ARCTIC
VOL. 56, NO. 1 (MARCH 2003) P. 82 – 90

Investigation of the Stock Structure of Atlantic Walrus (*Odobenus rosmarus rosmarus*) in Canada and Greenland Using Dental Pb Isotopes Derived from Local Geochemical Environments

P.M. OUTRIDGE,[1,2,3] W.J. DAVIS,[1] R.E.A. STEWART[2] and E.W. BORN[4]

(*Received 17 December 2001; accepted in revised form 10 July 2002*)

ABSTRACT. The chemical composition of animal tissues such as teeth appears to reflect an individual's exposure to its geochemical environment. In this study, the lead (Pb) isotope composition of dental cementum was used to investigate the stock structure of Atlantic walrus (*Odobenus rosmarus rosmarus*) in the Canadian Arctic and Greenland. The 12 communities providing walrus samples for this study represent most of the Canadian and Greenlandic villages where walrus still form an important part of the traditional Inuit diet. Significant differences between locations in mean Pb isotope ratios and the limited overlap of the ranges of values indicate that each village harvested walrus herds that exploited substantially different geological/geographical habitats. This geographic segregation based on isotopic signatures suggests that most walrus stocks (i.e., the groups of walrus that interact with hunters at each community) are more localized in their range than previously thought. $^{208}Pb/^{207}Pb$ and $^{208}Pb/^{204}Pb$ were the most important stock discriminators, reflecting the influence of local geological Th/U composition (i.e., ^{208}Pb) on Pb isotope composition in walrus teeth. ^{204}Pb-based isotope ratios in walrus were consistently higher (more radiogenic) and more homogeneous than those in regional terrestrial bedrock, a difference probably due to selective leaching of radiogenic Pb from mineral phases into seawater and mixing during weathering and transport. Dental Pb isotope signatures may have widespread application to stock discrimination of other coastal marine mammal species.

Key words: walrus, *Odobenus rosmarus rosmarus*, teeth, lead isotopes, stock discrimination

RÉSUMÉ. La composition chimique de tissus animaux tels que les dents semble refléter l'exposition d'un individu à son milieu géochimique. Pour la présente étude, on a utilisé la composition isotopique du plomb (Pb) contenu dans le cément pour examiner la structure du stock du morse de l'Atlantique (*Odobenus rosmarus rosmarus*) dans l'Arctique canadien et le Groenland. Les 12 communautés qui ont fourni les échantillons de morse pour ce projet représentent la majorité des villages canadiens et groenlandais où le morse constitue toujours une grande partie du régime alimentaire traditionnel des Inuits. Des différences marquées entre les sites dans la moyenne des rapports isotopiques du Pb et le faible recoupement des gammes de valeurs révèlent que chaque village prélevait des morses au sein de troupeaux qui exploitaient des habitats géologiques/géographiques bien distincts. Cette ségrégation géographique fondée sur des signatures isotopiques suggère que la plupart des stocks de morses (c.-à-d. le groupe de morses qui interagit avec les chasseurs dans chaque communauté) sont plus localisés dans leur territoire qu'on ne le pensait auparavant. $^{208}Pb/^{207}Pb$ et $^{208}Pb/^{204}Pb$ étaient les grands caractères discriminants des stocks, reflétant l'influence de la composition géologique locale Th/U (c-à-d. ^{208}Pb) sur la composition isotopique du Pb dans les dents du morse. Les rapports isotopiques fondés sur ^{204}Pb étaient constamment plus élevés (plus radiogéniques) et plus homogènes que ceux du substratum terrestre, la différence étant probablement due à la lixiviation sélective du Pb radiogénique passant des phases minérales dans l'eau de mer et à son mélange durant la météorisation et le transport. Les signatures isotopiques du plomb dentaire peuvent avoir de vastes applications dans la discrimination des stocks d'autres espèces de mammifères marins côtiers.

Mots clés: morse, *Odobenus rosmarus rosmarus*, dents, isotopes du plomb, discrimination des stocks

Traduit pour la revue *Arctic* par Nésida Loyer.

INTRODUCTION

Atlantic walrus (*Odobenus rosmarus rosmarus*) are an important part of traditional Inuit diets throughout much of the Arctic. There are indications that Atlantic walrus occur in separate stocks; however, the present population numbers, trends, and stock structures are poorly understood in several regions (Born et al., 1995). Such information is necessary to develop a management strategy adequate to prevent overhunting and assist the subspecies in re-establishing its pre-European contact distribution and population numbers (Born et al., 1995). In the present paper,

[1] Geological Survey of Canada, 601 Booth St., Ottawa, Ontario K1A 0E8, Canada
[2] Department of Fisheries and Oceans, 501 University Crescent, Winnipeg, Manitoba R3T 2N6, Canada
[3] Corresponding author: outridge@nrcan.gc.ca
[4] Greenland Institute of Natural Resources, P.O. Box 570, DK-3900 Nuuk, Greenland

"stocks" (or "management units") are defined as groups of walrus that interact with humans and can be exploited and managed independently of other groups (Royce, 1972). Because human exploitation of animals usually occurs in a series of hunting areas, stock definitions are also intrinsically geographical in nature. We consider a "population" to be a group of organisms with a substantially higher amount of genetic exchange within the group than outside it (Pianka, 1978). A population may have a much broader geographical distribution than a stock and encompass many stocks (harvested groups). A stock or management unit may include members of more than one population.

The structure and the interrelatedness of Atlantic walrus stocks are the subjects of on-going research using a variety of morphological (Knutsen and Born, 1994; Garlich-Miller and Stewart, 1998), tracking (Born and Knutsen, 1992; Wiig et al., 1996), and genetic techniques (Andersen et al., 1998; Andersen and Born, 2000; Born et al., 2001). Previous observations of Atlantic walrus distribution and the existence of independent management regimes suggested eight "regional stocks" (Born et al., 1995). Six of these occur in Canada and Greenland (see Fig. 1a): (1) Foxe Basin; (2) southern and eastern Hudson Bay; (3) northern Hudson Bay - Hudson Strait - southeastern Baffin Island - northern Labrador; (4) western Greenland; (5) "North Water" (Baffin Bay - eastern Canadian High Arctic); and (6) eastern Greenland. Exchange of individuals is thought to occur between stocks #2 and 3 and between stocks #3 and 4, although the extent of intermixing is unclear (Born et al., 1994, 1995).

Recently, a biogeochemical approach to walrus stock discrimination involving the analysis of trace elements and lead (Pb) isotopes in tooth cementum indicated previously unrecognized stocks within some of the putative regional groupings in the eastern Canadian Arctic (Outridge and Stewart, 1999). The approach, which was pioneered with African elephants (*Loxodonta africana*; van der Merwe et al., 1990; Vogel et al., 1990), is based on the fact that animals accumulate elements or stable isotopes from their surrounding environment in calcified tissues such as teeth and tusks. Groups of animals exploiting habitats with geochemical differences may reflect those differences in the characteristic element or isotopic compositions of their teeth. Thus, nonrandom geographic patterns in the chemical composition of teeth may be used to infer the previously unrecognized existence of groups of animals that exploit different habitats (i.e., stocks, sensu Royce, 1972). Walrus feed primarily on bivalves and other sedentary invertebrates (Fay, 1982; Fisher and Stewart, 1997), and the elemental and isotopic composition of their diet should reflect the local geochemical environment.

The key walrus stock diagnostics reported by Outridge and Stewart (1999) were Pb isotope ratios ($^{206}Pb/^{207}Pb$ and $^{208}Pb/^{207}Pb$) and concentrations of cobalt (Co), zinc (Zn), vanadium (V), and molybdenum (Mo) in teeth. However, the dental trace element contents of harvested walrus varied significantly over an eight-year span, suggesting that these may not be suitable as long-term diagnostics. The isotope ratios of heavy mass elements such as strontium (Sr) and Pb are controlled solely by geological processes and are not measurably affected by different feeding strategies or by physical, chemical, or biological processes (Dickin, 1995; Flegal and Smith, 1995; Outridge and Stewart, 1999; Blum et al., 2000). Of the four natural lead isotopes (^{204}Pb, ^{206}Pb, ^{207}Pb, and ^{208}Pb), the latter three are derived respectively from radiogenic decay of ^{238}U, ^{235}U, and ^{232}Th in the continental crust or mantle (Dickin, 1995). Lead isotope ratios in High Arctic bivalve shells and in walrus teeth from Igloolik, Canada, have remained constant for at least the past 500 to 6000 years (Outridge et al., 1997, 2000). Stability over such time scales makes these ratios more reliable than element concentrations for stock discrimination.

The present study arose from the work of Outridge and Stewart (1999). It expands the geographic coverage of that study, and provides complete and high-precision Pb isotope data for a subset of animals using a second analytical technique. Walrus teeth were obtained from three additional communities in Greenland (Thule, Sisimiut, and Scoresbysund) and three in Canada (Repulse Bay, Coral Harbour, and Loks Land), as well as new samples from Grise Fiord. These teeth were analyzed for $^{206}Pb/^{207}Pb$ and $^{208}Pb/^{207}Pb$ by inductively coupled plasma mass spectrometry (ICP-MS) for comparison with the earlier study. Selected samples from most sites were also analyzed by thermal ionization mass spectrometry (TIMS), which provides about a 10-fold improvement in the precision of isotope ratio measurement over ICP-MS (Hinners et al., 1998) and measures the least abundant Pb isotope, ^{204}Pb. TIMS analyses are time-consuming and many times more expensive per sample than ICP-MS, so they are not routinely applied to all samples but are used to resolve subtle differences between locations that could not be resolved by ICP-MS. The ^{204}Pb-based isotope ratios are also readily compared to data on basement rocks in the various regions, and this paper evaluates the degree of correspondence between Pb isotopic composition in walrus and that in local geology.

MATERIALS AND METHODS

Walrus were sampled as part of subsistence hunts and were assigned for statistical purposes to the communities where they were landed. Although the exact capture locations of walrus were not usually recorded, anecdotal reports from Foxe Basin suggest that hunters rarely travel more than 150 km from their communities (Riewe, 1992). Sample sizes at each site vary depending on the number of walrus captured each year. At several sites, animals from multiple years of harvesting were available for this study. Capture dates ranged from 1988 to 1996.

Mandibular teeth were extracted at time of capture (or, in the case of Greenland samples, from mandibles in the laboratory) for later sectioning and ageing by enumeration of dental cementum growth layers (Garlich-Miller et al., 1993). Teeth were chosen as indicator tissues for isotope analysis because they grow incrementally through life and are not resorbed (Fay, 1982; Hillson, 1986). The Pb isotope value for each walrus therefore represents an integrated average of lifetime Pb ingestion and accumulation in teeth. The procedures for preparation and ICP-MS analysis of the samples followed Outridge and Stewart (1999). Briefly, a thin section of cementum including all growth layers was excised and acid-digested before preconcentration of the Pb by chelation ion chromatography. The isotopes ^{206}Pb, ^{207}Pb, and ^{208}Pb were measured by solution nebulization ICP-MS. Replicates of National Institute of Standards and Technology (NIST) 1400 Bone Ash Standard Reference Material (SRM) were interspersed with the tooth samples. Although NIST 1400 is not certified for Pb isotopic composition, it was analyzed by the TIMS laboratory used here as part of an inter-laboratory study (Hinners et al., 1998; see Laboratory "C" in that study). Isotopic values as determined by TIMS were 1.1721 ± 0.0002 for ^{206}Pb/^{207}Pb and 2.4639 ± 0.0003 for ^{208}Pb/^{207}Pb (mean ± S.E., N = 7; note that the error values quoted in Hinners et al. (1998) are incorrect). ICP-MS analysis in the present study gave the following results for NIST 1400: 1.173 ± 0.002 for ^{206}Pb/^{207}Pb and 2.462 ± 0.006 for ^{208}Pb/^{207}Pb (mean ± S.D., N = 10), which agreed closely with the information values provided by Hinners et al. (1998) and were within 0.6% of the results reported by Outridge and Stewart (1999) of 1.166 ± 0.006 and 2.458 ± 0.005, respectively (N = 13). Analytical error for the ICP-MS technique was defined as three times the S.D. of the NIST 1400 analyses, i.e., ± 0.006 for ^{206}Pb/^{207}Pb and ± 0.018 for ^{208}Pb/^{207}Pb. Because the Pb concentrations in digest solutions of the NIST 1400 SRM and tooth samples were similar, analytical errors are also similar.

Other sections of cementum from selected teeth (N = 25) were removed for TIMS analysis. Each sample was decontaminated by immersing it briefly in 10% HNO_3 and distilled deionized (DD) water and then washed in DD water in an ultrasonic bath. Preparation and analytical techniques followed Hinners et al. (1998; Laboratory "C"). Briefly, the Pb was separated and concentrated from tooth material by passing acid-digested samples through anion-exchange columns. Lead isotopes were measured by single-filament TIMS, using NIST 981 SRM to correct for mass fractionation. Reproducibility, estimated from replicate analyses of NIST 981, was 0.05% per amu (1δ/mass unit). The median difference in isotopic ratios for samples analyzed by both ICP-MS and TIMS was 0.38% for ^{206}Pb/^{207}Pb and 0.10% for ^{208}Pb/^{207}Pb. Differences between methods (ICP-MS and TIMS) were compared using paired t-tests. There was a significant difference between methods for ^{206}Pb/^{207}Pb ($p = 0.03$), but not for ^{208}Pb/^{207}Pb ($p = 0.31$).

Isotope ratios were arc-sine square root (x/10) transformed before statistical analysis. Relationships between Pb isotopic composition and age or gender were tested by one-way analyses of variance grouped by site for locations with relatively large numbers of landed animals (Hall Beach, Igloolik, Thule, and Scoresbysund). No significant age or gender effects were found, and thus the subsequent tests were for site-related differences only. Differences between sites were tested with a one-way analysis of variance followed by a Tukey HSD test for unequal numbers of replicates. Significant differences cited in the text are at $p < 0.05$. Because the samples from Repulse Bay, Loks Land, and Resolute animals were limited (N ≤ 5), they are discussed in the text but not included in the statistical comparisons. For comparison with these communities, walrus landed at other locations that differed by more than analytical error were regarded as being isotopically differentiated.

RESULTS

For the sake of completeness, the ICP-MS data in this report include the 109 walrus reported by Outridge and Stewart (1999). New samples analyzed by ICP-MS consisted of 74 animals from Greenland sites and 24 additional animals from Canada. Differences between walrus landed at various communities will be discussed in the context of the regional stocks identified by Born et al. (1995).

ICP-MS analysis indicated that the mean ^{206}Pb/^{207}Pb or ^{208}Pb/^{207}Pb values (or both) of animals landed by most of the communities were significantly different from those at any other community in the same stock area (Table 1). In most cases, the ranges of Pb isotope ratios at adjacent sites differed by more than analytical error, with negligible overlap. Within the N Hudson Bay–SE Baffin Island stock (stock #3; see Fig. 1a), most Coral Harbour animals were different from those landed at Repulse Bay and Loks Land. Although sample numbers were small at the latter two sites, the animals landed there differed by at least 7% in terms of ^{206}Pb/^{207}Pb, which is a large margin in a global context (see Sangster et al., 2000). Limited overlap occurred between the radiogenic (higher) end of the Coral Harbour range and Repulse Bay, and between the nonradiogenic portion of the Coral Harbour range and Loks Land (Fig. 2a), suggesting that a few Coral Harbour walrus shared common habitats with some of the animals landed at those communities. Overlap also occurred between Coral Harbour and Loks Land in stock #3 and Akulivik in the adjacent SE Hudson Bay stock (#2) (Fig. 2a). Akulivik and Sisimiut (stock #4) were largely different, with a few overlapping values. Sisimiut walrus were also clearly different from stock #3, with no evidence of individuals common to both stocks. As reported by Outridge and Stewart (1999), Inukjuak walrus (stock #2) were isotopically differentiated from those at Akulivik, and the new data show that they were significantly different from animals landed from stocks #3 and #4 as well.

Within the proposed North Water regional stock (#5), approximately 80% of the animals landed at Thule and

TABLE 1. Mean (± S.D.) $^{206}Pb/^{207}Pb$ and $^{208}Pb/^{207}Pb$ ratios in teeth of walrus landed at Inuit communities in Canada and Greenland. Measurements by ICP-MS. Arranged in increasing order of isotope ratios for locations tested statistically. Resolute, Repulse Bay, and Loks Land were not included in statistical tests because of small numbers of replicates. Sites which are not significantly different from each other at $p < 0.05$ are joined by a line.

Site	Scoresby-sund	Inukjuak	Grise Fiord	Sisimiut	Akulivik	Thule	Coral Harbour	Hall Beach	Igloolik	Repulse Bay	Resolute Bay	Loks Land
N	18	11[a]	8[b]	16	11[a]	39	13	35[a]	43[a]	5	4[a]	4
$^{206}Pb/^{207}Pb$	1.182 ± 0.010	1.229 ± 0.033	1.256 ± 0.030	1.257 ± 0.018	1.263 ± 0.018	1.281 ± 0.030	1.319 ± 0.032	1.386 ± 0.077	1.423 ± 0.035	1.369 ± 0.020	1.237 ± 0.005	1.245 ± 0.012

Site	Scoresby-sund	Inukjuak	Grise Fiord	Thule	Akulivik	Sisimiut	Coral Harbour	Hall Beach	Igloolik	Repulse Bay	Resolute Bay	Loks Land
$^{208}Pb/^{207}Pb$	2.463 ± 0.008	2.505 ± 0.034	2.556 ± 0.024	2.573 ± 0.034	2.597 ± 0.027	2.639 ± 0.037	2.666 ± 0.050	2.696 ± 0.082	2.721 ± 0.036	2.743 ± 0.032	2.543 ± 0.007	2.550 ± 0.021

[a] Data that were previously examined by Outridge and Stewart (1999).
[b] Three more walrus are reported here in addition to the five reported by Outridge and Stewart (1999).

20% of those landed at Grise Fiord had dissimilar signatures, indicating that they were not shared between the two communities (Fig. 2b). Resolute animals could not be distinguished from the other stock #5 sites with ICP-MS data. Scoresbysund walrus (stock #6) contained the most nonradiogenic Pb of any group in the study area, while Igloolik and Hall Beach animals (stock #1) contained the most radiogenic Pb (Table 1). A number of communities, especially Hall Beach, Thule, Sisimiut, Grise Fiord and Inukjuak, landed several walrus that exhibited quite different isotopic signatures from most of the animals harvested there. These "outliers" resulted in relatively high within-site variances at these locations and may represent displaced or migrating individuals (R. Stewart and P. Outridge, unpubl. data).

The findings based on ICP-MS data were corroborated and extended by the high-precision data on ^{204}Pb-based ratios determined by TIMS (Fig. 3). The small number of samples per site analyzed by TIMS precluded a statistical comparison, but differences between sites that exceeded TIMS analytical error indicated that the walrus contained leads of distinctly different composition. The data showed that Resolute walrus were clearly different from Grise Fiord and Thule animals (Fig. 2b), while the similarities between some Grise Fiord and Thule walrus were confirmed.

DISCUSSION

Implications for Walrus Stock Structure

From the perspective of stock discrimination (sensu Royce, 1972), the significant differences and limited overlap of Pb isotopic values between locations suggest that across the Canadian/Greenland Arctic, hunters harvested walrus from local stocks. The analysis of whole-cementum samples means that each data point represents an integrated lifetime average of an individual's exposure to bioavailable Pb. Therefore, significant mean isotopic differences between locations can be interpreted as indicating groups of individuals that exploited substantially different geochemical/geographical environments (habitats) when averaged over their lifetimes and when averaged over all individuals. The approach used here does not allow us to test the possibility that certain stocks may temporarily move and share habitat with adjacent stocks or the possibility that a few individuals may temporarily exploit habitats that are different from those of most other members of their stock. In situ microanalyses of Pb isotopes in tooth annuli are underway to examine these possible variations in individual and stock movement patterns that are likely to be obscured by whole-cementum analyses.

The results of this study and Outridge and Stewart (1999) indicate that most of the regional groupings proposed by Born et al. (1995) contain two or more local stocks. Foxe Basin walrus (regional stock #1) landed at Hall Beach were distinguished from those at Igloolik on the basis of dental $^{206}Pb/^{207}Pb$, while Akulivik and Inukjuak walrus in SE Hudson Bay (stock #2) were different in terms of $^{208}Pb/^{207}Pb$. Regional stock #3 (N Hudson Bay to SE Baffin Island) is of particular interest because of its location between the first two stocks, and because of the possible movement of stock #3 walrus to and from W Greenland (stock #4) and SE Hudson Bay (stock #2). Two of the villages in the stock #3 area (Repulse Bay and Loks Land) land only a few walrus (and sometimes none) each year, limiting the sample numbers available to us. Despite this limitation, the results of the present study, especially the large isotopic differences between Loks Land and Repulse Bay animals, suggest that stock #3 includes local

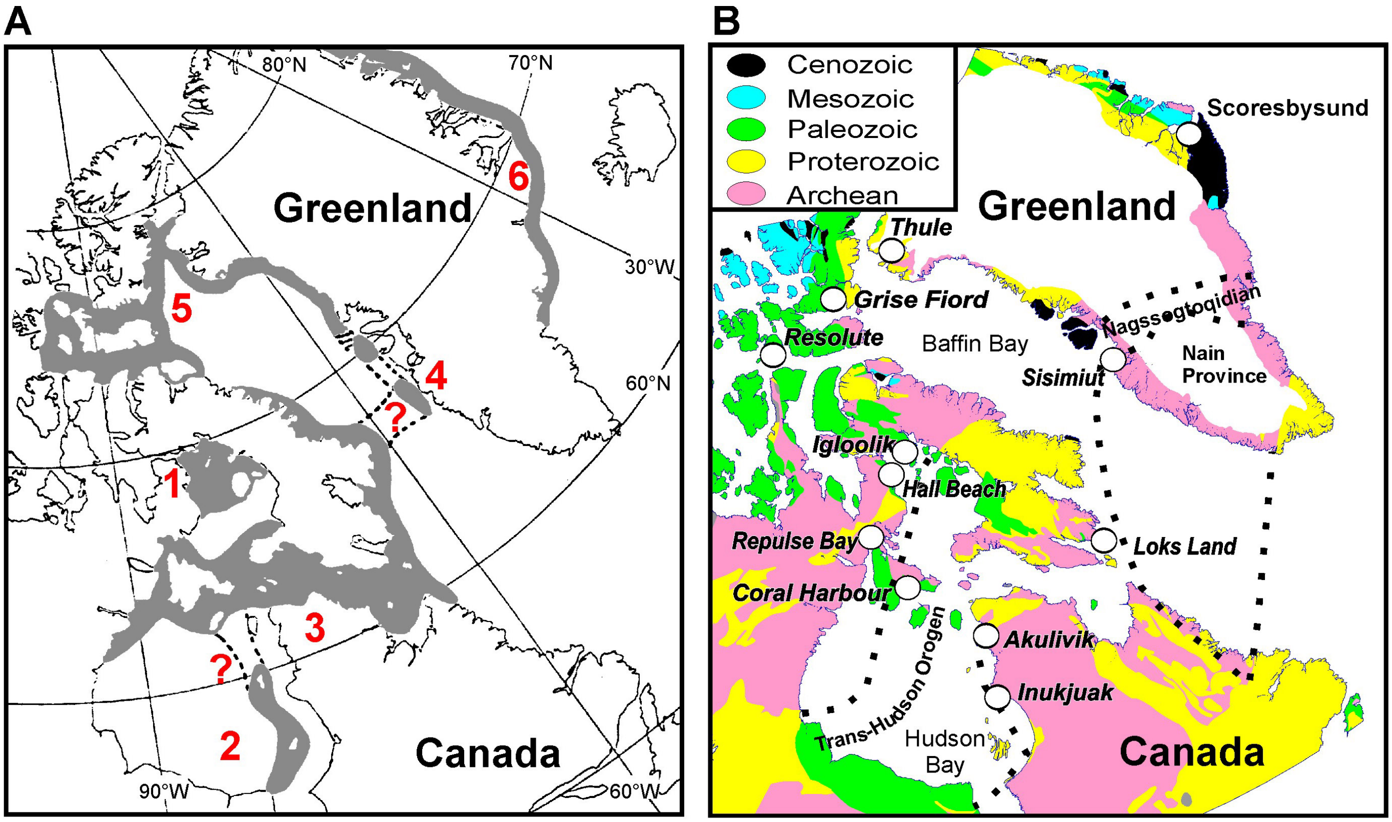

FIG. 1. (A) Map of the regional stock boundaries of Atlantic walrus in the study area, as proposed by Born et al. (1995). (B) a geological map of the study area, showing communities where walrus were landed. Boundaries of the Trans-Hudson and Nagssugtoqidian orogens and of Nain Province are indicated by dotted lines. Sources of geological data: GSC (1996) and Kirkham et al. (1995).

stocks at Coral Harbour, Loks Land, and Repulse Bay, with some degree of overlap between the catches of adjacent villages. It is unknown at present whether this overlap indicates temporary or partial sharing of habitat by the individual stocks or hunters' taking a few animals from the stocks hunted by adjacent communities. There was no evidence in this study of exchange between Coral Harbour/Loks Land and Sisimiut walrus (stock #4) or between Coral Harbour/Repulse Bay and Foxe Basin animals (stock #1). However, ion microprobe analysis of Pb isotopes in the growth annuli of teeth from some Hall Beach walrus suggested a degree of exchange between northern Foxe Basin and the Coral Harbour/Repulse Bay area (R. Stewart and P. Outridge, unpubl. data). The Coral Harbour stock on average was also isotopically distinct from that of Akulivik (stock #2) but with some similar individual signatures, again suggesting either movement between areas or a hunting area shared by both communities for part of their catches.

The present study suggests that the "North Water" stock (#5) identified by Born et al. (1995) could also be subdivided. High-precision TIMS analysis showed that Resolute walrus, although few in number, were clearly different from those at Grise Fiord and Thule. Some of the walrus landed at Thule and Grise Fiord were different from each other, but others exhibited similar isotopic signatures even in TIMS analyses. This overlap suggests that part of the catches of both communities came from a common stock, possibly in northern Baffin Bay. The putative common stock comprised approximately 80% of the Grise Fiord-harvested animals but only about 20% of the Thule animals. Andersen and Born (2000) found significant genetic heterogeneity among male walrus sampled at Thule during winter and suggested that this reflected males from different "sub-groups" wintering in the Thule area. Within the NE High Arctic of Canada and northern Baffin Bay, walrus are known to winter in several recurrent polynyas that are separated by hundreds of kilometres of consolidated ice (e.g., Kiliaan and Stirling, 1978). This winter distribution pattern may tend to favour fragmentation of the region's walrus into several local stocks, as indicated here.

The stocks identified by this study are in some respects consistent with the regional groupings proposed by Born et al. (1995) because there was no evidence of walrus moving or being hunted across those regional boundaries. However, it is unclear whether in all cases the regional groups and the local stocks identified here are comparable. Part of the difficulty lies in the use of different methods of delineating "stocks." The regional groups were based primarily on distribution and movement data. These data have subsequently been supported by other types of information that suggest the groups may represent a mixture of "stocks" and "populations" (using the definitions by Royce [1972] and Pianka [1978] that are employed here). Genetic

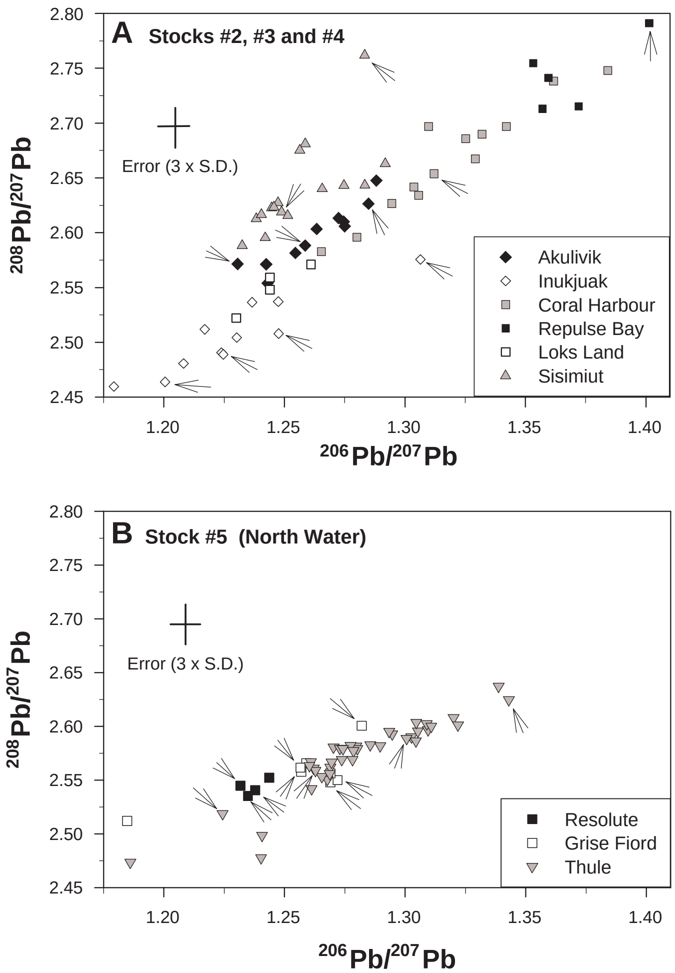

FIG. 2. $^{208}Pb/^{207}Pb$ and $^{206}Pb/^{207}Pb$ data for walrus captured by communities in (A) regional stock areas #2, #3 and #4, and (B) regional stock #5, the "North Water" stock. Analyzed by ICP-MS. In plot A, diamonds indicate stock #2 communities in SE Hudson Bay, squares indicate stock #3 communities in N Hudson Bay to SE Baffin Island, and triangles indicate stock #4 in W Greenland. Arrows indicate walrus that were subsequently analyzed by TIMS (see Fig. 3). Error bars represent 3δ of concurrent analyses of NIST 1400 Bone Ash SRM.

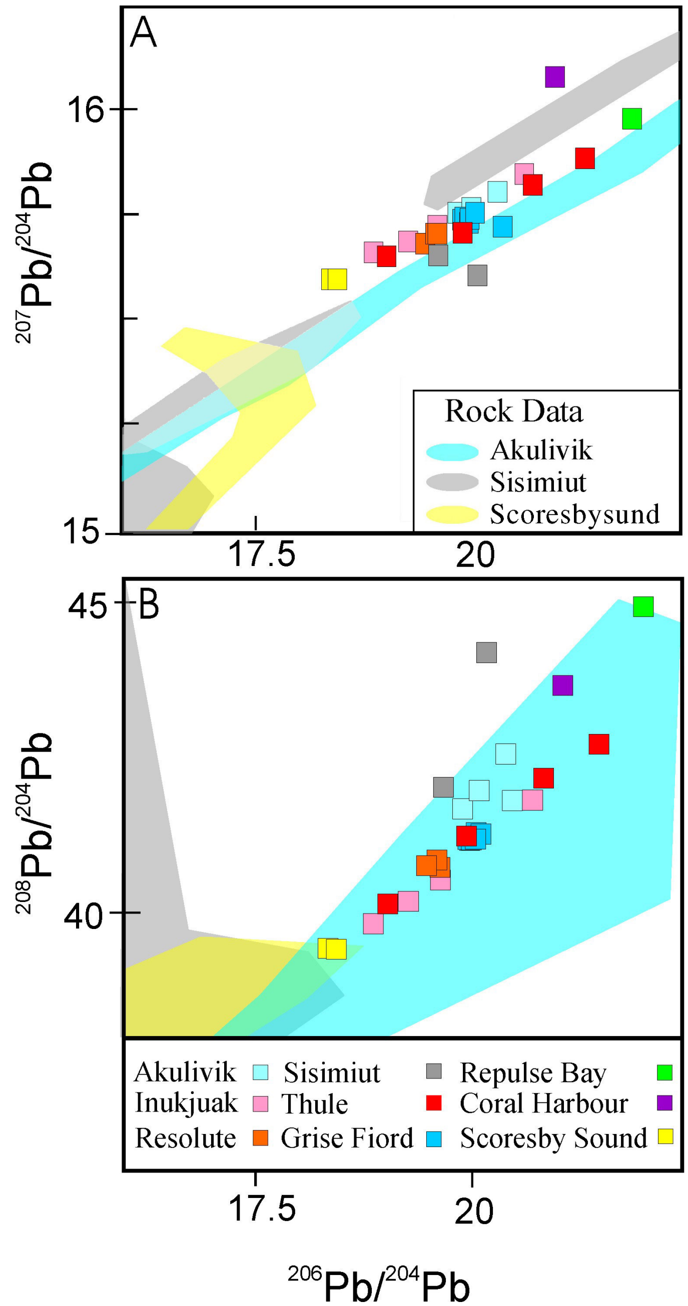

FIG. 3. (A) $^{207}Pb/^{204}Pb$ vs $^{206}Pb/^{204}Pb$, and (B) $^{208}Pb/^{204}Pb$ vs $^{206}Pb/^{204}Pb$ for walrus from nine communities and the upper range of values in bedrock surrounding Akulivik, Sisimiut, and Scoresbysund. The coloured polygons in A and B indicate the bedrock isotope data around Scoresbysund, Akulivik, and Sisimiut (Legend in A). Walrus values determined by TIMS; 3δ error bars around data are smaller than the symbols. Legend for walrus landed at different communities is shown in B. Data used to define the bedrock Pb isotopic composition came from Taylor and Kalsbeek (1990), Hegner and Bevier (1991), Taylor et al. (1992), Whitehouse et al. (1998), and Hansen and Nielsen (1999).

studies by Andersen et al. (1998), Andersen and Born (2000), and Born et al. (2001) indicated that walrus in NW, W, and E Greenland (stocks #4, 5, and 6) belonged to separate populations (sensu Pianka, 1978), which is consistent with the findings of separate "stocks" in the present study. Analyses of persistent organic pollutants in animals from NW and E Greenland and SE Baffin Island (i.e., stocks #3, 5, and 6) also indicated that they were different stocks (Muir et al., 2000) in the sense used here. One possible explanation is consistent with both genetic and biogeochemical data: Atlantic walrus may be distributed in local stocks that are in some cases part of larger populations, with the "regional stock" areas approximating the boundaries of distinctly different populations.

Biogeochemical approaches to studies of stock definition (sensu Royce, 1972), which use stable isotopes or elemental signatures, provide information that complements but is fundamentally different from that obtained in genetic studies of populations (sensu Pianka, 1978). Genetics and biogeochemistry in this context are measures of two distinctly different processes. Genetics measures interactions between individuals over generational time scales, while biogeochemistry measures interactions between an individual and its environment within the individual's lifetime. Genetic analysis is not directly informative about an individual's or group's exploitation of its habitat, although inferences may be made on the basis of genetic relationships between and within populations. Conversely, geochemistry is not informative about an individual's familial relationships. From a stock discrimination perspective, biogeochemical information is directly relevant; however, it also has limits to what can be determined with certainty. Different geochemical signatures (isotopes or elements) between sites indicate that the animals hunted by the communities exploited their environment differently. Similar geochemical signatures do not necessarily indicate that the communities hunted the same stock. In a geochemically homogeneous environment, different groups of animals may exist that become recognized only when the appropriate stock indicator (contaminants, biochemical indices, radioactive contaminants, etc.) is employed.

Relationships between Pb in Walrus and Geology

The heterogeneous Pb isotope pattern in walrus across the Arctic suggests an association, direct or indirect, between Pb in walrus and that in local geological sources. Weathering of continental crust ultimately causes Pb to enter aquatic systems, with most of the Pb transported in particulate material (Allegre et al., 1996). Isotopic studies of suspended material in rivers have shown a strong correlation between particulate Pb isotope ratios and the geological age of the catchment area (Asmerom and Jacobsen, 1993; Allegre et al., 1996). These local terrestrial inputs should control Pb isotope composition in most Arctic coastal waters. Atmospheric (industrial) Pb inputs have had no measurable impact on Pb isotope ratios in either walrus teeth from Igloolik (Outridge et al., 1997) or marine bivalve shells north of the Arctic Circle (Outridge et al., 2000) in Canada. Oceanic inflows of Pb from other areas of the Arctic Ocean are also unlikely to be significant because the residence time of Pb in nearshore seawater is short—approximately two years (Flegal and Patterson, 1983; MacDougall, 1991).

A detailed explanation of the relationship between geology and walrus requires an understanding of the processes that govern geological Pb isotopic composition and the processes that convey the Pb from bedrock to marine ecosystems. The Pb isotopic composition of continental crust is generally a function of its geological age, its initial Pb isotopic composition, and its U/Pb and Th/Pb ratios (Dickin, 1995). A geological age effect apparently occurs in some parts of the study area. For example, the least radiogenic Pb occurred in walrus from Scoresbysund in east Greenland, a region characterized by Tertiary basaltic lavas to the south and relatively young crustal ages (400–1000 Ma) elsewhere. More radiogenic leads in walrus occurred in Thule and Repulse Bay, areas characterized by Proterozoic or Archean crust reworked in the Proterozoic.

However, relating the Pb composition in walrus teeth to geology is complicated by a number of factors. First, the geological Pb isotope database for the Arctic is geographically restricted, and the geology of the study area is complex, with extensive reworking of geological units at several times in the past. Second, differential weathering may lead to isotopically variable contributions of bioavailable Pb from specific mineral phases or rock types (or both). Isotopic data are lacking across the Arctic for materials such as till deposits or river water, which are intermediate between bedrock and seawater in the weathering/transport process.

^{204}Pb-based isotope ratios in walrus teeth in each area are generally more radiogenic than average surrounding bedrock (Fig. 3), although rock units with radiogenic Pb that matches walrus Pb composition are locally present. For example, ^{206}Pb/^{204}Pb values exceeding 19.5 are common in the walrus data but relatively uncommon in the rock record (Fig. 3a); the minimum ^{206}Pb/^{204}Pb values in bedrock are as low as ca. 14.0. This dichotomy suggests that a fractionated, radiogenic, and bioavailable Pb component is preferentially transferred from continental areas to the marine environment, where it is incorporated into the walrus food chain. Most likely the pattern reflects the preferential weathering of minerals damaged by high U contents (e.g., Harlavan and Erel, 1999). From a global perspective, the walrus Pb isotopic compositions are more radiogenic than is typical for river-transported Pb from Precambrian terranes (Asmerom and Jacobsen, 1993; Allegre et al., 1996) and are considerably higher than those in central Arctic Ocean seawater (Winter et al., 1997). The walrus also exhibited a greater degree of isotopic homogeneity than bedrock, both Arctic-wide and within a given area. This homogeneity indicates a high degree of mixing and integration of geological leads, presumably during weathering and transport of terrestrial material, as well as the incorporation by walrus of any isotopic variation occurring among feeding areas. The latter phenomenon may explain the significant Pb isotopic variations found between individual growth annuli of walrus teeth (Stern et al., 1999), variations which are homogenized by whole-tooth analyses like those here.

^{208}Pb/^{204}Pb ratios in walrus were more variable and deviated more significantly from a simple linear array than ^{206}Pb/^{204}Pb or ^{207}Pb/^{204}Pb (Fig. 3b), making ^{208}Pb the single most important discriminant of walrus stocks across the study area. Greater ^{208}Pb/^{204}Pb variation compared to ^{206}Pb/^{204}Pb or ^{207}Pb/^{204}Pb predominantly reflects long-term compositional control, specifically a Th/U ratio that varies from area to area. Walrus from Akulivik, Sisimiut, Coral Harbour, and Repulse Bay are all characterized by relatively high ^{208}Pb/^{204}Pb, with the Sisimiut samples showing very high values. All of these sites are located within or near Proterozoic rocks of the Trans-Hudson orogen in Canada or the Nagssugtoqidian orogen in Greenland (see Fig. 1b). The source of this high Th/U component is not readily identified, although many bedrock samples in the Sisimiut region have elevated ^{208}Pb/^{204}Pb values (Fig. 3b). In contrast, walrus harvested from Inukjuak, dominated by

Archean crust, have among the lowest $^{208}Pb/^{204}Pb$ values, indicating low Th/U values for this area.

In summary, there are some associations between terrestrial geological age and walrus Pb composition, but geological age alone cannot predict the range of values for walrus from a given area. Other geological processes, including contributions from glacial till and differential weathering, may have played a role in determining the isotopic composition of bioavailable Pb entering the walrus food chain. ^{208}Pb was particularly important as a discriminator between stocks, reflecting the compositional control (Th/U ratio) of local terrestrial materials on walrus Pb isotope compositions. Local terrestrial inputs appear to control the Pb composition of coastal seawater and food chains, and so Pb isotopes may be particularly useful to resolve the stock structure of other nearshore marine species at a fine spatial scale.

ACKNOWLEDGEMENTS

We thank the hunters and the communities' hunting and trapping associations who supplied samples from their annual hunts. Reg Theriault, Claudia Moore, and Linda Cataldo (GSC) and Blair Dunn and Anna Chambers (DFO) provided technical support. We thank Joseph Graney and two anonymous reviewers for their comments. This work was financially supported by the Nunavut Wildlife Management Board (Canada), the Geological Survey of Canada, Fisheries and Oceans Canada, the Greenland Institute of Natural Resources, and the Aage V. Jensen Foundation.

REFERENCES

ALLEGRE, C.J., DUPRE, B., NEGREL, P., and GAILLARDET, J. 1996. Sr-Nd-Pb isotope systematics in Amazon and Congo River systems: Constraints about erosion processes. Chemical Geology 131:93–112.

ANDERSEN, L.W., and BORN, E.W. 2000. Indications of two genetically different sub-populations of Atlantic walruses (*Odobenus rosmarus rosmarus*) in West and Northwest Greenland. Canadian Journal of Zoology 78:1999–2009.

ANDERSEN, L.W., BORN, E.W., GJERTZ, I., WIIG, Ø., HOLM, L.-E., and BENDIXEN, C. 1998. Population structure and gene flow of the Atlantic walrus (*Odobenus rosmarus rosmarus*) in the eastern Atlantic Arctic based on mitochondrial DNA and microsatellite variation. Molecular Ecology 7:1323–1336.

ASMEROM, Y., and JACOBSEN, B.S. 1993. The Pb isotopic evolution of the Earth: Inferences from river water suspended loads. Earth and Planetary Science Letters 115:245–256.

BLUM, J.D., TALIAFERRO, E.H., WEISSE, M.T., and HOLMES, R.T. 2000. Changes in Sr/Ca, Ba/Ca and 87Sr/86Sr ratios between trophic levels in two forest ecosystems in the northeastern U.S.A. Biogeochemistry 49:87–101.

BORN, E.W., and KNUTSEN, L.Ø. 1992. Satellite-linked tracking of Atlantic walrus (*Odobenus rosmarus rosmarus*) in northeastern Greenland, 1989–1991. Zeitschrift für Säugetierkunde 57: 275–287.

BORN, E.W., HEIDE-JØRGENSEN, M.P., and DAVIS, R.A. 1994. The Atlantic walrus (*Odobenus rosmarus rosmarus*) in West Greenland. Meddelelser om Grønland, Bioscience 40. 33 p.

BORN, E.W., GJERTZ, I., and REEVES, R.R. 1995. Population assessment of Atlantic walrus (*Odobenus rosmarus rosmarus*). Meddelelser No. 138. Oslo: Norsk Polarinstitutt. 100 p.

BORN, E.W., ANDERSEN, L.W., GJERTZ, I., and WIIG, Ø. 2001. A review of the genetic relationships of Atlantic walrus (*Odobenus rosmarus rosmarus*) east and west of Greenland. Polar Biology 24:713–718.

DICKIN, A.P. 1995. Radiogenic isotope geology. Cambridge: Cambridge University Press. 490 p.

FAY, F.H. 1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illger. North American Fauna No. 74. Washington, D.C.: U.S. Fish and Wildlife Service. 279 p.

FISHER, K.I., and STEWART, R.E.A. 1997. Summer foods of Atlantic walrus, *Odobenus rosmarus rosmarus*, in northern Foxe Basin, Northwest Territories. Canadian Journal of Zoology 75:1166–1175.

FLEGAL, A.R., and PATTERSON, C.C. 1983. Vertical concentration profiles of lead in the central Pacific at 15˚ and 20˚. Earth and Planetary Science Letters 64:19–32.

FLEGAL, A.R., and SMITH, D.R. 1995. Measurements of environmental lead contamination and human exposure. Reviews of Environmental Contamination and Toxicology 143:1–45.

GARLICH-MILLER, J.L., and STEWART, R.E.A. 1998. Growth and sexual dimorphism of Atlantic walruses (*Odobenus rosmarus rosmarus*) in Foxe Basin, Northwest Territories, Canada. Marine Mammal Science 14:803–813.

GARLICH-MILLER, J.L., STEWART, R.E.A., STEWART, B.E., and HILTZ, E.A. 1993. Comparison of mandibular with cemental growth-layer counts for ageing Atlantic walrus (*Odobenus rosmarus rosmarus*). Canadian Journal of Zoology 71: 163–167.

GSC (GEOLOGICAL SURVEY OF CANADA). 1996. Geological map of Canada. Map 1860A, 1:5,000,000. Ottawa: Geological Survey of Canada.

HANSEN, H., and NIELSEN, T.F.D. 1999. Crustal contamination in Palaeogene East Greenland flood basalts: Plumbing system evolution during continental rifting. Chemical Geology 157: 89–118.

HARLAVAN, Y., and EREL, Y. 1999. The release of lead and rare earth elements during granitoid dissolution. Abstracts, 9th Annual V.M. Goldschmidt Conference, Harvard University, Cambridge, Massachusetts, U.S.A., 22–27 August 1999.

HEGNER, E., and BEVIER, M.L. 1991. Nd and Pb isotopic constraints on the origin of the Purtuniq ophiolite and Early Proterozoic Cape Smith Belt, northern Québec, Canada. Chemical Geology 91:357–371.

HILLSON, S. 1986. Teeth. Cambridge: Cambridge University Press.

HINNERS, T.A., HUGHES, R.J., OUTRIDGE, P.M., DAVIS, W.J., SIMON, K., and WOOLARD, D. 1998. Inter-laboratory comparison of mass spectrometric methods for lead isotopes and trace elements in NIST SRM 1400 Bone Ash. Journal of Analytical and Atomic Spectrometry 13:963–970.

KILIAAN, H.P.L., and STIRLING, I. 1978. Observations of overwintering walruses in the eastern Canadian High Arctic. Journal of Mammalogy 59:197–200.

KIRKHAM, R.V., CHORLTON, L.B., and CARRIERE, J.J. 1995. Generalized geology of the world. In: Generalized geological map of the world and linked databases. Geological Survey of Canada, Open File 2915d.

KNUTSEN, L.Ø., and BORN, E.W. 1994. Body growth in Atlantic walruses (*Odobenus rosmarus rosmarus*) from Greenland. Journal of Zoology (London) 234:371–385.

MacDOUGALL, J.D. 1991. Radiogenic isotopes in seawater and sedimentary systems. In: Heaman, L., and Ludden, J.N., eds. Applications of radiogenic isotope systems to problems in geology. Mineralogical Association of Canada, Short Course Handbook, Vol. 19. 337–364.

MUIR, D., BORN, E.W., KOCZANSKY, K., and STERN, G. 2000. Temporal and spatial trends of persistent organochlorines in Greenland walrus (*Odobenus rosmarus rosmarus*). Science of the Total Environment 245:73–86.

OUTRIDGE, P.M., and STEWART, R.E.A. 1999. Stock discrimination of Atlantic walrus (*Odobenus rosmarus rosmarus*) in the eastern Canadian Arctic using lead isotope and element signatures in teeth. Canadian Journal of Fisheries and Aquatic Science 56:105–112.

OUTRIDGE, P.M., EVANS, R.D., WAGEMANN, R., and STEWART, R.E.A. 1997. Historical trends of heavy metals and stable lead isotopes in beluga (*Delphinapterus leucas*) and walrus (*Odobenus rosmarus rosmarus*) in the Canadian Arctic. Science of the Total Environment 203:209–219.

OUTRIDGE, P.M., McNEELY, R., and DYKE, A. 2000. Historical trends of stable lead isotopes, mercury and other trace metals in marine bivalve shells from the Canadian Arctic. Proceedings, 11th International Conference on Heavy Metals in the Environment, Ann Arbor, Michigan. August 6–10, 2000. Abstract No. 1179 (CD-ROM).

PIANKA, E. 1978. Evolutionary ecology. 2nd ed. New York: Harper and Row.

RIEWE, R., ed. 1992. Nunavut Atlas. Edmonton: Canadian Circumpolar Institute and Tungavik Federation of Nunavut.

ROYCE, W.F. 1972. Introduction to fisheries science. New York: Academic Press.

SANGSTER, D.F., OUTRIDGE, P.M., and DAVIS, W.J. 2000. Stable lead isotope characteristics of lead ore deposits of environmental significance. Environmental Reviews 8: 115–147.

STERN, R.A., OUTRIDGE, P.M., DAVIS, W.J., and STEWART, R.E.A. 1999. Reconstructing lead isotope exposure histories preserved in the growth layers of walrus teeth using the SHRIMP II ion microprobe. Environmental Science and Technology 33:1771–1775.

TAYLOR, P.N., and KALSBEEK, F. 1990. Dating the metamorphism of Precambrian marbles: Examples from Proterozoic mobile belts in Greenland. Chemical Geology 86: 21–28.

TAYLOR, P.N., KALSBEEK, F., and BRIDGWATER, D. 1992. Discrepancies between neodymium, lead and strontium model ages from the Precambrian of southern East Greenland: Evidence for a Proterozoic granulite-facies event affecting Archaean gneisses. Chemical Geology 94:281–291.

VAN DER MERWE, N.J., LEE-THORP, J.A., THACKERY, J.F., HALL-MARTIN, A., KRUGER, F.J., COETZEE, H., BELL, R.H.V., and LINDEQUE, M. 1990. Source-area determination of elephant ivory by isotopic analysis. Nature 346:744–746.

VOGEL, J.C., EGLINGTON, B., and AURET, J.M. 1990. Isotope fingerprints in elephant bone and ivory. Nature 346:747–749.

WHITEHOUSE, M.J., KALSBEEK, F., and NUTMAN, A.P. 1998. Crustal growth and crustal recycling in the Nagssugtoqidian orogen of West Greenland: Constraints from radiogenic isotope systematics and U-Pb zircon geochronology. Precambrian Research 91:365–381.

WIIG, Ø., GJERTZ, I., and GRIFFITHS, D. 1996. Migration of walruses (*Odobenus rosmarus*) in the Svalbard and Franz Josef Land area. Journal of Zoology (London) 238:769–784.

WINTER, B.L., JOHNSON, C.M., and CLARK, D.L. 1997. Strontium, neodymium and lead isotope variations of authigenic and silicate sediment components from the Late Cenozoic Arctic Ocean: Implications for sediment provenance and the source of trace metals in seawater. Geochimica Cosmochimica Acta 61:4181–4200.