Energy deposition of common minke whales (*Balaenoptera acutorostrata*) during the feeding season in Icelandic waters.

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ABSTRACT

This paper presents the results of a feasibility/pilot study on seasonal energy deposition in minke whales from Icelandic waters. Energy deposition was estimated from measured increase in weight and energy density of different tissues. Weight data from Norwegian waters were also used for estimating seasonal increase. According to these results, minke whales increase their weight by 27% during an assumed 180 day feeding season. However, due to large increases in energy density of tissues, the total increase in energy content of the body is much higher, or around 90% over the feeding season. Most of the energy is stored in adipose tissue (blubber and visceral fat), but posterior dorsal muscle and bone tissue are also important sites for energy storage. Further data collection (e.g. from commercial catches) and additional energy measurements from existing samples would improve the precision of these estimates e.g. with respect to reproductive status.

INTRODUCTION

Migratory baleen whales (mysticetes) are generally considered capital breeders that cover the costs of reproduction at the winter breeding grounds from the energy deposited in blubber and other tissues at the summer feeding grounds (Lockyer, 1981, 1987b, 2007; Kasuya, 1995; Armstrong and Siegfried, 1991; Nordøy *et al*., 1995). Temporal trends in blubber storage can provide important insights into the behavioural ecology of these species (Haug *et al*., 2002; Konishi *et al*., 2008, 2009; Miller *et al*., 2011). Lockyer (1987a) and Víkingsson (1995) estimated the total energy content of fin whale (*Balaenoptera physalus)* carcasses and absolute seasonal energy storage from weighings and chemical analysis of different organs and tissues. These fin whale studies demonstrated that, in addition to blubber, energy is also stored in large quantities in the muscle tissue. They also revealed a clear distinction related to reproductive status where pregnant females deposited most energy during the feeding season (Lockyer 1981, 1987a, 1987b; Víkingsson 1990, 1995).

Among the sub-projects of the special permit research programme on common minke whales (*Balaenoptera acutorostrata)* in Icelandic waters were several studies on energetics (Marine Research Institute 2003). These included development of a new method for estimating blubber mass (SC/F13/SP8), investigations on the relationship between female reproductive condition and foetal growth SC/F13/SP5_Rev) and estimations of seasonal increase in weight and energetic density of various tissues (SC/F13/SP11_Rev and SC/F13/SP10_Rev). The IWC expert review panel (SC/65A/Rep3) recommended that the results of these energetic studies be integrated into a single paper. Here, an integrated examination of seasonal energy storage is presented based on the above mentioned data collected during 2003-2007. These Icelandic data are also compared with data from previous Norwegian research catches (Lydersen et al. 1991).

MATERIAL AND METHODS

The total weight of 21 minke whales was determined by weighing all tissues of the animals in a similar manner as described for fin whales (Lockyer and Waters, 1986; Víkingsson, 1995). The mean total weights of these 21 animals was 4,084kg (standard error (s.e.) = 296) and the mean length was 750cm (s.e. = 18). Of these, 11 were pregnant females, with a mean weight of 4,459kg and a mean length of 771cm. From previous Norwegian special permit catches (Lydersen et al. 1991) total weight, length was available for 11 males and seven females caught in 1988 and 1989. .Partial weights (i.e. weight of blubber, visceral fat and/or muscle) were available from additional 85 Icelandic animals and 224 Norwegian minke whales. These data are described in greater detail in SC/F13/SP11_Rev.

Because of the low sample size of total weighings, the present analysis included only the following four categories of partial weighings: blubber, visceral fat, muscle, bones and the category "*Other*". The proportions of these categories of total weight were calculated from all available Icelandic and Norwegian weight data. Trends in the weight of organs and tissues were calculated from the combined Icelandic and Norwegian data set using a log-linear model with day within season (from day 180), log(length), and the factors "area" and "pregnancy status" as explanatory variables, *cf.* SC/F13/SP11_Rev.

A total of 168 minke whales had all three measurements of energy density i.e. muscle and blubber at dorsal position 5 (D5 in Figure 1) and visceral fat. The methodology for determining enery density and a detailed description of the total sample is given in SC/F13/SP10_Rev. The energy density of blubber at position D5 and visceral fat (thoracic and abdominal) was very similar (SC/F13/SP10_Rev) and so was also their trends within season in a log-linear model. Therefore, the visceral fat was combined with the blubber for the present analysis (n=150). The visceral fat comprises 0 to 10% of this combined category of two adipose tissue types.

The total mid season (day 180) mean body energy content was calculated as the sum of the average energy content of each tissue category. The mean energy content of each tissue category of the Icelandic minke whales was found by multiplying the whole body mean weight, the body weight proportion of the tissue category, and the tissue's mean energy density.

A log-linear model was fitted to energy density of each tissue as a function of day within season from day 180, log-length, and factors for area (for tissue weight only) and pregnancy status. The sum of the temporal change parameters from the energy density and tissue weight relationships multiplied by the total energy gives the change in energy per day in each tissue category. The standard errors of the total temporal change of tissue weight and energy density were calculated assuming independence of the energy density and weight measurements. However, 27 of the animals are in both groups, hence these s.e. are underestimates due to uncorrected positive correlation in the measurements.

Two types of bone tissue (rib and the flipper) were routinely collected. As a pilot study on potential importance of bones as energy storage site, lipid content was measured in nine pairs from 2007 close to the beginning and end of the feeding season. These bone measurements were averaged and used for the whole skeleton. The larger bones (e.g. skull and vertebrae) appear more porous and might therefore be able to hold more lipid than the bones measured in this study.

Bones have been weighed separately for fin and sei whales (Lockyer and Waters, 1986; Víkingsson *et al*., 1988) and comprised around 15% of total body weight. This number is used here and no increase in bone weight assumed over the season (for animals of same length).

RESULTS AND DISCUSSION

The details of the results on weight and energy density are given in papers SC/F13/SP10_Rev and SC/F13/SP11_Rev, respectively. Estimates of energy deposition over the feeding period based on combination of these two datasets are given in Table 1. After subtracting the muscle (37.3%), adipose tissue (blubber + visceral fat) (13.2%) and assumed bone (15%) weights from the total body weight the remaining weight (category *Other*) was on average 34.5% of the total (S.E. 0.9%, n=37). The error in the weight proportions is small in relation to other errors and a shift from one category to another has in some cases no effect on the energy estimates so this variance is ignored here.

Some tissues/organs in the category *Other* were measured for energy content in a subsample containing the same individuals as had been measured for energy content of bones above. These organs, heart muscle (mean 18.4kg, 630kJ/g), liver (65kg, 621kJ/g) and kidneys (14.2kg, 519kJ/g) showed little variation and no apparent trend over the season. No samples were collected from other organs such as the tongue (around 2% of total weight in fin whales and highly variable in energy content), lungs and digestive tract. Some of the tissues in the category *Other* such as baleen are very unlikely to change in energy content over the season, while growth and wear may be higher during the feeding season. Lowest energy density was found in the kidney and this density was therefore conservatively chosen as a proxy for this category (*Other*) and no increase assumed over the season although there is certainly some deposition of fat there and fat deposits on for instance the heart.

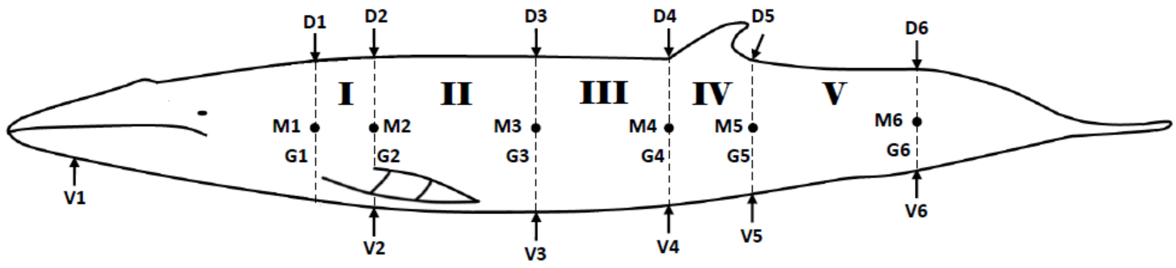

Figure 1. Sampling and measurement sites on the body of minke whales (Figure from SC/F13/SP8).

Measurements derive mostly from the same animals. However, the total s.e. of the temporal changes was calculated by summing the s.e. of both relationships (assuming zero correlation) and therefore the total s.e. is overestimated (Table 1a).

Based on these results from the log-linear model, an estimated seasonal increase in weight and total energy over an assumed 120 day feeding season is given in Figures 2a and 2b respectively. According to these estimates an average sized minke whale (7.5m) deposits 976kg and 22,320MJ over the feeding season (Figure 2a). This corresponds to an increase of 27% in total weight and 90% in terms of total energy content of the body. The increase in weight is relatively evenly spread between fat, muscle and the category *Other*. However, in terms of energy content, more than half (57%) of the seasonal deposition is attributable to adipose tissue (blubber and visceral fat).

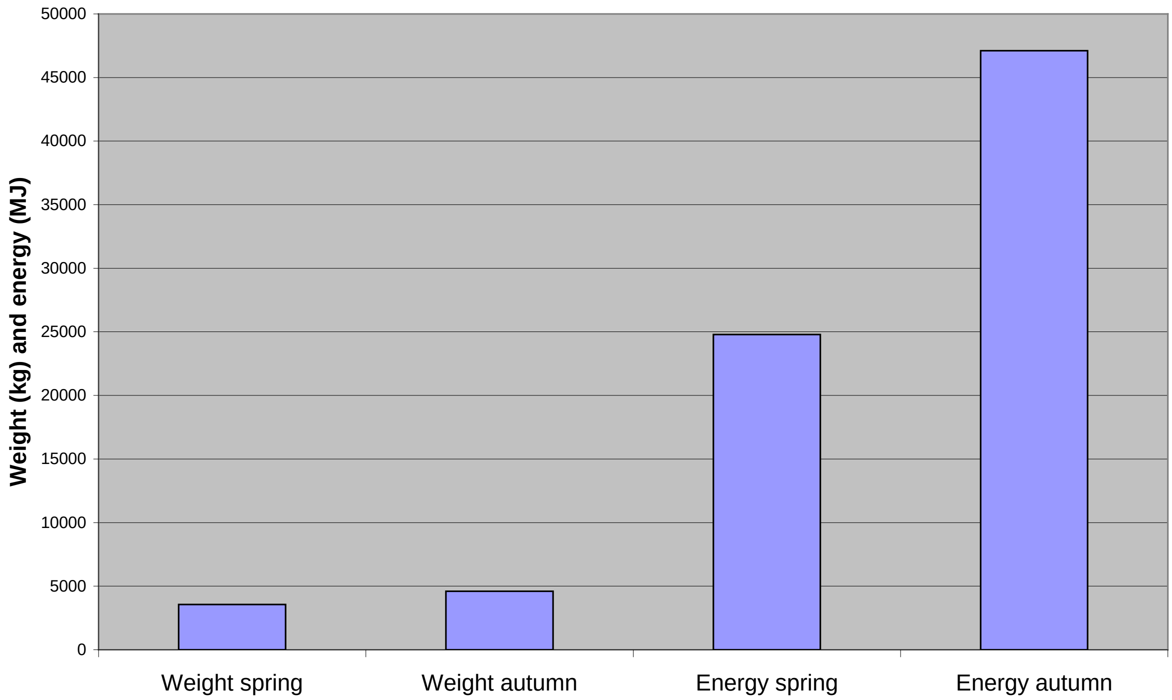

Figure 2a. Estimated increase in total weight and total energy content of an average sized (7.5m) minke whale over a feeding season of 180 days.

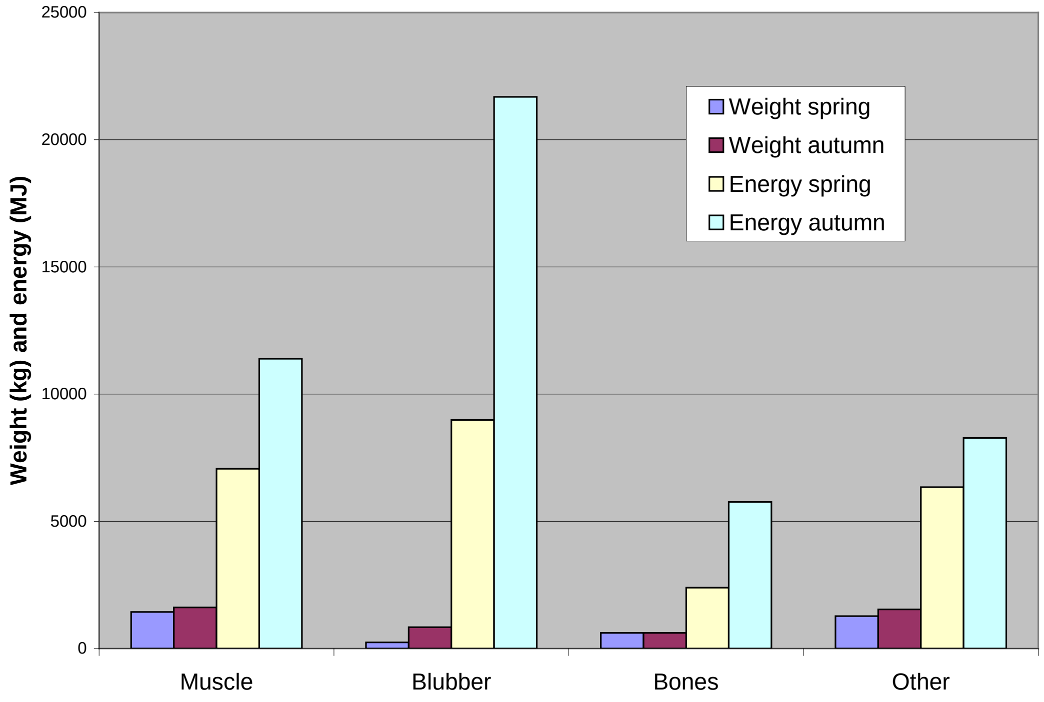

Figure 2b. Estimated increase in weight and energy content of different tissues of an average sized (7.5m) minke whale over a feeding season of 180 days.

Table 1a. Results of log-linear model on NA minke whale energy deposition measurements at position D5 and on tissue weights including day within season, log(length), the factor pregnant, and a factor for area in the case of tissue weights. Deposition per day (d) for an average sized animal of constant length (7.5m) mid season is used as a reference. The proportional weight of bone tissue is assumed to be the same as for fin whales. MJ=Mega-Joule; s.e. = standard error.

Mean body energy	Change per day						Deposition rate		Prop. body weight	Category
MJ	Energy density rate d^{-1}	s.e.	Weight (tissue) rate d^{-1}	s.e.	Sum of rates d^{-1}	s.e.	MJ/d	s.e.		
11,890	0.0047	0.00056	0.0015	0.00032	0.0062	0.00063	73.7	7.5	0.373	Muscle
16,850	0.0038	0.00086	0.0050	0.00079	0.0088	0.0012	148.3	20.2	0.132	Blubber+fat
4,074	0.0069	0.0038	0	0	0.0069	0.0038	28.1	15.5	0.15	Bones
7,313	0	NA	0.0022	0.0010	0.0022	0.0010	16.1	7.3	0.345	Other
40,127							266.2	50.5	1.00	Whole

Table 1b. Seasonal energy deposition where blubber and muscle energy density at several body sites are used instead of only D5 in Table 1a. by measurements at other positions of the same 9 animals for which bone energy was measured.

Mean body	Change per day			Deposition rate	Category
MJ	Energy density rate d^{-1}	Weight (tissue) rate d^{-1}	Sum of rates d^{-1}	MJ/d	
9,227	0.0024	0.0015	0.0039	36.0	Muscle
15,334	0.0019	0.0050	0.0069	105.8	Blubber+fat
4,074	0.0069	0	0.0069	28.1	Bones
7,313	0	0.0022	0.0022	16.1	Other
35,948				186.0	Whole

The energy measurements for muscle and blubber in table 1a are from position D5, *i.e.* dorsally and posteriorly on the body (Figure 1). This site has the thickest blubber and highest energy density (Christiansen *et al*., 2013; SC/F13/SP10_Rev) and appears to be an important energy storage site as in other baleen whales (Lockyer 1987a; Víkingsson 1995). Energy measurements were also used from sites D3, D1, M5, M3, M1, V5, and V3 from 9 animals (same as above). Energy density is lower at these sites and there is less change within season. While it is unknown how large a portion of the total muscle or blubber each sample represents, we have taken a conservative simple average of all these sites (together with D5?) instead of only D5 for these 9 animals . The average energy in muscle is then 78% of that of D5 and the seasonal change in energy density is 50% of the rate using only D5. These 9 animals have average blubber energy density at the 8 sites amounting to 91% of that of D5 and the energy density change is 70% of the rate using only D5.

These adjusted figures are presented in table 1b and should be regarded as conservative estimates. The daily deposition of total energy changes from 0.67% to 0.52%. There are no estimates of the variances in Table 1b but a CV on the daily deposition should be attainable within that of Table 1a or 0.19 (50.5/267.2) provided some more energy density measurement in existing samples of bones and blubber were carried out. However, most valuable in this respect would be additional energy measurements in tissues of the weighed animals.

The lowest lipid content of bone tissue was 2% for a pregnant female in April (n=4) and the highest values are around 33% in August and September (n=5). There was no change in the mineral density of the measured bones over the season, while lipid increases. If lipid replaces water in the bones concurrent with more lipid in the blubber and muscle, the buoyancy of the animals must be changing over the season. If this would be compensated for by an increase in bone mass rather than in the category *Other*, the estimated daily deposition in table 1b would be 4% higher.

A Von Bertalanffy growth curve was fitted to length at age in SC/F13/SP12. When applied to an animal of 750cm and assuming that growth does not differ by season, additional 5 and 2 MJ are required for a female and male respectively for growth per day through the year.

Christiansen *et al.* (2013) used blubber thickness measurements to estimate blubber increase over the season at 2.4 and 2.8 liters per day for pregnant females (n=49) and non-pregnant mature animals (n=66), respectively. The estimate from the weighings of blubber is 2.9kg per day (s.e. 0.46, n=26) for a mean animal mid season with no significant difference in the trend for pregnant. Thus, these two independent methods provided similar results regarding seasonal deposition of blubber. However, the results from the chemical analyses demonstrate the importance of energy density in addition to increase in weight. Thus, while the increase in body weight during the 180 day feeding season is “only” 27%, the total energy content of the body almost doubled during the same period.

The estimates of energy deposition in adipose tissue (blubber and visceral fat) are similar to that found in Norwegian minke whales (Nordøy *et al*., 1995). However, these authors did not consider energy deposition in the porous bones which appear to make an important contribution to the energy budget according to the present study.

Additional measurements of skeletal samples for comparison to the bones already measured would be valuable for a more precise estimation of the energy stored in bones. Weights of the minke whale skeleton are lacking and weights and chemical analyses of the various skeletal parts are needed if differences are to be revealed within the skeleton. If whole body weighings are carried out, care should be taken to measure all parts separately to get an estimate of the fluid loss.

Conclusion

This study clearly indicates the importance of seasonal deposition of energy reserves as has been demonstrated in the larger Balaenopterids (Lockyer 1987a; Víkingsson 1995). Although this feasibility/pilot study gives good approximations of the magnitude of energy deposition, larger sample sizes are needed for a more precise quantification, including potential differences between reproductive categories. Multiple energy measurements were made on tissues from only nine animals. Difference in energy content and deposition between position D5, which was measured for the whole sample size, and other positions is considerable. Additional energy measurements are therefore needed at the other body positions. Deposition of lipid in bones in these animals appears to be considerable and therefore more bone measurements are also needed.

The pattern of energy deposition is broadly similar to that found in fin whales in Icelandic waters (Lockyer 1987a; Víkingsson 1995). Posterior dorsal blubber and muscle are important sites for energy storage where pregnant females have the highest lipid levels in both species. The difference between reproductive classes is however less pronounced in minke whales, but this may be due to small sample size in some reproductive classes in the present study. The estimated rate of energy deposition in common minke whales is somewhat lower than that estimated for fin whales (Víkingsson, 1995). While this may be indicative of more winter feeding in minke whales as suggested by Nordøy *et al*. (1995), it might also reflect poor feeding conditions during the sampling period in the present study (SC/F13/SP2_Rev).

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