presumably due to geographic differences in the distribution and abundance of potential prey (Haug *et al.*, 2002). In general, the whales find capelin and herring (*Clupea harengus*) and, occasionally, krill more preferably than other prey, which usually comprised of gadoid fish (cod, *Gadus morhua*; saithe, *Pollachius virens* and haddock, *Melanogrammus aeglefinus*). In the northeastern Atlantic, regional differences in stomach contents were found. Consumption of herring was almost exclusively confined to the Vestfjorden/Lofoten (EC) and the Barents Sea (EB) areas whereas consumption of krill was most pronounced in the Svalbard (ES) area (Folkow *et al.*, 2000). In the latter area, capelin was important prior to the collapse of the Barents Sea capelin stock in 1992-1993 (Haug *et al.*, 2002). In 1999, herring was a predominant food item in the Norwegian Sea whereas sand eel dominated (86.6% by weight) the minke whale food in the North Sea. In this latter area, mackerel (*Scomber scombrus*) made up 9.3% and other fish (e.g. herring) the remainder of food items (Olsen and Holst, 2001). These diets (stomach contents) are very different from those in Greenland waters where cod (*Gadus* sp.) has only been reported in a limited number of stomachs and herring in none (*cf.* Neve, 2000). The cod stock in Greenland during the 1990s has been very small (Anon., 2001) and herring, mackerel, saithe and haddock are almost absent (H.

Hovgård, Danish Fisheries Institute, DFU, pers. comm., 2001).

Although minke whales are euryphagous, and despite the fact that there are both inter-annual and inter-seasonal variation in their food, it is clear that their overall food selection is determined by prominent regional differences in the distribution and abundance of various prey types. Likely, these regional differences in prey availability are recorded as differences in signatures of FAs in the blubber of the minke whales. We believe that differences in the foraging ecology of minke whales among regions is recorded in the blubber layers. The deep layer likely provides a record of a more recent history in contrast to an older history recorded in the superficial blubber. However, there are no comparable data on regional differences in FAs in the fish species or in other prey of minke whales to allow for a thorough discussion on the trophic importance of the signatures found in the minke whales (e.g. Dietz *et al.*, 1998).

Comparison with other studies

Only one other study exists on regional differences in blubber FA signatures in North Atlantic baleen whales. Olsen (2002) used FAs to differentiate between minke whales sampled in the North Sea and the Norwegian Sea in 1999. The findings by Olsen (2002) supported the results of Møller *et al.* (2002) and this study, that minke whales from the North Sea constitute a group that is different from those summering further north in the NE Atlantic region.

The present study indicates the existence of population sub-structuring in North Atlantic minke whales on a large geographical scale. This is in accordance with other studies using the same material from 1998 but applying different analytical techniques. Genetic analyses, which included both mitochondrial and nuclear DNA suggested the existence of four genetically distinct subpopulations: (1) West Greenland; (2) East Greenland and Jan Mayen; (3) North East Atlantic (Svalbard, Barents Sea Vestfjorden/Lofoten); and (4) the North Sea (2002). Andersen *et al.* (2002) had access to a larger sample from East Greenland than the present study, which only included three samples from this region. This is the likely explanation for Andersen *et al.*'s (2002) finding that CG constitutes a separate unit.

A regional comparison of PCBs and organochlorine (OC) pesticides showed that minke whales from the Barents Sea (EB) had significantly higher concentrations of ΣPCBs than those from the Vestfjorden/Lofoten, the North Sea and Svalbard, as well as significantly higher ΣDDT concentrations compared to West Greenland animals (Hobbs *et al.*, 2002). The similarities and differences in concentrations suggested that minke whales from West Greenland and East Greenland represent one group of whales, distinct from both the Jan Mayen minke whales and those from other IWC defined stocks within the range covered by the present study. However, principal component analysis using proportions of OCs did not reveal any major differences among groups. With the exception of the Barents Sea and West Greenland, there was a general similarity in mean levels and proportions of OC contaminants among minke whales in the northeastern Atlantic suggesting that the minke whales are quite mobile and may feed in multiple areas.

Multivariate and principal component analyses of signatures of stable isotopes of Pb, C and N and 19 other elements in muscle, kidney, liver and baleen of the minke whales that were sampled in 1998 suggested the existence of sub-structuring of the minke whale population within the explored geographical range. In particular, minke whales in

West Greenland, the North Sea and the Vestfjorden/Lofoten areas appeared to be different from those in other areas (Born, *et al.*, 2003). Finally, Born *et al.* (2002) found the highest caesium-137 concentration in minke whales from the North Sea, and that the mean Cs-137 levels in minke whales from Svalbard and the North Sea differed significantly from mean levels in the other areas. This difference supports the indications from other studies that groups of minke whales are resident for some time at their feeding grounds in the North Atlantic and may occur in separate stocks during summer.

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