

RESEARCH ARTICLE

Minke whales maximise energy storage on their feeding grounds

Fredrik Christiansen^{1,*}, Gísli A. Víkingsson², Marianne H. Rasmussen³ and David Lusseau^{1,4}

¹Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen AB24 2TZ, UK, ²Programme for Whale Research, Marine Research Institute, PO Box 1390, 121 Reykjavik, Iceland, ³Húsavík Research Center, University of Iceland, Hafnarstett 3, 640 Húsavík, Iceland and ⁴Marine Alliance for Science and Technology for Scotland, University of Aberdeen, Aberdeen AB24 2TZ, UK

*Author for correspondence (f.christiansen@abdn.ac.uk)

SUMMARY

Seasonal trends in energy storage of the minke whale (*Balaenoptera acutorostrata*), a capital breeder, were investigated in Iceland, a North Atlantic feeding ground. The aim was to better understand the energy acquisition strategies of minke whales and the energetic costs that different reproductive classes face during the breeding season. We modelled total blubber volume, using blubber thickness and morphometric measurements of individual whales. Blubber volume was influenced by body length, and was higher for pregnant females than mature whales. Blubber volume increased linearly through the feeding season at the same rate for mature (mean \pm s.e.m. = $0.0028 \pm 0.00103 \text{ m}^3 \text{ day}^{-1}$; $N=61$ male, 5 female) and pregnant whales ($0.0024 \pm 0.00100 \text{ m}^3 \text{ day}^{-1}$; $N=49$), suggesting that minke whales aim to maximise energy storage while on the feeding grounds. The total amount of blubber accumulated over the feeding season ($0.51 \pm 0.119 \text{ m}^3$ for mature and $0.43 \pm 0.112 \text{ m}^3$ for pregnant whales), together with energy stored as muscle and intra-abdominal fats, constitutes the total amount of energy available for reproduction (fetus development and lactation) on the breeding grounds, as well as migration, daily field metabolic rates, growth and body maintenance. No seasonal variation was observed for immature whales ($N=4$ male, 12 female), suggesting that they are investing most of their excess energy into growth rather than reproduction, in order to reach the length of sexual maturity faster and start reproducing earlier. Our novel modelling approach provides insight into large whale bioenergetics and life history strategies, as well as the relationship between single-site measurement of blubber thickness and total blubber volume.

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INTRODUCTION

Life history describes how an animal allocates energy to growth, reproduction and survival (maintenance) through its lifetime to maximize fitness (Stearns, 1992). A distinction can be made between species that use current energetic income and those that use previously stored energy to finance reproduction, commonly known as income and capital breeders, respectively (Costa, 1993; Jönsson, 1997; Stephens et al., 2009). Baleen whales (mysticetes) are capital breeders because they meet the costs of reproduction on the breeding grounds with stored energy acquired on the feeding grounds (Lockyer, 1987b; Kasuya, 1995).

Like most mysticete species, minke whales (*Balaenoptera acutorostrata* Lacépède 1804) undertake long-distance seasonal migrations between highly productive feeding grounds in the summer and less productive breeding grounds in the winter. The Icelandic continental shelf area constitutes a high-density feeding ground for minke whales with abundance estimates of up to 43,633 animals (95% CI=30,148–63,149) from recent sightings surveys (Borchers et al., 2009). Other important North Atlantic feeding grounds are located around Eastern Canada, Greenland, Iceland, the Norwegian Sea, Jan Mayen and Svalbard islands, the North Sea, the coast of Norway and the Barents Sea (Horwood, 1990). Breeding grounds are unknown but are believed to be located close to the equatorial waters of the Atlantic (Vikingsson and Heide-Jørgensen,

2005). Although the species has been sighted in all months, minke whales are most common in Icelandic waters between mid-April and mid-October every year, when they come to feed on a number of prey species, including krill (*Thysanoessa* spp. and *Meganyctiphanes* spp.), capelin (*Mallotus villosus*), sandeel (*Ammodytes* sp.) and cod (*Gadus morhua*) (Sigurjónsson and Vikingsson, 1997; Vikingsson and Elvarsson, 2010).

In mysticetes, most of the energy needed during the breeding season is stored in the form of blubber (Lockyer, 1987a; Lockyer, 1987b; Kasuya, 1995), a specialized organ of adipose tissue supported by connective tissue, vasculature and nerves, which forms part of the integument between the epidermis and the underlying muscle (Parry, 1949; Sokolov, 1960; Haldiman and Tarpley, 1993; Reeb et al., 2007). Apart from serving as a site for energy storage, blubber also provides thermal insulation and structural support, aids in locomotion and streamlining, and contributes to buoyancy (Lockyer, 1991; Folkow and Blix, 1992; Næss et al., 1998; Koopman et al., 2002; Evans et al., 2003; Struntz et al., 2004; Dunkin et al., 2005; Koopman, 2007; Montie et al., 2008; Dunkin et al., 2010). The stored energy in the blubber layer of mysticetes comes from excess energy acquired during the feeding season, the surplus of energy remaining after the whale has satisfied its own energetic needs for metabolism, maintenance and growth (Parry, 1949). Although considerable amounts of energy are also stored in muscle

and intra-abdominal fat, approximately half of the total amount of deposited energy goes into the blubber layer (Nordøy et al., 1995). The blubber storage is thus a good indicator of the energy balance of mysticetes (Miller et al., 2011). Storing blubber is a necessity for whales as it constitutes the primary source of energy during the breeding season, when the whales migrate to less productive equatorial waters to breed (Kasuya, 1995; Lockyer, 2007). Blubber storage is crucial and body fat condition influences fecundity in fin whales (*Balaenoptera physalus*) (Lockyer, 1987a). Blubber plays an important role as energetic support for mysticetes during reproduction, as has been shown in female right whales (*Eubalaena* sp.): blubber was significantly thicker when measured prior to the start of pregnancy, and the quantity of blubber decreased markedly during lactation (Miller et al., 2011).

Variations in body condition and energy storage are often reflected as changes in blubber thickness of cetaceans (Lockyer, 1987a; Lockyer, 1987b; Koopman et al., 2002; Struntz et al., 2004; Dunkin et al., 2005). For migratory mysticetes, the temporal segregation between feeding and breeding is often reflected as seasonal changes in blubber thickness, with an increase during the summer feeding season and a decrease during the winter breeding season (Lockyer, 1987a; Næss et al., 1998; Víkingsson, 1990; Víkingsson, 1995; Konishi et al., 2008; Konishi et al., 2009). Apart from thickness, blubber can also vary in lipid content and fatty acid composition within the blubber layer itself, across the body of the animal and seasonally, which influences energy storage (Lockyer, 1987a; Lockyer, 1991; Koopman et al., 1996; Víkingsson, 1995; Næss et al., 1998; Evans et al., 2003; Olsen and Grahl-Nielsen, 2003; Struntz et al., 2004; Dunkin et al., 2005; Koopman, 2007; Montie et al., 2008; Dunkin et al., 2010).

Seasonal trends in blubber storage can provide valuable information for a number of study areas. The strong relationship between energy storage and reproduction in mysticetes (Lockyer, 1987b) makes it possible to estimate the energetic costs of reproduction by measuring the total amount of blubber acquired at the end of the feeding season when the whales stop feeding and leave for the breeding grounds. The cost of reproduction is one of the main drivers of the life history of species (Stearns, 1992), and is a key component in any study attempting to understand the bioenergetics of mysticetes (Lockyer, 2007). Because capital breeders mainly store energy for reproduction, it is likely that blubber storage will differ between mature and immature whales, with the former allocating more energy to storage (larger seasonal variation) and the latter investing a larger proportion of their energy into growth. Temporal trends in blubber storage can also provide important insights in the behavioural ecology of these species (Haug et al., 2002; Konishi et al., 2008; Konishi et al., 2009; Miller et al., 2011). Finally, seasonal trends in blubber storage can provide valuable information about the behavioural strategies individuals employ to meet their life history needs.

Most studies looking at seasonal trends in energy storage of mysticetes have used single-site measurements of blubber thickness as a proxy for body condition (Moore et al., 2001; Konishi et al., 2008; Konishi et al., 2009; Miller et al., 2011). A few studies have used multiple sites of blubber thickness (Víkingsson, 1990; Víkingsson, 1995; Haug et al., 2002) or blubber thickness in relation to length or girth (Víkingsson, 1990). Other studies have used girth in relation to length as a proxy for body condition (Víkingsson, 1990; Haug et al., 2002). However, blubber thickness as well as the rate of deposition of blubber has been shown to vary across the body of cetaceans (Lockyer, 1981; Víkingsson, 1990; Folkow and Blix, 1992; Koopman, 1998).

Seasonal variations in blubber thickness, or girth, based on single-site measurements might therefore not be representative of seasonal trends in energy storage of the whale. Further, such measurements provide only relative estimates of energy storage and can thus not be used to quantify the total amount of stored energy (in absolute units of energy) in cetaceans.

In this study we analysed seasonal trends in blubber storage of Icelandic minke whales, caught during the special permit research programme in Iceland between 2003 and 2007 (Marine Research Institute, 2003). Rather than using a single measurement for blubber thickness as an index for blubber storage, this study used novel techniques to model the total blubber volume of minke whales, estimated from multiple measurement sites of blubber thickness together with morphometric data (girth and length measurements). We then used linear models to determine which factors best explain the total blubber volume of minke whales. By assessing trends in blubber deposition over the feeding season, we aim to infer the energetic acquisition strategy of minke whales. To infer the costs that different reproductive classes face during the breeding season, we compared variation in blubber volume between different reproductive classes as well as between sexes. Finally, we assessed the feasibility of using single site measurement of blubber thickness to infer the total blubber volume of minke whales, which would allow the use of non-invasive methods (Moore et al., 2001; Miller et al., 2011) to measure energy storage of free-living animals.

MATERIALS AND METHODS

Sampling protocol

Blubber thickness and morphometric data were collected by the Marine Research Institute of Iceland from minke whales ($N=151$) caught in Icelandic waters between 2003 and 2007. Blubber thickness was measured *in situ* on the whale perpendicular from the skin to the blubber–muscle interface at 18 positions (Fig. 1). These were standard sites used in other studies (Víkingsson, 1990). During sampling, the whales were lying on the side and measurements were taken within 1 h post mortem (mostly within 30 min). To minimize measurement variability due to the fibroelastic nature of the blubber, causing protraction and retraction of the tissue *in situ*, blubber was measured at each site after a 5×5 cm core was removed. Although measurements by ultrasound may be more accurate (Moore et al., 2001), our method was comparable to previous research performed on cetaceans (from catches, bycatches and strandings). Half girth measurements, from the dorso-median line to the centre of the ventral side, were also measured at six positions along the body (Fig. 1). Distance from the rostrum tip to each measurement site, as well as the total body length (tip of the rostrum to the notch of the tail fluke), of each whale was also taken according to standard morphometric methods (Víkingsson, 1988). Males were classified into mature, pubertal or immature classes based on histological examination of the testis tissue (Víkingsson, 1990). Females were classified into immature, mature (non-pregnant resting whales) and pregnant classes, based on examination of the ovaries and uterus (Lockyer, 1984). The presence of a corpus luteum or corpus albicans in the ovaries and/or the presence of a fetus in the uterus were used as criteria for maturity and pregnancy, respectively. As the reproductive activity of pubertal whales is unknown, this reproductive class was removed from analyses to simplify the biological interpretation of the results and to minimise the number of parameters in the model.

Total blubber volume

The total blubber volume of minke whales was estimated from the blubber thickness and morphometric data. Because the head, fins

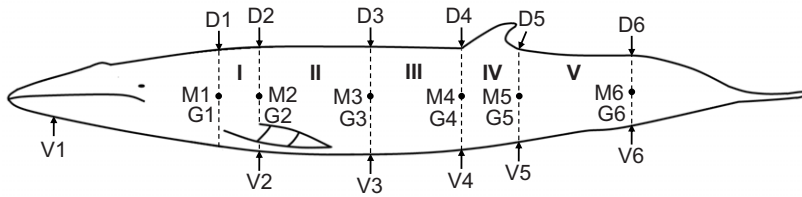


Fig. 1. Measuring sites for blubber thickness and girth measurements. G1–G6 are the girth measurement positions. D1–D6, M1–M6 and V1–V6 are the dorsal, medial and ventral sites where blubber thickness was measured. The different body sections used for the frustum volume estimations are marked with roman numerals I–V.

and tail fluke of cetaceans contain relatively little blubber (Parry, 1949; Brodie, 1975; Lockyer, 1991; Koopman, 1998), the body of a whale can theoretically be modelled as a series of frustums connected to each other at each girth measurement site. By modelling the body as a series of frustums, rather than cylinders or cones, the variation in girth between measurement sites could be taken into consideration, to better represent the true shape of the animal. As girths were measured at six sites, the body of the whale could be divided into five frustum sections (Fig. 1), with the volume of a frustum, V_F , equal to (Poyla, 1965):

$$V_F = \frac{1}{3}\pi h (r^2 + rR + R^2), \quad (1)$$

where h is the height (i.e. distance) between two girth measurements, r is the radius of the smaller girth measurement and R is the radius of the larger girth measurement. Two frustum volumes were estimated for each frustum section, one including the blubber layer, with the girth radii (r and R) estimated directly from the girth measurements [r or $R = G/(2\pi)$], and one excluding the blubber layer, with the girth radii (r and R) estimated by subtracting the average blubber thickness of that section from the total girth radius [r or $R = G/(2\pi) - (D+2M+V)/4$, where D , M and V refer to the dorsal, medial and ventral measurement sites, respectively]. For the first girth measurement (G1), the blubber thickness measurement at site V2 was used instead of V1 to estimate the average blubber thickness of that section, as the former is located closer to the actual measurement position of G1 (Fig. 1). The blubber volume for each frustum (V_{Bi}) was then estimated by subtracting the smaller frustum volume (excluding blubber) from the larger volume (including blubber). The total blubber volume (V_{BTotal}) of the whale was then estimated by summing the blubber volume of all frustums:

$$V_{BTotal} = \sum_{i=1}^5 V_{Bi} = V_F(\text{inc. blubber})_i - V_F(\text{exc. blubber})_i. \quad (2)$$

This index for energy storage accounts for variations in blubber thickness between measurement sites and provides an absolute, rather than relative, estimate of energy storage of minke whales. This estimate can then be converted into blubber mass and energy content, provided that potential differences in the constituents of the blubber along and around the body of the whale (Lockyer, 1987a; Vikingsson, 1995) are measured and accounted for.

Blubber growth

We developed linear models to determine which factors best explained the total blubber volume of minke whales. The covariates used in the model were sex, reproductive class, total body length, day and year. The covariate day represents the number of days into the feeding season, counted from 27 April, which is the earliest date in any year that a minke whale was caught in the sampling programme. Day was used to analyse the seasonal variation in total blubber volume of minke whales throughout the feeding season.

In the model selection process, covariates and interactions between covariates were added sequentially to the null model based on biological explanation, and the F -statistic for the ANOVA F -

test was estimated for each model and compared with that of the previous model, using R 2.14 (R Development Core Team, 2011). Different polynomial non-linear factors were used to test the relationship between the dependent and independent variables. The best-fitting model was selected using Akaike's information criterion (AIC), which provides a relative measure of the goodness-of-fit of statistical models.

To test whether there was a difference between reproductive classes in the relative importance of each covariate in explaining the total blubber volume, we ran separate analyses looking at the effect of length, sex and day on total blubber volume for immature, mature and pregnant whales independently. The relative importance of each covariate in explaining the total blubber volume for each of these reproductive classes was compared using the coefficient of determination (R^2).

Across-body variation in blubber deposition was investigated by comparing the rate of increase in blubber thickness through the feeding season at each measurement site (Fig. 1), using linear models. Separate analyses were run for immature, mature and pregnant whales to determine whether site-specific deposition of blubber varied between reproductive classes. Apart from day, length and year were included as covariates in the linear models to account for non-seasonal variations in blubber thickness.

Model validation

For all models, model validation tests were run to identify potential violations of the assumptions of the linear model. Scatter plots of residuals *versus* fitted values and residuals against each explanatory variable indicated equal variances (homogeneity) in the model. Normality of residuals was interpreted from quantile–quantile plots and from residual histograms, which showed no deviation from normality. We also looked for influential points and outliers using leverage and Cook's distance, but found no extreme values.

Collinearity between the explanatory variables in the model was investigated using variance inflation factor (VIF) [car package (Fox and Weisberg, 2011)]. VIF quantifies the severity of collinearity by providing an index that measures how much the variance of an estimated model parameter is increased because of collinearity. VIF was estimated for the full set of explanatory variables. A threshold value of three was used to remove collinear variables (Fox and Weisberg, 2011). Collinear variables were removed one at a time, starting with the one with the highest AIC value, and VIF values were then recalculated until all the remaining explanatory variables in the model had VIF values below three.

The sampling scheme was designed for representative sampling of the Icelandic continental shelf area (Marine Research Institute, 2003). Apart from prohibiting catches of suckling calves with females (which are seldom observed on feeding grounds), there was no deliberate selection bias in the size or sex of the whales caught in the scientific programme in Iceland. Still, naturally occurring spatial heterogeneity in the size and sex distribution of whales around Iceland could exist (Laidre et al., 2009). Such spatial dependence could potentially bias the data if catches are concentrated in areas

Table 1. Composition of the minke whale catches in the 2003–2007 scientific programme in Iceland by reproductive class and sex

Reproductive class	Sex	2003	2004	2005	2006	2007	Total	% of total
Immature	M	3	0	0	1	0	4	2.6
Pubertal	M	2	1	2	3	0	8	5.3
Mature	M	15	8	13	24	1	61	40.4
Unknown	M	0	0	4	2	0	6	4.0
Immature	F	0	1	7	3	1	12	7.9
Mature (resting)	F	0	1	0	4	0	5	3.3
Pregnant	F	8	10	6	16	9	49	32.5
Unknown	F	2	3	0	1	0	6	4.0

Only animals for which total blubber volume could be estimated are shown. In the model selection process (Table 2), only animals of known sex and reproductive class were included, whereas all animals, including unknowns, were included in the measurement site analysis (Table 3). M, male; F, female.

where certain sex or reproductive classes dominate. We tested for spatial independence of the linear model both visually, plotting the standardized residuals of the linear regression model against their spatial coordinates, and analytically, fitting variograms using the gstat package (Pebesma, 2004). Spatial independence was further investigated by incorporating various spatial auto-correlation structures (Gaussian, linear, spherical, exponential and rational quadratic) in the model and comparing the model fit with the original (without correlation structure) model, using AIC.

Single-site predictive power

Finally, the ability to predict total blubber volume of minke whales from blubber thickness measurements at specific sites was assessed using linear models (Fig. 1). The coefficient of determination was estimated for each measurement site to quantify the predictive power of each site and assess which blubber measurement site best followed the variations in total blubber volume of the animal.

RESULTS

Sample size

From a total of 192 minke whales sampled in the scientific programme in Iceland between 2003 and 2007, full blubber thickness and morphometric data were obtained for 151 whales (Table 1), and these data were consequently used in the linear models. There was an unequal sex ratio in the sample of immature ($N=4$ male, 12 female) and mature ($N=61$ male, 5 female) whales. The majority of mature females caught were pregnant ($N=49$ pregnant, 5 resting).

Blubber growth

The best-fitting model explaining the total blubber volume of minke whales included as covariates: total body length, reproductive class, day in the feeding season, year and an interaction term between

reproductive class and day (model 10 in Table 2). All main effects of the covariates were significant or very close to significant. The R^2 -value indicates that the total model explains 79.0% of the total variance in the data. Length explained most of this variance (56.2%), followed by day (14.1%), reproductive class (5.6%) and year (2.1%) (model 10 in Table 2). The interaction term between day and reproductive class explained a further 1.1% of the variance in total blubber volume.

We tested for non-linear change in blubber volume throughout the feeding season by adding a quadratic polynomial term for the day effect, but this did not improve model fit ($F_{3,117}=0.537$, $P=0.658$), nor did adding a quadratic polynomial term for total body length ($F_{1,119}=2.667$, $P=0.105$).

The total blubber volume depended on the body length of the whale, with longer animals having a higher total blubber volume (supplementary material Fig. S1). Blubber volume increased by a mean (\pm s.e.m.) of $0.176\pm0.016\text{ m}^3\text{ m}^{-1}$ body length. Day and reproductive class both had a significant effect on minke whale blubber volume, with pregnant females having a larger mean blubber volume than mature whales throughout the season. The effect of day varied between reproductive classes (Fig. 2). For immature whales, there was no significant variation in blubber volume through the feeding season. In contrast, mature and pregnant whales showed an increase in blubber volume through the feeding season at a mean (\pm s.e.m.) rate of 0.0028 ± 0.00103 and $0.0024\pm0.00100\text{ m}^3\text{ day}^{-1}$, respectively (Fig. 2). The rate of increase for mature and pregnant whales did not vary significantly from each other ($t_2=0.686$, $P=0.494$). From day 1 (27 April) to day 157 (8 September), which represents the time period covered, the total blubber volume of mature and pregnant whales almost doubled, from 0.34 m^3 (95% CI=0.231–0.456) to 0.79 m^3 (95% CI=0.709–0.865) and from 0.53 m^3 (95% CI=0.437–0.628) to 0.91 m^3 (95% CI=0.829–0.983), respectively. There was also a difference in the

Table 2. Results of linear model for model selection

Model	Variables	F	d.f. (among)	d.f. (within)	P	R ²	AIC	ΔAIC
1	BV ~ Length	165.4	1	129	<0.0001	0.56	-119.0	78.6
2	BV ~ Sex	12.8	1	129	0.0004	0.09	-23.3	174.3
3	BV ~ Reproductive class	41.3	2	128	<0.0001	0.39	-74.1	123.5
4	BV ~ Day	14.4	1	129	0.0002	0.10	-24.8	172.8
5	BV ~ Year	2.8	4	126	0.0304	0.08	-15.9	181.7
6	BV ~ Length + Reproductive class	68.5	3	127	<0.0001	0.62	-133.0	64.6
7	BV ~ Length × Reproductive class	41.6	5	125	<0.0001	0.62	-131.3	66.3
8	BV ~ Length + Reproductive class + Day	99.3	4	126	<0.0001	0.76	-191.3	6.3
9	BV ~ Length + Reproductive class × Day	70.2	6	124	<0.0001	0.77	-194.9	2.7
10	BV ~ Length + Reproductive class × Day + Year	45.3	10	120	<0.0001	0.79	-197.6	0
11	BV ~ Length + Reproductive class × Day × Year	18.4	27	103	<0.0001	0.84	-189.9	7.7

BV, total blubber volume.

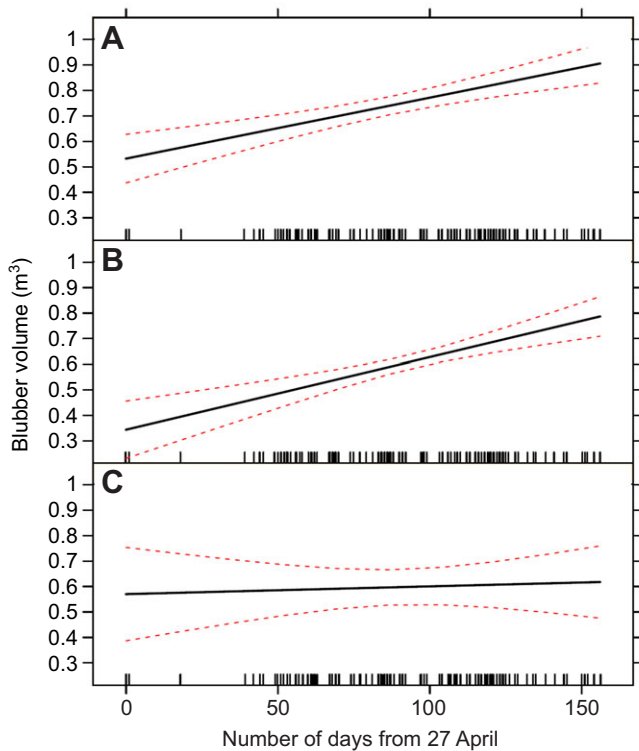


Fig. 2. Partial effect plots of total blubber volume as a function of day for (A) pregnant ($N=49$), (B) mature ($N=61$ male, 5 female) and (C) immature ($N=4$ male, 12 female) minke whales. Day 1 corresponds to 27 April. The red dashed lines represent 95% confidence intervals. Rug plots show the distribution of the data points.

average blubber volume between years, with minke whales in 2006 having a lower total blubber volume than minke whales in other years.

Sex also had a significant effect on total blubber volume and, as a single covariate, explained 9.1% of the total variation (model 2 in Table 2). However, because sex was correlated to reproductive class, which as a single covariate explained 39.2% of the total variation (model 3 in Table 2), only the latter was used as a variable in the analysis. This justified the separate analyses on the different reproductive classes to investigate the influence of different covariates, including sex, on blubber volume. For immature whales, length as a single covariate had a significant effect ($F_{1,12}=57.292$, $P<0.0001$) and explained 81.4% of the total variance (Fig. 3). Length also had a significant effect for mature ($F_{1,62}=87.796$, $P<0.0001$) and pregnant whales ($F_{1,46}=27.984$, $P<0.0001$); however, the covariate only explained 38.1 and 30.0% of the total variance, respectively. As shown by the best-fitting model (Fig. 2), day had no significant effect on total blubber volume for immature whales ($F_{1,12}=1.105$, $P=0.314$), explaining only 1.6% of the total variance. In contrast, day had a significant effect for both mature ($F_{1,62}=80.520$, $P<0.0001$) and pregnant whales ($F_{1,46}=19.344$, $P<0.0001$), explaining 35.0 and 20.7% of the total variance, respectively (Fig. 3). There was no difference between sexes in total blubber volume for both immature ($F_{1,12}=0.011$, $P=0.917$) and mature whales ($F_{1,62}<0.001$, $P=0.976$), with the covariate in each model explaining less than 0.1% of the total variance. However, given the low number of immature males ($N=4$ of 16) and mature females ($N=5$ of 66; Table 1), the lack of difference between sexes in both mature and immature whales could be a result of low sample sizes.

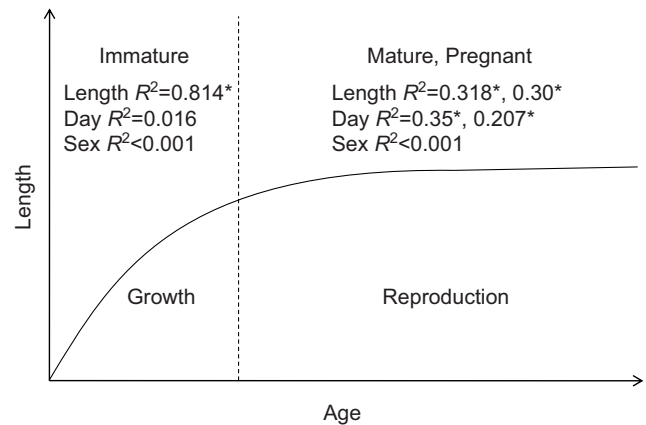


Fig. 3. Conceptual minke whale energy investment for different reproductive classes and the corresponding growth curve for that reproductive class. The R^2 values show the proportion of variation in total blubber volume explained by the explanatory variables length, day and sex. Covariates with a statistically significant effect ($P<0.05$) on total blubber volume are indicated with an asterisk. The shape of the growth curve is based on the age-length relationships presented in Horwood (Horwood, 1990). Note that there was considerable inter-individual variability in body length for immature (mean \pm s.d.= 6.30 ± 0.915 m, min.=4.61 m, max.=7.62 m, $N=16$), mature (mean \pm s.d.= 7.52 ± 0.612 m, min.=5.02 m, max.=8.70 m, $N=66$) and pregnant whales (mean \pm s.d.= 8.00 ± 0.450 m, min.=6.82 m, max.=8.71 m, $N=49$) and also an overlap between reproductive classes.

The rate of blubber deposition varied between body measurement sites and reproductive classes (Fig. 4). In accordance with total blubber volume, immature whales showed little or no seasonal variation in blubber thickness across different body regions, with only five sites (28%) showing a significant increase. In contrast, almost every measurement site showed an increase in blubber thickness for mature (100%) and pregnant whales (83%; Fig. 4). The highest increase in blubber thickness across all body sites occurred for mature whales. In both mature and pregnant whales, most of the blubber was deposited dorsally and ventrally in the posterior region of the body, close to the area of the dorsal fin, while the lateral and anterior part of the body showed a smaller relative increase. For pregnant females, there was no increase in blubber around the tail region.

Model validation

The VIF analyses showed collinearity between the explanatory variables in the model. Both sex and reproductive class had VIF values above three, suggesting that collinearity would be a major issue if both of the variables were kept in the model (the standard error for the coefficient of reproductive class would be almost nine times larger than if it was uncorrelated with the other independent variables). Removing sex from the model greatly improved the VIF values for the remaining explanatory variables in the model, which were all below three, indicating that there was no collinearity between the remaining explanatory variables.

The residuals of the linear model showed no clear sign of spatial auto-correlation (spatial dependence) between data points (Fig. 5). The experimental variograms showed no visible increase of points with increased distances or presence of low values that could indicate spatial dependence. Also, adding a spatial auto-correlation structure to the model did not improve model fit (log-likelihood ratio test, $L<0.001$, d.f.=2, $P=1$). The yearly effect on total blubber volume is thus not an effect of sampling heterogeneity when looking at the absence of spatial dependence in the data.

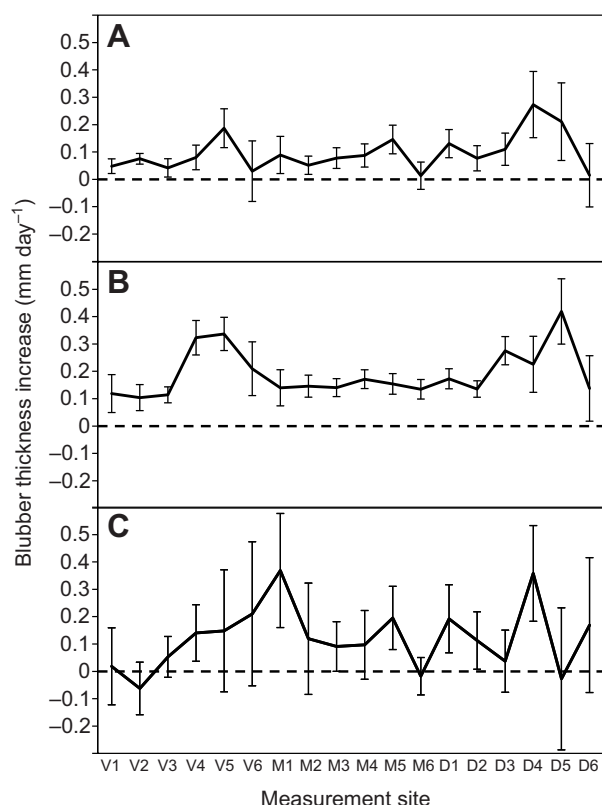


Fig. 4. Rate of blubber thickness increase at different measurement sites for (A) pregnant ($N=49$), (B) mature ($N=61$ male, 5 female) and (C) immature ($N=4$ male, 12 female) minke whales. Error bars represent 95% confidence intervals. The dashed lines represent the level where blubber thickness remains constant through the feeding season. The position of the different measurement sites can be seen in Fig. 1.

Single-site predictive power

The relationship between total blubber volume and site-specific blubber thickness was significant for all measurement sites; however, the coefficient of determination showed large variations between sites (Table 3). The measurement sites that had the closest relationship with total blubber volume were D1 ($R^2=0.613$), D5 ($R^2=0.594$) and D4 ($R^2=0.576$; Fig. 1, Table 3). An increase in blubber thickness of 1 mm at D1 corresponded to a mean (\pm s.e.m.) increase in total blubber volume of $0.01497 \pm 0.00098 \text{ m}^3$, while the same increase in thickness at D5 and D4 corresponded to an increase in total blubber volume of 0.00547 ± 0.00037 and $0.00668 \pm 0.00047 \text{ m}^3$, respectively.

DISCUSSION

The aim of this study was to investigate seasonal trends in energy storage, measured as total blubber volume, of Icelandic minke whales. Although immature minke whales showed no seasonal variation in blubber storage, the blubber volume of mature and pregnant whales increased linearly through the feeding season (Fig. 2). The rate of increase in blubber volume was similar for both mature and pregnant whales, at 0.0028 ± 0.00103 and $0.0024 \pm 0.00100 \text{ m}^3 \text{ day}^{-1}$ (mean \pm s.e.m.), respectively. Assuming that the time of residency for an individual minke whale on the feeding ground is ~ 180 days (Folkow et al., 2000) [analogous with the relative seasonal abundance of minke whales in Icelandic waters, which remains relatively constant between mid-April and mid-

October (Sigurjónsson and Víkingsson, 1997)], the total amount of blubber accumulated over the feeding season would equal approximately 0.51 ± 0.119 and $0.43 \pm 0.112 \text{ m}^3$ (mean \pm s.e.m.) for mature and pregnant whales, respectively. This increase corresponds to roughly a doubling in the amount of blubber over the feeding season, which shows that Icelandic waters constitute important feeding grounds for minke whales in the North Atlantic. With blubber having a density of 1.0412 g cm^{-3} (Parry, 1949) the seasonal increase in blubber mass of an average-sized mature minke whale (7.5 m) in Iceland is approximately $532 \pm 123.8 \text{ kg}$, and $449 \pm 116.2 \text{ kg}$ (mean \pm s.e.m.) for pregnant whales. The 95% confidence interval falls within the upper boundary estimated for adult minke whales in the Northeast Atlantic (225–442 kg) by Nordøy et al. (Nordøy et al., 1995) (given that their results are extrapolated to 180 days rather than the measured 112 days). The energetic content of minke whale blubber is between 27.5 and 30.6 kJ g^{-1} (Nordøy et al., 1995). Using these estimates, the total amount of energy that an average size minke whale deposit in their blubber storage during the feeding season is $\sim 15.5 \pm 3.60$ and $13.0 \pm 3.37 \text{ GJ}$ (mean \pm s.e.m.) for mature and pregnant whales, respectively. This amount, together with the energy stored as muscle and intra-abdominal fats, constitutes the total amount of energy that minke whales have available to finance the costs of reproduction (fetus development and lactation) on the breeding grounds, and to cover the costs of migration as well as their daily field metabolic rates, growth and body maintenance (Nordøy et al., 1995).

For both mature and pregnant whales, blubber deposition was highest towards the posterior end of the body on both the dorsal and ventral sides (Fig. 4). This corresponds well with the findings of Næss et al. (Næss et al., 1998), with the exception of the tail region itself (V6, M6 and D6), which showed a small and non-existent increase in thickness for mature and pregnant whales, respectively (Fig. 4). Blubber from the tailstock of small toothed whales (odontocetes) is relatively metabolically inert, containing more collagen and water than the thorax blubber, and is assumed to play a structural rather than a metabolic role by providing aid during locomotion and streamlining the caudal body (Koopman et al., 1996; Koopman et al., 2002; Struntz et al., 2004; Dunkin et al., 2010). The tail region of minke whales could play a similar structural role, which would explain the small seasonal variation.

The total blubber volume of minke whales increased with the length of the animal (supplementary material Fig. S1), following an increase in the surface area of the whale. Similarly, Næss et al. (Næss et al., 1998) found a linear relationship between blubber weight and body length of minke whales in the Northeast Atlantic. In the present study, there was also a difference in average blubber volume between reproductive classes, with pregnant females having a relative higher blubber volume than mature whales (Fig. 2). With 61 (92.4%) of the 66 mature non-pregnant whales sampled being males [most females conceive every year (Sigurjónsson et al., 1990)] (Table 1), this difference could be a confounding effect of sex (male *versus* female, rather than mature *versus* pregnant whales). Mysticete cetaceans exhibit sexual dimorphism, with females reaching an asymptotic length 5% longer than that of males (Ralls and Mesnick, 2008). Blubber has also been shown to be thicker in female minke whales of the Northeast Atlantic (Haug et al., 2002), Antarctic minke whales (*Balaenoptera bonaerensis*) (Konishi et al., 2008) and other mysticete species (Lockyer, 1987a; Víkingsson, 1990; Konishi et al., 2009). Our separate analyses of immature and mature whales showed no difference in blubber volume between sexes for either of the reproductive classes (Fig. 3), showing that the effect of sex that was found during the model selection process (model 2 in

Table 3. Result of measurement site analysis, showing the predictive power (R^2) for each blubber thickness measurement site in predicting total blubber volume of minke whales in Icelandic waters

Model	Mean \pm s.d. (mm)	F	R^2	AIC	Δ AIC
BV ~ V1	42.0 \pm 11.6	35.6	0.194	-50.7	110.1
BV ~ V2	41.7 \pm 7.4	45.4	0.235	-58.6	102.2
BV ~ V3	32.4 \pm 7.0	75.4	0.338	-80.2	80.6
BV ~ V4	54.2 \pm 12.6	107.3	0.420	-100.2	60.6
BV ~ V5	53.0 \pm 15.7	65.4	0.307	-73.4	87.4
BV ~ V6	73.7 \pm 20.9	71.8	0.327	-77.8	83.0
BV ~ M1	61.0 \pm 13.6	56.8	0.277	-67.1	93.7
BV ~ M2	36.8 \pm 9.7	109.7	0.426	-101.6	59.2
BV ~ M3	33.4 \pm 9.2	170.6	0.536	-133.5	27.3
BV ~ M4	34.3 \pm 9.6	148.9	0.502	-122.9	37.9
BV ~ M5	35.5 \pm 10.6	168.8	0.533	-132.6	28.2
BV ~ M6	26.0 \pm 8.7	88.3	0.374	-88.6	72.2
BV ~ D1	40.8 \pm 11.7	234.3	0.613	-160.8	0
BV ~ D2	35.7 \pm 10.0	186.7	0.558	-140.8	20.0
BV ~ D3	41.3 \pm 13.3	166.0	0.529	-131.3	29.5
BV ~ D4	93.0 \pm 25.5	201.4	0.576	-147.3	13.5
BV ~ D5	151.0 \pm 31.5	216.3	0.594	-153.6	7.2
BV ~ D6	139.1 \pm 27.0	136.0	0.479	-116.2	44.6

BV, blubber volume. The position of the different measurement sites (D, M and V) can be seen in Fig. 1. The degrees of freedom for the ANOVA were 1 (among) and 148 (within) for all models, and all P -values were <0.0001 .

Table 2) was a confounding effect of maturity class. Still, the large confidence interval caused by the low sample size for resting females ($N=5$) made it impossible to distinguish this group from either mature males or pregnant females (supplementary material Fig. S2).

Similar to our study, Haug et al. (Haug et al., 2002) found a seasonal increase in girth and blubber for mature and pregnant minke whales, but not for immature whales. In contrast, studies on odontocetes have shown a higher total blubber lipid content for immature and pregnant animals than non-pregnant adults (Dunkin et al., 2005; Montie et al., 2008). The different results are likely due to differences in the predominant role that the blubber layer plays in the two suborders. In odontocetes, thermal insulation was hypothesized to be causing the difference in blubber thickness between immature and mature animals, with the former requiring a thicker blubber layer due to their relatively larger surface area to volume ratio (Struntz et al., 2004; Dunkin et al., 2005; Montie et

al., 2008). Although this is also likely to be the case in mysticetes, the large amount of stored blubber needed for reproduction for mature and pregnant whales is likely to mask and even reverse this pattern (Lockyer, 1991; Evans et al., 2003). The fact that immature minke whales did not increase their blubber volume through the feeding season could reflect a difference in diet and/or feeding rates between reproductive classes. Differences between maturity classes in body condition between years, resulting from differences in diets, were found for minke whales in the Barents Sea (Haug et al., 2002). Though spatial variations in the diet of minke whales exist around Iceland (Vikingsson and Elvarsson, 2010), our spatial analysis did not find any spatial segregation between maturity classes of minke whales (Fig. 5), which could indicate a difference in diet between reproductive classes. In terms of feeding rates, mature whales are likely to consume relatively more prey than immature whales, based on their larger body mass and hence field metabolic rate (Nordøy

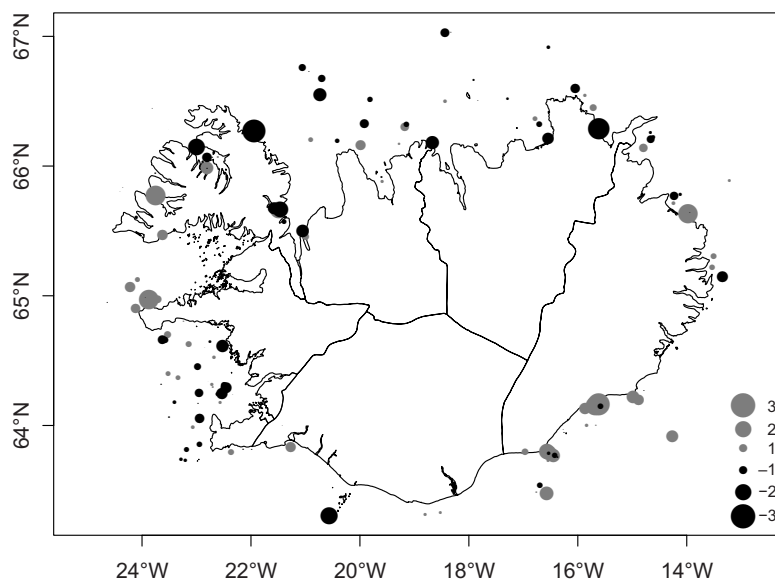


Fig. 5. Standardised residuals of the linear regression model (the deviation in minke whale total blubber volume between the model prediction and the observed values) plotted against their spatial coordinates. The grey and black circles indicate positive and negative residuals, respectively. Symbol size denotes standardised residual magnitude (see key). There was no clear sign of spatial auto-correlation. $N=131$.

et al., 1995). The feeding efficiency could also vary between reproductive classes; however, no study to date has been able to investigate this for minke whales. Although North Atlantic fin whales showed similar patterns in seasonal fattening between reproductive classes (Vikingsson, 1990), only marginal differences in feeding efficiency (relative frequency of empty fore-stomachs) were found between sexes and no differences were observed between reproductive classes (Vikingsson, 1997).

Assuming that immature minke whales acquire the same relative amount of energy as mature and pregnant whales, the lack of seasonal blubber variation in immature whales indicates that their excess energy must go somewhere else. It is unlikely that this excess would be deposited as visceral fat, given the findings of Nordøy et al. (Nordøy et al., 1995), who showed that adult and growing minke whales deposit the same relative proportion of their energy into blubber, muscle and visceral fat. Instead, a more plausible explanation is that immature whales invest most of their excess energy into growth. Minke whales in Icelandic waters reach sexual maturity at around 6 years for females and 5 years for males. However, it seems for mysticetes that sexual maturity is determined more by length than age (Horwood, 1990; Sigurjónsson et al., 1990). For North Pacific fin whales, human exploitation led to a decline in age at sexual maturity, while length at maturity remained constant (Ohsumi, 1986). Thus, by investing more energy into growth, immature minke whales can reach their length at sexual maturity [average approximately 7.2–7.3 m for females and 6.4–7.0 m for males (Horwood, 1990)] faster, and consequently start reproducing earlier. This would help explain the relatively rapid increase in body size of immature minke whales during their first years of life (Horwood, 1990), which must require considerable amounts of energy. That mature and pregnant whales invest more energy into blubber storage is not merely a consequence of them no longer growing, as many of the animals in both reproductive classes had lengths far below the species maximum (8–9 m). The relatively large overlap in body length between immature (mean \pm s.d.=6.30 \pm 0.915 m, min.=4.61 m, max.=7.62 m, $N=16$), mature (mean \pm s.d.=7.52 \pm 0.612 m, min.=5.02 m, max.=8.70 m, $N=66$) and pregnant whales (mean \pm s.d.=8.00 \pm 0.450 m, min.=6.82 m, max.=8.71 m, $N=49$) gives further support to the hypothesis that immature whales invest most of their excess energy into growth while mature and pregnant whales invest in reproduction.

There was no difference in the rate of increase in blubber between mature and pregnant minke whales (Fig. 2). Given the high proportion of males in the mature class (61 of 66), this suggests that the reproductive costs for males are similar to those of females. High reproductive costs for males, even exceeding those of females, have been recorded in mammalian species exhibiting both female defence and scramble competition mating systems (Forsyth et al., 2005; Lane et al., 2010). Little is known about the mating systems of minke whales. Genetic analyses indicate that the species mate promiscuously (Skaug et al., 2007), suggesting a scramble competition mating system. In such a mating system, sexual selection would favour males that devote energy and time in searching for mates, which can result in high energetic costs for males, as shown for other taxa (Lane et al., 2010). However, our model does not take into account variation in lipid content of tail blubber and muscle, which plays an important role in energy deposition for some mysticete species (Lockyer, 1987a; Vikingsson, 1995; Næss et al., 1998). Lockyer (Lockyer, 1987a) found a seasonal increase in the lipid content in the posterior dorsal blubber and muscle for resting and pregnant fin whales, but not for other reproductive classes. Although Næss et al. (Næss et al., 1998) found

the muscle lipid content of minke whales to increase through the feeding season (mainly behind the dorsal fin), low sample size prevented comparison between reproductive classes. Therefore, it is currently unknown whether pregnant minke whale females are depositing more energy into storage, by increasing blubber and muscle lipid content, than is apparent from trends in blubber volume alone. Further, our model does not take body heat loss into consideration, which should be considerably smaller for females because of their larger blubber thickness. With heat loss accounting for more than 50% of the total energy expenditure of minke whales (Folkow and Blix, 1992; Blix and Folkow, 1995), this reduction could, to some extent, balance the added cost of pregnancy and nursing for females on the breeding grounds, and help explain the similar rates of increase in blubber for males and females.

The rate of increase in blubber for mature and pregnant whales did not level off throughout the feeding season (Fig. 2), which indicates that minke whales aim to maximise energy acquisition (food intake) while on the feeding grounds. Such a behavioural strategy would reflect on the feeding rate of minke whales, which should be at its maximum, assuming that feeding rates during the feeding season are constrained more by the animals' digestive rate than by prey availability. Future research should aim to test this hypothesis.

The total blubber volume of minke whales varied between years, with minke whales in 2006 having a smaller blubber volume than in other years. Our model accounted for both temporal (model 10 in Table 2) and spatial (Fig. 5) heterogeneity in sampling between years. Yearly variation in blubber thickness has also been found for North Pacific minke, sei (*Balaenoptera borealis*) and Bryde's whales (*Balaenoptera edeni*) (Konishi et al., 2009). Positive relationships between body condition and prey abundance have been found for Antarctic minke whales (Ichii et al., 1998) and North Atlantic fin whales (Lockyer, 1987b; Sigurjónsson, 1992), and yearly variation in blubber thickness in North Atlantic right whales (*Eubalaena glacialis*) was shown to be positively correlated to the relative prey abundance between years (Miller et al., 2011). Variations in prey abundance, caused by oceanographic variations between years, could explain the observed yearly variation in total blubber volume of Icelandic minke whales. The density of sandeels, for example, one of the most important prey species for minke whales in the south and west of Iceland, has shown great inter-annual variability since regular monitoring began in 2006 (Bogason and Lilliendahl, 2009; Vikingsson and Elvarsson, 2010). However, from the limited sandeel data, the variation in sandeel density does not appear to follow that of minke whale blubber volume measured in this study. Given the euryphagous nature of the minke whales (Horwood, 1990; Haug et al., 1995; Folkow et al., 2000; Haug et al., 2002) and the large spatial variations in prey of minke whales around Iceland (Vikingsson and Elvarsson, 2010), it is unlikely that the observed yearly variations in blubber volume of minke whales in Iceland can be attributed solely to a single prey species. The same conclusion was reached by Haug et al. (Haug et al., 2002), who found only a weak correlation between yearly variations in minke whale body condition (measured as a girth and blubber index) and prey abundance in the Northeast Atlantic. In accordance with optimal foraging theory (Stephens and Krebs, 1986), Haug et al. (Haug et al., 2002) argued that minke whales must broaden their diets if the abundance of favourable prey declines. The measured blubber increase of mature and pregnant whales in this study indicates that Icelandic waters constitute important feeding grounds for minke whales in the North Atlantic. Further monitoring of prey type, abundance and availability in Faxaflói Bay and other areas around

Iceland is therefore needed to better understand how prey is influencing the yearly variations in blubber volume of minke whales.

This study used total blubber volume, rather than single-site measurement of blubber thickness or girth, to investigate seasonal trends in the energy storage of mysticetes. Even though Lockyer (Lockyer, 1987a) and Víkingsson (Víkingsson, 1995) used a similar approach to estimate the blubber volume for fin and sei whales, our method is novel in the sense that we model the body shape of whales as a series of frustums (rather than cylinders or cones), which takes into consideration variation in measurement locations (the relative distance from the rostrum tip to each measurement site; see Fig. 1), something that could vary considerably between individuals. Our model for total blubber volume thus accounts for not only individual variation in body shape (length and girth measurement), but also variation in measurement sites. No single measurement site explained more than about 60% of the observed variation in total blubber volume (Table 3), which indicated that across-body variations in blubber deposition are too large to be captured by a single measurement site. Across-body variations in blubber thickness have been measured for mysticetes in several studies (Lockyer, 1981; Víkingsson, 1990; Folkow and Blix, 1992; Næss et al., 1998). For example, Folkow and Blix (Folkow and Blix, 1992) tried to account for across-body variations in blubber thickness when estimating the body heat loss of minke whales, using a weighting factor for the different blubber thickness measurement sites.

Despite its limitations, there are instances in which using single-site blubber thickness measurements to infer energy storage is the only logistically feasible option; for example, if data from direct or indirect catches or strandings are not available or if repeated measurements of the same animals are required. In these cases, the use of non-invasive amplitude-mode ultrasound techniques to measure the blubber thickness of free-living cetaceans (Moore et al., 2001; Miller et al., 2011) can be a realistic alternative. If single measurement sites are to be used to make inferences about the overall blubber storage of the animal, the relationship between specific measurement sites and the total blubber volume (mass) of the animal must be established. The present study shows the relationship between single-site blubber thickness measurements and total blubber volume for minke whales in Icelandic waters (Table 3). The measurement sites that showed the strongest relationship with total blubber volume were D1, D5 and D4, which explained 61.3, 59.4 and 57.6% of the total variance in blubber volume, respectively (Table 3). All three measurement sites are located on the dorsal side of the whale's body (Fig. 1), which makes them accessible to *in situ* ultrasound measurements (Moore et al., 2001; Miller et al., 2011). The predictive power of each measurement site can be further improved if the length of the animal is added to the model. This would increase the amount of variance explained from 61.3 to 87.2%, 59.4 to 75.1% and 57.6 to 78.5% for D1, D5 and D4, respectively. Minke whale body length can be determined in the field by measuring the distance between the blowhole and the anterior part of the dorsal fin, using photogrammetric techniques (supplementary material Fig. S3) (Ratnaswamy and Winn, 1993; Miller et al., 2004). Coupled with the present results, non-invasive ultrasound measurements of single-site blubber thickness together with photogrammetric techniques can thus, at least in theory, provide estimates of total blubber storage in free-living minke whales.

Conclusions

This study provides a novel technique for modelling the total blubber volume of large whales, accounting for individual variation in body

shape. The estimated seasonal variation in blubber volume provided important information about the life history of minke whales and the costs that different reproductive classes face during the breeding season. We showed that while mature and pregnant minke whales deposit blubber for reproduction, immature whales appeared to be investing this excess energy into growth, to reach the length of sexual maturity faster and start reproducing earlier. The rate of blubber deposition for mature and pregnant whales also provided insight into the energy acquisition strategy used by minke whales on the feeding grounds, which is to maximise energy intake. Finally, this study demonstrates how single-site point measurements of blubber thickness can be used to make inferences about total blubber volume in minke whales, which will be useful for the application of less invasive techniques (Moore et al., 2001; Miller et al., 2011) in the future. This study is therefore important to the advancement of modelling techniques necessary for assessing the bioenergetics of large whales, including free-living animals, to provide valuable information about life history strategies and physiological ecology.

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