Body mass, muscle, blubber and visceral fat content and their seasonal, spatial and temporal variability in North Atlantic common minke whales

T. Gunnlaugsson[1], G.A. Víkingsson[1], S.D. Halldórsson[1], B.Þ. Elvarsson[1], T. Haug[2] and C. Lydersen[3]

Contact e-mail: thgunn@gmail.com

ABSTRACT

Total body mass and increase over the feeding season is important for estimating energy deposition used in ecological modelling. Weighing total whales is difficult, even in parts, while measurements of length, girth and blubber thickness can easily be obtained from catches at sea. The exponent for predicting total body mass from body length has been studied in many species and here data on common minke whales in the North Atlantic are added from both Icelandic and Norwegian research catches. The exponent was found to be not significantly different from 3 as is expected if there is little change in shape with growth. The exponent for how blubber mass increases with length was estimated to be significantly lower than 3. In addition, seasonal changes in body mass and in the parts of muscle, blubber and visceral fat are reported. In all cases a significant increase over the season was detected, in particular for the mature animals, and also in blubber thickness and girth measurements, particularly in girth at the posterior part of the body. Pregnant females had significantly more blubber than other whales. These results agree with studies on blubber thickness measurements and tissue energy content of the Icelandic whales and observed changes in the ecosystem around Iceland during the research period 2003 to 2007.

KEYWORDS: CLIMATE CHANGE; ENERGETICS; FEEDING GROUNDS; GROWTH; MINKE WHALE; MORPHOMETRICS; NORTH ATLANTIC; SEGREGATION

INTRODUCTION

Migratory baleen whales are capital breeders and cover the costs of reproduction at the winter breeding grounds from energy that is deposited at the summer feeding grounds (Armstrong and Siegfried, 1991; Kasuya, 1995; Lockyer, 1987a; 2007; Nordøy *et al.*, 1995). Temporal trends in blubber storage can provide important insights into the behavioural ecology of these species (Haug *et al.*, 2002; Konishi *et al.*, 2009; 2008; Miller *et al.*, 2011; Solvang *et al.*, 2017). Lockyer (1987b) and Víkingsson (1995) estimated the total energy content of fin whale carcasses and absolute seasonal energy storage from weighings and from chemical analysis of different organs and tissues. This study on the North Atlantic common minke whale (*Balaenoptera acutorostrata acutorostrata*), reports on seasonal trends in total body mass and masses of skeletal muscle (meat, not including tissue such as heart and tongue), blubber and visceral fat of Icelandic catches under a special permit research programme undertaken by Iceland from 2003 to 2007 (Marine Research Institute, 2003) and earlier Norwegian special permit research catches between 1988 and 1994 (Haug *et al.*, 1996). The Icelandic blubber data has been analysed in Christiansen *et al.* (2013); this paper compares these with the larger sample from Norway. The sampled animals are of different body lengths and, for comparison of mass, scaling is needed, therefore determining the exponent of length for predicting mass is essential. For most caught animals weighing is not practical, so for ecological modelling, body mass has to be predicted from measurements of length and possibly girth, while blubber thickness may be used for blubber mass.

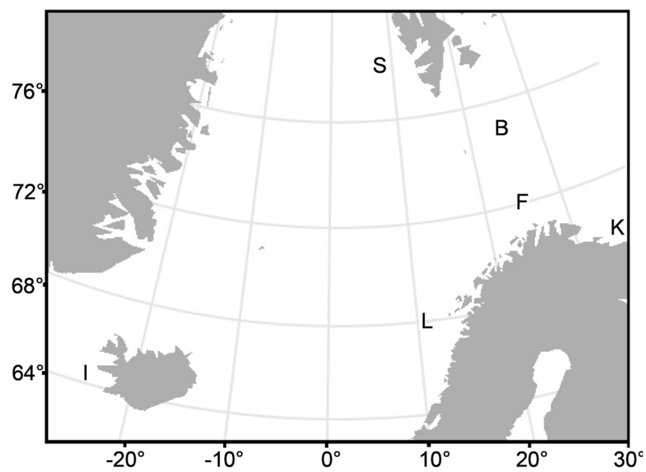

Fig 1. Sample locations off Iceland (I) and Norway: Lofoten Vesterålen (L); Finnmark (F); Björnöya (B); Spitsbergen (S); and Kola (K).

MATERIAL AND METHODS

Catches under the Icelandic special permit[4] were distributed based upon observed abundance from surveys undertaken around the country (Borchers *et al.*, 2009) and standardised measurements of length, girth and blubber thickness were taken from all animals caught. The subset of the sample with total or part weights was however only obtained from animals caught to the West of Iceland. The additional sampling areas off Norway are shown in Fig 1. Part weights were given for the whole Norwegian dataset and total weights for a subset from the first years with a small number of other kinds of measurements. More measurements were

[4] *https://iwc.int/permits.*

[1] *Marine and Freshwater Research Institute, Skúlagata 4 121, Reykjavík, Iceland.*
[2] *Institute of Marine Research, Fram Centre, PO Box 6606 Langnes, N-9296, Tromsø, Norway.*
[3] *Norwegian Polar Institute, N-9296, Tromsø, Norway.*

Table 1

Number and mean length (cm) of all the Icelandic research sample by years, sex and pregnancy. Measurements were made of girth G1–6 and blubber thickness dorsally (D1–6), median (M1–6) and ventrally (V1–6). Missing values are 3–5% – 140 out of the 190 whales have all the measurements and that includes all weighed whales.

	Number			Length (cm)			
Year	Males	Females	Pregnant	Males	Non-pregnant	Pregnant	Sampling period
2003	23	13	9	722	670	801	Late Aug.–Sep.
2004	10	15	10	764	670	809	Jun.–early Jul.
2005	20	14	7	723	695	822	Jul.–mid Aug.
2006	31	27	18	743	717	796	Late Jul.– arly Aug.
2007	12	25	21	772	693	787	Late Apr.–Aug.
All	96	94	65	738	692	799	Late Apr.–Sep.

Table 2

Number, mean length (cm) and mean total weight (kg) for the sample of total weights from Iceland (I) and Norway at Lofoten-Vesterålen (L) and Svalbard (S) by year, sex and pregnancy. The only measurement available for the Norwegian sample is G2 (girth under flipper).

		Number			Length (cm)			Total weight (kg)			
Year	Area	Males	Females	Pregnant	Males	Non-pregnant	Pregnant	Males	Non-pregnant	Pregnant	Sampling period
1988	L	11	1	0	742	510	–	4,895	1,150		Early Aug.
1989	S	0	6	2	–	659	735	–	2,725	4,428	Early Jul.
2004	I	0	1	0	–	–	774	–	–	4,607	Jun.
2005	I	6	3	2	716	762	798	3,466	3,528	5,474	Jul.–mid Aug.
2006	I	2	1	1	745	–	732	4,016	–	3,216	Late Jul.
2007	I	1	7	7	731	–	769	4,358	–	4,325	Late Apr., late Aug.
All		20	19	13	735	651	766	4,352	2,596	4,494	

added in the later years. The numbers by area and sex and the kind of measurements available are given in Tables 1–3. Average weights by year and country are given in Table 3b.

Maturity

Maturity was determined by inspection of sexual organs and hormone measurements for most of the animals caught off Iceland (Gunnlaugsson and Víkingsson, 2013), but only a few of the 1992–1994 Norwegian animals (except those observed with a foetus), so this had to be assigned based on standard length measurements. Males longer than 6.75m and females longer than 7.15m were considered mature according to Christensen (1981).

The percentage of mature specimens in the Icelandic sample was 80% for males and 90% for females, 75% of the latter were pregnant. The Norwegian data shows signs of segregation (Table 3a), where the Spitsbergen animals were all but one female, and out of 32 caught there in 1992 and 1993, 27 were classified as mature based on length, however only four of these were observed to be pregnant. In contrast, in 1994 only two out of 12 were classified as mature based on length and both were pregnant. In the sample from the Kola area taken in the midsummer period of 1992, seven of the eight females were mature and six of these were pregnant. In the combined sample from the Norwegian areas, about 40% were females, 50% of these mature and around 66% of the mature females were pregnant. Around 66% of the males were mature.

Measurements

The body length measurement (cm) is made on a flat surface in a straight line from tip of snout to the notch of fluke

Table 3a

Sample of muscle weights by area and year from late April–September. Same sample of blubber weights except for two missing values, and visceral fat weights the same except for 5 more missing values and all missing 1993, while 59 additional Icelandic animals had weights only of visceral fat. Girth G2 available for whole sample and by 1992 G4 and by 1993 G5, Blubber thickness first available at the three sites D1, D5, M2 in 1992 and the 10 sites D1, D3–6, M2, M4–5, V3 and V6 in 1993 and 1994. In the Kola (K) sample (only available for 1992) the D5 blubber thickness measurement was mostly below the range of measurements from other areas and was excluded. Of these missing girth and blubber thickness were 3–5%. Björnöya (B), Finnmark (F), Kola (K), Lofoten-Vesterålen (L) and Svalbard (S).

Year	Area	Males	Females	Pregnant	Sampling period
1988	L	12	3	0	Aug.
1989	B	0	1	0	Mid Jul.
1989	L	1	0	0	Mid Jul.
1989	S	1	7	3	Early Jul.
1989	All	2	8	3	Jul.–Aug.
1992	B	14	5	3	Jul.
1992	F	14	6	3	Jul.–early Aug.
1992	K	11	8	6	Jul.–early Aug.
1992	L	10	7	1	Jul.–early Aug.
1992	S	1	15	4	Jul.–early Aug.
1992	All	51	48	20	Jul.–early Aug.
1993	B	5	8	1	late Jun., mid Sep.
1993	F	7	6	4	late Jun., mid Sep.
1993	L	15	5	2	May–mid Sep.
1993	S	0	17	0	Jun.–Sep.
1993	All	27	36	7	May–Sep.
1994	B	4	17	7	May–Sep.
1994	F	10	9	4	May–Sep.
1994	L	10	7	1	May–Sep.
1994	S	1	12	2	Late Jul.
1994	All	25	45	14	May–Sep.
2004	I	5	2	1	Jun.
2005	I	6	3	2	Jul.–mid Aug.
2006	I	2	1	1	Late Jul.
2007	I	1	7	7	Late Apr., late Aug.

Table 3b

Weights available from Norway (N) and Iceland (I) Björnöya (B), Finnmark (F), Kola (K), Lofoten-Vesterålen (L) and Svalbard (S) – number, mean length and mean total weight by sex and pregnancy.

	Number			Length (cm)			Total weight (kg)		
Area	Males	Females	Pregnant	Males	Non-pregnant	Pregnant	Males	Non-pregnant	Pregnant
N	11	7	2	742	629	735	4,895	2,410	4,428
I	9	12	11	724	762	771	3,964	3,793	4,811
All	20	19	13	733	651	765	4,476	3,283	4,752
							Muscle weight kg		
B	23	31	11	736	675	820	1,811	1,347	2,260
F	30	21	11	761	581	806	1,847	803	1,956
K	11	8	6	695	723	743	1,599	1,490	1,641
L	48	22	4	750	623	832	1,964	1,053	2,239
S	3	51	9	682	702	771	1,247	1,362	1,944
N	115	133	41	743	668	795	1,850	1,241	2,017
I	14	13	11	737	723	771	1,416	1,253	1,472
							Blubber weight		
N	113	133	41	734	723	771	489	533	700
I	14	13	11	742	668	795	572	427	717
							Visceral fat weight		
N	85	95	34	750	653	788	30	14	30
I	40	40	30	741	683	802	22	24	64

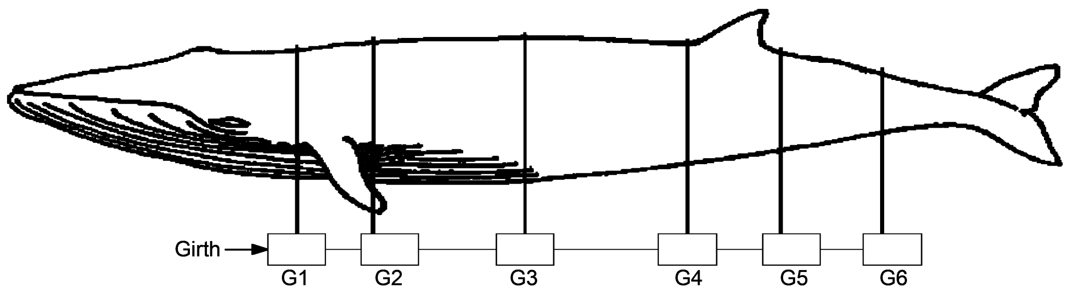

Fig. 2. Sites of measurements of girth (G1–6) and blubber thickness: dorsal (D1–6); median (M1–6); and ventral (V1–6) along the whale body. 1: Axilla, anterior insertion of flipper. 2: Axillary under flipper, posterior insertion. 3: End of ventral grooves. 4: Anterior edge of dorsal fin. 5: Posterior edge of dorsal fin base. 6: Midway between site 5 and insertion of tail.

(standard length) and was available for the whole sample. Complete girth measurements (cm) were taken during the Norwegian catches in 1988 and 1989, while half girth measurements (dorsally from top of back to ventrally the abdominal centre) were taken during the other catches and multiplied by two. Icelandic girth measurements were taken at six points along the body (see Fig. 2): G1 axillary in front of the flipper; G2 axillary under the flipper at the point of insertion; G3 at the end of the longest ventral grooves; G4 in front of the dorsal fin; G5 behind the fin; and G6 midway between G5 and the anterior edge of tail insertion. The Norwegian data have comparable girth G2 measurements and by 1992 and 1993 G4 and G5 data were collected respectively. There are a small number of missing values (about 3%) but few of these were for weighed whales.

Blubber thickness measurements (mm) from the skin surface perpendicular to the muscle connective tissue interface were available at all six girth sites dorsally (D1–6), median (M1–6) and ventrally (V1–6) in the Icelandic sample. There were about 5% missing values, and 140 out of the 190 whales had all the measurements and that included all the weighed whales. Norwegian blubber thickness measurements were first available at three sites D1, D5 and M2 in 1992 and 10 sites D1, D3–6, M2, M4–5, V3 and V6 in 1993 and 1994. In the Kola data (only available for 1992), the D5 blubber thickness measurement was mostly below the range of measurements from other areas and was excluded.

Total weights

During the Icelandic research catch the first whales weighed were towed to shore, including one weighed as a whole in 2004 and nine weighed in parts in 2005 (Table 2). The towing was generally short and no loss of tongue (a potential problem in heavy seas) was observed. In 2006 and 2007, 11 whales were weighed in parts on board the largest vessel. Blood and fluid lost during dissection was therefore not included in the total weights of part weighed whales. The whales were caught off West Iceland in April and from June to late August, during a short period each year. In total, the Icelandic material included total weights from 2 males and 1 immature female and 7 mature males and 11 pregnant females.

From the previous Norwegian research catch under special permit (Lydersen *et al.*, 1991; Nordøy and Blix, 1992) total weight, length and one comparable girth measurement (G2, axillary under flipper, Fig 2) was available for 11 males (6 mature) and 1 immature female, caught in the Lofoten and Vesterålen (L) area in August 1988, and 6 females (2 pregnant) caught West off Svalbard (S) in July 1989. The 18 Norwegian whales had been bled and were weighed whole including stomach contents, but they were also dissected and weighed in parts. Fluid loss during dissection was estimated at 7.5% (±2.4; Ryg *et al.*, 1993) and the remaining total weights based on part weights were corrected by that amount. This correction for fluid loss during dissection was also applied to estimate total weights in the Icelandic data. This correction is similar to observed fluid loss (7.4%) during dissection of fin whale foetuses (Víkingsson *et al.*, 1988).

Stomach contents were subtracted from the total weights of the animals that were weighed whole, while foetuses were always included.

The data from Iceland and Norway used here represent the only total weights of North Atlantic common minke whales that we are aware of.

Muscle, blubber and visceral fat weights

In addition to total weights, part weights of muscle (Table 3a) and blubber were available from more animals. In the Icelandic catch, five mature males and one immature female had been weighed in parts except for bones. Visceral fat weights (abdominal and thoracic combined) were also available for most of the part weighed animals and from an additional 59 animals.

The Norwegian data with total weights from 1988 and 1989 also had part weights. In addition, part weights were available for 1 mature male and 2 immature females in 1988, and 1 mature and 1 immature male and 1 immature and 1 pregnant female in 1989. Part weights were also available from the Norwegian research catch under special permit in 1992, 1993 and 1994 (Naess *et al.*, 1998; Table 3; Fig. 1). Visceral fat weights (Fig. 4) were missing for 1993 and there were blank values in the Norwegian data particularly early in the season. It is unclear whether the blanks represented zeros or missing values, but they have generally been assumed to be zero unless otherwise indicated (for instance by other missing values) resulting in 24% of the weights being assumed to be zero. Zeroes represented 10% of the visceral fat weights in the Icelandic data.

Analyses

Log-normal stepwise regression was performed using the *R* package (R Development Core Team, 2017) using the *lm* function on all girth and blubber thickness measurements with an exponent of length as a predictor, along with seasonal timing (catch day within year) and covariate factors for sex (male, maturity, pregnancy), year and area or country with interactions of these with the seasonal timing as the maximal model. Note that country is fully captured by year as there was no overlap of sampling years in Norway and Iceland. Unless otherwise stated, the best model was selected on the basis of the Akaike Information Criterion (AIC; Akaike, 1974).

The same regression was performed on total body mass, muscle, blubber and visceral fat mass separately. Potentially girth and blubber thickness measurements also predict the total mass, and thus girth and blubber thickness measurements have been presented first. As some of the visceral fat measurements were 0, before taking logarithms, an appropriate constant was added that was estimated to be 2kg (Box and Cox, 1964). Visceral fat was also regressed directly in a linear model to estimate absolute change.

A categorical variable indicating the Icelandic catches as either Northern or Southern on the continental shelf was tested but had no noticeable effect. Icelandic waters were therefore treated as a single area in the analyses presented here.

The null hypothesis in these regressions was that mass is in direct relation to the length cubed (*Condition Index* in Naess *et al.,* 1998 is Weight/Length^3×100), or girth squared times length, but some other estimated combinations of the exponents on length and girth that sum to 3 might outperform these if the girth measurements were less precise. Similarly, blubber thickness was expected to be in direct relation to blubber mass. This was tested using the *offset* setting of the *lm* function in *R.*

RESULTS

Girths and blubber thickness

As shown in Table 4, the largest combined data set of girth measurements was at site G2 (axillary under flipper) and gave an exponent on length of 0.89 (SE 0.025); significantly lower than the offset value 1 but this was not the case at G4 (in front of the fin) or G5 (behind the fin). The estimated increase per day was 0.1% at G2 and G4 and 0.13% at G5 with a CV of 0.1 in all cases. For a given length, G5 was significantly (6–10%) larger in Iceland than in Norway and area was significant and highest in Kola (only available in 1992 at G2 and G4). The measurements at sites G1, G3 and G6 (Iceland only) gave similar but less precise results and all with an exponent on length significantly less than 1 by respectively –0.19, –0.1 and –0.12 (SE 0.05). Girth for females (at some sites the model selected had pregnant females) was about 3–5% larger (SE 1%) and the seasonal increase was always lower and (slightly) significant only at G2. There was a significant year effect at girths G4 and G6 that were lowest in 2006.

Fitting the same model on the Icelandic blubber thickness measurements, the estimated exponent on length was not

Table 4

Log-linear regression on girth at site G2 (behind flipper) with offset 3*log(length). Sex, maturity and year insignificant. Predicted 359cm (CV 0.005) for a 750cm long non-pregnant common minke whale on day of year (DoY) 180.

R-squared: 0.8027 on 421 degrees of freedom. Significance Codes: 0 ‘***’ ‘.’ 0.1 ‘ ’ 1.

Coefficients	Estimate	Std.Error	t-value	Pr(>|t|)	Significance
(Intercept)	–0.1419	0.167	–0.850	0.396	
log(length)+3	–0.085	0.025	–3.4	7e–4	***
DoY–180	0.0010	0.00012	8.533	2e–16	***
pregnant	0.0525	0.0092	5.700	2.26e–8	***
DoY: pregnant	–0.0004	0.00022	–1.813	0.070	.

significantly lower than 1 around the fin (D4 and D5) or at D6 but at other sites ranged from 0.35 to 0.7 and lowest ventrally (V5 and V6). The exponent on the mean of all blubber thickness measurements was 0.68 (SE 0.11). The seasonal increase was highest around the middle of the animal and lowest (around 0.2%) per day at the front (site 1) and D6. Table 5 shows the regression results using the combined Icelandic and Norwegian data at site D3 where the seasonal effect was greatest (0.50% for non-pregnant animals). Pregnant females showed less seasonal effect at this site and this was also significant at M2 and M4 and negative (less seasonal effect) at all sites. Though not significant at all sites, blubber was consistently thicker for pregnant than nonpregnant females while males were thinnest. Mature animals had marginally thicker blubber only at the single site V6. The Kola measurements (D1, M2) were the highest. Other areas differ significantly, but not consistently where Svalbard was thinnest at D3 and M5 but thickest at D6 and V6. The greatest difference between countries was Iceland, thicker at M5 by 30%.

Table 5

Log-linear regression on blubber thickness at site D3 (dorsally between flipper and fin). Predicted 36.3mm (CV 0.036) for a 750cm long non-pregnant female on day of year (DoY) 180 off Iceland R-squared: 0.4439 on 304 degrees of freedom. Significance Codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Coefficients	Estimate	SE	t-value	Pr(>|t|)	Significance
(Intercept)	–0.235	0.738	–0.319	0.750	–
log(length)	0.578	0.1134	5.097	6.0e–7	***
DoY –180	0.0049	0.00043	11.389	<2e–16	***
pregnant	0.143	0.045	3.14	0.0018	**
pregnant:doy	–0.0019	0.0008	–2.407	0.016	*
male	–0.1409	0.0384	–3.673	2.8e–4	***
Björnöya	–0.128	0.0453	–2.825	0.005	**
Finnmark	–0.10978	0.0447	–2.444	0.015	*
Lofoten	0.0035	0.0425	0.082	0.934	–
Spitsbergen	0.2095	0.0522	–4.011	7.6e–5	***

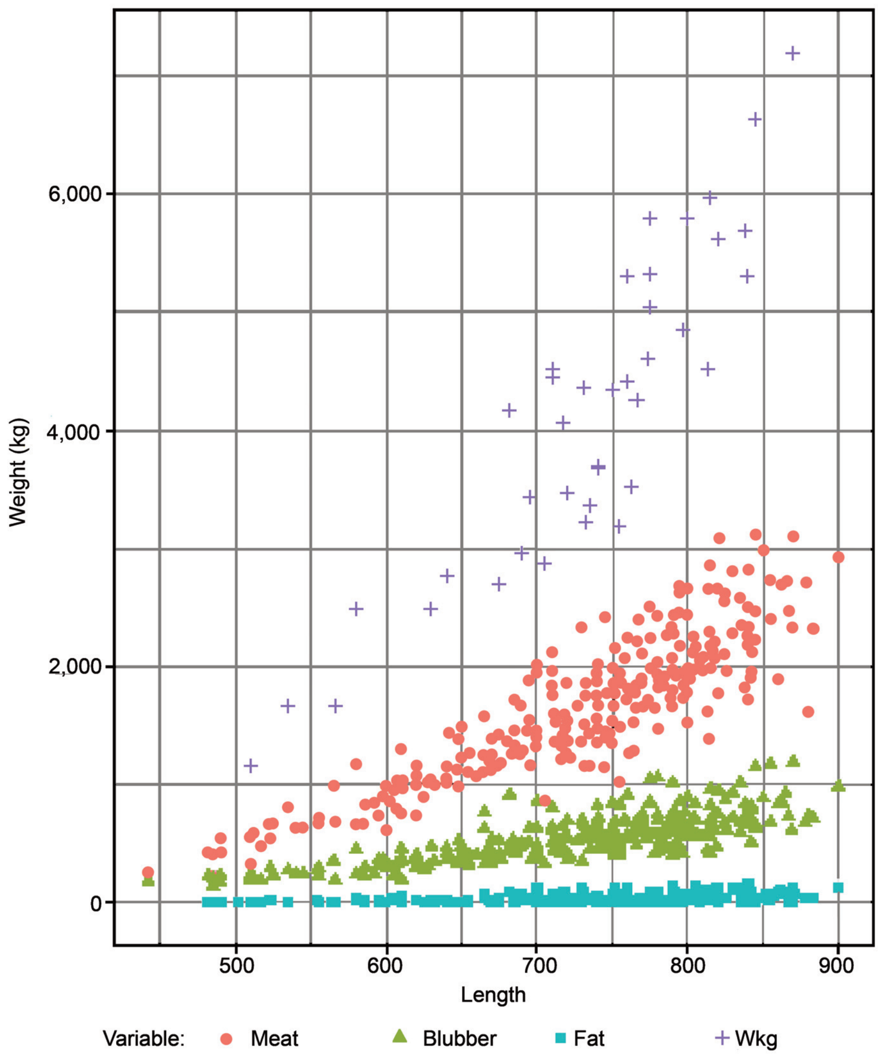

Fig 3. Icelandic and Norwegian weight data of North Atlantic common minke whales 1988–2007 showing total weights (Wkg); meat (skeletal muscle); blubber; and visceral fat (fat).

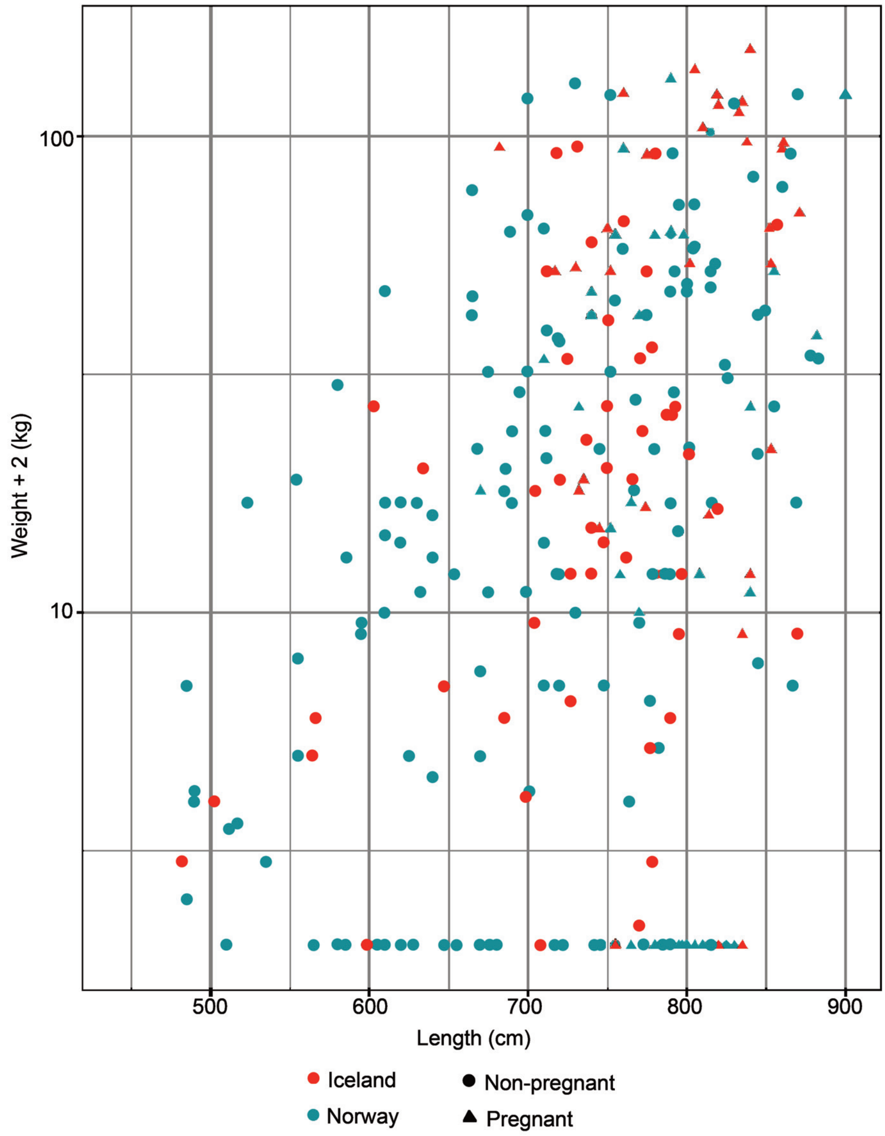

Fig 4. Icelandic and Norwegian visceral fat mass data of North Atlantic common minke whales 1988–2007 on a logarithmic scale.

For further comparison, the data from the Icelandic fin whale research catches 1986 to 1989 ($n = 122$) was checked and gave an exponent on length of 0.65 (CV 0.19) on mean blubber thickness, lower for males than females and lower for immature than mature animals.

Total body mass

All weight data are plotted in Fig. 3. The regression on Icelandic and Norwegian total body mass gave the exponent on body length of 2.91 (SE 0.15). This is not significantly different from 3 and was subsequently fixed at 3. The estimated 0.2% increase in body mass per day of the year was significant. The whales caught by Norway were on average 10% heavier, while interaction of area and both the day within year and body length was not significant. Pregnant animals were significantly (25%) heavier than non-pregnant animals for a given length. Males were 19% heavier than non-pregnant females of the same length and, although not significantly lower than pregnant females, were included as separate group in the model, as grouping them with either pregnant or non-pregnant females was considered unreasonable. There was no significant interaction of the sex, maturity and pregnancy factors with body length or the day within year. Year had no significant effect in these regressions.

Including the only available Norwegian girth measurement (G2) for the Norwegian weighed whales (Lydersen *et al.*, 1991) increased the difference by country (Table 7). The sum of the exponents of body length and girth was 2.93 (SE 0.13) and not significantly different from 3 but deviated significantly from 1 on length and 2 on girth, (1.9 and 1.1, respectively). As the girth was increasing over the season, including girth measurements in the model on body mass reduced the estimated increase over the season, but not significantly.

Restricting analyses to the Icelandic data, the girth at G4 gives an AIC of –8.6, lower than at G2 and the mass increase over the season is non-significant. The exponent on the girth was 1.3 (SE 0.3). Adding blubber thickness to this model with the exponents on length and girth fixed at 1 was in most cases non-significant and this was also the case using the mean of the blubber thickness measurements. The best fit was obtained with blubber thickness V2 with exponent 0.49 (SE 0.12) and AIC lower by –3.5, but mature animals still had significantly more mass.

Table 6

Log-linear regression of length in cm on total weight (corrected for fluid loss) of common minke whales. Offset 3*log(length). Predicted 3410kg (CV 0.052) for a 750cm nonpregnant female day of year (DoY) 180 off Iceland and approximately the mass increases by 0.2% per day, pregnant 22% heavier, males 17% heavier and all Norwegian minke whales 10% heavier. R-squared: 0.9392 on 34 degrees of freedom. Significance Codes: 0 '***' 0.001 '**' 0.01 '*'.

Coefficients	Estimate	SE	t-value	Pr(>|t|)	Significance
(Intercept)	–11.73	0.05.2	–223.591	<2e–16	***
DoY–180	0.00201	0.00056	3.592	0.0010	**
pregnant	0.223	0.0558	4.004	0.0003	***
male	0.166	0.048	3.435	0.00158	**
Norway	0.098	0.0367	2.672	0.0115	*

Table 7

Log-linear regression on total weight (corrected for fluid loss) including girth G2.
Offset log(length)+2*log(G2). R-squared: 0.9568 on 33 degrees of freedom. Significance Codes: 0 '***' 0.001 '**' 0.01 '*'

Coefficients	Estimate	SE	t-value	Pr(>|t|)	Significance
(Intercept)	–10.94	0.206	–53.124	<2e–16	***
DoY–180	0.0016	0.00048	3.280	0.00245	**
pregnant	0.143	0.0512	2.790	0.00869	**
male	0.105	0.0435	2.404	0.02200	*
Norway	0.150	0.336	4.459	9.01e–5	***
log(length/G2)	0.900	0.283	3.172	0.00326	**

Table 8a

Log-linear regression on muscle mass with offset 3*log(length). Predicted 1,430kg (CV 0.044) for a 750cm immature female on day of year (DoY) 180 off Iceland. R-squared: 0.885 on 269 degrees of freedom.
Significance Codes: 0 '***' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Coefficients	Estimate	SE	t-value	Pr(>|t|)	Significance
(Intercept)	–14.03	0.739	–18.991	<2e–16	***
log(length)+3	0.217	0.115	1.882	0.061	.
DoY–180	0.0014	0.0003	4.469	1.2e–5	***
Male	0.0749	0.019	3.870	1.3e–4	***
Mature	–0.082	0.034	–2.436	0.015	*
Norway	0.1807	0.032	5.603	5.2e–8	***

Table 8b

Log-linear regression of length in cm on muscle mass (kg) of NA common minke whales. Offset 2*log(G4)+log(length).
R-squared: 0.9214 on 235 degrees of freedom. Significance Codes: 0 '***' 0.001 '**'.

Coefficients	Estimate	SE	t-value	Pr(>|t|)	Significance
(Intercept)	–11.493	0.095	–120.680	<2e–16	***
male	0.040	0.015	2.631	0.009	**
Norway	0.222	0.024	9.152	<2e–16	***
log(length/G4)	0.774	0.097	7.942	8e–14	***

In the Icelandic data, including the five heaviest foetuses in the regression of length on mass was also tested and this gave an exponent on length of 2.92 (SE 0.04).

Muscle mass and blubber

For muscle, the exponent on length was estimated marginally higher than 3 (Table 8). Males had more muscle by 7% and mature animals less muscle by 8.2% (CV 0.3), while pregnancy appeared to have no effect. When the exponent was fixed at 3, maturity became non-significant with regard to muscle mass. Muscle increased with day by 0.13% (CV 0.04). The estimate for the exponent on length for blubber mass was significantly less than 3 but gave a daily mass increase over the season of 0.32% (CV 0.09) both with the exponent on length estimated or fixed at 3 (Table 9). Pregnant females had significantly more blubber by 17% (CV 0.2). The increases over the season did not differ between categories of animals. Not shown in the tables here were some significant differences between years and areas: the Kola area (1992 only) had the highest blubber mass overall; high blubber mass years were 2006 for Iceland and 1988 and 1989 for Norway. Muscle mass was highest in 1988 in Spitsbergen and it was around 20% higher in all Norwegian areas compared to Iceland. In Iceland, muscle mass decreased each year 2004 to 2007 (Marginally significant).

As shown in Table 8b, when predicting muscle mass with the girth measurement G4, the sum of the exponents (2.98) was not significantly different from 3, but the exponent on length was 1.8, significantly higher than 1 (and less than 2 at 1.2 on girth). The seasonal increase was fully captured by the girth. Maturity was non-significant, but males still had more muscle. The larger sample with girth measurement G2 gave similar results, but maturity and day in season were

Table 9

Log-linear regression on blubber mass predicted from length, day of year (DoY) and pregnancy, (sex, maturity and country insignificant). Offset 3*log(length). R-squared: 0.8008 on 268 degrees of freedom. Significance Codes: 0 '***' 0.001 '**'.

Coefficients	Estimate	SE	t-value	Pr(>|t|)	Significance
(Intercept)	–8.8417	0.5509	–16.048	<2e–16	***
log(length) +3	–0.7267	0.0841	–8.635	<6e–16	***
DoY–180	0.0036	0.0003	9.953	<2e–16	***
Pregnant	0.1742	0.0301	5.784	2.03e–8	***

Table 10

Log-linear regression on blubber mass predicted from girth G2, and as above.
R-squared: 0.8255 on 265 degrees of freedom. Significance Codes: 0 '***'.

Coefficients	Estimate	SE	t-value	Pr(>|t|)	Significance
(Intercept)	–8.5048	0.5198	–16.359	<2e–16	***
log(length)	1.2978	0.1729	7.503	9.4e–13	***
log(G2)	1.0384	0.1647	6.303	1.21e–9	***
DoY–180	0.0026	0.0003	7.218	5.5e–12	***
Pregnant	0.1219	0.0294	4.134	4.80e–5	***

Table 11

Log-linear regression on blubber mass (kg) predicted from average blubber thickness (BT) at sites V3+M2+M4+M5+D1+D3+D5 (mm) and as above.
R-squared: 0.8733 on 143 degrees of freedom. Significance Codes: 0 '***'.

Coefficients	Estimate	SE	t-value	Pr(>|t|)	Significance
(Intercept)	–7.7617	0.6185	–14.282	<2e–16	***
log(length)	1.7871	0.1072	16.670	<2e–16	***
DoY–180	0.0017	0.0003	4.563	1.08e–05	***
pregnant	0.1391	0.0324	4.288	3.30e–05	***
log(BT)	0.5512	0.0822	6.706	4.32e–10	***

Table 12

Log-linear regressions on blubber weight by different blubber thickness measurements and combinations thereof, length, day of year (DoY) and pregnancy. The sum of the coefficients for blubber thickness and length around 2.3 for larger sample (D1+5+M2) and 2.2 for smaller sample.

	Thickness	SE	DoY	SE	Pregnant	SE	RSE	Df
1992–2007								
D1	0.243	.044	.0027	.00032	.17	.026	0.150	242
D5	0.338	.066	.0023	.00034	.16	.027	0.144	222
M2	0.259	.046	.0025	.00033	.16	.026	0.150	241
D1+5+M2	0.49	.071	.0019	.00034	.14	.027	0.139	221
1993–2007								
V3	0.209	.061	.0028	.00035	.17	.034	0.152	151
V6	0.047	.042	.0032	.00036	.19	.035	0.158	150
M4	0.263	.049	.0024	.00035	.16	.035	0.145	146
M5	0.188	.041	.0026	.00035	.17	.033	0.147	151
D3	0.265	.045	.0023	.00035	.16	.032	0.143	151
D4	0.095	.034	.0028	.00036	.18	.035	0.154	152
D6	0.282	.086	.0028	.00035	.20	.033	0.152	152
V3M45D3	0.38	.063	.0019	.00037	.14	.033	0.141	144

marginally significant. Using the much smaller sample with G5, only maturity had a significant effect on muscle mass; the exponent on length was even higher at 2.3 (and correspondingly smaller on girth). In all cases the difference of Iceland and Norway remained the same.

The results of predicting blubber mass with girth are given in Table 10 and with blubber thickness in Table 11. The sum of the exponents on length and girth was significantly lower than 3 and in particular the exponent on girth is low and only marginally lowers the estimate of the coefficient for the increase in blubber mass with day of season. When the exponent on girth was fixed at 2, the coefficient for increase by day of season in blubber mass was estimated to be lowest when including girth measurement G5 but was still 0.09% per day. The exponent on blubber thickness was low for individual measurement sites, but higher when the sample is larger (D1, D5 and M2) (data for more years from Norway). The exponent was also higher when the sum of the individual measurements was used (Table 12). The higher the estimated exponent on blubber thickness, the lower the estimated coefficient for increase with day of season, but as the exponent was always considerably less than 1, blubber thickness did not fully capture the seasonal trend or differences due to pregnancy. Adding girth measurements to

Table 13

Log-linear regression on log(Visceral fat +2kg) with offset 3*log(length).
R-squared: 0.3922 on 258 degrees of freedom. Significance Codes: 0 '***' 0.001 '**'.

Coefficients	Estimate	SE	t-value	Pr(>|t|)	Significance
(Intercept)	–17.8100	3.350	–5.316	2.29e–7	***
DoY–180	0.0236	0.0023	10.191	<2e–16	***
Pregnant	0.4208	0.1598	2.633	0.00897	**

Table 14

Linear regression on visceral fat (kg), length (cm), day of year (DoY), sex and sexual condition.
R-squared: 0.3418 on 258 degrees of freedom. Significance Codes: 0 '***'.

Coefficients	Estimate	SE	t-value	Pr(>|t|)	Significance
(Intercept)	–57.770	14.27	–4.047	6.85e–5	***
length	0.094	0.019	4.708	4.09e–6	***
DoY–180	0.518	0.061	8.404	2.9e–15	***
Pregnant	19.28	4.26	4.517	9.54e–6	***

the model was marginally significant and highest for G4 when the coefficient for day of season was lower but still highly significant.

Visceral fat mass

Visceral fat increased by 0.52kg (SE 0.06) or 2.4% (SE 0.3%) per day (Table 13 and 14). Pregnancy added significantly to this (52%, on average 19kg). The parameter with log(length) (exponent on length) was 3.0 (SE 0.51) i.e. much less precise than other regressions. The factors country and year were insignificant. In the linear regression, an additional metre in body length added 9kg to visceral fat. Fitting length squared or cubed in the linear model made a negligible difference. There were some differences by year and area; animals from the Björnöya area and Iceland in 2003 and 2006 had the least visceral fat. When limited to the Icelandic data (with very few zeroes) the results were similar with an increase of 1.8% (SE 0.3) per day and a greater difference among pregnant and other types. Similarly restricting to animals over 650cm made little difference. Including girths lowered the estimated coefficient for increase with day of season, the highest was for G4 (1.8% or 0.35kg per day). Effects of explanatory factors varied greatly depending on whether the linear or log-linear model was used.

DISCUSSION

Considerations of area and other factors

The Norwegian dataset of total weights is smaller than the Icelandic and unbalanced by sex and segregated by geographical origin. Segregation by sex has been observed consistently in catches from different areas within Norwegian waters (Øien, 1988). Some of the Norwegian areas were only present in this sample in a single year and month, so not surprisingly these data add little to the precision regarding any day within year effect. Despite this, sex, maturity status and area had little effect on the within year trend on either total or partial mass. The lower mass (by length) in the Icelandic data might be real, as there are other indications that conditions around Iceland were poor and getting poorer during the investigated period (Astthórsson *et al.*, 2007; Víkingsson *et al.*, 2013; Víkingsson *et al.*, 2014) and a decrease in common minke whale occurrence has been observed in abundance surveys around Iceland in recent years (Víkingsson *et al.*, 2015). However, at least part of the difference may be due to differences in the weighing methods used in Iceland versus Norway, in particular the large difference in muscle mass and girth and blubber thickness at certain sites. When the most widely available girth measurement (G2, axillary under flipper) was included in the regression on total mass, the difference between areas increased, which was contrary to expectation if the condition of the animals differed by areas and if this was reflected in the girth. Neither did fitting girth on muscle mass reduce the difference by country. Either mass deposition is not well reflected at this site or the difference was due to factors such as fluid loss in the Icelandic total weighing, but that would not explain why muscle and blubber mass is also lower in the Icelandic area. The G5 girth (behind dorsal fin) measurement is about 10% less in the Icelandic data, but this might also be due to some difference in the body positioning of this measurement where blubber thickness decreases sharply with distance from the fin. There were other differences between areas and years (not all detailed here) that were not consistent among sites and were unlikely to reflect persistent biological differences. There were also some inconsistencies within area and year such as blubber mass versus muscle mass. For example, blubber mass for Iceland was highest in 2006, but blubber thickness at some sites was low. This raises the question as to whether there was some difference in measurements and tissue classification between the expeditions (such as more meat left on the bones in Iceland). However, this did not, in general, affect other estimates such as the trend over the season.

Pampoulie *et al.* (2013) found no genetic structure on the feeding grounds in the North Atlantic. It is therefore unlikely that the observed differences between areas are of genetic origin, rather that they are coincidental, or reflect segregation by body condition or the feeding conditions at the areas prior to sampling.

In their studies of seasonal variations in minke whale body condition in Norwegian waters, Naess *et al.* (1998) observed an increase in visceral fat and blubber thickness from snout to tail over the summer that varied with site on the whale body, with more depositions on the dorsal and lateral than on the ventral sides. The present paper confirms the largest increase is mid-body dorsally (D3) but with less on the tail and close to head, however this can be sensitive to what exponent on length is obtained at each site. Visceral fat increases the most over the season and greater care in collecting these data and avoiding zero values should be a primary objective if additional data are collected.

Due to the limited information on sexual condition, pubertal animals could not be assigned to a separate category. The immature size limit probably includes pubertal animals. There are indications (Víkingsson *et al.*, 2013) that pubertal animals are more similar to mature than immature animals with regards to fat deposition and this would therefore have blurred the differences of these categories.

Exponent on length

When girth is included in a regression on weight, an exponent on length close to 1 is expected and an exponent on girth close to 2, since the girth is reflecting two dimensions (breath and height). However, the best fit obtained showed almost the opposite in that the exponent on length was found to be close to 2 and that for girth close to 1. As there have been no hints of an allometric change, this is likely a function of lower precision in the girth measurements where both the point of measurement along the body is uncertain and the top dorsal and ventral points in the half-girth measurements are unclear. When length was dropped from the regression whilst retaining girth, the fit was poorer than in the model with length and no girth. The sum of the exponents of length and girth was, however, as expected close to 3.

Blubber thickness measurements are the least precise measurements given the variation in exactly how and where the blubber is cut. The exponent on blubber thickness (and the sum of the exponents on blubber thickness and length) increased with sample size and this was not a function of the position of measurement as when the measurements with the larger sample (D1, D5 and M3 $n = 224$) were restricted to the smaller sample at other positions ($n = 150$), the exponent on blubber thickness was lowered by 0.13, while using the average of different measurement positions reduces noise and increases the exponent (Table 12).

Hauksson *et al.* (2013) found an exponent on length of 2.76 (SE 0.2) for weighed common minke whale foetuses. The exponent on length when some large foetuses were included in this dataset was close to 3 as expected, since the girth to length ratio in large foetuses is very similar to the ratio in adults, indicating that little relative morphometric change is taking place from foetus to adult (transforming into a more flattened or elongated form would take the exponent on length down).

In the regression on girth, the exponent on length was above 0.8 in all cases and 1 at sites G4 and G5. In the regression on blubber thickness the exponent on length was also 1 at these sites dorsally (D4 and D5 in front of and behind the fin) and also at D6, but for blubber thickness at other sites the exponent on length was 0.3–0.7 and for blubber mass the exponent on length was significantly lower than 3. This implies that the blubber thickness does not increase proportionally with the length of the animal and this is similar to observations in other whale species (e.g. Miller *et al.*, 2011) and other marine mammals as can be derived from equations 1 and 12 of Ryg *et al.* (1993), where the minke whale mean blubber thickness came from the Norwegian samples from 1988 and 1989.

Solvang *et al.* (2017) regressed length on blubber thickness behind the blow hole (approximately D1), at D5 and M2 in whales caught by Norway 1993 to 2013 and decided not to use length in their model. These findings do not support the use of the *condition index* suggested by Naess *et al.* (1998). Once the whale has reached optimal blubber thickness for keeping warm while not overheating during exercise, and assuming that the BMR increases with the power 2/3 on mass (the power 2 on length), the increased heat production with length will match the increased surface and there will be no need for thicker blubber for insulation. Assuming a power of 3/4 for BMR on mass (Kleiber, 1932), the optimal blubber thickness for insulation would decrease with size. Larger animals may store proportionately more reserves as visceral fat as implied by the exponent on length exceeding 3. Considerable cooling must result from engulfing large amounts of sea water while feeding, but that would not apply to suckling calves where the need for thick insulating blubber is believed to be reduced by being born in warmer waters.

Model considerations

The regression presented here should give a good prediction of mass for a dataset similar to the one used here, but while the estimated parameters are unbiased by errors in the dependent variable there are probably some errors in the explanatory variables such that the exponent (slope) will not reflect the true exponent in the population, but be biased towards zero (Carroll *et al.*, 2006). This may explain why the exponent on length when explaining total mass is not 3 as expected but lower. When girth measurements were included in the model, the sum of the exponents on length and girth was around 2.9. The day within year is unlikely to contain errors (animals are numbered and a date out of sequence would be noticed). However, the feeding season may not be the same for all animals within each category, some starting early and others late and moving between areas as they gain weight and this will have the same effect as an error in measurement. Therefore, the trend within season is also probably underestimated. Girth represents two dimensions in the body and the increase in the cross sectional area scales with the square of the increase in the circumference (girth). It is therefore of no surprise that the estimated coefficient for seasonal increase in girth is about half that in blubber thickness and mass. Since the dataset is small and the length measurements have some unquantified errors, we do not attempt here any between species comparison such as performed by Lockyer (1976). This also implies that any formula obtained in the present study will not be optimal for body mass estimation from length measurements that have a different range.

CONCLUSION

The exponent of length regressed on total body and skeletal muscle mass was not significantly different from 3. When girth measurements were included in the model, the sum of the exponents of girth and length was closer to 3, while the exponent on visceral fat may be higher. The blubber mass proportion decreased with length (the exponent of length was lower than 3) and the blubber thickness only increased by around the square root of length. A significant increase was detected in body mass for a given length over the summer in Icelandic waters and in muscle, blubber and visceral fat. This is similar to observations made in Norwegian waters for 1992–1994 (Naess *et al.*, 1998) and the present results were strengthened by including the Norwegian data. Immature animals showed less increase in mass for a given length, probably due to them growing more in total length during the season. The increase in mass was not fully explained by the increase in the available girth measurements. Girth measurements showed more fattening towards the caudal part of the body. Females have less muscle while pregnant females are heavier and have more visceral fat, blubber mass and blubber thickness from the start of the season. A lower increase over the season seen in blubber thickness of pregnant females at three sites was not clearly reflected in the much smaller blubber mass sample. Pregnant females must have gained weight earlier in the season and/or only those females with good reserves became pregnant. The predicted increase in mass for a given length over the season estimated here is in addition to any increase in mass due to growth in body length over the season. In particular, females increase in length after maturation (Víkingsson *et al.*, 1988). These results confirm the seasonal increase in blubber thickness measurements in the Icelandic sample (Christiansen *et al.*, 2013), here incorporating also a large Norwegian sample. Increased tissue energy content over the season, such as lipid replacing water in bones in these whales, as reported by Víkingsson *et al.* (2013), comes on top of the increase in mass.

ACKNOWLEDGEMENTS

The authors are grateful for the useful comments of two anonymous reviewers. We also wish to thank all those who worked tirelessly to bring this paper to publication.

REFERENCES

Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19(6): 716–23.

Armstrong, A.J. and Siegfried, W.R. 1991. Consumption of Antarctic krill by minke whales. *Antarct. Sci.* 3(1): 13–18.

Astthórsson, O.S., Gislason, A. and Jonsson, S. 2007. Climate variability and the Icelandic marine ecosystem. *Deep-Sea Res. II* 54: 2456–77.

Borchers, D., Pike, D., Gunnlaugsson, H. and Víkingsson, G. 2009. Minke whale abundance estimation from the NASS 1987 and 2001 aerial cue-counting surveys taking appropriate account of distance estimation errors. *NAMMCO Sci. Publ.* 7: 95–110.

Box, G.E.P. and Cox, C.R. 1964. An analysis of transformations. *J. Roy. Stat. Soc. (Series B)* 26: 211–46.

Carroll, R.J., Ruppert, D., Stefanski, L.A. and Crainiceanu, C.M. 2006. *Measurement Error in Nonlinear Models: A Modern Perspective.* 2nd Edn. Chapman and Hall/CRC, Florida. 484pp.

Christensen, I. 1981. Age determination of minke whales, *Balaenoptera acutorostrata*, from laminated structures in the tympanic bullae. *Rep. Int. Whal. Commn* 31: 245–53.

Christiansen, F., Víkingsson, G., Rasmussen, M. and Lusseau, D. 2013. Minke whales maximise energy storage on their foraging grounds. *J. Exp. Biol.* 216: 427–36.

Gunnlaugsson, T. and Víkingsson, G.A. 2013. Changes in blood testosterone and progesterone concentrations in the North Atlantic common minke whale (*Balaenoptera acutorostrata*) during the feeding season in Icelandic waters. Paper SC/F13/SP13 presented to the IWC Scientific Committee Icelandic Special Permit Expert Panel Review Workshop, 18–22 February 2013, Reykjavík, Iceland (unpublished). 7pp. [Paper available from the Office of this Journal].

Haug, T., Lindstrøm, U. and Nilssen, K.T. 2002. Variations in minke whale *Balaenoptera acutorostrata* diets in response to environmental changes in the Barents Sea. *Sarsia* 87: 409–22.

Haug, T., Lindstrøm, U., Nilssen, K.T., Røttingen, I. and Skaug, H.J. 1996. Diet and food availability for northeast Atlantic minke whales, *Balaenoptera acutorostrata*. *Rep. Int. Whal. Commn* 46: 371–82.

Hauksson, E., Víkingsson, G.A., Ólafsdóttir, D., Halldórsson, S.D. and Sigurjónsson, J. 2013. Sexual differences in the morphology of the common minke whale (*Balaenoptera acutorostrata* Lacepède, 1804) caught in Icelandic waters in the period 2003–2009. Paper SC/F13/SP12 presented to the IWC Scientific Committee Icelandic Special Permit Expert Panel Review Workshop, 18–22 February 2013, Reykjavík, Iceland (unpublished). 40pp. [Paper available from the Office of this Journal].

Kasuya, T. 1995. Overview of cetacean life histories: an essay on their evolution. pp.481–97. *In*: Blix, A.S., Walløe, L. and Ulltang, O. (eds). *Whales, Seals, Fish and Man: Proceedings of the International Symposium on the Biology of Marine Mammals in the Northeast Atlantic*. Elsevier, Amsterdam. 720pp.

Kleiber, M. 1932. Body size and metabolism. *J. Agric. Sci.* 6(11): 315–53.

Konishi, K., Tamura, T., Goto, M., Bando, T., Kishiro, T., Yoshida, H. and Kato, H. 2009. Trend of blubber thickness in common minke, sei and Bryde's whales in the western North Pacific during JARPN and JARPN II periods. Paper SC/J09/JR20 presented to the Expert Workshop to Review Results of JARPN II, 26–30 January 2009, Tokyo, Japan (unpublished). 4pp. [Paper available from the Office of this Journal].

Konishi, K., Tamura, T., Zenitani, R., Bando, T., Kato, H. and Walløe, L. 2008. Decline in energy storage in the Antarctic minke whale (*Balaenoptera bonaerensis*) in the Southern Ocean. *Polar Biol.* 31: 1509–20.

Lockyer, C. 1976. Body weights of some species of large whales. *Journal du Conseil International pour l'Exploration de la Mer* 36(3): 259–73.

Lockyer, C. 1987a. The relationship between body fat, food resource and reproductive energy costs in North Atlantic fin whales (*Balaenoptera physalus*). *Symposia of the Zoological Society, London* 57: 343–61.

Lockyer, C. 1987b. Evaluation of the role of fat reserves in relation to the ecology of North Atlantic fin and sei whales. pp.183–203. *In*: Huntley, A.C., Costa, D.P., Worthy, G.A.J. and Castellini, M.A. (eds). *Approaches to Marine Mammal Energetics*. Society for Marine Mammalogy, Lawrence, Kansas. xviii+253pp.

Lockyer, C. 2007. All creatures great and smaller: a study in cetacean life history energetics. *J. Mar. Biol. Ass. UK.* 87: 1035–45.

Lydersen, C., Weslawski, J.M. and Øritsland, N.A. 1991. Stomach content analysis of minke whales (*Balaenoptera acutorostrata*) from the Lofoten and Vesterålen areas, Norway, August 1988. *Holarctic Ecology* 14: 219–22.

Marine Research Institute. 2003. A programme for a two year feasibility study on cetaceans in Icelandic waters. Paper SC/55/O2 presented to the IWC Scientific Committee, May 2003, Berlin (unpublished). 63pp. [Paper available from the Office of this Journal].

Miller, C.A., Reeb, D., Best, P.B., Knowlton, A.R., Brown, M.W. and Moore, M.J. 2011. Blubber thickness in right whales *Eubalaena glacialis* and *Eubalaena australis* related to reproduction, life history status and prey abundance *Mar. Ecol. Prog. Ser.* 438: 267–83.

Naess, A., Haug, T. and Nilssen, E.M. 1998. Seasonal variation in body condition and muscular lipid contents in Northeast Atlantic minke whales *Balaenoptera acutorostrata*. *Sarsia* 83(3): 211–18.

Nordøy, E.S. and Blix, A.S. 1992. Diet of minke whales in the northeastern Atlantic. *Rep. Int. Whal. Commn* 42: 393–98.

Nordøy, E.S., Folkow, L.P., Martensson, P.E. and Blix, A.S. 1995. Food requirements of northeast Atlantic minke whales. pp.307–17. *In*: Blix, A.S., Walløe, L. and Ulltang, O. (eds). *Whales, Seals, Fish and Man: Proceedings of the International Symposium on the Biology of Marine Mammals in the Northeast Atlantic*. Elsevier, Amsterdam. 720pp.

Øien, N. 1988. Length distributions in catches from the northeastern Atlantic stock of minke whales. *Rep. Int. Whal. Commn* 38: 289–95.

Pampoulie, C., Danielsdottir, A. and Víkingsson, G. 2013. Genetic structure of the North Atlantic common minke whale (*Balaenoptera acutorostrata*) at feeding grounds: a microsatellite loci and mtDNA analysis. Paper SC/F13/SP17 presented to the IWC Scientific Committee Icelandic Special Permit Expert Panel Review Workshop, 18–22 February 2013, Reykjavík, Iceland (unpublished). 17pp. [Paper available from the Office of this Journal].

R Development Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available at: *http://www.R-project.org/*].

Ryg, M., Lydersen, C., Knutsen, L.Ø., Bjørge, A., Smith, T.G. and Øritsland, N.A. 1993. Scaling of insulation in seals and whales. *J. Zool*. 230(2):193–206.

Solvang, H.K., Yanagihara, H., Øien, N. and Haug, T. 2017. Temporal and geographical variation in body condition of minke whales (*Balaenoptera acutorostrata acutorostrata*) in the Northeast Atlantic. *Polar Biol.* 40: 667–83.

Víkingsson, G.A. 1995. Body condition of fin whales during summer off Iceland. pp.361–69. *In*: Blix, A.S., Walløe, L. and Ulltang, O. (eds). *Whales, Seals, Fish and Man: Proceedings of the International Symposium on the Biology of Marine Mammals in the Northeast Atlantic.* Elsevier, Amsterdam. 720pp.

Víkingsson, G., Auðunsson, G., Elvarsson, B. and Gunnlaugsson, H. 2013. Energy storage in common minke whales (*Balaenoptera acutorostrata*) in Icelandic waters 2003–2007 – chemical composition of tissues and organs. Paper SC/F13/SP10 presented to the IWC Scientific Committee Icelandic Special Permit Expert Panel Review Workshop, 18–22 February 2013, Reykjavík, Iceland (unpublished). 13pp. [Paper available from the Office of this Journal].

Víkingsson, G., Elvarsson, B., Olafsdóttir, A., Sigurjónsson, J., Chosson, V. and Galan, A. 2014. Recent changes in the diet composition of common minke whales (*Balaenoptera acutorostrata*) in Icelandic waters. A consequence of climate change? *Mar. Biol. Res.* 10: 138–52.

Víkingsson, G.A., Pike, D.G., Valdimarsson, H., Schleimer, A., Gunnlaugsson, T., Silva, T., Elvarsson, B.Þ., Mikkelsen, B., Øien, N., Desportes, G., Bogason, V. and Hammond, P.S. 2015. Distribution, abundance, and feeding ecology of baleen whales in Icelandic waters: have recent environmental changes had an effect? *Front. Ecol. Evol.* 3: 6.

Víkingsson, G., Sigurjónsson, J. and Gunnlaugsson, T. 1988. On the relationship between weight, length and girth dimensions in fin and sei whales caught off Iceland. *Rep. Int. Whal. Commn* 38: 323–26.