

Female body condition affects foetal growth in a capital breeding mysticete

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

¹Institute of Biological and Environmental Sciences and ⁴Marine Alliance for Science and Technology for Scotland, University of Aberdeen, Aberdeen, AB24 2TZ, UK

²Programme for Whale Research, Marine Research Institute, P.O. Box 1390, 121 Reykjavik, Iceland

³Húsavík Research Center, University of Iceland, Hafnarstett 3, 640 Húsavík, Iceland

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

Abstract

Understanding how female body condition (FBC) influence foetal development, and hence offspring production, is fundamental for our understanding of species reproductive physiology and life history. In this study we demonstrate for the first time that FBC can affect foetus growth in minke whales, a capital breeding K-strategy species. Pregnant minke whales were sampled around Iceland during the summer feeding seasons between 2003 and 2007 and the length and weight of their foetuses were measured. FBC was modelled as the relative difference between measured blubber volume and the average expected blubber volume of individual whales. Linear models were used to test the effect of FBC on foetus length, while accounting for the daily growth in foetus size through gestation, as well as other covariates. Similar to previous studies, foetus length increased linearly through the study period at a rate of 0.918 cm day⁻¹ (SE=0.111). The effect of FBC on foetal length was nonlinear, showing an almost linear positive relationship for females in poorer body condition (FBC<0), which levelled off at better body conditions (FBC>0). This curvilinear relationship was confirmed by fitting a generalized additive model and by running separate analyses on two subsets of data containing females in poorer and better condition. Our findings suggest that females that are in poorer body condition reduce their energetic investment in their foetus proportionately to their condition, in order to maintain high adult survival. That foetus length did not continue to increase at better body condition suggest that maternal size causes physiological constraints to the maximum length that the offspring can attain at birth, in order to avoid labour complications. Reducing the size at birth by reducing the gestation period is unlikely, since the reproductive cycle of balaenopterids is strongly linked to their seasonal migration between feeding grounds and breeding grounds.

INTRODUCTION

A species life history dictates how an animal allocate energy throughout its life between growth, reproduction and survival to maximize fitness (Stearns 1992). K-strategy species differ from r-strategy species in that they maximize lifetime reproductive success by having a low reproductive potential but high survivorship (MacArthur & Wilson 1967). With their large adult body size, high lifetime expectancy, iteroparity, small litter size and delayed reproduction, cetaceans are typical K-strategists (Lockyer 1984). In terms of financing reproduction, cetaceans can be further divided into income breeders, which use current energetic income to finance reproduction, and capital breeders, which use previously stored energy to finance reproduction (Costa 1993; Jönsson 1997; Stephens *et al.* 2009). Most odontocetes can be considered income breeders, since they continue to feed throughout the reproductive cycle (the period including mating, conception, gestation, parturition, lactation and weaning). In contrast, mysticetes can be considered capital breeders since they finance the costs of reproduction on low latitude breeding grounds with stored energy acquired on high latitude feeding grounds (Lockyer 1987a; Kasuya 1995).

Their capital breeding strategy allow mysticetes to undertake long distance seasonal migrations between highly productive feeding grounds in the summer and less productive breeding grounds in the winter, where they mate and give birth. Most of the energy needed during the breeding season is stored in the form of blubber (Lockyer 1987a; b; Kasuya 1995; Nordøy *et al.* 1995; Miller *et al.* 2011; Christiansen *et al.* in press), although some energy is also stored in muscle and intra-abdominal fat (Lockyer 1987b; Vikingsson 1995; Næss, Haug, & Nilssen 1998). The stored energy constitute the excess energy acquired during the feeding season, after the whale has covered its own energetic needs for metabolism, maintenance and growth (Parry 1949). The relative amount of blubber therefore provides a good measure of the energy balance, and therefore body condition, of mysticetes (Miller *et al.* 2011).

Icelandic waters constitute important feeding grounds for minke whales (*Balaenoptera acutorostrata*) in the North Atlantic (Borchers *et al.* 2009; Christiansen *et al.* in press), with minke whales being present between mid April and mid October every year (Sigurjónsson & Víkingsson 1997), although some animals can be seen year around. The exact location of the breeding grounds are unknown, they are believed to be located somewhere close to the equatorial waters of the Atlantic (Vikingsson & Heide-Jørgensen 2005).

Like other mysticetes, the reproductive cycle of minke whales is closely synchronized with their annual migration pattern (Laws 1959; Lockyer 1984). While most balaenopterids have a two year reproductive cycle, comprised of about a year of gestation, half a year of lactation and half a year of resting (Lockyer 1984), minke whales are considered annual breeders, with calving rates above 90% (Jonsgård 1951; Horwood 1990). In the north Atlantic the peak of conception occurs around February (Sergeant 1963; Lockyer 1984) (Lockyer 1984), although there are considerable variation in conception dates (Frazer & Huggett 1973; Wang 1985; Horwood 1990; Kato & Miyashita 1991; Kato 1992). The period of gestation has been estimated to about 10 months (Sergeant 1963; Ivashin & Mikhalev 1978; Masaki 1979; Best 1982; Wang 1985; Horwood 1990), after which the female gives birth to a single calf between 240 and 280cm in length (Sergeant 1963; Ivashin & Mikhalev 1978; Wang 1985) or about 305 kg in mass (Lockyer 1981). Although empirical data is missing, the lactation period is believed to last between four and six months (IWC 1979; Best 1982; Lockyer 1984; Kato & Miyashita 1991), at which time the calf has normally reached a length somewhere between 430 and 550 cm (Jonsgård 1951; Best 1982; Lockyer 1984). Ovulation occurs again about four months after parturition (Best 1982), meaning that most mature females are still lactating when they ovulate and conceive (Jonsgård 1951; Best 1982; Kato & Miyashita 1991). Consequently, although minke whales exhibit annual reproduction, the actual reproductive cycle, or calving interval, is believed to be closer to 14 months (IWC 1979; Lockyer 1981, 1984; Best 1982). There is no evidence of delayed implantation in mysticetes (Lockyer 1984), something which is commonly exhibited in pinnipeds (Boyd 1996).

Foetus development in mammals can generally be described by a slow growth phase during the beginning of pregnancy, followed by a more rapid accelerating phase following the full establishment of the placental circulation (Huggett & Widdas 1951; Laws 1959). This later phase, known as the late prenatal phase, is characterised by a constant growth rate in foetus length, or the cube root of foetus weight, up until parturition (Huggett & Widdas 1951; Frazer & Huggett 1959, 1973). In balaenopterids, the late prenatal growth phase is believed to start somewhere between 60 (Horwood 1990) and 74 days (Lockyer 1984) after conception, which coincides more or less with the arrival of the females on the feeding grounds (Rice 1983; Lockyer 1984). Up until then the female has been relying on the stored energy in her blubber to finance the costs of ovulation and mating, as well as the growth of the foetus during the

first months of gestation, since no feeding takes place on the breeding grounds. Minke whales are believed to spend about six months in the feeding grounds (Folkow *et al.* 2000), during which they nearly double their blubber volume (Christiansen *et al.* in press), before migrating back to the breeding grounds. This means that during this final period of gestation (roughly the last fifth), and also during parturition and lactation, the female once again needs to rely on the energy stored in her blubber. After birth, the calf is weaned before or during the migration back to the feeding grounds (Kato & Miyashita 1991). With the periods of lactation and ovulation overlapping in minke whales, females will commonly have to support the growth of her new foetus while simultaneously supporting her newborn calf (Jonsgård 1951; Best 1982; Lockyer 1984; Kato & Miyashita 1991).

In order to produce large offsprings with high survival, and to have their reproductive cycle synchronized with their annual migratory cycle, balaenopterids have evolved some of the highest foetus growth rates among mammals (Frazer & Huggett 1959, 1973). Such high growth rates suggest that the energetic investment during gestation must be very high (Lockyer 1986), and that adequate nutrition will be key to reproductive success and recruitment (Pitcher, Calkins, & Pendleton 1998). Since most of the energy required during gestation is supported by energy stored in the blubber layer of the females, one should expect a close relationship between foetus growth and female body condition (FBC). While high investment in the foetus growth will increase size at birth and hence calf survival (Kovacs & Lavigne 1986; Pontier, Gaillard, & Allainé 1993; Boltnev, York, & Antonelis 1998; Boltnev & York 2001; McMahon & Burton 2005; Huang, Chou, & Ni 2009; Huang *et al.* 2011), it will lead to a gradual depletion of female energy reserves, throughout the reproductive cycle, most noticeable as a decrease in blubber thickness (Lockyer 1984, 2007; Miller *et al.* 2011). Poorer body condition can lead to a decrease in adult survival (Le Boeuf *et al.* 2000). Because cetaceans are highly iteroparous species, life history dictates that the females should gear energy investment during pregnancy toward maximizing their own survival over that of their current offspring in order to maximize lifetime reproductive success (Peacock 1991; Pontier *et al.* 1993; Lockyer 2007). Thus, females in poor body conditions are more likely to reduce investment in their offspring rather than jeopardizing their own survival.

There are a number of ways in which a female can reduce the investment in her offspring. This includes altering her own metabolism to reduce her own energy expenditure (maintenance costs), decreasing the rate of energy investment in the foetus by producing a smaller offspring, or shortening the gestation period by making an earlier switch from gestation to lactation (Peacock 1991). In cetaceans, relatively little is known about the relationship between FBC and reproduction. In odontocetes, female harbour porpoises (*Phocoena phocoena*) produced smaller calves during years of lower prey intake (Read 2001). In mysticetes, Lockyer (1990) found that female body mass influenced the weight-length relationship of foetuses in fin whales (*Balaenoptera physalus*), with foetuses being leaner in years when females were in poorer body condition. These findings suggests that female cetaceans can reduce the energetic investment in their offspring by producing smaller calves, by decreasing the growth rate of the foetus (Kovacs & Lavigne 1986; Pontier *et al.* 1993; Read 2001; Boltnev & York 2001). The size at birth will influence the size at weaning, which will strongly influence neonatal survival (Kovacs & Lavigne 1986; Baker & Fowler 1992; Pontier *et al.* 1993; Boltnev & York 2001; McMahon & Burton 2005; Huang *et al.* 2009, 2011). Because of this, there is a need for empirical studies looking at the relationship between FBC and foetus growth in cetaceans.

This study aims to inform the link between FBC and foetus growth in minke whales. Using data collected from the Icelandic feeding ground, the effect of FBC, expressed as relative blubber volume of females, on foetus length and weight through the feeding season, as well as the effect of FBC on the length-weight relationship of foetuses.

MATERIAL AND METHODS

Sampling protocol

Foetus lengths and weights of minke whales in Icelandic waters were collected by researchers from the Marine Research Institute of Iceland (Hafrannsóknastofnunin) between 2003 and 2007 as part of the Scientific Research Programme on minke whales. Foetus length was measured to the nearest mm along a straight line from the tip of the upper jaw to the notch of the tail flukes (or to the tip of the tail for foetuses smaller than about 20 cm in length). Body weight was measured to the nearest gram for small (<1 kg) foetuses and to the nearest 10g for larger foetuses. With reproductive status also being determined from the ovaries of females, the likelihood of missing a foetus was considered very small. Females carrying more than one foetus were removed from the data set, since litter size has been shown to influence the growth rate of individual foetuses (Huggett & Widdas 1951).

Female body condition (FBC)

Relative blubber volume was used as an index of FBC of minke whales, since most of the energy needed during the breeding season is stored as blubber (Lockyer 1987a; b; Kasuya 1995; Miller *et al.* 2011; Christiansen *et al.* in press). Christiansen *et al.* (in press) estimated the blubber volume of individual minke whales caught in the Scientific whaling programme in Iceland (N=131), using blubber thickness measured from 17 sites across the body of the whale, together with 6 measures of girth, the full body length of the animal and the distance between measurement sites. By investigating the effect of a number of covariates, they found that the variation in blubber volume could largely be explained by the animal's body length, reproductive class, the day in the feeding season and year (for details, see Christiansen *et al.* in press). The year effect was believed to be caused by variation in prey abundance (Lockyer 1987a; Sigurjónsson 1992; Ichii *et al.* 1998; Haug, Lindstrøm, & Nilssen 2002; Miller *et al.* 2011), and was therefore already accounting for some of the variance in body condition of minke whales. To avoid the year effect masking the effect of FBC on foetus growth, year as a covariate was removed from the blubber volume model. After removing year from the model, the total blubber volume, BV (m³), of pregnant females could be modelled as (Christiansen *et al.* in press):

$$BV_i = -0.796 + 0.176L_i + 0.00244D_i + \varepsilon_i \quad (1)$$

Where L is the body length of the whale (m), D is the number of days into the feeding season (counted from April 27) and ε_i is the residual errors (normally distributed with zero mean and constant variance, $\varepsilon_i \sim N(0, \sigma^2)$). The total model explained 78% (R^2) of the total variance in the data. The positive values for the length (0.176) and day parameters (0.00244) indicate that blubber volume increase with the size of the animal and that pregnant females increase their blubber volume at a constant rate throughout the feeding season (Christiansen *et al.* in press). The model residual (ε_i) represent the difference, in m³, between the observed blubber volume (BV_{obs}) and the expected, or average blubber volume (BV_{exp}), and thus provide a good measure of FBC. However, although the model accounts for seasonal variation in blubber volume (i.e. day), the residual provides an absolute rather than relative value, which will vary depending on when in the feeding season body condition was measured (assuming that the residual

difference was caused by variation in the rate of blubber increase (the slope parameter) and not by variation in absolute blubber (the intercept parameter)). Therefore, a more appropriate measure of condition is the relative FBC (%):

$$FBC = \frac{BV_{Obs} - BV_{Exp}}{BV_{Exp}} \quad (2)$$

Where BV_{Obs} is the observed blubber volume (m^3) and BV_{Exp} is the expected blubber volume (m^3). Since the effect of day was included in the model of blubber volume (equation 1), our index of FBC accounts for temporal variation in blubber volume between individuals, which allow comparison of body condition between females caught at different times in the feeding season. Another important feature of the index is that it accounts for the size (i.e. length) of the animal (equation 1), which affect the blubber volume and therefore body condition of the animal.

Effects on foetus length

Linear Models were developed in R 2.14 (R Development Core Team 2011) to determine the relationship between FBC and foetus size. Foetus length rather than weight was used as a measure of foetus size, since the former measurement is most often presented in the cetacean literature, as a result of technical difficulties in weighing either very small or very large foetuses (Ivashin & Mikhalev 1978). This is unlikely to affect the measured effect of FBC,

since foetus length and weight have been found to be closely related as $L^3 \propto W$ (Huggett &

Widdas 1951; Laws 1959; Ivashin & Mikhalev 1978). However to confirm this, the same analyses were also carried out using foetus weight as a response variable (see Supporting information).

To avoid confounding effects of other factors, the model selection tested for a number of covariates and their influence on foetus length. The most obvious covariate to include was day, since the length of the foetus will increase through the study period, following the process of gestation, which needed to be accounted for. The effect of maternal size (i.e. length) was also investigated, since studies on both cetaceans (Lockyer 1990, 2007) and pinnipeds (Kovacs & Lavigne 1986; Baker & Fowler 1992; Boltnev & York 2001) have showed that maternal size can greatly influence the size, and thus growth rate, of the foetus. Collinearity between explanatory variables was investigated using variance inflation factor (VIF) with a threshold value of three (`car` package, Fox and Weisberg, 2011).

Apart from linear relationships, different polynomial non-linear relationships between the dependent and independent variables were tested. A generalized additive model (GAM) with a thin plate regression spline smoother was also used to look for potential non-linear relationships outside the range possible for linear models. The best fitting model was selected using Akaike's Information Criterion (AIC), which provides a relative measure of the goodness of fit of statistical models.

To be able to differentiate a potential effect of FBC on foetus growth from naturally occurring variations resulting from variation in conception dates between females, the data set was separated into two subsets, one comprised of females in poorer body condition ($FBC < 0$) and

females in better body condition ($FBC > 0$). The same model selection procedure was then carried out as for the full data set.

Effects on foetus weight-length

To test if FBC had an effect on the weight-length relationship (the leanness) of foetuses (Lockyer 1990; Peacock 1991), the relationship between foetus weight and length was first investigated, using generalized linear models (GLM) with a log link to bind the fitted values above zero (foetus weight cannot be negative). The effect of FBC on the relationship between foetus weight and length was then measured by including FBC as an interaction term in the model.

Model validation

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

Sensitivity analysis

The blubber volume model (equation 1) used to estimate FBC (equation 2), comes with a level of uncertainty, which if sufficiently large could affect the FBC estimates and hence the measured effect on foetus growth. To quantify the effect of this uncertainty, bootstrapping resampling methods were used, running 1000 simulations. For each simulation new values of blubber volume, taken from a random normal distribution defined by the mean and SE around the predicted blubber volume for each individual whale, were used to re-estimate FBC. After the bootstrapping simulation, the effects of on foetus length were assessed by visual examination.

RESULTS

Sample size

192 minke whales were sampled in the scientific programme in Iceland between 2003 and 2007, of which 82 were pregnant females. One female was found carrying multiple foetuses (twins), and was therefore removed from the data set. From the remaining females, body condition could be estimated for 48 whales, which ranged between -28.5 and +43.3%. Length and weight was obtained from 62 and 31 foetuses, respectively. The sampling period stretched from April 27 to September 18. The foetuses varied in size from 2 to 178cm in length and from 0.117 to 59kg in weight. Visual inspection of the foetus length distribution through the feeding season showed no obvious deviation from a normal distribution (Fig. 1). The data was thus not temporally biased towards smaller foetuses at the end of the study period, as a result of females in late pregnancy already having started their migration back to the breeding grounds (Laws 1959; Frazer & Huggett 1973; Ivashin & Mikhalev 1978; Kato & Miyashita 1991). Instead, the smaller peak in foetus lengths that becomes visible in the second half of the study period represent the reduced size foetuses of females in poorer body condition (Fig. 1).

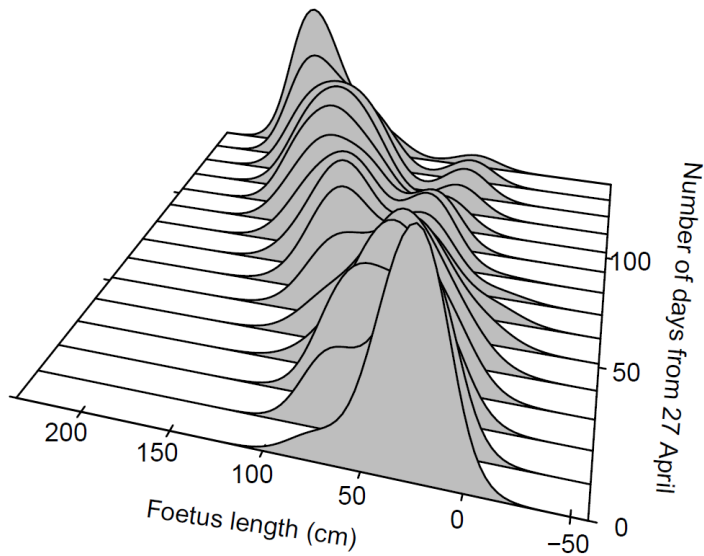


Fig. 1. Conditional density plot (`hdcde` package, Hyndman, Bashtannyk, & Grunwald 1996) of foetus length as a function of day for minke whales. Day 1 corresponds to April 27.

Effects on foetus length

The best fitting model included day and FBC as covariates ($F_{3,44}=28.94$, $P<0.0001$, model 9 in Table 1). There was no interaction between the two explanatory variables (model 7 in Table 1), which showed that the effect of body condition on foetus length remained same throughout the study period. Female body size (i.e. length) had not affect on foetus length (models 4 and 5 in Table 1), although the range of female lengths used in the analyses was quite restricted, between 6.8 and 8.7m (mean=8.0, SE=0.45). There were no collinearity between the explanatory variables in the model ($VIF<3$).

Table 1. Results of linear model selection for minke whale foetus length. Length(F)=Foetus length, Length(M)=Female (maternal) length, FBC=Female body condition.

Model	Variables	F-statistic	df(among)	df(within)	P-value	R ²	AIC	ΔAIC
1	Length(F)~Day	53.7	1	46	<0.0001	0.54	472.9	11.2
2	Length(F)~Length(M)	0.4	1	46	0.5219	0.01	509.6	47.9
3	Length(F)~FBC	3.5	1	46	0.0679	0.07	506.5	44.8
4	Length(F)~Day+Length(M)	26.4	2	45	<0.0001	0.54	474.8	13.1
5	Length(F)~Day*Length(M)	17.6	3	44	<0.0001	0.55	476.2	14.5
6	Length(F)~Day+FBC	37.7	2	45	<0.0001	0.63	464.8	3.1
7	Length(F)~Day*FBC	24.6	3	44	<0.0001	0.63	466.7	5.0
8	Length(F)~Day+FBC ²	33.9	2	45	<0.0001	0.60	468.0	6.3
9	Length(F)~Day+(FBC+FBC ²)	28.9	3	44	<0.0001	0.66	461.7	0.0

Foetus length increased linearly through the feeding season ($F_{1,44}=70.47$, $P<0.001$) at a rate of $0.918 \text{ cm day}^{-1}$ (SE=0.111) (Fig. 2a). It was not possible to fit a segmented regression line through the data (splitting the regression line into two separate lines with different growth rates), confirming that the growth rate was constant throughout the feeding season. The rate of increase in foetus length remained virtually constant when accounting for model uncertainties (Fig. 2b).

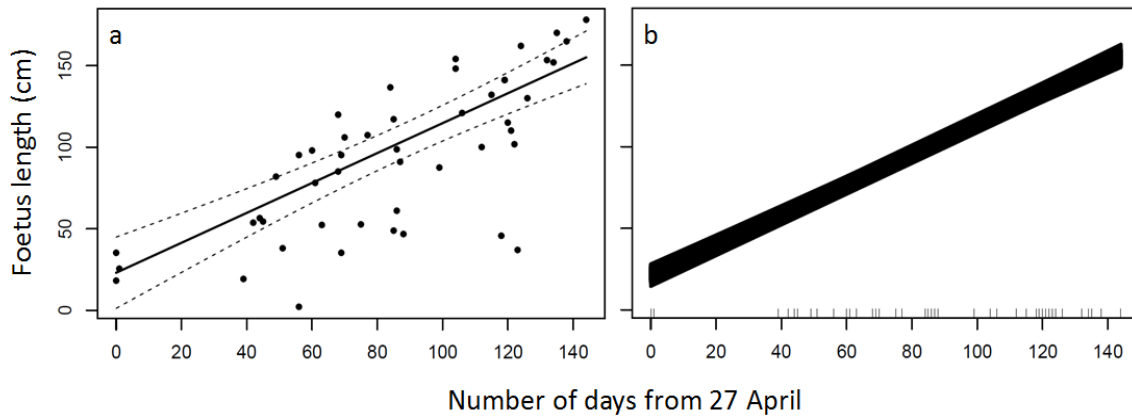


Fig. 2. Partial effect plot of foetus length as a function of day for minke whales, showing (a) the results of the best fitting linear model (model 9 in Table 1) together with (b) the output of the sensitivity analysis (the influence of uncertainty on FBC). Day 1 corresponds to April 27. FBC has been fixed at zero. The dashed lines represent 95% confidence interval. $n=48$.

The relationship between foetus length and FBC was best described by a quadratic polynomial relationship ($F_{2,44}=8.17$, $P<0.001$), which explained significantly more than a linear relationship ($L=4.906$, $df=1$, $P=0.032$). The curvilinear relationship was similar to a logistic growth curve, showing an almost linear positive relationship at poorer body condition ($FBC<0$), which then levelled off at better body condition ($FBC>0$) (Fig. 3a). The relationship remained largely the same when accounting for model uncertainties (Fig. 3b) and although the curve varied largely in shape at higher FBC values, the spread corresponded well with the confidence interval given by the linear model. The linear model explained 66.4% of the variance in foetus length, with day explaining 53.9% and FBC 12.5%. The sex of the foetus did not influence the length ($F_{1,29}=1.47$, $P=0.235$) or the rate of seasonal increase of the foetus ($F_{1,29}=1.14$, $P=0.294$). The same nonlinear effect of FBC was also found for foetus weight (Fig. S1, Supporting information).

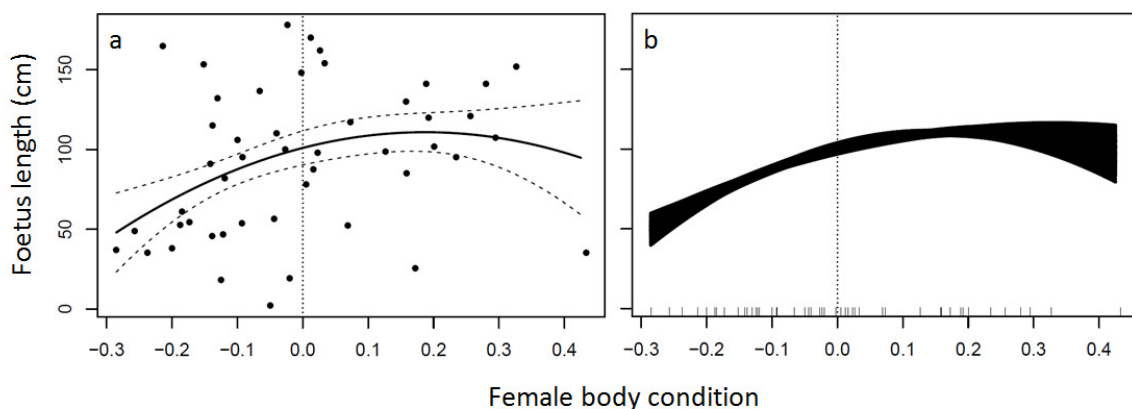


Fig. 3. Partial effect plots of foetus length as a function of FBC for minke whales, showing (a) the results of the best fitting linear model (model 9 in Table 1) together with (b) the output of the sensitivity analysis (the influence of uncertainty on FBC). Day has been fixed at 85 (July 20), which is the mean sampling date in the feeding season. The dashed lines represent 95% confidence interval and the dotted vertical line crossing the x-axis at zero represent the average FBC. $n=48$.

The nonlinear relationship between foetus length and FBC was further supported by the GAM ($F_{2,33,43.67}=5.27$, $P=0.003$), which showed that the flat part of the curve continued at higher

FBC values (FBC>0.2) (Fig. 4a). The sensitivity analysis also showed a much narrower spread of the curve at higher FBC values (Fig. 4b), again confirming that the relationship remained flat for females in better body condition (FBC>0).

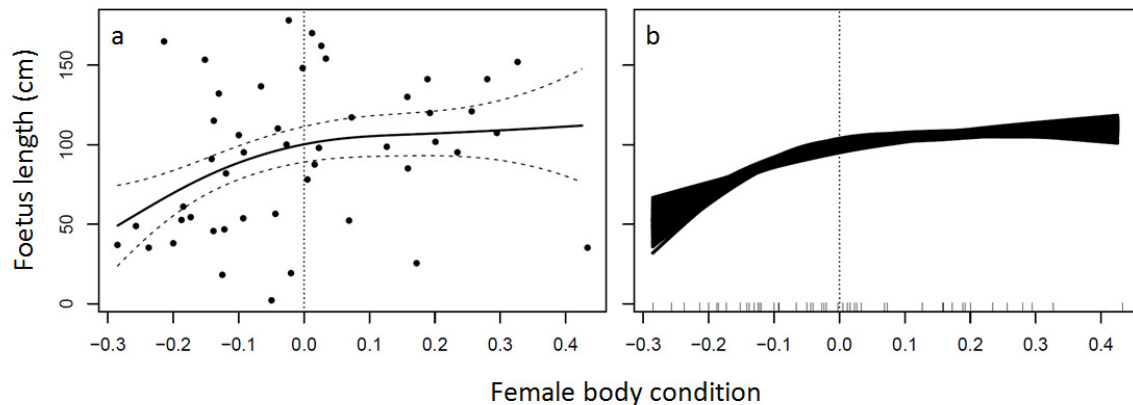


Fig. 4. Partial effect plots of foetus length as a function of FBC for minke whales, showing (a) the results of the GAM together with (b) the output of the sensitivity analysis (the influence of uncertainty on FBC). Day has been fixed at 85 (July 20), which is the mean sampling date in the feeding season. The dashed lines represent 95% confidence interval and the dotted vertical line crossing the x-axis at zero represent the average FBC. n=48.

Additional support of the nonlinear relationship between foetus length and FBC was provided by the separate analyses. As expected, there was still a significant effect of FBC on foetus length ($F_{1,24}=5.48$, $P=0.028$) for females in poorer condition (FBC<0), however the effect could equally well be described by a linear function as a quadratic polynomial ($L=2.425$, $df=1$, $P=0.133$). In contrast, there was no effect of FBC on foetus length ($F_{1,18}=0.00$, $P=0.960$) for females in better body condition (FBC>0), as could be expected given the flat relationship of the linear model (Fig. 3) and the GAM (Fig. 4) at higher FBC. Again, day had a significant effect in both models (FBC<0: $F_{1,24}=25.47$, $P<0.001$; FBC>0: $F_{1,18}=62.77$, $P<0.001$) and the rates of increase (FBC<0: $0.942 \text{ cm day}^{-1}$, $SE=0.181$; FBC>0: $0.9068 \text{ cm day}^{-1}$, $SE=0.117$) did not differ significantly from that obtained from the full model ($0.918 \text{ cm day}^{-1}$, $SE=0.111$).

Effect on foetus weight-length

The GLM analyses showed a quadratic polynomial relationship between foetus weight and length ($F_{2,24}=417.66$, $P<0.0001$, Fig. 5a). A likelihood ratio test indicated that the quadratic polynomial model was considerable better than a linear model ($L=28.65$, $df=1$, $P<0.001$). The relationship was very strong, having a R^2 value at 97.2%. The weight-length relationship was unaffected by FBC ($F_{2,22}=1.061$, $P=0.363$), also when accounting for uncertainty in the FBC estimate (Fig. 5b). This suggests that a potential reduction in female energy investment in the offspring did not result in leaner foetuses. Also, the sex of the foetus did not influence the weight-length relationship ($F_{2,19}=3.22$, $P=0.062$).

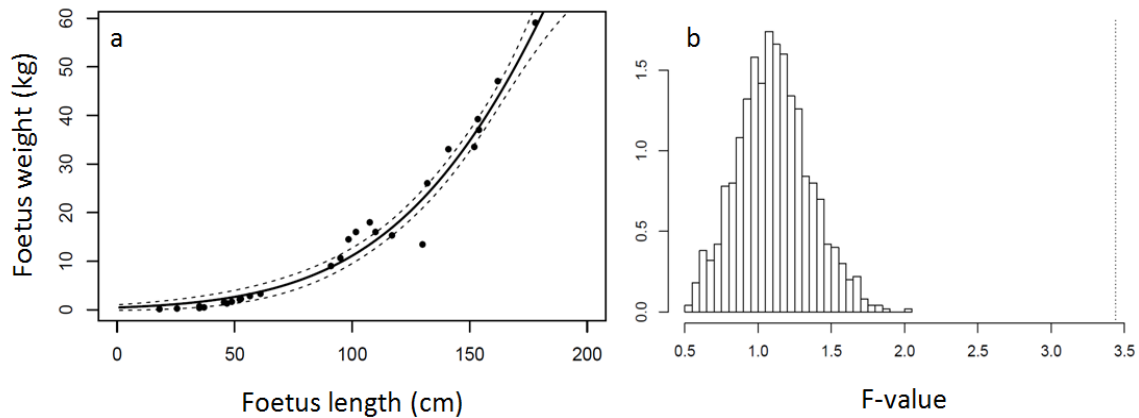


Fig. 5. (a) Foetus weight as a function of foetus length for minke whales. The dashed lines represent 95% confidence interval. (b) Density distribution of F-values obtained from the sensitivity analysis, showing the effect of FBC on the foetus weight-length relationship. The dotted vertical line crossing the x-axis represents the critical value of the F statistic ($F_{\text{critical}_{2,22}}=3.44$) for the 0.05 level of significance. $n=27$.

DISCUSSION

This study shows that FBC can affect foetus growth in minke whales, a capital breeding mysticete. Although Lockyer (1990) found that the relationship between foetus weight and length differed between periods of years for Northeast Atlantic fin whales, with the slope being much less steep during a period coinciding with low prey availability and also low adult body weight (Lockyer 2007), she was not able to directly link foetus growth to individual variation in FBC. Similarly, while Read (2001) found a relationship between prey intake and calf size, he was not able to show if this was an effect of FBC on foetus growth rate. This study is thus the first to directly link FBC to foetus growth rates in cetaceans.

Effects of FBC and foetal growth rates has been documented in a number of mammal species, including humans (Peacock 1991), ungulates (Guinness, Albon, & Clutton-Brock 1978; Mellor & Murray 1982; Skogland 1984; Byers & Moodie 1990; Byers & Hogg 1995) and pinnipeds (Kovacs & Lavigne 1986; Trites 1991; Georges & Guinet 2001). These studies suggest that species most susceptible to variations in FBC are those with relatively high maternal investment (Byers & Moodie 1990; Byers & Hogg 1995). In pronghorns (*Antilocapra americana*), females are near the maximum level of maternal expenditure, which means that they are limited in their ability to support foetal and neonatal growth rates during years of poor nutrition (Byers & Moodie 1990; Byers & Hogg 1995). In contrast, bighorn sheep (*Ovis canadensis*) have relatively low maternal expenditure, and therefore sufficient energetic margins to maintain normal foetus growth rates during years of poor nutrition (Byers & Hogg 1995). Cetaceans, and in particular balaenopterids, exhibit some of the highest foetal growth rates in mammals (Frazer & Huggett 1959, 1973), suggesting that the energetic costs of reproduction must be very high (Lockyer 1986). It was therefore not surprising that we found an effect of FBC on foetal growth rates.

In accordance with the foetal growth pattern of the late prenatal growth phase (Huggett & Widdas 1951; Frazer & Huggett 1959, 1973), our results show a linear increase in foetus length through the study period. The rate of increase ($0.918 \text{ cm day}^{-1}$; $\text{SE}=0.111$) is similar to other studies on minke whales in the North Atlantic (Jonsgård 1951; Sergeant 1963; Horwood 1990), although slightly lower than those estimated for southern minke whales (Ivashin & Mikhalev 1978; Kato & Miyashita 1991). This difference could be explained by differences in

the average adult body size between the two hemispheres, with southern minke whales being relatively larger than their northern counterpart (Horwood 1990).

The curvilinear relationship between minke whale foetus length and FBC can be explained by the species life history. The iteroparous nature of mysticetes dictates that females in poorer body condition will reduce energetic investment in their offspring rather than lowering their own body condition further, to maintain high adult survival. The reduction in energy to the foetus should be proportionate to the body condition of the female, which explains the linear positive relationship between foetus size and body condition for females in poorer body condition ($FBC < 0$). That foetus length did not continue to increase at better body condition ($FBC > 0$) suggest that maternal size causes physiological constraints to the maximum length that the offspring can attain at birth, which sets an upper limit to foetal growth rates, in order to avoid labour complications (Gluckman & Hanson 2004; Huang *et al.* 2011). Overcoming this by shortening the gestation period is also unlikely, since the reproductive cycle of mysticetes is strongly linked to the seasonal migration of the female between the feeding grounds and breeding grounds (Laws 1959; Rice 1983; Lockyer 1984). Alternatively, the apparent asymptote in foetus growth rate might be caused by an absolute limitation on the capacity of the mother and placenta to supply nutrients to the foetus (Gluckman & Hanson 2004).

Since foetuses were not aged, it could be argued that the measured effect of FBC on foetus size is the effect of variation in conception dates between females. Minke whales exhibit considerable variation in conception dates (Frazer & Huggett 1973; Wang 1985; Horwood 1990; Kato & Miyashita 1991; Kato 1992), most likely caused by their 14 month reproductive cycle (Best 1982), which means that females gradually gets out of sync with their seasonal migration pattern (Best 1982; Rice 1983). Females that conceive earlier also arrive earlier in the feeding grounds to start building up their blubber reserves, than those conceiving later (Kato & Miyashita 1991; Kato 1992, 1995). As a result, at any point in the feeding season these females will be in relatively better body condition and carry larger foetuses, compared to females that conceived later and therefore arrived later in the feeding grounds. This should result in a linear positive relationship between FBC and foetus length throughout the range of body conditions. Our results however show that this is clearly not the case, since foetus lengths levelled off at higher FBC. This support our conclusion that the measured effect of FBC on foetus length is caused by a reduction in energy investment in the offspring, and not a confounding effect of variation in conception dates.

A reduction in foetus growth rates, caused by poor FBC, will reduce the size of the calf at birth. This in turn is likely to have negative effects on neonatal survival (Kovacs & Lavigne 1986; Baker & Fowler 1992; Pontier *et al.* 1993; Boltnev & York 2001; McMahon & Burton 2005; Huang *et al.* 2009, 2011), possibly caused by poorer insulation and lowered buoyancy (Lockyer 1990). Theoretically this could be avoided by increasing the length of gestation, similarly to some pinnipeds species (Boyd 1996). However since female mysticetes are food deprived during the final part of gestation, delaying the time of parturition would not give them more time to acquire energy. And even if the female could potentially channel more energy towards the foetus, by reducing her own body condition further, this would most likely result in her being in such a poor body condition in the following years breeding season, that she would be forced to skip a year of breeding in order to rebuild her energy reserves (Lockyer 1986). Either way, this would have negative effects on calf production, and hence reproductive success.

If a reduction in offspring investment (i.e. reduction in foetus growth rate) is not enough to counterbalance a reduction in body condition, the only way for the female to avoid risking her own survival, and to maximize lifetime reproductive success, is to terminate the reproduction event by aborting the foetus (Guinet *et al.* 1998; Pitcher *et al.* 1998; Trites & Donnelly 2003; Gibbens, Parry, & Arnould 2010). Although partially reabsorbed prenatal dead fetuses have been observed in a number of balaenopterids species, little is known about prenatal death in cetaceans and its relationship with FBC (Ichihara 1962). Lockyer (1987b) found that the fecundity of fin whales (measured as the proportion of females with a corpus luteum) decreased during periods of years with low adult body weight, but could not determine whether this reduction was caused by an increase in cessation in ovulation or an increase in abortion, or both. Similarly, Le Boeuf *et al.* (2000) found that calf production in gray whales was particularly low during a year when adult whales were in poorer body condition, but again could not conclude if this was caused by a reduction in ovulation rates or an increase in abortions.

Studies on other mammals suggest that reproductive failure should occur at the point in the reproductive cycle when the cost of offspring production is highest in relation to the energy intake of the female (Trites & Donnelly 2003). This in turn, will depend on the life history of the species. In mysticetes, the initial costs of gestation during the slow growth phase is believed to be minimal (Rice 1983; Lockyer 1984), which is probably why female minke whales can afford being pregnant and lactating at the same time (Lockyer 1981). Instead, the crucial periods in the reproductive cycle seem to come later in the gestation period when the energetic demands of the foetus start to increase faster (Trites 1991; Pitcher *et al.* 1998). Since the faster growth phase begins when the mother arrives on the summer feeding grounds (Laws 1959; Rice 1983), the female will initially be able to cover the increasing costs of the foetus by feeding. However, towards the last half or third of gestation the costs of gestation start to increase rapidly (Lockyer 1984), following an almost exponential increase in foetus weight (Fig. S2, Supporting information). Whether or not the female will have enough body reserves to support the costs of the foetus at this critical period will not be “known” at the time she ovulates (Trites 1991; Pontier *et al.* 1993), which suggests that ovulation rates should not be affected much by FBC, as been shown in pinnipeds (Pitcher *et al.* 1998; Trites & Donnelly 2003). Instead, reproductive failure resulting from poor FBC is more likely to occur in the form of prenatal abortions in the late stages of pregnancy (Guinet *et al.* 1998; Pitcher *et al.* 1998; Trites & Donnelly 2003; McKenzie *et al.* 2005; Gibbens *et al.* 2010), when the costs of the foetus become higher and the female is able to “assess” her future body condition after having been feeding for some time (Pitcher *et al.* 1998). In support of this, Ichihara (1962) found that the rate of abortion in fin whales is about three times higher in the later stages of pregnancy than earlier on. Where the threshold of prenatal abortion lies, in terms of FBC and time in gestation, is unknown, but critical to our understanding of how FBC influence offspring production, and hence reproductive success. To date no records of abortions (reabsorbed fetuses) have been documented for minke whales despite considerable research effort (G Víkingsson, personal observation). This, together with pregnancy rates above 90% (Jonsgård 1951; Horwood 1990), indicates that abortions are not common in minke whales, at least in the first half of pregnancy. However, with almost all data on minke whales coming from the feeding grounds, it is possible that this vital information will be missed if females abort later in the gestation period, on the way to or on the breeding grounds, as was found for fin whales (Ichihara 1962). Thus, although this study shows that FBC can affect foetus growth in minke whales, further research is needed to link these effects to offspring production and survival, and thus reproductive success.

ACKNOWLEDGMENTS

We are grateful to all the scientists and technicians of the MRI that participated in the sampling process as well as the captains and crew of the sampling vessels. We thank the University of Aberdeen Graduate School Competitive Studentship grant scheme for financial support. We thank E Pirota for his constructive feedback on the analyses. We are grateful to D S Janiger for providing many of the older articles discussed in this paper.

LITERATURE CITED

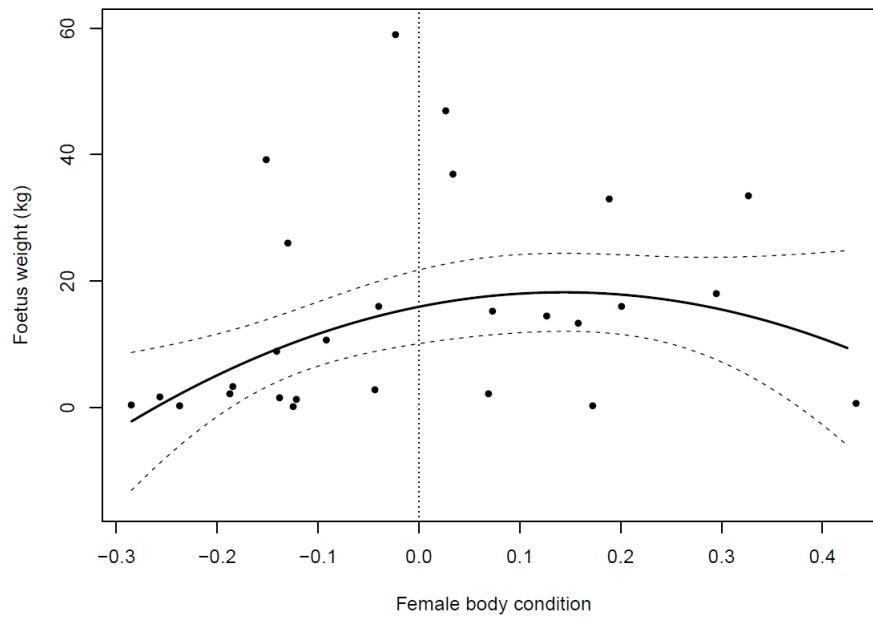
- Baker, J.D. & Fowler, C.W. (1992) Pup weight and survival of northern fur seals *Callorhinus ursinus*. *Journal of Zoology (London)*, **227**, 231–238.
- Best, P.B. (1982) Seasonal abundance, feeding, reproduction, age and growth in minke whales off Durban (with incidental observations from the Antarctic). *Reports of the International Whaling Commission*, **32**, 759–786.
- Le Boeuf, B.J., Pérez-Cortés M, H., Urbán R, J., Mate, B.R. & Ollervides U, F. (2000) High gray whale mortality and low recruitment in 1999: potential causes and implications. *Journal of Cetacean Research and Management*, **2**, 85–99.
- Boltnev, A.I. & York, A.E. (2001) Maternal investment in northern fur seals (*Callorhinus ursinus*): interrelationships among mothers' age, size, parturition date, offspring size and sex ratios. *Journal of Zoology (London)*, **254**, 219–228.
- Boltnev, A.I., York, A.E. & Antonelis, G.A. (1998) Northern fur seal young: interrelationships among birth size, growth, and survival. *Canadian Journal of Zoology*, **76**, 843–854.
- Borchers, D.L., Pike, D.G., Gunnlaugsson, T. & 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.
- Boyd, I.L. (1996) Individual variation in the duration of pregnancy and birth date in Antarctic fur seals: the role of environment, age, and sex of fetus. *Journal of Mammalogy*, **77**, 124–133.
- Byers, J.A. & Hogg, J.T. (1995) Environmental effects on prenatal growth rate in pronghorn and bighorn: further evidence for energy constraint on sex-biased maternal expenditure. *Behavioral Ecology*, **6**, 451–457.
- Byers, J.A. & Moodie, J.D. (1990) Sex-specific maternal investment in pronghorn, and the question of a limit on differential provisioning in ungulates. *Behavioral Ecology and Sociobiology*, **26**, 157–164.
- Christiansen, F., Vikingsson, G.A., Rasmussen, M. & Lusseau, D. (in press) Minke whales maximise energy storage on their feeding grounds. *Journal of Experimental Biology*, **X**, XX–XX.
- 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., Haug, T., Nilssen, K.T. & 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.
- Fox, J. & Weisberg, S. (2011) *An R Companion to Applied Regression, Second Edition*. Sage Publications, Thousand Oaks, CA.
- Frazer, J.F.D. & Huggett, A.S.G. (1959) The growth rate of foetal whales. *Journal of Physiology London*, **146**, 21–22.
- Frazer, J.F.D. & Huggett, A.S.G. (1973) Specific foetal growth rates of cetaceans. *Journal of Zoology (London)*, **169**, 111–126.
- Georges, J.Y. & Guinet, C. (2001) Prenatal investment in the subantarctic fur seal, *Arctocephalus tropicalis*. *Canadian Journal of Zoology*, **79**, 601–609.
- Gibbens, J., Parry, L.J. & Arnould, J.P.Y. (2010) Influences on fecundity in Australian fur seals (*Arctocephalus pusillus doriferus*). *Journal of Mammalogy*, **91**, 510–518.
- Gluckman, P.D. & Hanson, M.A. (2004) Maternal constraint of fetal growth and its consequences. *Seminars in fetal & neonatal medicine*, **9**, 419–425.

- Guinet, C., Roux, J.P., Bonnet, M. & Mison, V. (1998) Effect of body size, body mass, and body condition on reproduction of female South African fur seals (*Arctocephalus pusillus*) in Namibia. *Canadian Journal of Zoology*, **76**, 1418–1424.
- Guinness, F.E., Albon, S.D. & Clutton-Brock, T.H. (1978) Factors affecting reproduction in red deer (*Cervus elaphus*) hinds on Rhum. *Journal of Reproduction and Fertility*, **54**, 325–334.
- Haug, T., Lindstrøm, U. & 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.
- Huang, S.L., Chou, L.S. & Ni, I.H. (2009) Comparable length at weaning in cetaceans. *Marine Mammal Science*, **25**, 875–887.
- Huang, S.L., Chou, L.S., Shih, N.T. & Ni, I.H. (2011) Implication of life history strategies for prenatal investment in cetaceans. *Marine Mammal Science*, **27**, 182–194.
- Huggett, A.S.G. & Widdas, W.F. (1951) The relationship between mammalian foetal weight and conception age. *Journal of Physiology*, **114**, 306–317.
- Hyndman, R.J., Bashtannyk, D.M. & Grunwald, G.K. (1996) Estimating and Visualizing Conditional Densities. *Journal of Computational and Graphical Statistics*, **5**, 315–336.
- Ichihara, T. (1962) Prenatal dead foetus of baleen whales. *Scientific reports of the whales research institute Tokyo*, **16**, 47–60.
- Ichii, T., Shinohara, N., Fujise, Y., Nishiwaki, S. & Matsuoka, K. (1998) Interannual changes in body fat condition index of minke whales in the Antarctic. *Marine Ecology Progress Series*, **175**, 1–12.
- Ivashin, M. V & Mikhalev, Y.A. (1978) To the problem of the prenatal growth of minke whales *Balaenoptera acutorostrata* of the southern hemisphere and of the biology of their reproduction. Document SC/29/Doc 20. The Scientific Committee of the International Whaling Commission, Canberra, Australia.
- IWC. (1979) Report of the special meeting on southern hemisphere minke whales. *Reports of the International Whaling Commission*, **29**, 348–358.
- Jonsgård, Å. (1951) Studies on the little piked whale or minke whale (*Balaenoptera acutorostrata* Lacépède). *Norsk Hvalfangst-Tidende*, **40**, 209–232.
- 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. *Whales, seals, fish and man* (eds A.S. Blix, L. Walløe & Ø. Ulltang), pp. 481–498. Elsevier Science, Amsterdam.
- Kato, H. (1992) Body length, reproduction and stock separation of minke whales off Northern Japan. Document SC/43/Mi31. The Scientific Committee of the International Whaling Commission, Glasgow, UK.
- Kato, H. (1995) Migration strategy of southern minke whales to maintain high reproductive rate. *Whales, seals, fish and man* (eds A.S. Blix, L. Walløe & Ø. Ulltang), pp. 465–480. Elsevier Science, Amsterdam.
- Kato, H. & Miyashita, T. (1991) Migration strategy of southern minke whales in relation to reproductive cycle estimated from foetal lengths. Document SC/42/SHMi24. The Scientific Committee of the International Whaling Commission, Reykjavik, Iceland.
- Kovacs, K.M. & Lavigne, D.M. (1986) Maternal investment and neonatal growth in phocid seals. *Journal of Animal Ecology*, **55**, 1035–1051.
- Laws, R.M. (1959) The foetal growth rates of whales with special reference to the fin whale, *Balaenoptera physalus* Linn. *Discovery reports*, **29**, 281–308.
- Lockyer, C. (1981) Estimation of the energy costs of growth, maintenance and reproduction in the female minke whale, (*Balaenoptera acutorostrata*), from the Southern hemisphere. Document SC/32/Mi19. The Scientific Committee of the International Whaling Commission, Cambridge, UK.
- Lockyer, C. (1984) Review of baleen whale (Mysticeti) reproduction and implications for management. *Reports of the International Whaling Commission (special issue)*, **6**, 27–50.

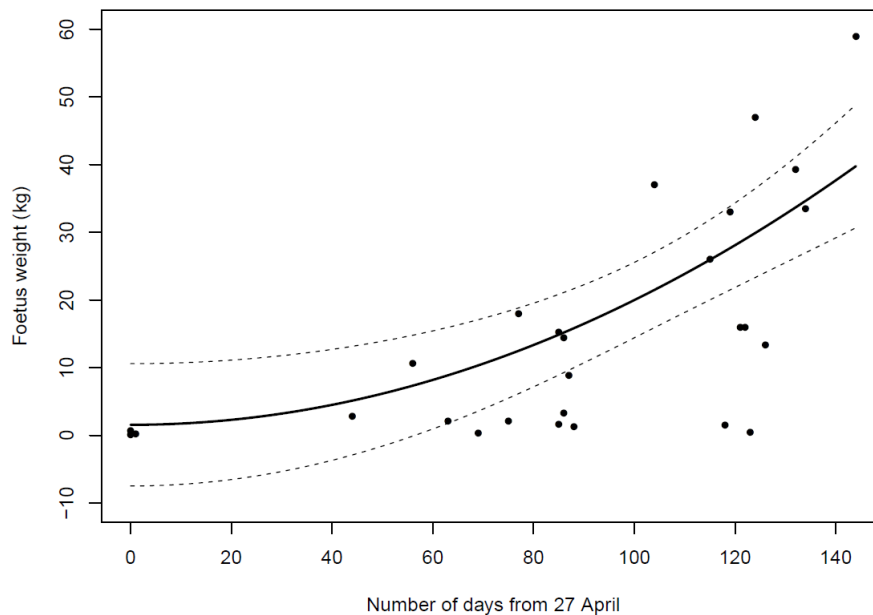
- Lockyer, C. (1986) Body fat condition in northeast Atlantic fin whales, *balaenoptera physalus*, and its relationship with reproduction and food resource. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 142–147.
- Lockyer, C. (1987a) The relationship between body fat, food resource and reproductive energy costs in North Atlantic fin whales (*Balaenoptera physalus*). *Symposium of the Zoological Society of London*, **57**, 343–361.
- Lockyer, C. (1987b) Evaluation of the role of fat reserves in relation to the ecology of North Atlantic fin and sei whales. *Approaches to Marine Mammal Energetics. Special Publication No 1* (eds A.C. Huntley, D.P. Costa, G.A.J. Worthy & M.A. Castellini), pp. 183–203. Society for Marine Mammalogy, Lawrence.
- Lockyer, C. (1990) The importance of biological parameters in population assessments with special reference to fin whales from the N. E. Atlantic. *North Atlantic Studies*, **2**, 22–31.
- 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.
- MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- Masaki, Y. (1979) Yearly change of the biological parameters for the Antarctic minke whale. *Reports of the International Whaling Commission*, **29**, 375–395.
- McKenzie, J., Parry, L.J., Page, B. & Goldsworthy, S.D. (2005) Estimation of pregnancy rates and reproductive failure in New Zealand fur seals (*Arctocephalus forsteri*). *Journal of Mammalogy*, **86**, 1237–1246.
- McMahon, C.R. & Burton, H.R. (2005) Climate change and seal survival: evidence for environmentally mediated changes in elephant seal, *Mirounga leonina*, pup survival. *Proceedings of the Royal Society B*, **272**, 923–928.
- Mellor, D.J. & Murray, L. (1982) Effects of long term undernutrition of the ewe on the growth rates of individual fetuses during late pregnancy. *Research in Veterinary Science*, **32**, 177–180.
- Miller, C.A., Reeb, D., Best, P.B., Knowlton, A.R., Brown, M.W. & 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.
- Nordøy, E.S., Folkow, L.P., Mårtensson, P.E. & Blix, A.S. (1995) Food requirements of Northeast Atlantic minke whales. *Whales, seals, fish and man* (eds A.S. Blix, L. Walløe & Ø. Ulltang), pp. 307–318. Elsevier Science, Amsterdam.
- Næss, A., Haug, T. & Nilssen, E.M. (1998) Seasonal variation in body condition and muscular lipid contents in Northeast Atlantic minke whale *Balaenoptera acutorostrata*. *Sarsia*, **83**, 211–218.
- Parry, D.A. (1949) The structure of whale blubber and a discussion of its thermal properties. *Quarterly Journal Microscopical Science*, **90**, 13–25.
- Peacock, N. (1991) An evolutionary perspective on the patterning of maternal investment in pregnancy. *Human Nature*, **2**, 351–385.
- Pitcher, K.W., Calkins, D.G. & Pendleton, G.W. (1998) Reproductive performance of female Steller sea lions: an energetics-based reproductive strategy? *Canadian Journal of Zoology*, **76**, 2075–2083.
- Pontier, D., Gaillard, J.M. & Allainé, D. (1993) Maternal investment per offspring and demographic tactics in placental mammals. *Oikos*, **66**, 424–430.
- R Development Core Team. (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Read, A.J. (2001) Trends in the maternal investment of harbour porpoises are uncoupled from the dynamics of their primary prey. *Proceedings of the Royal Society London B*, **268**, 573–577.
- Rice, D.W. (1983) Gestation period and fetal growth of the gray whale. Document SC/34/PS11. The Scientific Committee of the International Whaling Commission, Cambridge, UK.
- Sergeant, D.E. (1963) Minke whales, *Balaenoptera acutorostrata* Lacepede, of the Western North Atlantic. *Journal of the fisheries research board of Canada*, **20**, 1489–1504.

- Sigurjónsson, J. (1992) Recent studies on abundance and trends in whale stocks in Icelandic and adjacent waters. *Proceedings of the symposium "Whales - Biology - Threats" - Conservation* pp. 77–111. Royal Academy of Overseas Sciences, Brussels.
- Sigurjónsson, J. & 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.
- Skogland, T. (1984) The effects of food and maternal conditions on fetal growth and size in wild reindeer. *Rangifer*, **4**, 39–46.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Stephens, P.A., Boyd, I.L., McNamara, J.M. & Houston, A.I. (2009) Capital breeding and income breeding: their meaning, measurement, and worth. *Ecology*, **90**, 2057–2067.
- Trites, A.W. (1991) Fetal growth of northern fur seals: life-history strategy and sources of variation. *Canadian Journal of Zoology*, **69**, 2608–2617.
- Trites, A.W. & Donnelly, C.P. (2003) The decline of Steller sea lions *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis. *Mammal Review*, **33**, 3–28.
- Víkingsson, G.A. (1995) Body condition of fin whales during summer off Iceland. *Whales, seals, fish and man* (eds A.S. Blix, L. Walløe & Ø. Ulltang), pp. 361–369. Elsevier Science, Amsterdam.
- Víkingsson, G.A. & Heide-Jørgensen, M.P. (2005) A note on the movements of minke whales tracked by satellite in Icelandic waters in 2001-2004. Document SC/57/O9. The Scientific Committee of the International Whaling Commission, Ulsan, Republic of Korea.
- Wang, P. (1985) Studies on the breeding habits of the minke whale (*Balaenopera acutorostrata*) in the Yellow Sea. *Chinese Journal of Oceanology and Limnology*, **3**, 37–47.

SUPPORTING INFORMATION



Supplementary Figure S1. Partial effect plot of foetus weight (W_F) as a function of FBC for minke whales, showing the results of the best fitting linear model: $W_F \sim \text{Day}^2 + (\text{FBC} + \text{FBC}^2)$. Day has been fixed at 88 (July 23), which is the mean sampling date in the feeding season. The dashed lines represent 95% confidence interval and the dotted vertical line crossing the x-axis at zero represent the average FBC. The effect of FBC was statistically significant ($F_{2,23}=3.80$, $P=0.038$) and explained 12.3% of the observed variance in foetus weight. $n=27$.



Supplementary Figure S2. Partial effect plot of foetus weight (W_F) as a function of day for minke whales, showing the results of the best fitting linear model: $W_F \sim \text{Day}^2 + (\text{FBC} + \text{FBC}^2)$. Day 1 corresponds to April 27. FBC has been fixed at zero. The dashed lines represent 95%

confidence interval. The effect of day was statistically significant ($F_{1,23}=31.13$, $P<0.001$) and explained 50.4% of the observed variance in foetus weight. $n=27$.