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Journal of Marine Systems 43 (2003) 1–17
JOURNAL OF MARINE SYSTEMS
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Population substructure of North Atlantic minke whales (*Balaenoptera acutorostrata*) inferred from regional variation of elemental and stable isotopic signatures in tissues

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Received 10 February 2003; accepted 21 May 2003

Abstract

Information on population structure is essential for estimating population demographics and managing the impacts of exploitation of North Atlantic minke whales (*Balaenoptera acutorostrata*). New approaches including assessment of geochemical signatures in tissues can assist in defining such structure.

This study determined regional variations in long-term elemental diagnostics of stock differences among 159 minke whales harvested in West Greenland, the Northeast Atlantic Ocean and the North Sea in 1998. The diagnostics tested included mercury (Hg), selenium (Se) and cadmium (Cd) in various tissues, and the trace and major element composition of baleen. Supporting data was also gathered on $\delta^{15}N$ and $\delta^{13}C$ and stable lead isotope ratios.

For female whales, significant differences in at least one long-term diagnostic element occurred between several areas. Existence of the following population substructure was inferred: (a) West Greenland, (b) a central group represented by whales from Jan Mayen, (c) a northeastern stock encompassing the Barents Sea, Svalbard and coastal Norway, and (d) the North Sea. These groups were consistent with those defined genetically by Andersen et al. [Mar. Ecol., Prog. Ser. 247 (2003) 263]. Males appeared to fall into similar groupings to females but because of smaller sample sizes fewer significant differences occurred between areas.

Stable-isotopic values in minke whales suggested lower trophic-level feeding in this species than hitherto suspected, with significant dietary differences between areas. Variations in feeding habits appeared to explain part of the geographical variation in tissue Cd, but not tissue Hg or Se.

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doi:10.1016/S0924-7963(03)00085-X

Differences among elements with a relatively long biological half-life in specific tissues suggested that groups of minke whales have fidelity to certain summer feeding areas at least for several years.
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Keywords: Minke whale; *Balaenoptera acutorostrata*; North Atlantic; Element signatures; Stable isotopes; Subpopulation

1. Introduction

Uncertainty exists about population substructure in North Atlantic minke whales (*Balaenoptera acutorostrata*). Studies involving analyses of, for example, genetics, morphometrics, and distributional and catch data indicated some substructuring but generally failed to find a clear distinction between minke whales from various regions of the North Atlantic (reviewed in van Waerebeek et al., 1999; Andersen et al., 2003). However, Andersen et al. (2003) identified four genetically discrete groups of minke whales: (1) West Greenland, (2) a central group (East Greenland and Jan Mayen), (3) a northeastern group (Svalbard, Barents Sea, Vestfjorden/Lofoten in NW Norway), and (4) the North Sea. Andersen et al. (2003) hypothesised that these groups had evolved as a response to the existence of profound ecological differences among the summer feeding areas of North Atlantic minke whales, and the long-term affinity of the whales to specific feeding grounds.

The present study employs a relatively new approach to investigation of minke whale population substructure by examining the geographical variation in composition of certain elements and isotopes in minke whale tissues across the North Atlantic Ocean from West Greenland to the North Sea. The main purpose of the study was to identify minke whale groups (i.e. subpopulations or management stocks) that on a long-term scale have been geographically separated at those North Atlantic summering grounds where Greenland and Norway catch minke whales for human consumption (Grønvik, 1998; Witting, 2000).

The concepts of animal "populations" and "stocks" are explicitly different in theory and in empirical definition. According to Anon. (2002a), a biological stock or biological population encompasses all the individuals in an area that are part of the same reproductive process. They form a self-contained unit, with emigration/immigration rates far lower than initial rate of population growth. In contrast, a management stock (or management unit) is a human construct in the context of management that may or may not be equivalent to a single biological stock. It refers to animals that happen to be present in a defined region and defined season where management is taking place or is contemplated (Anon., 2002a). In the following, we use the term "management stock" for the groups of whales identified irrespective of whether or not they may also represent subpopulations in a biological sense.

Apparently, North Atlantic minke whales feed little, if at all, when wintering between about 11° and about 45°N latitude. Pairing likely takes place from December to May, and calving predominantly from October to March, during a period when minke whales are mostly absent from North Atlantic waters. During spring the minke whales migrate north to their boreal, subarctic and arctic summer feeding grounds; some, likely few, individuals may stay farther south during summer. The females summer further north compared to males. Although the whales may occur in deeper waters in the North Atlantic during summer (e.g. Anon., 1997), they concentrate on traditional feeding grounds: eastern Canada (Gulf of St. Lawrence, Nova Scotia, Newfoundland-Labrador), off West and Southeast Greenland, around Iceland and Jan Mayen, off Svalbard and in the Barents Sea, off western Norway and in the North Sea (Mackintosh, 1965; Jonsgård, 1962, 1966; Øien, 1988; Larsen and Øien, 1988; Horwood, 1990; Mitchell, 1991; Folkow and Blix, 1991; Anon., 1997; van Waerebeek et al., 1999).

About a decade ago, the International Whaling Commission (IWC) defined a number of "management units" for management of large cetaceans—including minke whales—in the North Atlantic based largely on the distribution of the whales at these feeding grounds (Anon., 1993; Fig. 1).

Within the North Atlantic, no one organism forms the dominant food supply for minke whales (e.g. Skaug et al., 1997). The greater variety of food in the northern hemisphere as compared to that in the southern can be partly attributed to the more complex

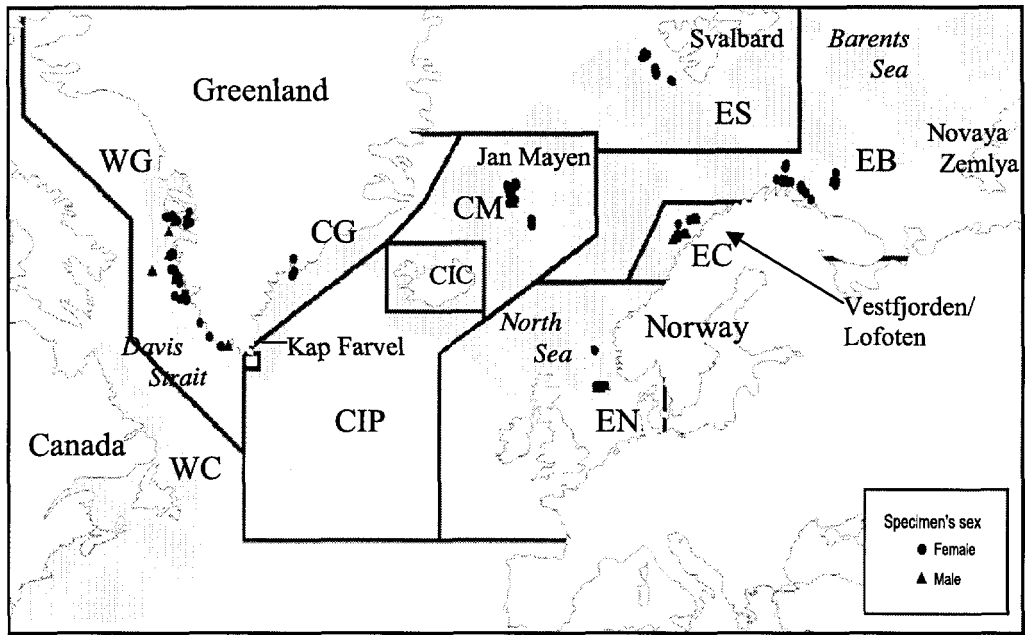

Fig. 1. Map showing the location of sampling of tissues from 159 minke whales at seven North Atlantic summer feeding grounds in 1998 (For number of samples per area see Table 1). Boundaries of the International Whaling Commission (IWC) management areas (Anon., 1993) are shown. Approximate minke whale summer range (Stewart and Leatherwood, 1985; Donovan, 1991a,b; Anon., 1997) is indicated in darker grey. IWC acronyms of different management areas are as follows: 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) and EN (East, North Sea).

topography and water conditions in the north (Mackintosh, 1965). Although the shallow continental shelf-areas where minke whales feed are areas of great productivity, they differ substantially with respect to oceanography (Mann and Lazier, 1991; Anon., 2003): (1) The West Greenland area is influenced by a mixture of waters from the cold East Greenland Current and the warmer and more saline Irminger Current. (2) The East Greenland–Jan Mayen area is dominated by the East Greenland Current that brings cold low-saline polar water south along the eastern coast of Greenland resulting in heavy pack ice almost all year round. (3) The western coast of Svalbard is an area of mixing between polar water and a branch of the warm North Atlantic Current, and (4) the Barents Sea is a relatively shallow area that is dominated by the North Atlantic Current. These latter two areas are ice-covered for part of the year. (5) The northwestern coast of Norway is greatly influenced by the North Atlantic Current and the Norwegian Coastal Current resulting in relatively high water temperatures. (6) The North Sea is confined between the British Isles, southern Norway and Denmark, and is influenced by water from the North Atlantic Current as well as land runoff from the surrounding countries. Ice is never present along western Norway and in the North Sea.

These regions also differ with respect to fish and crustacean fauna as reflected in differences among areas in minke whale prey preferences. Capelin (*Mallotus villosus*) and sand eel (*Ammodytes* sp.) are important food for minke whales in West Greenland waters whereas polar cod (*Boreogadus saida*) seems to be of greater importance in the East Greenland region (reviewed by Neve, 2000). Krill (*Thysanoessa* sp.) and herring (*Clupea harengus*) are two of the most prominent prey items in the diet of minke whales in the Northeast Atlantic where gadoid fish (cod, *Gadus morhua*, saithe, *Pollachius virens*, and haddock, *Melanogrammus aeglefinus*) are also important prey (reviewed by Haug et al., 2002). Within the NE Atlantic

area, there are regional differences in prey preferences. Consumption of herring is almost exclusively confined to the Barents Sea and the northwestern coast of Norway whereas consumption of krill is more pronounced in the Svalbard area (Folkow et al., 2000; Haug et al., 2002). Herring is a predominant food item in the Norwegian Sea whereas sand eel dominate the minke whale food in the North Sea. In this latter area, mackerel (*Scomber scombrus*) and other fish (e.g. herring) constitute the remainder of food items (Olsen and Holst, 2001). During the last decade or so, Atlanto-boreal species like Atlantic cod, saithe, haddock, herring, mackerel and whiting have either not been present in Greenland waters or have occurred there in such low numbers that they have been insignificant as minke whale food (e.g. Anon., 2001).

There exist a number of complementary approaches to the delineation of whale stocks including studies of ratios of stable isotopes of C and N ($\delta^{13}C$ and $\delta^{15}N$), and various biochemical indicators of provenance (cf. Hobson, 1999; Anon., 2002a; Wang, 2002). The biogeochemical approach used in the present study of population structure was originally pioneered with African elephants (*Loxodonta africana*; Vogel et al., 1990; van der Merwe et al., 1990; Koch et al., 1995). It has subsequently been widely utilised in studies of marine and freshwater fish stocks (reviewed by Campana, 1999; Campana and Thorrold, 2001), but less commonly with marine mammals (Uspensky et al., 1985; Outridge and Stewart, 1999; Tolley and Heldal, 2002; Born et al., 2002; Outridge et al., 2003). The approach is based on the rationale that animals accumulate in their tissues bioavailable compounds via water and food from their environment. Groups of animals exploiting geochemically different habitats may reflect those differences in characteristic element or isotopic compositions ("signatures") of tissues. If such differences are found in element/tissue combinations which are not subject to rapid turnover, they may indicate the existence of "ecological separation", or management stocks/subpopulations.

Two types of long-term diagnostics are used in the present study: (1) concentrations of Hg, Cd and Se in kidney, liver and muscle, which have relatively long biological half-lives (reviewed by Dietz et al., 1998); and (2) concentrations of 19 major and trace elements in baleen plates which are believed to represent at least several years of life (Ruud, 1940, 1945).

Supplementary information was also included: (1) Ratios of stable isotopes of C and N in muscle were determined; they likely represent integrations based on a 1–2 month period (Hobson and Clark, 1992) and reflect dietary differences between areas that could explain the elemental composition data. Stable nitrogen isotopes in the whales and their prey were used to infer relative trophic level—TL (e.g. Hobson et al., 2002)—values for whales in each sampling area; (2) lead isotope ratios ($^{206}Pb/^{207}Pb$ and $^{208}Pb/^{207}Pb$) were determined in kidneys. While renal Pb has a short half-life (possibly 3–4 weeks, Scheuhammer, 1991) compared to soft tissue Hg, Cd and Se, the isotopic ratios of Pb have the advantage of being solely under geological control and unaffected by dietary, chemical or physical processes (Flegal and Smith, 1995; Dickin, 1995). They thus provide a short-term yet unequivocal indicator of stock differences between areas that can be compared to the long-term diagnostics mentioned above.

These methods were used to determine regional differences in a total of 159 individual minke whales that were sampled in the North Atlantic in 1998 (Fig. 1). Our hypothesis was: If groups of minke whales have long-term (i.e. inter-annual) affinity to specific feeding areas with different biotic and chemical environments, significant differences in long-term signatures have evolved among groups of whales, indicating the existence of different stocks.

2. Materials and methods

2.1. Field sampling

Tissue samples were available from a total of 159 minke whales that were taken during Greenland and Norwegian whaling operations from 6 May to 31 October 1998 in seven International Whaling Commission management units: West Greenland (WG), East Greenland (CG), Jan Mayen (CM), Svalbard (ES), the Barents Sea (EB), Vestfjorden/Lofoten (EC) on the NW coast of Norway, and the North Sea (EN) (Fig. 1; Table 1). The character of the whaling operations determined the sampling areas visited and the aggregate locations within areas exploited by Norwegian whalers (i.e. CM, ES, EB, EC and EN). However, overall the seasonal and spatial distribution of samples

Table 1
List of samples from 159 minke whales taken in 1998 in seven International Whaling Commission (IWC) management areas in the North Atlantic

Sampling area (acronym)	Sample type		Sex		Age category (*N* for muscle, liver and kidney samples)			Sampling period
	Baleen	Muscle, liver and kidney	M	F				
	N	*N*[a]			Mature	Immature	Unidentified	
West Greenland (WG)	34	45	10	35	17	25	3	6 May–31 Oct.
East Greenland (CG)	2	4	0	4	2	1	1	12 Jul.–16 Oct.
Jan Mayen (CM)	24	24	5	19	18	6	0	7 Jun.–1 Jul.
Svalbard (ES)	2	16	1	15	14	2	0	15 May–31 May
Barents Sea (EB)	31	33	3	30	23	10	0	23 May–25 Jun.
Vestfjorden/Lofoten (EC)	0	14	7	7	8	6	0	28 May–14 Aug.
North Sea (EN)	22	23	9	14	20	3	0	15 May–8 Jun.
Total	115	159	35	124	102	53	4	

Information on sex composition, maturity status and sampling period is given.
[a] For these tissues, the total number available for various analyses differed somewhat because in a few cases not all tissues (or length data) were available for each whale.

in the present study is representative of the Greenland (Witting, 2000) and Norwegian catches in 1998 (Øien, unpublished data). Greenland samples were collected by licensed whalers. Similar samples were collected by trained staff during licensed Norwegian pelagic and coastal whaling operations. For each whale, the following information was available: date and kill location as well as whale sex, body length, presence or absence of a foetus and its length. Samples included in the present study were baleen plates, muscle, liver and kidney. In a few cases, not all tissues were sampled from each whale which led to < 159 samples in each data set. About 2 l of stomach contents (compartment of the stomach not specified) were collected from the minke whales caught in West Greenland in 1998.

2.2. Sample handling and analytical methods

All tissue samples were stored at −20 °C until processed in laboratories at the Department of Arctic Environment (DAE), Roskilde, Denmark, the Geological Survey of Canada (GSC), Ottawa, and the Prairie and Northern Wildlife Research Center (PNWRC), Saskatoon, Canada.

2.2.1. Elements and Pb isotopes

Mercury (Hg), cadmium (Cd) and selenium (Se) in kidney, liver and muscle were analysed at DAE using the methods described in Dietz et al. (1996) and Asmund and Cleemann (2000). Lead isotopes (^{206}Pb, ^{207}Pb, ^{208}Pb) in kidney, and all elements in baleen except Hg were analysed by GSC. Lead concentrations in most of the other tissue samples were too low for reliable isotopic measurement. Preparation of samples and analysis of Pb isotopes and trace elements by inductively coupled plasma mass spectrometry—ICP MS (Elan 6100, Perkin Elmer SCIEX, Canada)—followed Outridge and Stewart (1999) except that ion chromatography was not used prior to instrumental analysis. For the baleen, a strip several millimeters wide was cut longitudinally along the entire length of one baleen plate from each animal and decomposed with acid digestion. This sampling procedure ensured that all growth increments in the plate were included. Baleen Hg was determined at laboratories of Fisheries and Oceans Canada, Winnipeg, using cold-vapour atomic absorption spectrometry. For other trace elements in baleen, digest solutions were analysed by ICP-MS using the isotopes indicated: scandium (^{45}Sc), vanadium (^{51}V), chromium ($^{52, 53}$Cr), manganese (^{55}Mn), cobalt (^{59}Co), nickel ($^{60, 62}$Ni), copper (^{65}Cu), zinc ($^{66, 68}$Zn), rubidium (^{85}Rb), strontium (^{88}Sr), molybdenum (^{95}Mo), silver (^{107}Ag), cadmium (^{111}Cd), antimony (^{121}Sb), caesium (^{133}Cs), barium (^{138}Ba), lanthanum (^{139}La), cerium (^{139}Ce), neodymium (^{142}Nd), europium (^{151}Eu), thallium (^{205}Tl), lead (^{206,207,208}Pb), thorium (^{232}Th), and uranium (^{238}U). The following major elements in baleen were analysed by ICP-optical emission spectrometry (ICP-OES; Optima 3000, Perkin Elmer

SCIEX): calcium (Ca), iron (Fe), potassium (K), magnesium (Mg) and sodium (Na). For all elemental analyses, standard reference materials (DORM-2 Dogfish Muscle, DOLT-2 Dogfish Liver and TORT-2 Lobster Hepatopancreas; National Research Council of Canada, Ottawa) included with the samples generally agreed to within 10% of certified values, with analytical precision typically <15% relative S.D. Cadmium in liver digests was analysed by both the DAE and GSC laboratories and the results showed good agreement (linear regression of data in μg g^{-1} dry weight/DW, $y=0.90x+0.37$; $r^2=0.94$, $df=142$, $P<0.001$). On average, dry matter constituted 16.8% in muscle, 28.0% in liver and 21.8% in kidney.

2.2.2. C and N isotopes

Stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) in muscle samples were determined by continuous-flow isotope-ratio mass spectrometry (CF-IRMS) according to Hobson et al. (2002). Prior to analysis, samples were dried, ground to a fine powder and lipids extracted using successive rinses in a 2:1 chloroform/methanol solution. Results are presented in the usual δ notation relative to PDB belemnite and atmospheric nitrogen (AIR) for $\delta^{13}C$ and $\delta^{15}N$, respectively. Analytical error is estimated to be ± 0.1 ‰ for $\delta^{13}C$ values and ± 0.3 ‰ for $\delta^{15}N$.

$\delta^{13}C$ and $\delta^{15}N$ were also determined in the stomach contents (grouped as krill, i.e. mainly euphausids, capelin, remains of unidentified fish and nematodes) of 31 West Greenland minke whales. Using a trophic-level (TL) model based on the food web of the North Water Polynya off northwestern Greenland (Hobson et al., 2002), minke muscle $\delta^{15}N$ values were used to quantify trophic differences among areas. This model is based on the assumption that the copepod *Calanus hyperboreus* occupies TL 2.0 and that there is a trophic enrichment factor of 3.8 ‰ between levels. The mod-

Table 2
Arithmetic mean (± S.D.) concentrations (μg g^{-1} DW) of Hg, Se and Cd in various tissues of minke whales sampled in seven areas of the North Atlantic in 1998

Element / Area (acronym)	Muscle			Kidney			Liver			Baleen		
	N	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.	*N*	Mean	S.D.
Hg												
West Greenland (WG)	38	0.288	0.185	39	0.856	0.84	36	1.00	1.12	32	0.068	0.060
East Greenland (CG)	4	0.403	0.135	2	2.70	1.67	2	1.92	0.39	2	0.281	0.151
Jan Mayen (CM)	20	0.791	0.326	23	2.38	1.63	24	2.04	0.73	22	0.255	0.166
Svalbard (ES)	14	0.315	0.166	16	0.69	0.34	16	0.73	0.35	1	0.230	–
Barents Sea (EB)	33	0.505	0.204	32	1.17	0.59	31	1.12	0.65	31	0.159	0.093
Vestfj./Lofoten (EC)	10	0.593	0.604	11	1.18	1.06	14	1.74	2.19	–	–	–
North Sea (EN)	23	0.902	0.400	21	2.45	1.48	22	2.04	1.26	21	0.163	0.07
Se												
West Greenland (WG)	38	0.653	0.187	39	5.59	1.55	36	4.88	2.23	–	–	–
East Greenland (CG)	4	0.685	0.352	2	6.06	1.21	2	3.77	0.20	–	–	–
Jan Mayen (CM)	20	0.976	0.305	23	7.06	2.34	24	4.68	0.86	–	–	–
Svalbard (ES)	14	0.847	0.282	16	6.81	1.11	16	5.53	1.02	–	–	–
Barents Sea (EB)	33	0.946	0.352	32	7.22	1.57	31	6.30	1.51	–	–	–
Vestfj./Lofoten (EC)	10	0.815	0.270	11	6.87	1.04	14	5.31	2.15	–	–	–
North Sea (EN)	23	1.01	0.26	21	9.23	2.29	22	7.07	2.14	–	–	–
Cd												
West Greenland (WG)	42	0.205	0.374	41	16.9	11.3	36	3.89	3.12	34	<0.018	–
East Greenland (CG)	4	0.191	0.187	2	35.5	26.2	2	5.26	2.90	2	0.030	0.029
Jan Mayen (CM)	21	0.101	0.073	23	20.4	10.6	24	3.96	1.64	23	<0.018	–
Svalbard (ES)	14	0.161	0.102	16	15.4	8.7	16	3.76	1.49	2	<0.018	–
Barents Sea (EB)	33	0.127	0.076	32	18.2	7.6	31	3.50	1.45	31	<0.018	–
Vestfj./Lofoten (EC)	10	0.062	0.058	11	10.5	5.8	14	2.39	1.86	–	–	–
North Sea (EN)	23	0.070	0.041	21	13.6	8.3	22	1.85	0.74	22	<0.018	–

el reasonably placed the amphipod *Themisto libellula* at TL 2.5, polar cod (*B. saida*) at TL 3.6, ringed seal (*Phoca hispida*) at TL 4.5, and polar bear (*Ursus maritimus*) at TL 5.5.

The sex of individual whales was determined genetically (Andersen et al., 2003).

2.3. Statistical analysis

Statistical analyses were performed using SAS software (SAS, 1999–2001). To avoid the effect of "below-detection limit" values during the statistical analyses of trace elements, these values were replaced with "dummy values" that were half of the detection limit. Data were $\log_e$-transformed in order to meet the assumptions of parametric statistical tests.

The two types of stock diagnostic employed—i.e. renal, hepatic and muscle Hg, Cd and Se as well as baleen Hg, and multiple elements in baleen—were statistically analysed with different techniques. Hg, Se and Cd differences between sampling areas were analysed with analysis of covariance (ANCOVA) which included the factor "sampling area", the co-variable "body length", and their first-order interaction.

Female minke whales grow to a longer asymptotic body length than males (e.g. Christensen, 1981) and hence it may be difficult to detect the influence of length and sex separately. It was therefore decided to carry out separate analyses for each sex.

Because there were few males in the areas Jan Mayen (CM), Svalbard (ES) and Barents Sea (EB), these data were pooled to form a group named "East". A possible biological justification for this pooling was that whales in these areas have a more northern distribution than in other areas. Differences in mean element concentrations between areas were tested pairwise using the least square means (LSMEAN; i.e. a length-adjusted mean value, applying a common relationship between $\log_e$-metal concentration and whale body length for all areas). This procedure was chosen because of the sex-specific difference in body growth pattern and concentrations of heavy metals tend to accumulate with age (e.g. AMAP, 1998).

The second stock diagnostic data set consisted of all 19 detectable elements (except Hg) in baleen. Principal Components Analysis (PCA) was used to examine similarities and differences in elements from the different areas (cf. Table 6 for elements included in the PCA). Element concentrations in each whale were normalised to have the sum of 1 prior to the analysis, and the PCA was performed on the correlation matrix. The principal components were VARIMAX rotated in order to facilitate the interpretation. One-way analysis of variance (ANOVA) was performed to test for differences in mean principal scores among sampling areas. Differences in mean metal concentrations between areas were tested by Tukey's post hoc test.

Table 3
Significant factors influencing concentrations of Hg, Se and Cd in tissues of minke whales sampled in seven areas of the North Atlantic in 1998 (analysis by ANCOVA of data in Table 2)

Metal—gender, tissue	Factor area	Co-variable body length	Interaction
Hg—males			
Muscle	*	*	
Liver	*	*	
Kidney	*	*	
Baleen	*		
Hg—females			
Muscle	*	*	*
Liver	*	*	*
Kidney	*	*	
Baleen	*	*	
Se—males			
Muscle	*	*	*
Liver		*	
Kidney	*		
Se—females			
Muscle	*		
Liver	*	*	
Kidney	*		*
Cd—males			
Muscle			
Liver		*	
Kidney	*	*	
Baleen[a]	–	–	–
Cd—females			
Muscle			
Liver	*	*	
Kidney	*		*
Baleen[a]	–	–	–

*: Indicates significance at the 5% level. Se concentrations were not determined in baleen.

[a] Too few concentrations of Cd in baleen were above detection limit.

Table 4
Results of pair-wise LSMEAN comparisons between seven North Atlantic areas for Hg, Se and Cd in soft tissues of female minke whales

Area, acronym	E Greenland CG	Jan Mayen CM	Svalbard ES	Barents Sea EB	Vestfj./Lofoten EC	North Sea EN
W Greenland, WG		Muscle: **Hg**, Se		Muscle: Se		Muscle: Hg, Se
					Liver: Cd	Liver: **Cd**
		Kidney: Hg		Kidney: Se		Kidney: Se
		Baleen: **Hg**	Baleen: **Hg**	Baleen: **Hg**		
E Greenland, CG		Muscle: Se		Muscle: Se		Muscle: Se
		Liver: **Hg**		Liver: Se		Liver: Hg, Se
			Kidney: **Hg**	Kidney: Se		Kidney: **Se**
Jan Mayen, CM			Muscle: **Hg**			
			Liver: **Hg**	Liver: Se	Liver: Cd	Liver: Se, **Cd**
			Kidney: **Hg**			
Svalbard, ES						Muscle: Hg
						Liver: Hg, Cd
						Kidney: **Hg**
Barents Sea, EB						Liver: Cd
Vestfj./Lofoten, EC						

Elements listed were significantly different between areas at $P<0.05$; those elements underlined and in bold typeface are different at $P<0.01$. Nonsignificant differences are not shown.

$\delta^{15}N$ and $\delta^{13}C$ values in muscle and $^{206}Pb/^{207}Pb$ and $^{208}Pb/^{207}Pb$ in kidney were normally distributed or differed only slightly from normality (in the case of $\delta^{13}C$). Differences among areas were tested using ANOVA followed by Tukey's post hoc test. Pearson's product-moment correlation was applied between $\delta^{15}N$ and $\delta^{13}C$ values and $\log_e$-transformed Hg, Se and Cd concentrations in tissues. Possible gender-related differences in $\delta^{15}N$, $\delta^{13}C$ and Pb isotope ratios were tested with *t*-tests but there were no significant gender differences in $\delta^{15}N$ and $\delta^{13}C$ ($P>0.05$) and therefore the data were pooled. There were also no gender differences in $^{206}Pb/^{207}Pb$ and $^{208}Pb/^{207}Pb$ except for the Barents Sea (females greater than males in both isotopic ratios; $P<0.02$) and Jan Mayen area (males greater than females; $P<0.03$). However, as these differences were in opposite directions, we concluded that they likely occurred by chance. Hence, in the following analyses of stable isotopes, the two sexes were treated together.

3. Results

3.1. Concentrations of Hg, Se and Cd and population substructure

Mean concentrations of Hg, Se and Cd are reported by tissue and area in Table 2. Se concentrations were positively correlated with Hg concentrations in all tissues ($r_{muscle}=0.44$, $P<0.001$, $N=142$; $r_{liver}=0.48$, $P<0.001$, $N=144$; $r_{kidney}=0.61$, $P<0.001$, $N=145$), which supports its inclusion as a possible long-term stock diagnostic.

ANCOVA showed that for Hg in all tissues of males and females, both sampling area and body length were significant factors with significant "area × length" interactions for females in muscle and liver (Table 3). Selenium in female kidney also exhibited a significant "area and length effect". Area and/or length were significant factors in Se in various tissues of males.

Table 5
Results of pair-wise LSMEAN comparisons between seven North Atlantic areas for Hg, Se and Cd in soft tissues of male minke whales

Area acronym	"East"	Vestfj./ Lofoten EC	North Sea EN
W Greenland WG	Muscle: Hg, **Se**	Muscle: Se	Muscle: Hg, **Se**
	Liver: Hg		Liver: Hg
	Kidney: Hg, **Se**	Kidney: Se	Kidney: Hg, **Se**
	Baleen: **Hg**		Baleen: Hg
"East"			Kidney: Cd
Vestfj./Lofoten EC			Kidney: Se

Elements listed were significantly different between areas at $P<0.05$; those elements underlined and in bold typeface are different at $P<0.01$. Nonsignificant differences are not shown. "EAST"= Whales from Jan Mayen, Svalbard and the Barents Sea pooled.

Table 6
Correlation coefficients (r) between 19 elements and principal components I–IV (Principal Component Analyses) in baleen of female ($N=90$) and male ($N=24$) minke whales from six areas of the North Atlantic (samples of baleen were not available from Vestfjorden/Lofoten; Table 1)

Principal component	I	II	III	IV
Females				
Element				
Ba	0.62	0.04	−0.06	0.32
Ca	−0.09	0.06	−0.08	**0.70**
Ce	0.54	0.23	0.02	−0.10
Co	0.24	**0.84**	−0.12	0.10
Cr	−0.24	**0.77**	0.30	0.19
Cu	0.17	0.04	−0.16	−0.09
K	0.04	−0.29	**0.72**	0.04
Mg	0.35	0.15	−0.02	**0.69**
Mn	0.27	**0.83**	0.03	−0.06
Mo	0.64	0.35	0.18	−0.06
Na	0.22	0.04	0.23	**0.78**
Ni	0.15	0.11	0.63	0.15
Pb	−0.39	0.14	0.22	0.31
Rb	0.03	0.08	**0.85**	−0.06
Sc	0.07	0.32	**0.65**	0.05
Sr	**0.71**	−0.03	0.26	0.41
U	**0.72**	0.13	0.26	0.16
V	0.42	0.64	0.33	0.35
Zn	−0.27	0.03	0.17	0.27
Total variance (%)	15.5	15.0	13.7	11.9
Males				
Element				
Ba	**0.77**	−0.05	−0.12	0.39
Ca	0.33	0.14	**0.72**	−0.25
Ce	0.56	0.17	−0.42	0.39
Co	0.33	0.25	0.07	−0.08
Cr	0.07	**0.82**	−0.07	0.09
Cu	0.14	−0.32	**0.78**	−0.02
K	0.20	0.001	0.04	**0.74**
Mg	**0.90**	0.20	0.20	0.07
Mn	0.58	0.03	0.24	0.17
Mo	0.41	0.16	−0.25	−0.005
Na	0.54	0.24	0.38	−0.34
Ni	0.09	**0.88**	0.09	0.14
Pb	0.07	**0.90**	0.22	0.05
Rb	0.12	0.14	−0.07	**0.88**
Sc	−0.10	0.55	−0.12	**0.65**
Sr	**0.88**	−0.01	0.24	0.04
U	−0.03	−0.05	−0.05	0.07
V	0.25	**0.66**	−0.38	−0.04
Zn	−0.01	0.29	**0.82**	0.07
Total variance (%)	19.2	18.2	13.7	12.2

Correlation coefficients greater than 0.65 are shown in bold. Only values for the first principal components are given.

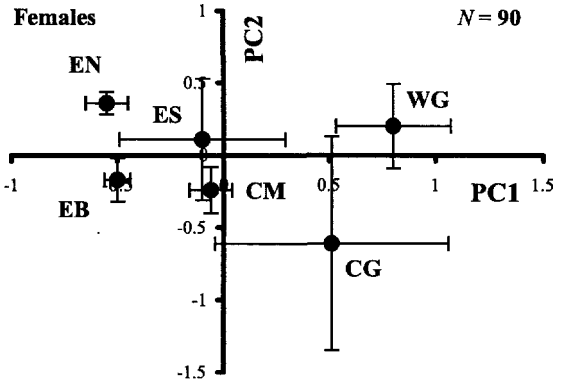

Fig. 2. Mean (± S.D.) plot for the first two principal components (PC1, PC2) based on 19 different elements in baleen (see Table 6) of female minke whales sampled in the North Atlantic in 1998. For explanation of area acronyms, cf. Fig. 1 and Table 1.

Cadmium generally displayed fewer significant relationships with area and length although males exhibited significant area and length effects on renal Cd while females showed similar effects on hepatic Cd.

Irrespective of gender, West Greenland whales generally had low Hg and Se concentrations and high Cd concentrations in all tissues compared with whales in other areas, while high Hg and Se and low Cd concentrations were generally found in whales from the North Sea and/or the northwestern coast of Norway (Vestfjorden/Lofoten).

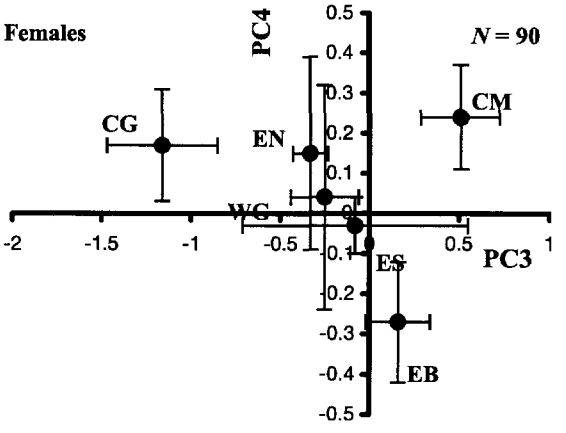

Fig. 3. Mean (± S.D.) plot for principal components 3 and 4 (PC3, PC4) based on 19 different elements (see Table 6) in baleen of female minke whales sampled in the North Atlantic in 1998. For explanation of area acronyms, cf. Fig. 1 and Table 1.

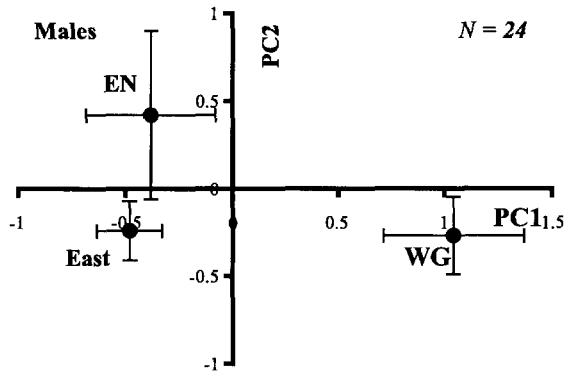

Fig. 4. Mean (± S.D.) plot for the first two principal components (PC1, PC2) based on 19 different elements (see Table 6) in baleen of male minke whales sampled in the North Atlantic in 1998. For explanation of area acronyms, cf. Fig. 1 and Table 1.

When area-related elemental data were adjusted for differences in body length and tested pair-wise (LSMEAN analysis), a number of significant differences between sampling areas became apparent. In females, significant differences in at least one long-term diagnostic element occurred between most adjacent areas (Table 4). The exceptions were females from Svalbard (ES), the Barents Sea (EB) and Vestfjorden/Lofoten (EC) which were indistinguishable from each other, while West and East Greenland females (i.e. WG and CG; only four females from east Greenland available for analyses), and Vestfjorden/Lofoten (EC) and North Sea (EN) females were also similar. However, North Sea females were different in terms of hepatic Cd from Svalbard and Barents Sea whales (Table 4). Hg was the most important diagnostic for many pair-wise comparisons, while Se was vital for some comparisons with Barents Sea females and Cd was important for North Sea and Vestfjorden/Lofoten. Differences among areas in males were less pronounced possibly because of smaller sample sizes (Table 5). West Greenland males were clearly different from North Sea, Vestfjorden/Lofoten and the combined "East" group (Jan Mayen–Svalbard–Barents Sea) in terms of several diagnostic elements while North Sea and Vestfjorden/Lofoten males were different in terms of kidney Se.

3.2. Population substructure inferred from element concentrations in baleen

PCA of 19 different elements in baleen yielded six principal components (PC) with eigen values above 1, explaining 69.6% and 75.2% of the total variance in females and males, respectively (Table 6). Among females, PC1 showed a significant difference among areas in mean component scores ($P<0.01$) with a latitudinal gradient of mean scores generally increasing from east to west (Fig. 2). Female whales from West Greenland (WG) had significantly higher ($P<0.01$) mean PC1 scores than whales from all other areas except East Greenland (CG; 4 whales). Some separation was also indicated by PC3 (Fig. 3) where

Table 7
Mean (± S.D.) values of stable isotopes (δ^{15}N and δ^{13}C) in muscle tissue of North Atlantic minke whales and the corresponding trophic level estimate (TL)

Area (acronym)	N	δ^{13}C (‰)	δ^{15}N (‰)	Trophic Level TL	Correlation coefficients		
					Metal (tissue)	δ^{13}C	δ^{15}N
West Greenland (WG)	43	−18.2 ± 0.4	12.2 ± 1.0	3.1	Hg (M)	−0.06	0.12
East Greenland (CG)	4	−19.7 ± 1.6	11.4 ± 0.5	2.9	Hg (K)	−0.15	0.11
Jan Mayen (CM)	23	−19.5 ± 0.5	11.5 ± 0.8	3.0	Hg (L)	−0.10	0.08
Svalbard (ES)	16	−19.7 ± 0.2	11.9 ± 0.9	3.1	Se (M)	−0.02	0.04
Barents Sea (EB)	33	−19.3 ± 0.5	12.6 ± 0.6	3.2	Se (K)	−0.16	0.11
Vestfjorden/Lofoten (EC)	14	−19.0 ± 0.5	13.0 ± 1.0	3.3	Se (L)	0.04	0.16
North Sea (EN)	22	−18.5 ± 0.5	13.2 ± 0.7	3.4	Cd (M)	0.04	−0.11
					Cd (K)	−0.09	−0.20*
					Cd (L)	−0.07	−0.37*

TL is based on a model presented in Hobson et al. (2002). Correlation coefficients (r) between stable isotope values and Cd, Hg and Se concentrations are listed.
M = muscle, K = kidney, L = liver.
* Indicates that r was significant at $P<0.05$.

Table 8
Statistical comparison of mean stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) in North Atlantic minke whales caught in 1998 in seven different areas of the North Atlantic

$\delta^{13}C$							$\delta^{15}N$						
WG	EN	EC	EB	CM	ES	CG	EN	EC	EB	WG	ES	CM	CG

Data arranged in order of decreasing concentrations. Continuous underlining indicates areas in which concentrations were not statistically different ($P>0.05$). For explanation of acronyms, see Table 7 or Fig. 1.

whales from East Greenland (CG) differed significantly from Jan Mayen (CM) whales ($P=0.04$).

PC1 scores in males also indicated a grouping among areas (Fig. 4). Males from West Greenland differed significantly from males from the North Sea and the "East" group ($P<0.01$). PC3 and PC4 did not separate among males ($P>0.05$; figure not shown).

3.3. Variation in stable C and N isotopes

Minke whales from a number of areas were significantly different from each other in terms of mean $\delta^{15}N$ and $\delta^{13}C$ values in muscle (Tables 7 and 8), with the highest $\delta^{13}C$ occurring in West Greenland (WG) and North Sea (EN) whales and the highest $\delta^{15}N$ found in whales from the North Sea (EN), Vestfjorden/Lofoten and the Barents Sea (EB). $\delta^{15}N$ values were significantly negatively correlated with Cd concentrations in kidney and liver (Table 7).

$\delta^{15}N$ and $\delta^{13}C$ values in prey items found in stomachs of West Greenland minke whales (Table 9) were similar to food-web values reported for High Arctic ecosystems such as Lancaster Sound in the NE Canadian Arctic (Hobson and Welch, 1992) and the Northeast and North Water polynyas off NE and NW Greenland, respectively (Hobson et al., 1995, 2002). Therefore, the trophic-level model developed by Hobson et al. (2002) was used to determine relative trophic levels among minke whale in the different areas (Table 7). This information will be used below to suggest reasons for elemental differences between areas.

Table 9
Mean concentrations ($\pm$ S.D.) of stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) in stomach contents of West Greenland minke whales (1998) and the whales' inferred trophic level (TL) as determined by the model in Hobson et al. (2002)

Prey item	N	$\delta^{15}N$ (‰)	Trophic level	$\delta^{13}C$(‰)
Krill	6	8.3 ± 0.8	2.1	-20.0 ± 0.9
Capelin	9	12.5 ± 0.9	3.2	-19.7 ± 1.0
Fish remains	12	12.3 ± 1.5	3.2	-19.9 ± 1.1
Nematodes	4	11.9 ± 2.4	3.1	-16.7 ± 0.6

Samples size refers to number of stomachs examined.

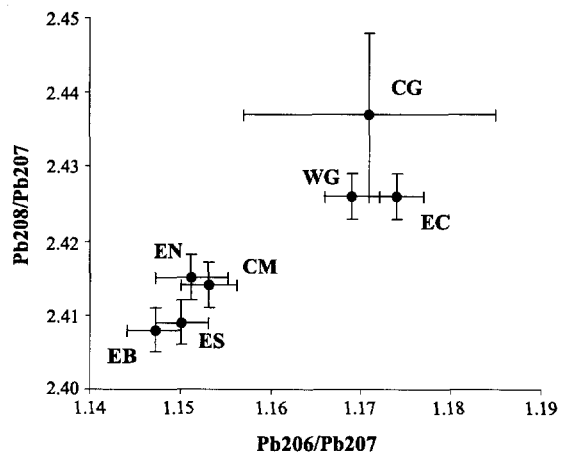

Fig. 5. Mean ($\pm$ S.D.) $^{208}Pb/^{207}$ and $^{206}Pb/^{207}$ isotope ratios in kidney of minke whales sampled in the North Atlantic in 1998. For explanation of area acronyms, cf. Fig. 1 and Table 1.

3.4. Variations in Pb isotopes

Although the ranges of mean $^{206}Pb/^{207}Pb$ and $^{208}Pb/^{207}Pb$ ratios among areas were narrow (1.147–1.174 and 2.408–2.437, respectively) (Fig. 5), significant differences in renal $^{208}Pb/^{207}Pb$ and $^{206}Pb/^{207}Pb$ were found. West Greenland (WG), East Greenland (CG), and Vestfjorden/Lofoten (EC) whales had significantly higher $^{206}Pb/^{207}Pb$ and $^{208}Pb/^{207}Pb$ values than those captured elsewhere ($P<0.05$).

4. Discussion

4.1. Concentrations of Hg, Se and Cd

Generally, the concentrations of Hg, Se and Cd found in the present study were similar to those reported in Johansen et al. (1980) who analysed Hg concentrations in muscle and liver of 15 minke whales

in West Greenland during 1972–1978, and in Hansen et al. (1990) who analysed 24 minke whales from the same area. To our knowledge, information has not been published about concentrations of the metals in minke whales from the Norwegian whaling areas.

4.2. Stability of long-term diagnostics (Hg, Cd, Se and baleen)

Ideally, discrimination among major groups of whales using tissue element signatures should use element/tissue combinations which are not subject to rapid turnover and replacement, and which are therefore long-term indicators of element accumulation. We believe that the elements and tissues chosen in the present study satisfied this requirement. The biological half-life of Hg in soft tissues of animals including marine mammals is probably several years (André et al., 1990; Dietz et al., 1998). Cadmium has a residence time in mammalian kidney and liver on the order of several years (Friberg et al., 1974; Nordberg et al., 1985; Scheuhammer, 1991).

Baleen is an archive of elements, since it is metabolically inactive following growth. Although not known with certainty (C. Lockyer, Age-Dynamics, Lyngby, Denmark, and E. Olsen, Institute of Marine Research, Bergen, Norway, personal communication, 2002) a baleen likely represent at least several years of life (Ruud, 1940, 1945).

The long-term stability of these element/tissue combinations suggests that the elemental differences found among groups of whales from different areas must be the product of at least several years of separation of the same groups of individuals on different summer feeding grounds. Whales which individually exploited different summer feeding grounds, either annually or within a year, and were then harvested together as a group in a particular area are unlikely to exhibit significant mean differences of tissue elements between areas. If this premise is correct, then the geochemical data suggest that groups of minke whales may have evolved with a "learned" fidelity over several years to their respective summering grounds. Andersen et al. (2003), who analysed the same suite of samples as used in the present study, suggested that such a mechanism may explain the existence of genetically distinct groups of minke whales in the North Atlantic. This is similar to the findings of Baker et al. (1994) who detected a population structure in the maternally inherited mitochondrial DNA in humpback whales (*Megaptera novaeanglia*), a species which shows strong fidelity to migration destinations such as feeding grounds possibly as a result of a transmission of feeding and migration strategies from mother to calf.

4.3. The influence of feeding habits and the variation in short-term diagnostics (stable isotopes)

Two possible explanations for the elemental differences in whales among areas are (1) that they reflect a geochemically heterogenous environment, or (2) that whales in different areas had varying food availability or preferences.

We suggest that profound geographical differences in types of prey available to minke whales explain the differences seen in element concentrations among areas. Although the minke whales are quite flexible in their choice of food, adapting well to local prey abundance situations, there are indications that they, given the choice, may prefer fish (capelin, herring) to krill (Skaug et al., 1997). The areas included in the present study differ substantially in types of fish present (see Introduction). Hence, minke whale prey preferences in the NE Atlantic and the North Sea are very different from those in West Greenland waters. These differences, as well as the significant negative correlations between tissue Cd concentrations and $\delta^{15}N$ values across the study area, suggest that prey selection differences of whales among sampling areas explains some of the differences in tissue elements. The absence of similar correlations between tissue Hg and $\delta^{15}N$ or $\delta^{13}C$ suggests that the inter-area variation in Hg concentrations is not as tightly controlled by diet as Cd.

A premise of our study is a geographical variation in trace element abundance among various areas. However, apparently only sparse and heterogenous information exists on geographical trends in elements within the area covered by the present study (for reviews cf. AMAP, 1998, Anon., 2000, 2002b). Mercury concentrations in ringed seal liver showed regional variation but no clear trends in the areas comparable to our study—West Greenland, western Norway and North Sea not included (Anon., 2002b). Mercury concentration in muscle of polar cod from South Greenland, Jan Mayen, Svalbard and the Barents Sea showed little

geographical variation. Within the same range, Cd in polar cod liver showed somewhat more geographical variability—the concentrations being highest in East Greenland (Anon., 2000).

Generally the trophic estimates for minke whales inferred from $\delta^{15}N$ in the present study are lower than that expected for animals feeding on a mixed diet of invertebrates and fish (e.g. Neve, 2000; Folkow et al., 2000) and suggest relatively more feeding on invertebrates such as krill. The range of $\delta^{15}N$ values for minke whales here is similar to that in the stenophagous blue whale, *Balaenoptera musculus* (Gendron et al., 2001), in which euphausids are a major food item (Gaskin, 1982), but lower than in the euryphagous fin whale, *Balaenoptera physalus* (Gendron et al., 2001).

Stable C and N isotope data can be informative about possible differences in average foraging behaviour among areas which may also be indicative of "ecological separation". Two primary interpretations for isotopic differences among groups of minke whales are: (1) that their diets (relative trophic level, represented by $\delta^{15}N$) and/or foraging locations (inshore/benthic vs. offshore/pelagic, represented by $\delta^{13}C$) differed among areas (Hobson and Welch, 1992; Michener and Schell, 1994), or (2) that food webs were isotopically distinct among the stocks (Hobson, 1999). The most likely explanation for the findings is the first option although it should be noted that Schell et al. (1998) documented substantial regional isotopic differences in the Bering Sea, an area of dynamic up-welling.

Adopting the first option (that stable isotopic differences among areas represent differences in dietary and foraging location preference), the results are interpreted to mean that East Greenland, Jan Mayen and Svalbard minke whales occupied the lowest trophic levels (range 2.9–3.1) of any area. The indications that minke whales at Jan Mayen and Svalbard primarily feed on krill is in accordance with analyses of stomach contents (Folkow et al., 2000; Haug et al., 2002). A greater consumption of krill by minke whales in these areas may also explain the higher Cd levels in whales from these areas compared to those from Vestfjorden/Lofoten (EC) and the North Sea (EN) (Table 2). Stable C and N isotopic data indicate increasing Cd concentrations with *decreasing* trophic level of whales (Michener and Schell, 1994; Hobson et al., 2002), and generally Cd concentrations in crustaceans are higher than in fish muscle (Dietz et al., 1996). Whales from Jan Mayen and Svalbard possibly were also more offshore feeders than those elsewhere (i.e. they had more depleted $\delta^{13}C$ values), although this may partly involve a trophic level effect also (Michener and Schell, 1994).

Minke whales from Vestfjorden/Lofoten on the western coast of Norway and from the North Sea were the highest trophic level feeders (3.3 and 3.4, respectively). A preference in these areas for fish was also indicated in other studies (Jonsgård, 1982; Olsen and Holst, 2001).

A greater consumption of krill by West Greenland minke whales may at least partly explain the relatively higher Cd levels in whales from this area (Table 2).

Tissue Pb is believed to turn over relatively rapidly in mammals (Scheuhammer, 1991) and therefore the Pb values are indicators of the provenance of whales over approximately the previous one to two months of life.

The Pb isotope data showed that West Greenland and Vestfjorden/Lofoten whales assimilated relatively radiogenic (higher isotope ratio) bioavailable Pb compared to those elsewhere in the study area. The higher ratios could be explained by significant inputs of natural Pb into coastal food chains from terrestrial sources. Riverine flows entering the North Atlantic Ocean contain relatively radiogenic Pb resulting from the weathering of ancient continental margins (Asmeron and Jacobsen, 1993). Elsewhere in the North Atlantic, the Pb isotope values of most minke whale kidneys fell within the range of European industrial Pb (Hamelin et al., 1989; Véron et al., 1993; Véron and Chuch, 1997), suggesting that anthropogenic Pb dominated the Pb found in seawater and minke whale food chains in pelagic areas. This may explain the lack of isotopic variation among whales from those areas.

The Pb isotopic data are not in conflict with the hypothesis that whales in the Vestfjorden/Lofoten area may be connected with whales in the North Sea and the northern areas because Pb isotope differences could develop in whales feeding in Vestfjorden/Lofoten for as little as 1–2 months each summer.

4.4. Management stocks or subpopulations inferred from the study

In female minke whales, we found significant differences among most areas in at least one of the

long-term diagnostic elements (Hg, Cd, Se), with West Greenland and North Sea females exhibiting the largest and more numerous differences from all other areas. In contrast, females from the Barents Sea, Svalbard area and Vestfjorden/Lofoten in the coastal region of Norway formed a group which was internally indistinguishable using the geochemical diagnostics employed here. PCA analyses of multiple elements in baleen indicated the existence of an east–west gradient in elemental patterns, and a significant difference was found between whales in West Greenland and the North Sea.

Overall, the following groups were inferred from these data: West Greenland, a central group represented by Jan Mayen animals, a northeastern stock encompassing the Svalbard, the Barents Sea and Vestfjorden/Lofoten, and the North Sea. Basically, this grouping was similar found in the genetic study by Andersen et al. (2003). Males appeared to fall into similar groupings to females but because of small sample sizes fewer areas could be tested. Nonetheless, males in West Greenland and the North Sea were significantly different from other areas in a pattern consistent with the females. Further sampling in subsequent years, especially in East Greenland and the northern stock area, is required to increase sample sizes and to verify the existence of these suggested stocks. While North Sea females were clearly different from Svalbard and Barents Sea females, they were not distinct from females in the adjacent area of Vestfjorden/Lofoten. One possible explanation is that the Vestfjorden/Lofoten area is a shared feeding area for some females between the North Sea and other northern management areas. A connection between minke whales in these areas has been suggested. According to Jonsgård (1951), adult minke whales pass through the Lofoten area during their spring migration to the feeding grounds in eastern North Atlantic waters.

This study is part of a broader, multi-disciplinary effort to better understand North Atlantic minke whale stocks and populations based on the same suite of samples. In addition to the genetic study (Andersen et al., 2003), the population substructure has been studied using regional variation in persistent organic pollutant (POP) burdens (Hobbs et al., 2003), blubber fatty acid (FA) composition (Møller et al., in press), and muscle ^{137}Cs concentrations (Born et al., 2002). All these studies included samples from the same whales as used in the present study. Proportions of POPs in minke whales from the North Sea differed from those from Greenland waters (Hobbs et al., 2003). Furthermore, whales from Greenland waters differed in POP burdens from those from the Jan Mayen area and from more eastern areas (Ibid.). Similar to the patterns of regional variation in POP, the ^{137}Cs concentrations did not reveal any major difference among groups except that ^{137}Cs levels in minke whales from the North Sea and Svalbard were significantly different from those in whales from the other areas (Born et al., 2002). The relatively low ^{137}Cs concentrations in samples from Svalbard supported the notion that the minke whales in this area are krill-eaters to a large extent. Regional variation in FA profiles indicated the existence of three different groups: a Greenland group (West and East Greenland), a central group (Jan Mayen–Svalbard–Barents Sea–Vestfjorden/Lofoten), and a North Sea group (Møller et al., in press). Although the different analyses grouped the whales somewhat differently, they all indicated that minke whales in West Greenland and the North Sea are different from those in the other areas. The status of minke whales in East Greenland cannot be considered to have been determined in these and the present study because the sample only consisted of four whales. However, the genetic study, in which the total sample from East Greenland was larger because samples taken in other years than 1998 (i.e. 1996, 1997 and 1999) were included, indicated that East Greenland minke whales differ significantly from those in West Greenland but are similar to those summering at Jan Mayen (Andersen et al., 2003).

The minke whales that were caught in seven different International Whaling Commision (IWC) management areas belonged by definition to different management stocks because IWC areas form the management units within which harvesting takes place. However, the four major groups identified in the present study might form the basis of a redefinition of management areas. Because these stocks apparently are similar to subpopulation identified genetically by Andersen et al. (2003), they may also be regarded as "subpopulations" in a biological sense. We suggest that these groups can be viewed as constituting a meta-population (i.e. a number of groups connected by dispersal of individuals between them, Stern, 2002). If a species is distributed into populations over a sufficiently large area, environ-

mental conditions may be more or less independent between areas; therefore, a catastrophe in one area will not affect other populations. Dispersal (to different feeding ground in case of minke whales) reduces the risk of population extinction by minimising the effects of chance environmental changes or changes in population demography (Stern, 2002).

5. Conclusions

From the elemental variation among minke whales caught in different areas of the North Atlantic, ecologically separated stocks are inferred to exist in the following summer feeding grounds: West Greenland (WG), a central group (CM), and a northeastern stock (ES, EB and EC), and the North Sea (EN). This result suggests a finer resolution of stock structure than was achieved with POPs, ^{137}Cs and FA and was similar to that indicated by the genetic study. Males appeared to fall into similar groupings to females but because of smaller sample sizes fewer significant differences occurred between areas.

Minke whales from neighbouring Canadian (WC) and Icelandic (CIP and CIC; Fig. 1) waters were not included in the present study. Future studies of minke whale population and stock structuring in the North Atlantic Ocean should ideally include samples taken from, for example, stranded animals from Canada and Iceland, and aim to expand the sample numbers of animals from the NE Atlantic and eastern Greenland harvests.

Acknowledgements

This study was funded by the Danish Ministry of the Environment (Program: DANCEA "Danish Co-operation for Environment in the Arctic") and the Greenland Institute of Natural Resources (GINR). The Institute of Marine Research, Bergen, and the Norwegian Institute of Fisheries and Aquaculture organized the sampling in the NE Atlantic and the North Sea. We wish to thank the Greenland and Norwegian fishermen and hunters and others who helped collect the samples. Co-operation during the sampling phase with the Directorate of Fisheries (Nuuk) and KNAPK (the Association of Greenland Hunters and Fishermen) is gratefully acknowledged. Thanks to Sofie Jeremiassen and Kirsten Rydahl (GINR), Gert Asmund, Sigga Joensen, Else Marie Nielsen, and Maja Kirkegaard (DAE), Linda Cataldo and Ryan Meeds (GSC) and Patricia Healy (PNNWRI) for help during the sampling and/or analysis. Stable isotope analyses were performed by Garth Parry (University of Saskatchewan).

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