

Energy storage in common minke whales (*Balaenoptera acutorostrata*) in Icelandic waters 2003-2007. – Chemical composition of tissues and organs.

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Abstract

This report details studies on chemical composition (total lipids, protein and water) of various tissues in common minke whales (*Balaenoptera acutorostrata*). Energy deposition was demonstrated by an increase in the percentage of lipids in blubber, muscle, visceral fat and bones. As in other balaenopterids, most lipids were deposited dorsally behind the dorsal fin. In addition, large amounts of energy are apparently stored as visceral fats and within bone tissue. Highest levels of lipids were found in pregnant females. Spatial variation within the Icelandic continental shelf area might be explained by corresponding variation in diet composition. A significant decrease over the research period 2003-2007 in lipid content of posterior dorsal muscle could be a result of a decrease in prey availability

Introduction

The common minke whale (*Balaenoptera acutorostrata*) is the most abundant baleen whale species in the Icelandic continental shelf area. Like other Balaenopterids, minke whales are migratory animals spending the summer at relatively high latitude feeding areas and the winters at lower latitude breeding areas (Horwood 1990). Although minke whales have been observed in Icelandic waters throughout the year they are most frequent during the summer (April to September) with peak abundance in July (Sigurjónsson & Víkingsson 1997). Different migration patterns are observed for females, males and juveniles and minke whales are highly segregated by sex on the feeding grounds (Laidre et al. 2009). Minke whales have a more coastal distribution than their larger relatives and feed on a wide variety of fish and invertebrates. In the North Atlantic, they consume both krill (*Thysanoessa* spp. and *Meganyctiphanes* spp.) and various fish species such as herring (*Clupea harengus*), capelin (*Mallotus villosus*), sandeel (*Ammodytidae*), cod (*Gadus morhua*), polar cod (*Boreogadus saida*), haddock (*Melanogrammus aeglefinus*) (Haug et al. 1995, 2002, Sigurjónsson et al. 2000, Víkingsson & Elvarsson 2011, SC/F13/SP2). The diet varies both spatially and seasonally. Inter-annual variations in diet composition, probably reflecting prey availability, have been noted in the Northeast Atlantic. In the Central-North Atlantic stock, research in Icelandic waters during 2003–2007, has shown appreciable spatial and temporal variation in diet composition (Víkingsson & Elvarsson 2011, SC/F13,SP2). Overall, sandeel was the most common prey and was particularly dominant in the more southern areas. Large benthic fish together constituted altogether 26% of the diet, with cod and haddock being the most important species. Other important prey species include planktonic

crustaceans (krill) and capelin. The total annual prey consumption by minke whales in Icelandic and adjacent waters has been estimated as around 2 million metric tons (Sigurjónsson & Víkingsson 1997).

Balaenopterids are generally characterized as capital breeders, storing energy during a summer feeding season for use in breeding at lower latitudes in winter when they feed at much reduced rates or not at all. Such energy storage strategy has been described in some detail for some larger baleen whale species such as fin whales (Lockyer et al. 1985, Lockyer 1986, 1987, Víkingsson 1990, 1995, Boyd et al. 1999) and large temporal variations in body condition have been reported for some species (Lockyer 1987, Víkingsson 1990, Sigurjónsson 1992, Konishi et al. 2008). Previous research on common minke whale body condition has, however been largely limited to analysis of blubber thickness. Haug et al. (2002) reported on changes in blubber thickness and girths in Norwegian waters and related those to abundance of prey. Næss et al. (1998) presented data on muscle lipid from Norwegian waters collected as a part of Norwegian Special Permit research in 1992-1994. In addition to blubber thickness they provided data on weights of blubber, muscle and visceral fat. Low sample size (n=59) in the chemical analysis precluded comparisons according to sex and reproductive status (Næss et al. 1998).

No systematic studies have been conducted on body condition or energetics of common minke whales in Icelandic waters. Therefore energetic studies were included as an important part of the Icelandic minke whale research programme (MRI 2003). Here we report on chemical analysis of various tissues, believed to be important in energy storage. Other aspects of body condition are considered in SC/F13/SP8, SC/F13/SP10 and SC/F13/SP11.

Material and methods

The material used in this study originates from MRI's minke whale research programme with sampling in the years 2003-2007 (Marine Research Institute 2003). Sampling of whales was distributed spatially and temporally in proportion to the abundance of minke whales as known from sightings surveys conducted during 1986-2001. The details of the sampling process are given in SC/F13/SP1 and in the original research proposal (Marine Research Institute 2003) and in annual reports on the progress of the programme (Víkingsson et al. 2004, 2005, 2006, 2007, 2008, 2009).

Extensive sampling was undertaken on every captured minke whale including tissue samples of blubber and the underlying muscle at 18 locations on the body (see Figure 2) for the various sub-projects of the study. Previous research on balaenopterids s.a. fin whales has shown the posterior dorsal site (D5 on Figure 1) to be most important for energy deposition in blubber and muscle (Lockyer 1986, 1987, Víkingsson 1990, 1995, Konishi 2006) and there are indications that this may also apply to common minke whales (Næss et al. 1998). Therefore, this site was chosen as the standard for blubber and muscle sampling, while the study also includes comparisons with other sites to verify if the above assumption applies to minke whales as well. Approximately 5x5cm full depth samples of blubber and about the same size of muscle meat underneath the blubber were taken within two hours after death, packed in plastic bags and stored frozen at -20°C until laboratory analyses.

In the laboratory all samples but blubber and bones were homogenized in a mincing machine. The blubber samples were first homogenized in a mixer (samples of 2003 and 2004) but due to difficulties in that work, all later samples were sliced thinly (60 µm) in a freezing microtome (Leica CN 1850) whereafter the samples were mixed well. In homogenizing the blubber, care was taken to include the whole core of the same diameter from skin to muscle of each sample to ensure that all possible layers of the blubber were present in the final sample. The bones were sawn to small cubes (about 1 cm³) suitable for analysis where subsamples of the pectoral flippers were taken in the middle of the bone while the samples from the ribs were taken about 10 cm from the outer ends.

The moisture content was determined by drying at 103°C for four hours using the method of ISO 6496. The protein content was determined by the Kjeldahl method in accordance with ISO 5983-2. The fat was determined by Soxhlet-extraction applying AOCS Official Method Ba 3-38 with a mixture of 50:50 (v/v) of petroleum ether and diethylether as an extraction solvent.

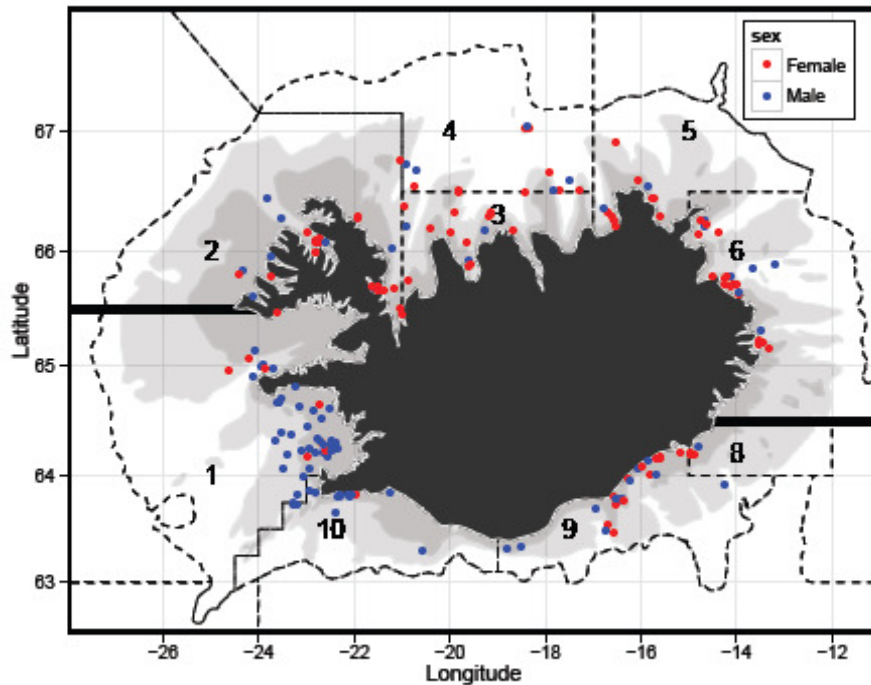


Figure 1. Catch positions of common minke whales for the research programme 2003-2007. The numbers (1-6 and 8-10) refer to the Bormicon areas .

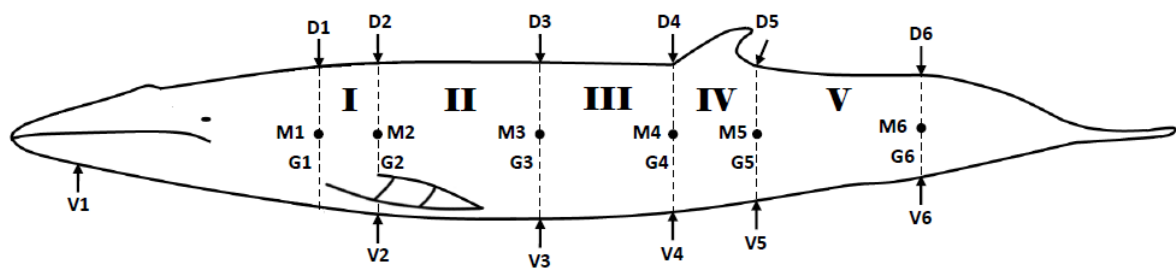


Figure 2. Sampling sites on the body of minke whales (Figure from SC/F13/SP8)

The sample distribution (n=502) among years was uneven with respect to dates and area (SC/F13/SP1). To take account of this variability, the results were analysed using generalized linear model using the R statistical software with percentage of total lipids as the dependent parameter. The explanatory parameters considered were length, year, day within a year (seasonal effect), maturity (separately by sex) as well as interactions between day within a year and maturity. The best model was selected on the basis of the Akaike Information Criterion (AIC), as discussed in Akaike (1974), by stepwise removal of the above parameters as follows:.

Parameter	Data	Reference point
Length	Numeric in cm	0
Year	Numeric (2003,2004,2005,2006,2007)	2002
Area	Factor. Bormicon areas 1,2,3,4,5,6,8,9. (see Fig. 1)	Area 1
Maturity	Factor. Immature males, Immature females, pubertal males, anoestrus females, pregnant females	Anoestrus females
Day within year	Numeric	Day 180 (29. June)

Results and discussion

Variation among different tissues and organs.

Table 1 gives the composition of different tissues and organs in terms of protein, lipid and water for pregnant females. The protein content of muscle shows little variation between sampling sites with means in the range of 22.3-25.9% on a wet weight basis (see Fig. 2 for sampling sites). In contrast, the lipid content of muscle is highly variable, where means are ranging 1.9-12.1%. Highest levels are found at sites D5 and D3.

There is much more variability in protein levels of the blubber across the body (Table 1). Highest levels are found anteriorly (see Table 1 and Figure 2). In particular the percentage of protein is high at site V1, representing the ventral grooves where a network of fibers is embedded in the blubber layer to enable great expansion during feeding in baleen whales. At this site, the mean lipid content is the lowest (19.2%), whereas the highest average lipid levels are found at site D5 behind the dorsal fin (75.3%).

This variability in lipid levels in muscle and blubber at different sites is similar to that found in other balaenopterid whales indicating that also for common minke whales, the posterior dorsal area is most important for energy storage within these tissues.

Both the investigated types of bone tissue contained on average more than 20% lipid on a wet weight basis (Table 1). As bones represent around 10% of the weight of baleen whales (Lockyer et al. 1985, Vikingsson 1995), these high levels show that bones are an important site of energy deposition in minke whales.

Lipid levels in visceral fat were generally high as expected, the means by reproductive classes ranging 66-84% (Table 2). However, protein levels are low as compared to blubber, and water content higher accordingly than in blubber.

The internal organs (heart, kidney and liver) had average lipid levels below 7% (Table 1) with a range of 1-15%.

Variation with respect to time, area and reproduction.

D5 muscle

For percentage lipid in the posterior dorsal muscle (D5) all the investigated parameters improved the model significantly except the interaction factor between maturity and day of the year.

The whales from the northern areas (Bormicon areas 6,8,9,10 in Fig.1) had higher lipid content than their more southern counterparts (Table 3). This seems to reflect pronounced differences in diet of minke whales in these two areas (SC/F13/SP2). Thus, the diet in the southern areas was dominated by fish species of high fat content such as sandeel (*Ammodytes marinus*) and herring (*Clupea haerengus*), while the diet was more diverse in the northern areas with high proportions of gadoids s.a. cod and haddock as well as higher occurrence of krill.

A simple mean of the total sample could indicate that the pubertal males had the highest lipid contents in the dorsal posterior muscle (Table 1). However, the sample size for this reproductive category is very small and in the statistical analysis they were treated with immatures. When the effects of area and season have been taken into account anoestrous females have the lowest lipid content of all classes while pregnant females have the highest lipid content followed by immature females (Table 3). This pattern is similar to that found in fin whales (Lockyer et al. 1985, Vikingsson 1990).

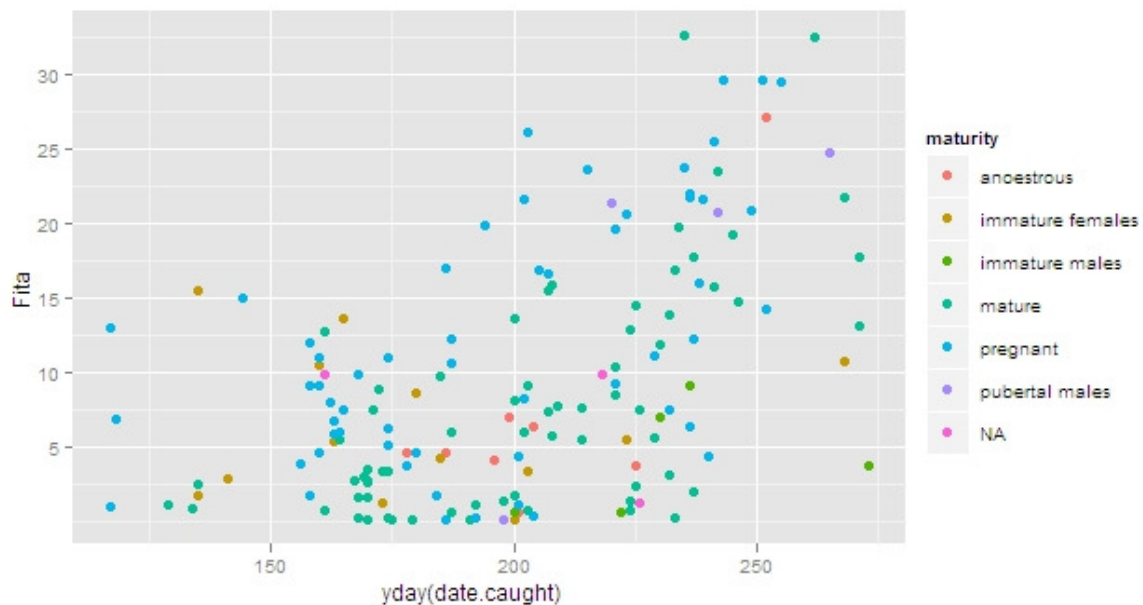


Figure 2. Lipid contents (Fita) of minke whale muscle (at position D5) plotted against the day of the year.

The lipid content of muscle at position D5 increased significantly over the feeding season (Table 3). The daily increase in percentage lipid content was estimated as 0.09 with no significant differences between reproductive classes.

There was a significant decrease in lipid content of muscle at position D5 over the research period 2003-2007. The year 2003 had by far the highest mean lipid content while the succeeding three years had similar levels with a minimum in 2006 (Figure 3). However, when account has been taken of sampling variability between years, a linear decrease of 1.39% lipid content per year was found over the period (Table 3). This coincides with a pronounced change in diet composition (SC/F13/SP2) following a collapse in the Icelandic sandeel population which may have contributed to the decrease in abundance of minke whales in coastal waters during this same period particularly in the southern areas (Bogason & Lilliendahl 2009, Borchers et al. 2009, Pike et al. 2011)

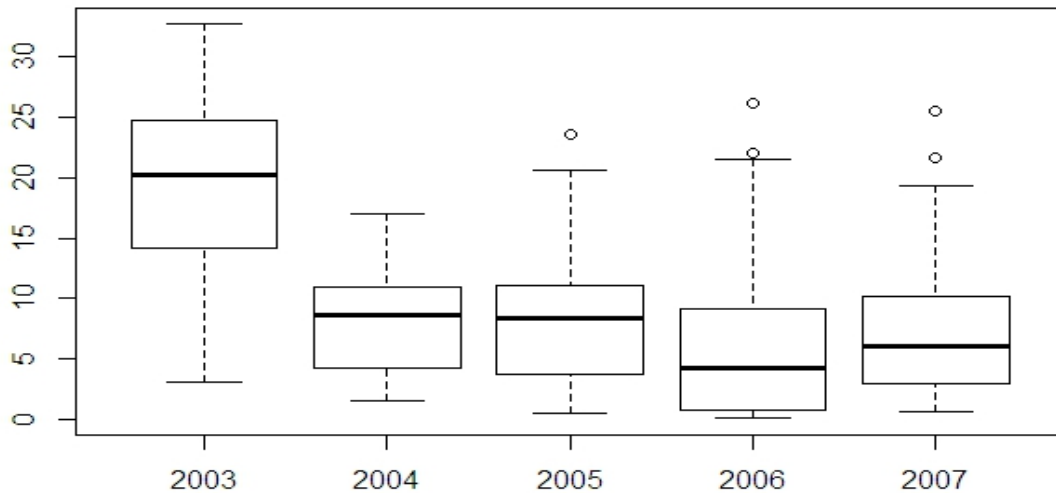


Figure 3. Boxplot (median, quartiles and range) of percentage lipid in posterior dorsal muscle (D5) according to year.

D5 blubber

For posterior dorsal blubber (D5), the only parameters that improved the model were day within the year (seasonal effect) and maturity status. Immature and pregnant females had highest levels of lipids in the blubber while mature males had the lowest (Table 4). The percentage lipid in the D5 blubber increased by 0.23 per day and this rate was not significantly different among reproductive classes.

Visceral fat

No differences were found between visceral fat in the thoracic and abdominal cavities (Table 1), so they are hereafter treated together. All the tested parameters except year did improve the model (Table 5). As for the posterior dorsal muscle, the southernmost areas had higher lipid content in visceral fat (Table 5) probably reflecting geographic differences in diet (SC/F13/SP2). The overall mean lipid levels were highest for pregnant females and immature+pubertal males but lowest in mature males and immature females (Table 2). However, the slope of the linear regression for seasonal effect was highest in the two latter classes (Table 5). Considering the mature animals, this indicates that the process of energy storage in visceral fat takes place earlier in the season for mature, and in particular pregnant, females than for mature males.

Conclusions

This study demonstrates that in addition to the increase in mass of important energy storage tissues, s.a. blubber and visceral fat (SC/F13/SP8, SC/F13/SP11), common minke whales store significant amounts of energy by increasing the lipid content of various tissues, thereby increasing the energy density per unit weight.

The results are consistent with previous studies on balaenopterids in that the most important blubber storage sites lie dorsally in the posterior part of the body. Significant amounts of energy are also stored in the posterior dorsal muscles as in fin whales (Lockyer et al. 1985, Vikingsson 1990, 1995) and supports indications detected by Næss et al. (1998) regarding minke whales. In addition, large amounts of energy are apparently stored as visceral fats and within bone tissue.

The pattern of variation among reproductive classes is broadly similar to that found for larger Balaenoptera with highest levels of lipids found in pregnant females.

The study has also shown interesting spatial variation within the Icelandic continental shelf area, which can be explained by corresponding variation in diet composition.

A significant decrease over the research period 2003-2007 in lipid content of posterior dorsal muscle could be a result of a decrease in prey availability. This is supported by the concurrent feeding ecology studies and recent changes in abundance of minke whales in the area. Thus, a massive decrease in the Icelandic sandeel population around or before 2005 explains decreased proportion of sandeels (apparently the preferred prey species) in the minke whale stomachs during 2003-2007 (ref?). Decreased abundance of minke whales in sightings surveys during 2007-2009, as compared to 2001, could thus reflect a shift in distribution as a result of food shortage.

This study has demonstrated the feasibility of using carcass analysis for estimating total energy storage throughout the season which would establish an important parameter for estimating food requirements as an input for multispecies modelling. Larger sample sizes (e.g. in connection with the commercial minke whaling operations) are however obviously required to increase the precision of such estimates.

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Table 1. Chemical composition of different tissues in pregnant females (% wet weight). Means, standard deviation (SD) and sample size (n).

Tissue	Location	Sample size	Protein		Lipid		Water	
			Mean	SD	Mean	SD	Mean	SD
Muscle								
	D1	7	25.55	0.97	2.31	2.47	71.27	2.55
	D3	7	22.32	2.85	11.04	10.72	66.03	10.77
	D5	57	22.69	1.97	12.07	8.36	61.62	6.99
	M1	7	23.40	1.61	1.88	2.09	71.89	3.53
	M3	6	24.47	1.40	3.73	3.29	69.57	5.49
	V3	7	25.87	1.02	1.85	1.59	71.54	2.17
	V5	6	22.59	2.73	7.85	8.59	64.95	10.97
Blubber								
	D1	7	16.31	5.74	53.81	12.89	33.60	12.36
	D3	7	14.09	4.48	59.68	13.63	28.04	8.71
	D5	47	5.78	3.24	75.27	17.44	15.83	15.28
	M1	7	12.86	5.74	61.05	15.77	26.87	11.78
	M3	6	11.36	3.49	66.87	12.79	22.80	9.23
	V1	6	20.35	1.70	19.18	11.41	61.36	6.78
	V3	6	12.36	5.54	55.57	16.16	27.73	10.14
	V5	6	10.75	4.69	64.77	8.32	22.65	8.90
Visceral fat								
	Thoracic	43	2.74	1.33	81.65	12.40	15.18	11.58
	Abdominal	43	3.00	2.47	79.71	19.41	16.72	17.43
Bones								
	Flipper	7			25.88	12.43		
	Rib	7			21.10	9.52		
Internal organs								
	Heart	5	18.31	0.91	6.95	6.96	76.64	2.92
	Kidney	7	15.23	0.47	6.50	5.84	76.99	6.00
	Liver	7	20.09	0.53	4.08	1.25	71.72	1.39
Total n								
		308						

Table 2. Chemical composition of blubber, muscle and visceral fat according to reproductive status. Means, standard deviation (SD) and sample size (n).

		Blubber (D5)					
Males	n	Protein	SD	Lipid	SD	Water	SD
Immature	3	3.54	2.92	81.02	5.63	14.73	5.12
Pubertal	5	6.08	2.41	71.37	30.73	21.64	24.80
Mature	66	6.87	3.74	65.66	24.52	25.87	21.69
Females							
Immature	15	4.56	1.43	76.93	10.81	16.07	10.36
Anestrous	6	5.26	2.98	74.12	18.07	15.12	10.84
Pregnant	47	5.78	3.24	75.27	17.44	15.83	15.28
		Muscle (D5)					
Males	n	Protein	SD	Lipid	SD	Water	SD
Immature	5	23.76	0.45	4.20	3.84	70.46	5.15
Pubertal	4	21.59	2.38	16.76	11.27	57.27	4.98
Mature	68	23.06	1.51	7.77	7.73	65.55	6.73
Females							
Immature	13	23.47	1.40	6.40	4.91	66.60	4.97
Anestrous	8	23.53	2.73	7.28	8.28	64.74	5.57
Pregnant	57	22.69	1.97	12.07	8.36	61.62	6.99
		Visceral fat					
Males	n	Protein	SD	Lipid	SD	Water	SD
Immature	3	2.28	0.67	84.00	9.00	15.39	12.22
Pubertal	5	2.91	1.73	81.37	13.08	15.22	11.89
Mature	77	3.89	3.11	69.70	27.86	26.26	25.61
Females							
Immature	15	4.72	3.54	66.43	26.44	28.59	23.60
Anestrous	14	4.70	4.15	71.79	23.08	23.23	18.34
Pregnant	91	2.78	1.96	81.34	16.03	15.34	14.56
Total n	502						

Table 3. Summary of the variables of the best model, in terms of AIC, for percent lipid in posterior dorsal muscle (D5). The intercept represents anoestrous females in Bormicon area 1 in the year 2002 on day 180, and the explanatory parameters are relative to that value.

		Estimate	Std. Error	t value	Pr(> t)
Intercept		-2.1416	7.9031	-0.27	0.7868
Time trend (year)		-1.3885	0.4408	-3.15	0.0020
Seasonal effect (day of year)		0.0901	0.0172	5.25	0.0000
Maturity status	Immature females	4.2664	3.0528	1.40	0.1645
	Immature males	1.6676	3.5073	0.48	0.6352
	Mature males	0.9337	2.5017	0.37	0.7096
	Pregnant females	6.4758	2.3748	2.73	0.0072
Whale length		0.0149	0.0092	1.61	0.1089
Bormicon area	2	-1.0857	1.6514	-0.66	0.5120
	3	-4.6614	2.0720	-2.25	0.0260
	4	-3.7139	2.1906	-1.70	0.0922
	5	-3.8405	2.5700	-1.49	0.1374
	5	3.6505	1.7973	2.03	0.0442
	8	6.9972	4.5992	1.52	0.1304
	9	1.2381	1.6115	0.77	0.4436
	10	1.6535	2.0079	0.82	0.4116

Table 4. Summary of the variables of the best model, in terms of AIC, for percent lipid in posterior dorsal blubber (D5). The intercept represents anoestrous females on day 180, , and the explanatory parameters are relative to that value.

		Estimate	Std. Error	t value	Pr(> t)
Intercept		67.2175	8.1165	8.28	0.0000
Seasonal effect (day of year)		0.2313	0.0494	4.68	0.0000
Maturity status	Immature females	6.1529	9.4708	0.65	0.5170
	Immature males	-1.8895	10.5751	-0.18	0.8585
	Mature males	-7.7819	8.3378	-0.93	0.3523
	Pregnant females	5.7206	8.5319	0.67	0.5037

Table 5. Summary of the variables of the best model, in terms of AIC, for percent lipid in Visceral fat. The intercept represents anoestrous females in Bormicon area 1 on day 180 and the explanatory parameters are relative to that value..

		Estimate	Std. Error	t value	Pr(> t)
	Intercept	77.2780	7.8090	9.90	0.0000
	Seasonal effect (day of year)	0.1942	0.2514	0.77	0.4407
	Immature females	-11.8000	9.7928	-1.20	0.2297
	Immature males	-0.1857	15.1179	-0.01	0.9902
	Mature males	-24.9214	7.9418	-3.14	0.0020
	Pregnant females	12.1188	7.3775	1.64	0.1021
Bormicon area	2	-9.9788	4.0128	-2.49	0.0138
	3	-23.6849	4.9088	-4.82	0.0000
	4	-26.4990	5.0687	-5.23	0.0000
	5	-8.7232	5.7123	-1.53	0.1284
	5	-3.6994	4.3944	-0.84	0.4010
	8	6.3118	10.9140	0.58	0.5637
	9	6.1226	4.1760	1.47	0.1443
	10	9.1402	7.1793	1.27	0.2046
Interaction day and maturity status	Day : Immature females	0.2355	0.3024	0.78	0.4370
	Day : Immature males	0.0984	0.3894	0.25	0.8008
	Day : Mature males	0.3804	0.2603	1.46	0.1456
	Day : Pregnant females	-0.1712	0.2572	-0.67	0.5063