

Minke whales maximise energy storage on their foraging grounds

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SUMMARY

Seasonal trends in energy storage of Minke whales (*Balaenoptera acutorostrata*), a capital breeder, were investigated in Iceland, a feeding ground in the North Atlantic. We modelled total blubber volume, using blubber thickness and morphometric measurements of individual whales. Total blubber volume was strongly influenced by the length of the animal, and there was a difference between reproductive classes, with pregnant females having a higher blubber volume than mature animals. While there was no seasonal variation in the blubber volume for immature whales, mature and pregnant whales showed a strong linear increase in blubber volume through the feeding season. This indicates that immature whales invested this energy in growth while mature and pregnant whales tended to reserve this energy for breeding. That the rate of increase in blubber for mature and pregnant whales did not level off through feeding season, further showed that Minke whales aim to maximize energy storage, and consequently food intake, while on the feeding grounds. The total amount of energy deposited into blubber through the feeding season was about 15.5 GJ for mature whales, and 13.0 GJ for pregnant whales. Being a capital breeder, this energy, together with that stored in muscles and visceral fats, is the total amount of energy available for reproduction on the breeding grounds.

Key words: Blubber, Capital breeder, Energy storage, Life history, Minke whale, Morphometric, Mysticete

Running title: Modelling the blubber storage of Icelandic Minke whales

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). Migratory baleen whales (mysticetes) are capital breeders since they meet the costs of reproduction on the breeding grounds with stored energy, in the form of blubber, acquired on the feeding grounds (Lockyer, 1987b; Kasuya, 1995).

As most mysticetes species, Minke whales (*Balaenoptera acutorostrata*) undertake long distance seasonal migrations between highly productive feeding grounds in the summer and less productive breeding grounds in the winter, where mating and calving takes place. The Icelandic continental shelf area constitutes a high density feeding ground with abundance estimates up to 43,633 (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 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 Víkingsson, 1997; Vikingsson and Elvarsson, 2010).

The stored energy in the blubber layer of mysticetes comes from excess energy acquired during feeding events, the surplus of energy remaining after the whale has satisfied its own energetic needs for metabolism, maintenance and growth (Parry, 1949). 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). With feeding being virtually absent on the breeding grounds, the energy deposited as blubber (as well as muscles and intra-abdominal fat) will be the only energy available to finance the costs of reproduction (Armstrong and Siegfried, 1991; Nordøy et al., 1995; Lockyer, 2007). Blubber storage is crucial and body fat condition influences fecundity in fin whales (*Balaenoptera physalus*) (Lockyer, 1987a). That blubber plays an important role as energetic support for Mysticetes during reproduction was also shown in female right whales (*Eubalaena* sp.), where blubber thickness decreased markedly during pregnancy and lactation (Miller et al., 2011).

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 quantify 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 costs of reproduction is one of the main drivers of the life history of species (Stearns, 1992), and will provide a key component in any study attempting to understand the bioenergetics of mysticetes (Lockyer, 2007). 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, 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, 2009; Miller et al., 2011). A few studies have used multiple sites of blubber thickness (Vikingsson, 1990, 1995; Haug et al., 2002) or blubber thickness in relation to length or girth (Vikingsson, 1990). Other studies have used girth in relation to length as a proxy for body condition (Vikingsson, 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; Vikingsson, 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 only provide 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. Lockyer (1987a) and Vikingsson (1995) estimated the total energy content of fin whale carcasses and absolute seasonal energy storage from weighings and chemical analysis of different organs and tissues.

In this study we look at seasonal trends in blubber storage of Icelandic Minke whales, caught in 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 uses 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 aim to infer the energetic acquisition strategy of Minke whales by assessing the trends in blubber deposition over the feeding season. We also compared variation in blubber volume between different reproductive classes as well as between sexes, to infer the costs different age/reproductive classes are meeting during the breeding season.

MATERIALS AND METHODS

Blubber thickness and morphometric data were collected by the Marine Research Institute of Iceland from Minke whales 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 (Vikingsson, 1990). 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 of each whale from the tip of the rostrum to the notch of the tail fluke were also taken according to standard morphometric methods (Vikingsson, 1988). Males were classified into mature, pubertal or immature classes based on histological examination of the testis tissue (Vikingsson, 1990). The presence of a *corpus luteum* or *corpus albicans* in the ovaries and/or the presence of a foetus in the uterus were used as a criterion for maturity and pregnancy in females.

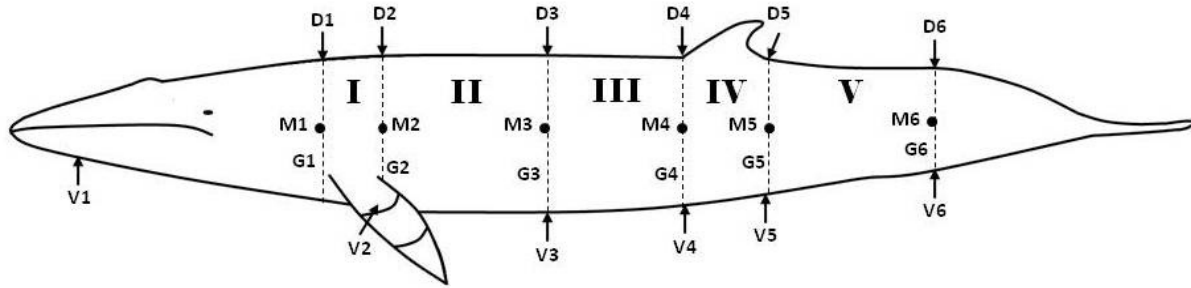


Fig. 1. Measuring sites for blubber thickness and girth measurements. G1-G6 are the girth measurement positions. D1-D6, M1-M6 and V1-V6 are the sites where blubber thickness was measured. The different body sections used for the frustum volume estimations are marked with roman letters I-V.

The total blubber volume of Minke whales was estimated from the blubber thickness and morphometric data. Since the head, fins and tail fluke of cetaceans contain relatively little blubber (Parry, 1949; Brodie, 1975; Koopman, 1998) the body of a whale can theoretically be modelled as a series of frustums connected with each other at each girth measurement site. Since 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 BV (Poyla, 1965):

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

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 radius' (r and R) being estimated directly from the girth measurements ($r=G/(2\pi)$), and one excluding the blubber layer, with the girth radius' (r and R) being estimated by subtracting the average blubber thickness of that section from the total girth radius ($r=G/(2\pi)-(D+M*2+V)/4$). 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, since the former is located closer to the actual measurement position of G1 (Fig. 1). The blubber volume (BV) for each frustum (i) was then estimated by subtracting the smaller frustum volume (excluding blubber) from the larger volume (including blubber). The total blubber volume (BV_{Total}) of the whale was then estimated by summing the blubber volume of all frustums:

$$BV_{Total} = \sum_{i=1}^5 BV_i = BV(\text{inc. blubber})_i - BV(\text{exc. blubber})_i \quad (2)$$

Where i is a frustum section. 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 which can easily be converted into blubber mass and energy content.

Blubber growth

We developed linear models to assess how total blubber volume (BV_{Total}) of Minke whales varied depending on sex, reproductive class, total body length, day and year. The covariate day represents the number of days into the feeding season, counted from April 27, which is the earliest date in any year that a Minke whale was caught in the sampling programme. Day

was used to look at 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 to 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).

Since 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 effect of day), while immature whales invest all their energy into growth (larger effect of length). To test this hypothesis, we ran separate analysis looking at the effect of length, sex and day on total blubber volume for immature and mature whales as well as pregnant females independently. The relative importance of each covariate in explaining the total blubber volume for each reproductive class was compared using the coefficient of determination (R^2).

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 were 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 and VIF values recalculated until all remaining explanatory variables in the model had a 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 bias the data if catches are concentrated in areas 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 (gstat package, Pebesma, 2012). 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.

We finally assessed the ability for each blubber measurement sites to predict total blubber volume using linear models (Fig. 1). The coefficient of determination were estimated for each measurement site to quantify the predictable power of each site and assess which blubber measurement site best followed the variations in total blubber volume of the animal.

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.

RESULTS

From a total of 192 Minke whales sampled in the scientific programme in Iceland between 2003 and 2007, full blubber thickness and morphometric data was obtained for 151 whales (Table 1), and were consequently used in the linear models. From the mature females caught (N=54), the great majority (91%, N=49) were pregnant. As the reproductive role of pubertal whales is unknown, this reproductive class was removed from analyses to simplify the biological interpretation of the results and to minimize the number of parameters in the model.

Table 1. Composition of the Minke whale catches in the 2003-2007 scientific programme in Iceland by reproductive class and sex. Only animals for which total blubber volume could be estimated are shown. M=Male, F=Female.

Reproductive class	Sex	2003	2004	2005	2006	2007	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
Immature	F	0	1	7	3	1	12	7.9
Mature (nonpregnant)	F	0	1	0	4	0	5	3.3
Pregnant	F	8	10	6	16	9	49	32.5
Unknown	-	2	3	4	3	0	12	7.9

The VIF analyses showed collinearity between the explanatory variables in the model (Table 2). 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 (Table 2).

Table 2. Variance inflation factors (VIF) for the full set of explanatory variables, with sex included (Model A) and excluded (Model B) from the model. VIF values above three indicate collinearity between the explanatory variables. BV=Total blubber volume.

Model A: $BV \sim L+S+D+Y+M$		Model B: $BV \sim L+D+Y+M$	
Variable	VIF	Variable	VIF
Length (L)	1.82	Length (L)	1.81
Sex (S)	4.72	Day (D)	2.17
Day (D)	2.19	Year (Y)	2.55
Year (Y)	2.62	Reproductive class (M)	2.09
Reproductive class (M)	8.65		

Blubber growth

The best model to explain the total blubber volume of Minke whales included an effect of total length, reproductive class, day in the feeding season, and an interaction term between reproductive class and day, as well as inter-annual variability (Table 3).

Table 3. Results of linear model for model selection. BV=Total blubber volume.

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

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 ($F_{3,117}=0.537$; $P=0.658$). Adding a quadratic polynomial term to length did not improve model fit either ($F_{1,119}=2.667$; $P=0.105$). The R^2 value indicates that the total model explains 79.0% of the total variance in the data. All main effects of the covariates were significant or very close to significant (Table 4). As single covariates, length explained most of the variance (56.2%), followed by day (14.1%), reproductive class (5.6%) and year (2.1%) (Table 3, 4). The interaction term between day and reproductive class explained a further 1.1% of the variance in total blubber volume.

Table 4. Analysis of variance table for the linear analysis for the best fitting model.

Variable	df	SS	SS/df	F-value	P-value
Length	1	3.788	3.788	321.701	<0.0001
Reproductive class	2	0.380	0.190	16.130	<0.0001
Day	1	0.950	0.950	80.703	<0.0001
Year	4	0.139	0.035	2.956	0.0227
Day*Reproductive class	2	0.072	0.036	3.059	0.0506
Residuals	120	1.413	0.012		

The model explains 79.0% of the variance in total blubber volume.

The residuals of the linear model showed no clear sign of spatial auto-correlation (spatial dependence) between data points (Fig. 2). 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, $L<0.001$; $df=2$; $P=1$). The absence of spatial dependence in the data rule out the possibility that the observed yearly effect on total blubber volume could be an effect of sampling heterogeneity.

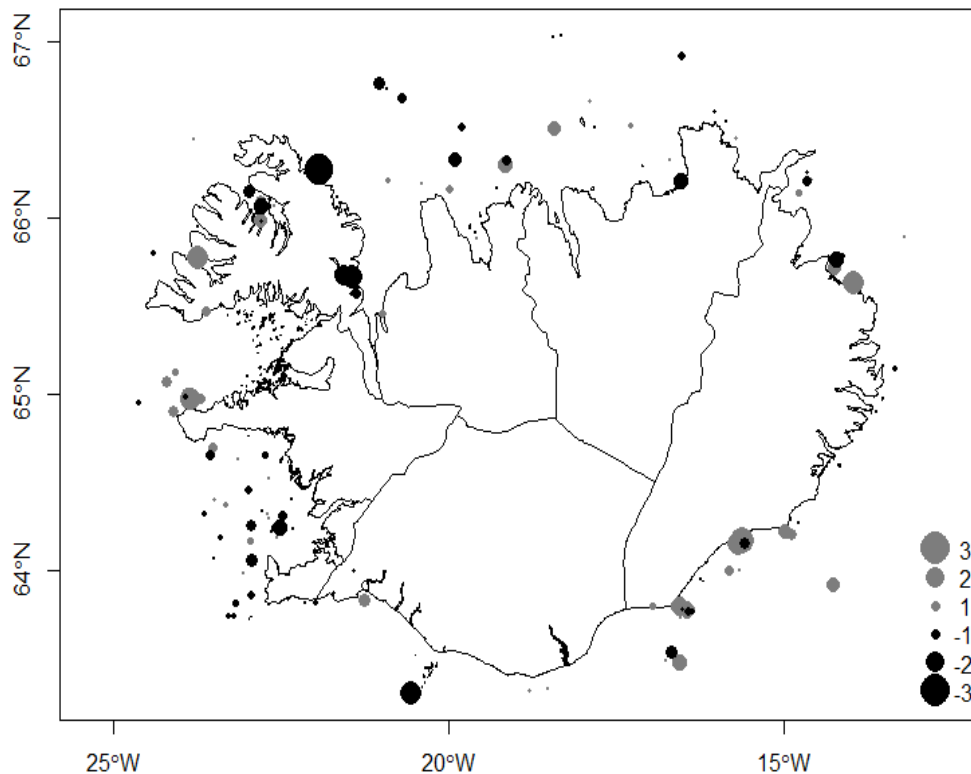


Fig. 2. Standardised residuals of the linear regression model plotted against their spatial coordinates. The grey and black dots indicate positive and negative residuals, respectively. Symbol size denotes standardised residual magnitude (see legend). N=131.

The total blubber volume depended on the body length of the whale, with longer animals having a higher total blubber volume (Fig. 3). The rate of increase in total blubber volume was $0.176 \text{ m}^3 \text{ m}^{-1}$ (s.e.m=0.016). 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. 4). 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 rate of about $0.0028 \text{ m}^3 \text{ day}^{-1}$ (s.e.m=0.00103) and $0.0024 \text{ m}^3 \text{ day}^{-1}$ (s.e.m=0.00100), respectively (Fig. 4). 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 one (April 27) to day 157 (September 8), which represents the time period covered, the total blubber volume of Minke 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) for mature and pregnant whales, respectively. There was also a difference in the average blubber volume between years, with Minke whales in 2006 having a lower total blubber volume than Minke whales in other years.

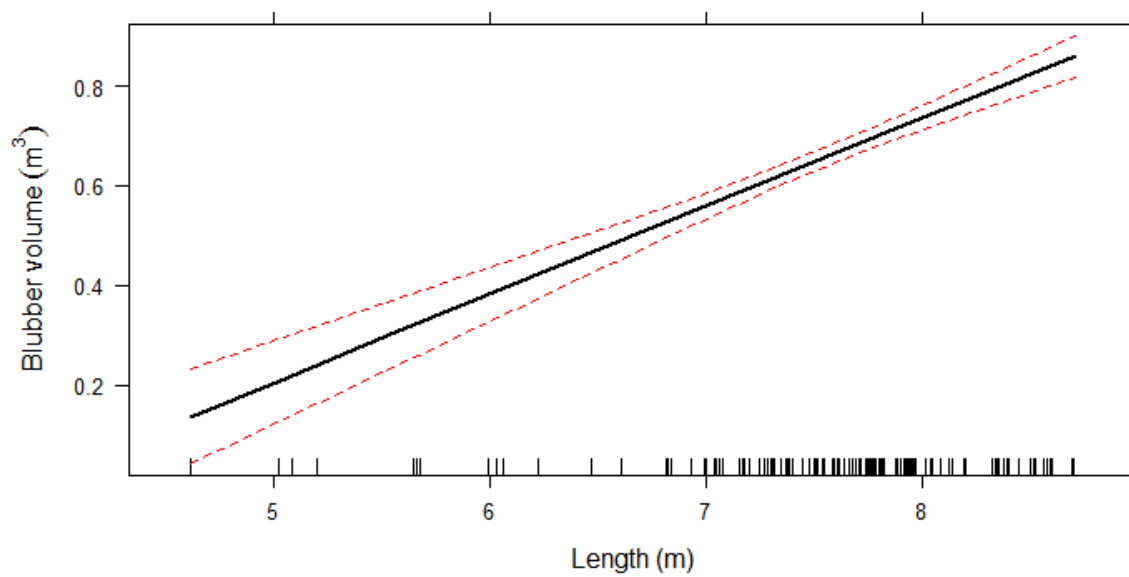


Fig. 3. Partial effect plots of total blubber volume as a function of length for Minke whales. The dotted lines represent 95% confidence interval. A rug plot showing the distribution of the data points is also shown. N=131.

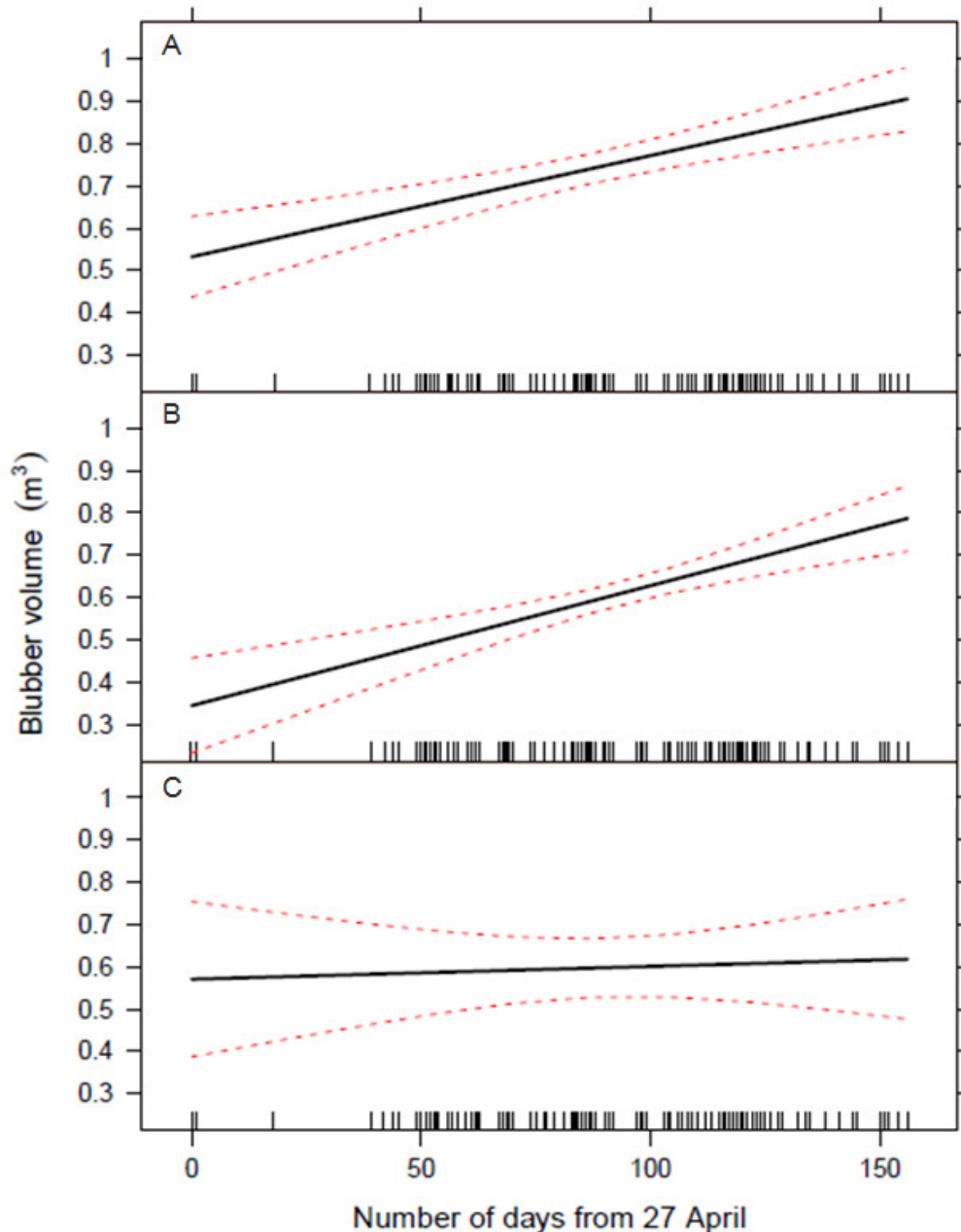


Fig. 4. Partial effect plots of total blubber volume as a function of day for (A) pregnant, (B) mature and (C) immature Minke whales. Day 1 corresponds to April 27. The dotted lines represent 95% confidence interval. Rug plots showing the distribution of the data points are also shown. $N=131$.

Sex also had a significant effect on total blubber volume, and as a single covariate explained 9.1% of the total variation (Table 3). However, since sex was correlated to reproductive class, which as a single covariate explained 39.2% of the total variation, only the later 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. 5). 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 (Table 3), 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. 5). 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. For all analyses the same model validation tests were run as for the initial model, which again showed support for the linear models.

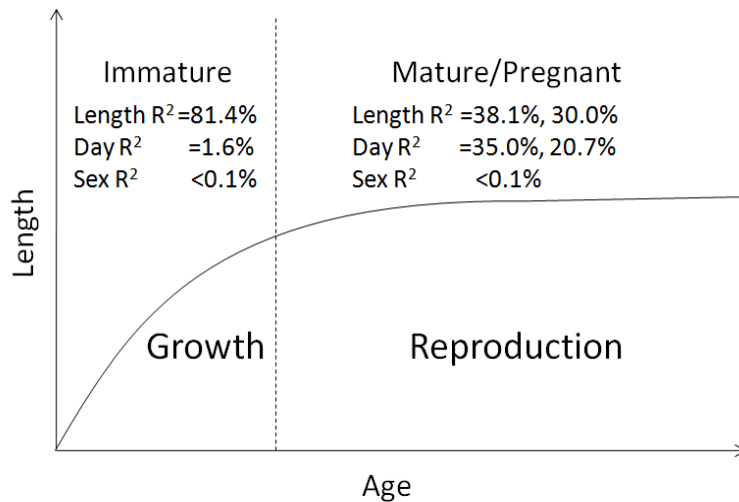


Fig. 5. A conceptual figure showing Minke whale energy investment for different reproductive classes and the corresponding growth curve for that reproductive class. The R^2 values show the proportion of variation in total blubber volume explained by the specific explanatory variables, length, day and sex. The shape of the growth curve is based on the age-length relationships presented in Horwood (1990). Observe that there is still considerable inter-individual variability in length for mature whales.

The relationship between total blubber volume and blubber thickness was significant for all measurement sites, however the coefficient of determination, R^2 , showed large variations between sites (Table 5). 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 5). One mm of increase in blubber thickness at D1 corresponded to 0.01497 m^3 (s.e.m=0.00098) of increase in total blubber volume, while D5 and D4 corresponded to a blubber volume increase of 0.00547 m^3 (s.e.m=0.00037) and 0.00668 m^3 (s.e.m=0.00047), respectively. For all models, the model validation tests showed no violation of the model assumptions.

Table 5. Result of measurement site analysis, showing the predictable power (R^2) for each blubber thickness measurement site in predicting total blubber volume of Minke whales in Icelandic waters. BV=blubber volume. The position of the different measurement sites can be seen in Fig. 1.

Model	F-statistic	df(among)	df(within)	P-value	R^2	AIC	ΔAIC
BV~V1	35.6	1	148	<0.0001	0.194	-50.7	110.1
BV~V2	45.4	1	148	<0.0001	0.235	-58.6	102.2
BV~V3	75.4	1	148	<0.0001	0.338	-80.2	80.6
BV~V4	107.3	1	148	<0.0001	0.420	-100.2	60.6
BV~V5	65.4	1	148	<0.0001	0.307	-73.4	87.4
BV~V6	71.8	1	148	<0.0001	0.327	-77.8	83.0
BV~M1	56.8	1	148	<0.0001	0.277	-67.1	93.7
BV~M2	109.7	1	148	<0.0001	0.426	-101.6	59.2
BV~M3	170.6	1	148	<0.0001	0.536	-133.5	27.3
BV~M4	148.9	1	148	<0.0001	0.502	-122.9	37.9
BV~M5	168.8	1	148	<0.0001	0.533	-132.6	28.2
BV~M6	88.3	1	148	<0.0001	0.374	-88.6	72.2
BV~D1	234.3	1	148	<0.0001	0.613	-160.8	0

BV~D2	186.7	1	148	<0.0001	0.558	-140.8	20.0
BV~D3	166.0	1	148	<0.0001	0.529	-131.3	29.5
BV~D4	201.4	1	148	<0.0001	0.576	-147.3	13.5
BV~D5	216.3	1	148	<0.0001	0.594	-153.6	7.2
BV~D6	136.0	1	148	<0.0001	0.479	-116.2	44.6

DISCUSSION

The aim of this study was to investigate seasonal trends in energy storage, measured as total blubber volume, of Icelandic Minke whales. Immature Minke whales did not increase their blubber storage during the feeding season (Fig. 4) and instead invest all their excess energy into growth (Horwood, 1990). In contrast, the blubber volume of mature and pregnant whales increased through the feeding season (Fig. 4), suggesting that both maturity classes put a significant proportion of their excess energy into blubber storage for reproduction. Blubber volume increased through the feeding season at a similar rate for both mature and pregnant whales, at $0.0028 \text{ m}^3 \text{ day}^{-1}$ (s.e.m=0.00103) and $0.0024 \text{ m}^3 \text{ day}^{-1}$ (s.e.m=0.00100), respectively. Assuming that the time of residency for an individual Minke whale on the feeding ground is about 180 days (Folkow et al., 2000) (which is consistent with the relative seasonal abundance of Minke whales in Icelandic waters, which is relatively constant between mid April and mid October, Sigurjónsson and Víkingsson, 1997), the total amount of blubber accumulated over the feeding season would equal about 0.51 m^3 (s.e.m=0.119) and 0.43 m^3 (s.e.m=0.112) 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 about 532 kg (s.e.m=123.8) and 449 kg (s.e.m=116.2) 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. (1995) (given that their results are extrapolated to 180 days rather than the measured 112 days). The energetic content of blubber is between 27.5 and 30.6 kJ g^{-1} (Nordøy et al., 1995). By using these estimates, the total amount of energy that an average size Minke whale deposit in their blubber storage during the feeding season is about 15.5 GJ (s.e.m=3.60) and 13.0 GJ (s.e.m=3.37) for mature and pregnant whales, respectively. This amount, together with the energy stored as muscles and intra-abdominal fats, constitute the total amount of energy that Minke whales have available to finance the costs of reproduction (foetus development and lactation) on the breeding grounds, and to cover the costs of their daily field metabolic rates, growth and body maintenance (Nordøy et al., 1995).

The total blubber volume of Minke whales was unsurprisingly affected by the length of the animal (Fig. 3), as the surface area of the whale increases with increased length, and hence also the blubber volume. There was also a difference between reproductive classes in the average blubber volume, with pregnant females having a relative higher blubber volume than mature whales (Fig. 4). With 61 (92.4%) of the 66 mature nonpregnant whales sampled being males, 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 males (Ralls and Mesnick, 2008). Higher blubber thickness for females have been found for Minke whales in the Northeast Atlantic (Haug et al., 2002), Antarctic Minke whales (*Balaenoptera bonaerensis*) (Konishi et al., 2008) and for 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. 5), showing that the effect of

sex that was discovered during the model selection process (Table 3) was actually a confounding effect of maturity class. Still, the large confidence interval caused by the low sample size for mature nonpregnant females made it impossible to distinguish this group both from mature males and pregnant females (see Fig. 1 in supplementary material).

There was no difference in the rate of increase in blubber between mature and pregnant Minke whales. This was surprising, since female Minke whales on the breeding grounds carry the added energetic costs of foetus development and lactation and would therefore be expected to deposit relatively more energy into blubber than males to cover these additional costs. Our model however, does not take into account variations in lipid content of tail blubber and muscle, which plays an important role in energy deposition for some mysticete species (Lockyer, 1987a; Víkingsson, 1995). Further, the fact that females have a larger total blubber volume, and thus blubber thickness, than males means that the rate of body heat loss (which is mainly driven by blubber thickness and sea temperature), and thus field metabolic rate, of females will be lower (Folkow and Blix, 1992). Thus, it could be that the added cost of pregnancy and nursing for females on the breeding grounds is to some extent balanced by lower field metabolic rates, owing to their thicker blubber layer. However further studies are needed to verify this.

The total blubber volume of Minke whales varied between years, with Minke whales in 2006 having a smaller blubber volume than other years. Our model accounted for both temporal (Table 3) and spatial (Fig. 2) heterogeneity in sampling between years. Yearly variations in blubber thickness has also been found for North Pacific Minke, Sei and Bryde's whales (*Balaenoptera edeni*) (Konishi et al., 2009). Positive relationships between body condition and prey abundance has 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 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, Víkingsson and Elvarsson, 2010). However, from the limited sandeel data the variation in sandeel density does not appear to follow that of Minke whale blubber thickness 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 (Víkingsson 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. (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), the authors argued that Minke whales broaden their diets if the abundance of favourable prey declines (Haug et al., 2002).

This study use 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 (1987a) and Víkingsson (1995) used a similar approach to estimate the blubber volume for fin and sei whales (*Balaenoptera borealis*), our method is novel in the sense that it takes into consideration between individual variation in measurement locations (the relative

distance from the rostrum tip to each measurement site, see Fig. 1), which could vary quite a bit between individuals. Our model for total blubber volume thus accounts not only for 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 5), which indicate that across body variations in blubber deposition is too large to be captured by a single measurement site. Across body variations in blubber thickness has been measured for mysticetes in several studies (Lockyer, 1981; Vikingsson, 1990; Folkow and Blix, 1992; Koopman, 1998). Folkow and Blix (1992) tried to account for across body variations in blubber thickness, when estimating the body heat loss of Minke whales, by using a weighting factor for the different blubber thickness measurement sites. Our model for total blubber volume accounts for individual variation in body shape (length and girth measurement) Despite its limitations, there are instances in which using single blubber thickness measurements to infer energy storage is the only logistically feasible 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. This study shows the relationship between single site blubber thickness measurements and total blubber volume for Minke whales in Icelandic waters. 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 5). All three of these measurement sites are located on the dorsal side of the whale's body (Fig. 1), which makes them accessible to *in situ* ultra-sound measurements (Moore et al., 2001; C. A. Miller et al., 2011). The predictable power of each measurement sites can be further improved if the length of the animal is added to the model. This would increase R^2 from 61.3-87.2%, 59.4-75.1% and 57.6-78.5% 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 (see Fig. 2 in supplementary material) (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

The seasonal variation in blubber volume observed in this study provides valuable insight into the life history of Minke whales. Immature Minke whales did not deposit additional blubber during the feeding season (Fig. 4, 5), and instead investing their acquired energy into growth. Minke whales in Icelandic waters reach sexual maturity 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 (Sigurjónsson et al 1990, Horwood, 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 about 7.2-7.3 m for females and 6.4-7.0 m for males, Horwood, 1990) faster, and consequently start reproducing earlier.

In contrast to immature whales, the blubber volume of mature and pregnant Minke whales increased through the feeding season (Fig. 4). That the rate of increase in blubber was similar

for mature and pregnant Minke whales suggests that the reproductive cost for males is similar to those of females. High male reproductive costs, even exceeding those of females, have been recorded in mammalian species both exhibiting female defence and scramble competition mating systems (Forsyth et al., 2005; Lane et al., 2010). As for other mysticetes, little is known about the mating systems of Minke whales, however genetic analyses indicate that the species mate promiscuously (Skaug et al., 2007). Even if Minke whales might not exhibit male-male competition like those displayed by humpback whales (*Megaptera novaeangliae*) (Tyack and Whitehead, 1982), a scramble competition mating system, under which sexual selection favour male searching behaviour on the breeding ground, could carry high energetic costs for males, as shown for other taxa (Lane et al., 2010).

The blubber storage of mature and pregnant Minke whales increased linearly through the feeding season (Fig. 4). This indicates that Minke whales aim to maximize 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 only constrained by the animals' digestive rate and not by prey availability. Future research should aim to test this hypothesis.

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REFERENCES

- Armstrong, A. J. and Siegfried, W. R.** (1991). Consumption of Antarctic krill by Minke whales. *Antarctic Science*, **3**, 13-18.
- Bogason, V. and Lilliendahl, K.** (2009). Rannsóknir á sandsíli (an initiation of sandeel monitoring in Iceland). Þættir úr vistfræði sjábvar 2008 (Environmental conditions in Icelandic waters 2008) Hafrannsóknir vol 145. Marine Research Institute, 36-42.
- Borchers, D. L., Pike, D. G., Gunnlaugsson, T., and Vikingsson, G. A.** (2009). Minke whale abundance estimation from the NASS 1987 and 2001 aerial cue-counting surveys taking appropriate account of distance estimation errors. *NAMMCO Scientific Publications*, **7**, 95-110.
- Brodie, P. F.** (1975). Cetacean Energetics , an Overview of Intraspecific Size Variation. *Ecology*, **56**, 152-161.
- Costa, D. P.** (1993). The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. *Symposia of the Zoological Society of London*, **66**, 293-314.

- Folkow, L. P. and Blix, A. S.** (1992). Metabolic rates of minke whales (*Balaenoptera acutorostrata*) in cold water. *Acta Physiologica Scandinavica*, **146**, 141-150.
- Folkow, L. P., Haug, T., Nilssen, K. T., and Nordøy, E. S.** (2000). Estimated food consumption of minke whales *Balaenoptera acutorostrata* in Northeast Atlantic waters in 1992-1995. *NAMMCO Scientific Publications*, **2**, 65-80.
- Forsyth, D. M., Duncan, R. P., Tustin, K. G., and Gaillard, J. M.** (2005). A substantial energetic cost to male reproduction in a sexually dimorphic ungulate. *Ecology*, **86**, 2154-2163.
- Fox, J. and Weisberg, S.** (2011). *An R Companion to Applied Regression*, Second Edition Sage Publications, Thousand Oaks, CA.
- Haug, T., Gjøsaeter, H., Lindstrøm, U., Nilssen, K. T., and Røttingen, I.** (1995). Spatial and temporal variations in northeast Atlantic minke whale *Balaenoptera acutorostrata* feeding habits. In, Blix, A. S., Walløe, L., and Ulltang, Ø. (eds), *Whales, seals, fish and man*. Elsevier Science, Amsterdam, pp. 225-239.
- Haug, T., Lindstrøm, U., and Nilssen, K. T.** (2002). Variations in Minke Whale (*Balaenoptera acutorostrata*) Diet and Body Condition in Response to Ecosystem Changes in the Barents Sea. *Sarsia*, **87**, 409-422.
- Horwood, J.** (1990). *Biology and Exploitation of the Minke whale* CRC Press, Florida.
- Ichii, T., Shinohara, N., Fujise, Y., Nishiwaki, S., and Matsuoka, K.** (1998). Interannual changes in body fat condition index of minke whales in the Antarctic. *Marine Ecology Progress Series*, **175**, 1-12.
- Jönsson, K. I.** (1997). Capital and Income Breeding as Alternative Tactics of Resource Use in Reproduction. *Oikos*, **78**(1), 57-66.
- Kasuya, T.** (1995). Overview of cetacean life histories: an essay in their evolution. In, Blix, A. S., Walløe, L., and Ulltang, Ø. (eds), *Whales, seals, fish and man*. Elsevier Science, Amsterdam, pp. 481-498.
- 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 Biology*, **31**, 1509-1520.
- 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. The Scientific Committee of the International Whaling Commission, Yokohama, Japan, p. Document SC/J09/JR20.
- Koopman, H. N.** (1998). Topographical Distribution of the Blubber of Harbor Porpoises (*Phocoena phocoena*). *American Society of Mammalogists*, **79**, 260-270.
- Laidre, K. L., Heagerty, P. J., Heide-Jørgensen, M. P., Witting, L., and Simon, M.** (2009). Sexual segregation of common minke whales (*Balaenoptera acutorostrata*) in

- Greenland , and the influence of sea temperature on the sex ratio of catches. *ICES Journal of Marine Science*, **66**, 2253-2266.
- Lane, J. E., Boutin, S., Speakman, J. R., and Humphries, M. M.** (2010). Energetic costs of male reproduction in a scramble competition mating system. *Journal of Animal Ecology*, **79**, 27-34.
- Lockyer, C.** (1981). Growth and energy budgets of large baleen whales from the southern hemisphere. In, FAO (ed), *Mammals in the Seas: General Papers and Large Cetaceans Volume 3*. FAO, Rome, pp. 379-484.
- Lockyer, C.** (1987a). Evaluation of the role of fat reserves in relation to the ecology of North Atlantic fin and sei whales. In, Huntley, A. C., Costa, D. P., Worthy, G. A. J., and Castellini, M. A. (eds), *Approaches to Marine Mammal Energetics. Special Publication No 1*. Society for Marine Mammalogy, Lawrence, pp. 183-203.
- Lockyer, C.** (1987b). The relationship between body fat, food resource and reproductive energy costs in North Atlantic fin whales (*Balaenoptera physalus*). *Symposium of the Zoological Society of London*, **57**, 343–361.
- Lockyer, C.** (2007). All creatures great and smaller: a study in cetacean life history energetics. *Journal of the Marine Biological Association of the UK*, **87**, 1035-1045.
- Marine Research Institute** (2003). A programme for a two year feasibility study on cetaceans in Icelandic waters. The Scientific Committee of the International Whaling Commission, Berlin, Germany, p. Document SC/55/O2-revised.
- 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 with reproduction, life history status and prey abundance. *Marine Ecology Progress Series*, **438**, 267-283.
- Miller, P. J. O., Johnson, M. P., Tyack, P. L., and Terray, E. A.** (2004). Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. *Journal of Experimental Biology*, **207**, 1953-1967.
- Moore, M. J., Miller, C. A., Morss, M. S., Arthur, R., Lange, W. A., Prada, K. G., Marx, M. K., and Frey, E. A.** (2001). Ultrasonic measurement of blubber thickness in right whales. *Journal of Cetacean Research and Management*, **2**, 301-309.
- Nordøy, E. S., Folkow, L. P., Mårtensson, P. E., and Blix, A. S.** (1995). Food requirements of Northeast Atlantic minke whales. In, Blix, A. S., Walløe, L., and Ulltang, Ø. (eds), *Whales, seals, fish and man*. Elsevier Science, Amsterdam, pp. 307-318.
- Ohsumi, S.** (1986). Yearly change in age and body length at sexual maturity of a fin whale stock in the eastern North Pacific. *The Scientific Reports of the Whales Research Institute*, **37**.
- Parry, D. A.** (1949). The structure of whale blubber and a discussion of its thermal properties. *Quarterly Journal Microscopical Science*, **90**, 13-25.

- Pebesma, E.** (2012). Spatial and spatio-temporal geostatistical modelling, prediction and simulation, the gstat package.
- Poyla, G.** (1965). *Mathematical Discovery: On Understanding, Learning, and Teaching Problem Solving*, Volume II John Wiley and Sons, New York.
- R Development Core Team** (2011). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ralls, K. and Mesnick, S.** (2008). Sexual Dimorphism. In, Perrin, W. F., Würsig, B., and Thewissen, J. G. M. (eds), *Encyclopedia of Marine Mammals, Second Edition*. Academic Press, San Diego, pp. 1005-1011.
- Ratnaswamy, M. J. and Winn, H. E.** (1993). Photogrammetric Estimates of Allometry and Calf Production in Fin Whales, *Balaenoptera physalus*. *Journal of Mammalogy*, **74**, 323-330.
- Sigurjónsson, J. Halldórsson, S.D. and Konráðsson, A.** (1990). New information on age and reproduction in minke whales (*Balaenoptera acutorostrata*) in Icelandic waters. Paper IWC SC/42/NHMi27, 17pp.
- Sigurjónsson, J.** (1992). Recent studies on abundance and trends in whale stocks in Icelandic and adjacent waters. In, *Proceedings of the symposium "Whales - Biology - Threats" - Conservation*. Royal Academy of Overseas Sciences, Brussels, pp. 77-111.
- Sigurjónsson, J. and Víkingsson, G. A.** (1997). Seasonal abundance of and estimated food consumption by cetaceans in Icelandic and adjacent waters. *Journal of Northwest Atlantic Fishery Science*, **22**, 271-287.
- Skaug, H. J., Bérubé, M., Rew, M. B., and Palsbøll, P. J.** (2007). Genetic analyses reveal promiscuous mating in female minke whales, *Balaenoptera acutorostrata*. The Scientific Committee of the International Whaling Commission, Anchorage, USA, p. Document SC/59/O1.
- Stearns, S. C.** (1992). *The evolution of life histories* Oxford University Press, Oxford.
- Stephens, D. W. and Krebs, J. R.** (1986). *Foraging theory* Princeton University Press, Princeton.
- Stephens, P. A., Boyd, I. L., McNamara, J. M., and Houston, A. I.** (2009). Capital breeding and income breeding: their meaning, measurement, and worth. *Ecology*, **90**, 2057-2067.
- Tyack, P. and Whitehead, H.** (1982). Male Competition in Large Groups of Wintering Humpback Whales. *Behaviour*, **83**, 132-154.
- Víkingsson, G. A.** (1988). Morphometric studies on the sei whale (*Balaenoptera borealis*) - A progress report. The Scientific Committee of the International Whaling Commission, San Diego, USA, p. Document SC/40/BA6.

- Vikingsson, G. A.** (1990). Energetic Studies on Fin and Sei whales caught of Iceland. *Reports of the International Whaling Commission*, **40**, 365-373.
- Vikingsson, G. A.** (1995). Body condition of fin whales during summer off Iceland. In, Blix, A. S., Walløe, L., and Ulltang, Ø. (eds), *Whales, seals, fish and man*. Elsevier Science, Amsterdam, pp. 361-369.
- Vikingsson, G. A. and Elvarsson, B. Þ.** (2010). Recent changes in diet composition of minke whales (*Balaenoptera acutorostrata*) in Icelandic waters. The Scientific Committee of the International Whaling Commission, Agadir, Morocco, p. Document SC/17/AS/06.
- Vikingsson, G. A. and Heide-Jørgensen, M. P.** (2005). A note on the movements of minke whales tracked by satellite in Icelandic waters in 2001-2004. The Scientific Committee of the International Whaling Commission, Ulsan, Republic of Korea, p. Document SC/57/O9.