Analyses on stable carbon and nitrogen isotope ratios in soft tissues of common minke whale (*Balaenoptera acutorostrata*) in Icelandic waters and its prey.

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Abstract

The objectives of the study were to evaluate the applicability of stable isotope analyses as an alternative method by means of non-lethal sampling in feeding ecology studies of the common minke whale. Three main questions were addressed: 1) How well do skin samples from the mid dorsal region (D4) resemble other tissues of the minke whale? 2) How do information on the minke whale diet obtained by stable isotope analyses compare to traditional stomach content analyses? 3) Can stable isotope ratio analyses lead to conclusive interpretations on the minke whale diet without supplementary information from stomach content analyses?

A total of 94 and 92 tissue samples were analyzed for δ13C or δ15N, respectively consisting of blood, muscle D4, skin M4.5, skin D4 from 36 whales in June to September in 2003, 2004 and 2006. Samples of common prey species of the minke whale were collected in 2003 to 2007.

The overall level of $\delta^{15}N$ in minke whale tissues was at the level of herring, above the levels of krill and sand eel and below adult cod fishes suggesting that krill and small sand eels may be important in the minke whale diet. The overall level of $\delta^{13}C$ was at level with adult codfishes but higher than krill, sand eel and the pelagic herring and capelin.

Paired comparison of isotope levels in skin-D4 to other tissue types revealed significant difference for $\delta^{13}C$ levels in muscle-D4 and for $\delta^{15}N$ levels in blood and muscle-D4 respectively. However, low significant difference in the intercept of the slopes suggests that biopsies may give representative information on the isotope levels in the other tissues and that the individuals' diet was relatively homogenous during the weeks prior to the sampling.

The glmm fitting best to the $\delta^{13}C$ data was based on the tissue type, region, length and period and for the $\delta^{15}N$ data on the tissue type and length. Comparison of the results from the stable isotope and stomach content analyses show somewhat lower trophic level in the isotope study. On the other hand, the spatial and temporal difference observed in the $\delta^{13}C$ is in line with the stomach content analyses, and suggest larger importance of prey of coastal origin in the SW and in 2003/04 compared to larger proportions of pelagic diet in the NE region and in 2006.

The generalist and opportunistic feeding behaviour of the minke whale make the interpretation of stable isotope analyses difficult without supplementary information from other sources. The method may however be useful in monitor signals of changes in the diet or changes further down the food chain.

Introduction

The common minke whale (*Balaenoptera acutorostrata*) in the North Atlantic migrates to the subarctic and arctic areas in the spring where it feeds during the boreal summer. The main concentrations are on the coastal shelf areas off eastern Canada, West and south Greenland, around Iceland, Jan Mayen and Svalbard, in the Barents Sea, along the Norwegian coast and in the North Sea (reviewed in Born et al., 2003) where the species plays considerable role in the coastal shelf ecosystems (Folkow et al., 2000).

Feeding studies of common minke whales have revealed generalist feeding behaviour and distinct geographical and temporal variance in the diet (Haug et al., 1995; Haug.T et al., 1996; Horwood, 1990; Jonsgard, 1982; Klinowska, 1991; Neve, 2000; Sigurjónsson et al., 2000; Tamura and Fujise, 2002; SC/F13/SP2). Studies on stomach content of the minke whale around Iceland revealed the importance of sand lance as food source in the South and Southwest areas whereas various codfishes were the modal prey species off the North and East coasts. Temporal changes were however observed probably due to fluctuations in prey abundance (Sigurjónsson et al., 2000; SC/F13/SP2)

While stomach content analyses may reveal detailed information about the diet including prey size and age constructed from hard particles such as bones and otoliths, the approach has been criticized for ignoring the effects of different digestibility of the prey. Easily digested prey is likely to be underestimated compared to prey of slowly digested hard particles (Hyslop, 1980; Jobling and Breiby, 1986; Santos et al., 2001). Furthermore, the conventional methods such as stomach content and scat analyses may only provide information on the last meal of the predator and may lead to oversimplified conclusions, especially in population with large geographical and temporal variations in food composition. In addition, the common reality of small sample sizes in many marine mammal foraging studies increases the risk of poorly representative overall sample in populations of generalist feeding behaviour.

Analysis of naturally occurring stable isotopes in predators' tissues and their prey have reached increased attention in marine mammal feeding ecology in the recent years as an alternative to the conventional methods and resolving at least one of the limitations listed above (Abend and Smith, 1997; Christensen and Richardson, 2008; Das et al., 2003; Hammill et al., 2005; Hobson et al., 1996; Lesage et al., 2001, 2002; Marcoux et al., 2007; Tucker et al., 2007). The utility of isotopes for the study of animal ecology is derived from the properties that the isotope signature of a food is incorporated into the consumers' tissues

(DeNiro and Epstein, 1978; Kelly, 2000). The most frequently used isotopes are carbon and nitrogen. The stable isotope ratios reflect the average diet over a prolonged period and may therefore be more appropriate in studies on generalist predator and small sample sizes.

The carbon isotope ratio ($^{13}C/^{12}C$) remains unchanged or slightly enriched through the food chain and the direct incorporation of the carbon-isotopes of plants into consumers' tissue gives information of the origin of the carbon. In terrestrial animals the signatures may reveal origin in C3 and C4 plants and in the marine food web a pelagic or coastal origin of the food source may be observed in the carbon isotope signatures. The heavy isotope of nitrogen (^{15}N) is preferentially incorporated into the tissues of the consumer from the diet, and therefore a systematic enrichment in nitrogen-isotope ratio ($^{15}N/^{14}N$) occurs with each trophic level. Stable isotopes of nitrogen have been used to assess position in food chains with the general assumption of 3-4 ‰ enrichment between trophic levels (Kelly, 2000). The enrichment rate is however species and tissue dependent and information on the enrichment profile for the species or the taxon is necessary for interpreting results on stable nitrogen values (Dalerum and Angerbjörn, 2005; Hobson et al., 1996).

Studies on tissues with different metabolic turnover rates may be used to analyze variations in the diet. Tissues with short turnover rate reflect recent food whereas tissues with high rates may give indications of the diet some days to weeks prior to the sampling (Podlesak et al., 2005; Sponheimer et al., 2006). Comparison of the isotope signatures in different tissues may therefore reveal information on temporal shifts in the diet (Dalerum and Angerbjörn, 2005; Phillips and Eldridge, 2006; Quillfeldt et al., 2008).

The aim of the present study was to investigate the representativeness of biopsy samples in stable isotope studies for minke whales and the overall applicability of stable isotope analyses compared to stomach content analyses by addressing the following questions:

- How well do skin samples from the mid dorsal region (D4) resemble other tissues of the minke whale?
- How do information on the minke whale diet obtained by stable isotope analyses compare to traditional stomach content analyses?
- Can stable isotope ratio analyses lead to conclusive interpretations on the minke whale diet without supplementing information from stomach content analyses?

Materials and methods

A total of 94 and 92 tissue samples were analyzed for $\delta^{13}C$ or $\delta^{15}N$, respectively. The samples consisted of four tissue types (blood, muscle D4, skin M4.5, skin D4) and were obtained from 36 whales landed in Icelandic waters in June to September in 2003, 2004 and 2006 (Table 1). For further description on the sampling procedure (see SC/F13/SP1).

Samples of common prey species of the minke whale were collected for the study in various research excursions in Icelandic waters in the years 2003 to 2007. Each sample consisted of five whole fish that were homogenized before the isotope analyses. Results on isotope levels for various fish species obtained from Pétursdóttir and Gíslason (2009) were included in the comparison.

Stable isotopes ratios were analysed at the Institute for Energy Technology (IFE), Kjeller, Norway. After drying the samples at 80°C to constant weight, they were homogenized in a mortar and finally defatted by Soxhlet extraction for 2 h using 93% dichloromethane and 7% methanol. Stable isotopes ratios ($\delta^{13}C$ and $\delta^{15}N$) were analysed on a Horizon Isotope Ratio Masspectrometer from NU-Instruments, Wales. The isotope enrichment (‰) relative to international isotopic standards is given by the following equation:

$$\delta X = \left[(R_{sample} / R_{s\tan dard}) - 1 \right] \times 1000$$

where δX is $\delta^{13}C$ or $\delta^{15}N$ and R is the ratio of either $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Pee Dee Belemnite (PDB: USGS 24) is the standard for $\delta^{13}C$ is while atmospheric air (IAEA-n-1 and IAEA-n-2) is the standard for $\delta^{15}N$.

Relationship between stable isotope ratios in skin D4 compared to blood, muscle-M4 and skin-M4.5 was evaluated using paired t-test and linear regression model in the R package (R Core Team 2012).

Models fitting the relationship of isotope ratios to a set of explanatory variables were built using generalised linear mixed model (glmmADMB package in R) (Skaug et al 2011) with a Gaussian link function. The variability of the model parameters was assessed by running *post hoc* Markow chain of 50000 MCMC iterations.

The explanatory variables used in the models were tissue type (blood, muscle d4, skin-D4, skin-M4.5), body length, period (2003/2004 and 2006) and region (SW: Látrabjarg south and east to Hornafjörður; NE: Látrabjarg north and east to Hornafjörður). Models testing for

interactions between region and period were evaluated. Whale ID was set as a random effect in the models tested.

Results

The results of the $\delta^{13}C$ and $\delta^{15}N$ (average +/-SD) in various tissues, regions and periods for the minke whale as well as common prey species are shown in Figure 1 and Table 1.

Paired t-test of isotope levels in skin-D4 samples compared to blood, muscle-D4 and skin-M4.5 respectively showed significant difference in $\delta^{15}N$ to blood and muscle-D4 at the 1% level and in $\delta^{13}C$ to blood at the 5% level (Table 2). Of the groups with significant difference in the paired t-test only skin-D4~muscle-D4 showed significant intercept in the regression analyses for $\delta^{15}N$ (Table 2, Figure 2 a, b).

The glmm fitting best to the $\delta^{13}C$ data was based on the tissue type, region, length and period and for the $\delta^{15}N$ data was based on the tissue type and length. Testing for interactions of area and periods did not improve the models (Table 3).

Discussion

The overall level of $\delta^{15}N$ in minke whale tissues is at the level of herring, above the levels of krill and sand eel and below adult cod fishes (Fig 1). Taking into account 3‰ to 4‰ enrichment between trophic levels this may lead to the assumptive conclusion that krill and small sand eel are of significant importance in the minke whale diet. The overall level of $\delta^{13}C$ in the minke whale tissues is at level with adult codfishes but lower than krill, sand eel and the pelagic herring and capelin. These somewhat contradictory results may suggest that the minke whale diet consists of prey species or populations not fully covered in the present study.

The low significant difference in the paired comparison of δ13C in skin-D4 samples and blood, muscle-D4 and skin-M4.5 respectively suggest that biopsy samples may give representative information on the isotope levels of the individual whale. Significance was only detected in paired comparison of δ13C in skin-D4 and blood. Paired comparison of δ15N in skin-D4 to other tissues showed significance at the 1% level for blood and muscle-D4. These results indicate that biopsy samples are less suitable to represent δ15N values in other tissues of the minke whale in these waters.

It is not known to what extent the various tissues of the minke whale represent different timing of food assimilation as reported previously for other species (e.g. Dalerum and Angerbjörn, 2005; Hobson et al., 1996; Lesage et al., 2001). The low significant difference in the various tissues suggests however that the source of diet is homogeneous with respect of trophic level and source of origin during the weeks or months reflected in the different tissues. The larger difference in δ13C values among tissue types suggest however, larger heterogeneity in the origin of prey than the trophic level.

The glmm model fitting best to the isotope data suggest that $\delta^{13}C$ values are highly dependent on tissue type, region and period and to a lesser extent the whale length. Interactions between regions or periods did not improve the fit. The best model for $\delta^{15}N$ suggests that tissue type and body length are the main explanatory parameters. These results for $\delta^{15}N$ suggest that the average trophic level of the minke whale diet is stable and does not vary geographically or by the size of the predator. Furthermore the relatively consequent $\delta^{15}N$ levels observed in the different tissue types and the two periods (2003/04 *vs* 2006) suggest little change in the average trophic level over shorter and longer time scale.

The somewhat more complex results of the δ13C analyses suggest that the diet in the NE region is by larger extent of pelagic origin than in the SW region. Furthermore, some shift towards diet of pelagic origin seems to have occurred from 2003/04 to 2006.

Comparison of the results from the stable isotope and stomach content analyses show somewhat lower trophic level in the isotope study. On the other hand, the spatial and temporal difference observed in the $\delta^{13}C$ is in line with the stomach content analyses, and suggest larger importance of prey of coastal origin in the SW and in 2003/04 compared to larger proportions of pelagic diet in the NE region and in 2006 (SC/F13/SP2).

In general it may be impossible to draw firm conclusions on the diet based solely on stable isotope signatures in a highly generalist and opportunistic predator as the minke whale. The diet consists of wide spectrum of prey species from different trophic levels and therefore it will be difficult to interpret the isotope data without supplementary information from other sources. The isotope levels may however prove useful as a monitoring tool and provide signals of changes in the minke whale diet or potential changes at lower trophic levels.

Improved mapping of information on isotope signatures in the ecosystem of the area as well as better knowledge on the turnover and enrichment rates in various tissues and predators is vital if the method will be applied in trophic ecology studies of the minke whale and other

organisms of the area. Factors such as body size, temperature, growth (addition of new material to the tissue) and catabolic turnover (replacement of material from the tissue as a result of catabolism) may also influence the incorporation of isotopes in the tissues causing increased complications in the interpretation of isotopic analyses (del Rio et al., 2009).

Tables

Table 1. Stable isotope ratios of minke whale blood, muscle and skin collected in Icelandic waters in 2003/4 and 2006 (A) and frequent minke whale prey species collected in Icelandic waters 2003-2007(B).

A) Minke whale	δ13C			δ15N		
Tissue/ Area/ Period	**N**	**δ13C**	**SD**	**N**	**δ15N**	**SD**
Blood						
NE						
2003/04	10	-18,18	0,57	10	11,48	1,42
NE Total	**10**			**10**		
SW						
2003/04	12	-17,54	0,46	11	11,15	1,02
SW Total	**12**			**11**		
Blood Total	**22**			**21**		
muscleD4						
NE						
2003/04	13	-17,70	0,50	12	11,55	1,06
2006	4	-18,15	0,47	4	11,30	0,65
NE Total	**17**			**16**		
SW						
2003/04	12	-17,19	0,42	12	11,43	0,77
2006	6	-17,72	0,38	6	11,75	1,69
SW Total	**18**			**18**		
muscleD4 Total	**35**			**34**		
skinD4						
NE						
2003/04	12	-17,91	0,56	12	11,88	1,73
NE Total	**12**			**12**		
SW						
2003/04	11	-17,16	0,62	11	12,00	1,28
SW Total	**11**			**11**		
skinD4 Total	**23**			**23**		
skinM4.5						
NE						
2003/04	7	-17,40	0,58	7	11,99	1,20
NE Total	**7**			**7**		
SW						
2003/04	7	-16,74	0,61	7	11,10	1,61
SW Total	**7**			**7**		
skinM4.5 Total	**14**			**14**		
Grand Total	**94**			**92**		

B) Prey species	N	δ13C	SD	N	δ15N	SD
M. norvegica/ Thysanoessa	2	-21,15	0,49	2	5,90	0,14
M. norvegica	3	-21,13	0,25	3	7,33	0,76
M. villosus	7	-20,24	0,24	7	11,29	0,48
C. harengus	5	-18,88	0,61	5	11,84	0,59
Ammodytae	6	-18,50	0,93	6	9,90	0,60
P. virens	5	-18,20	0,14	5	13,16	0,76
M. aeglefinus	8	-17,65	0,67	8	13,35	0,71
G. morhua all samples	7	-18,36	1,00	7	14,01	0,46
G. morhua 26-38cm	3	-18,73	1,12	3	13,60	0,45
G. morhua 51-64cm	4	-18,08	0,97	4	14,26	0,32

Table 2. Paired t-test and regression of $\delta^{13}C$ and $\delta^{15}N$ in skin-D4 to blood, muscle-D4 and skin-M4.5.

$\delta^{15}N$	Paired t-test					Regression				
	mean of difference	df	t	p		Intercept	SE	p		R^2
Blood	0,61	19	3,095	0,006	**	-0,40	1,89	0,833	ns	0,704
Muscle D4	0,49	21	2,849	0,010	**	-4,46	1,90	0,029	*	0,791
Skin M4.5	0,31	11	1,145	0,276	ns	3,23	2,00	0,137	ns	0,650
$\delta^{13}C$										
Blood	0,33	20	2,767	0,012	*	-3,01	3,64	0,418	ns	0,456
Muscle D4	-0,07	22	-0,642	0,528	ns	-2,04	3,79	0,596	ns	0,444
Skin M4.5	-0,43	11	-1,814	0,097	ns	-11,41	6,04	0.088	*	0,096

Table 3. 97.5% interval of glmm model parameters obtained from *post hoc* MCMC fitting

$\delta^{13}C$	2.5%	97.5%
(Intercept)	-1,99E+01	-1,83E+01
tissuemuscleD4	1,78E-01	6,16E-01
tissueskinD4	9,70E+02	5,54E-01
tissueskinM4.5	5,49E-01	1,09E+00
length	2,95E-04	2,57E-03
Area.codeSW	2,42E-01	8,13E-01
$\delta^{15}N$	2.5%	97.5%
(Intercept)	4,54E+00	8,32E+00
tissuemuscleD4	-1,98E+00	5,01E-01
tissueskinD4	2,46E-01	9,80E-01
tissueskinM4.5	-3,12E-02	8,21E-01
length	4,08E-03	9,49E-03

Figures

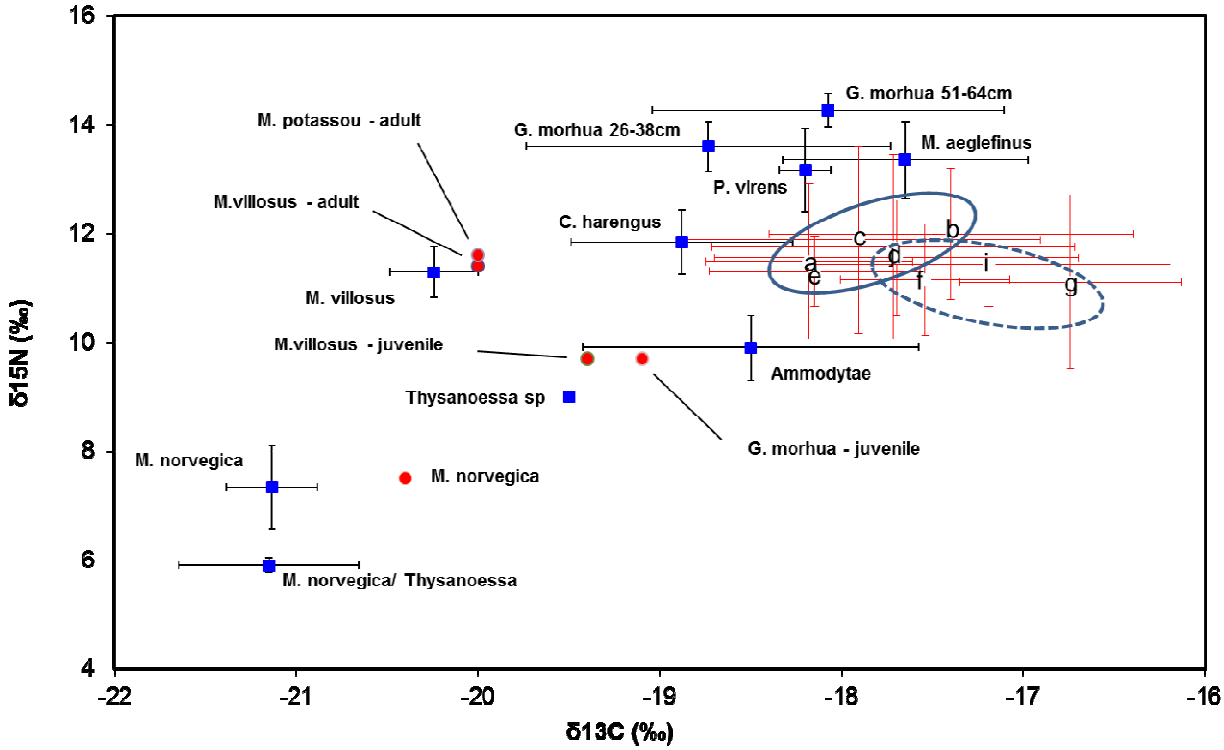
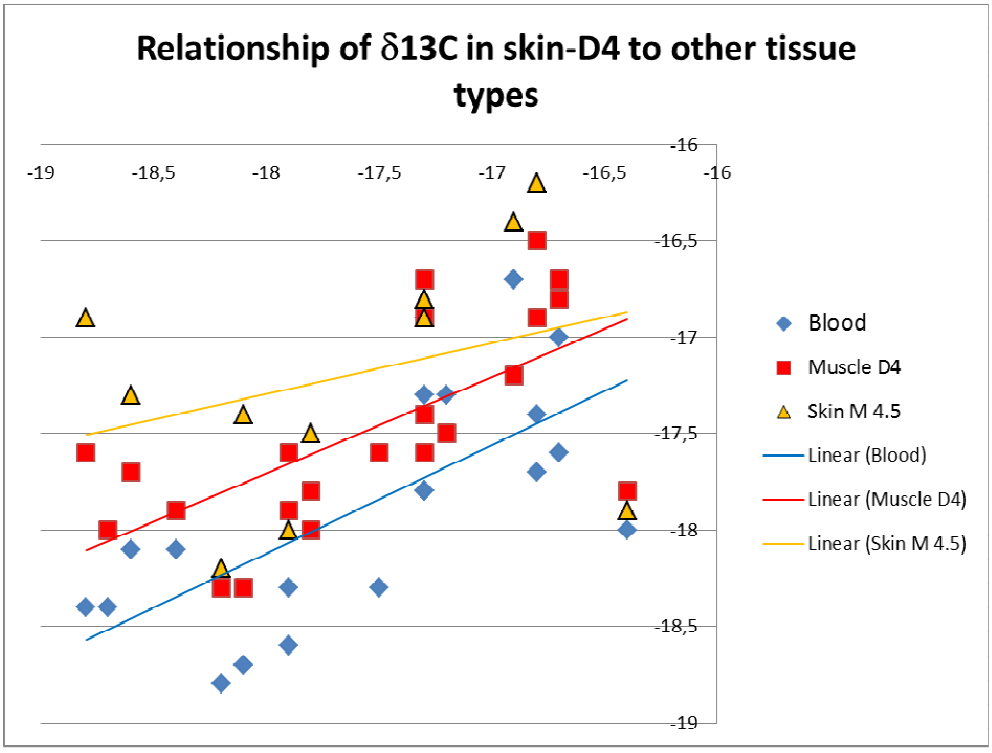
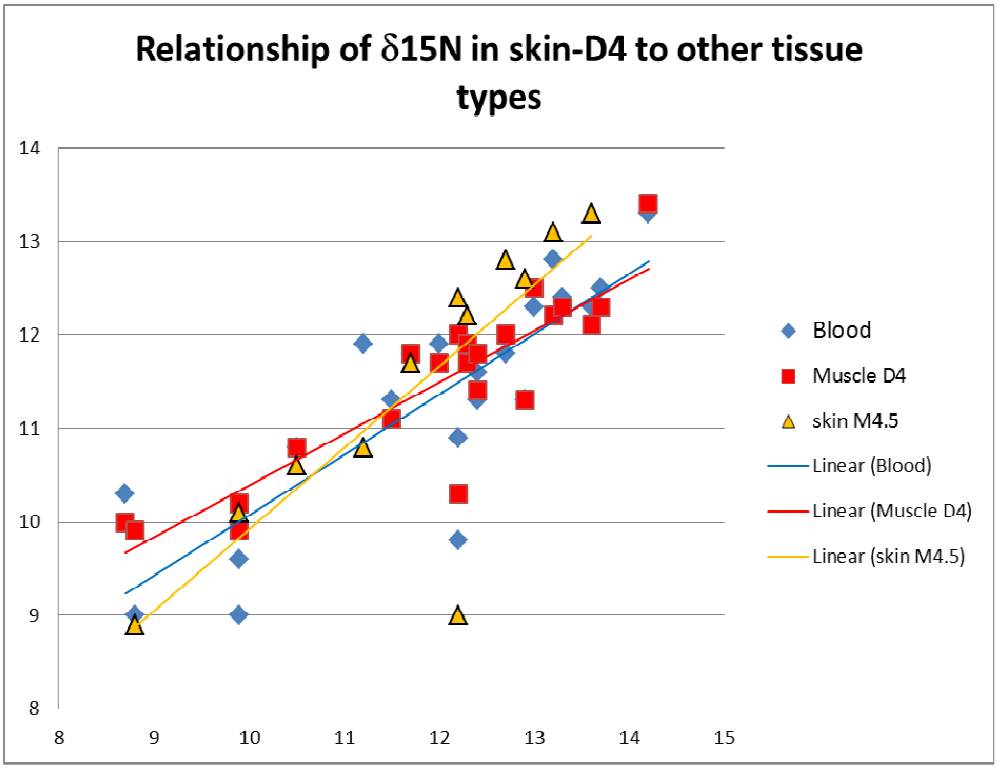


Figure 1. $\delta^{13}C$ and $\delta^{15}N$ levels in minke whale tissues (a-g) and common prey species (average +/- SD).
a. 2003-4/NE-blood, **b:** 2003-4/NE-skin-m4.5, **c:** 2003-4/NE-skin-d4, **d:** 2003-4/NE-muscle-d4, **e:** 2006/NE-muscle-d4, **f:** 2003-4/SW-blood, **g:** 2003-4/SW-skin-m4.5, **h:** 2003-4/SW-skin-d4, **i:** 2003-4/SW-muscle-d4, **j:** 2006/SW-muscle-d4

Circles with solid line: NE region and broken line: SW region. Red symbols represent data from Pétursdóttir and Gíslason (2009).



a)



b)

Figure 2. Relationship of a) δ13C, b) δ^{15}N in skin-D4 to other tissue types.

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