Fetal growth, birth size and energetic cost of gestation in southern right whales

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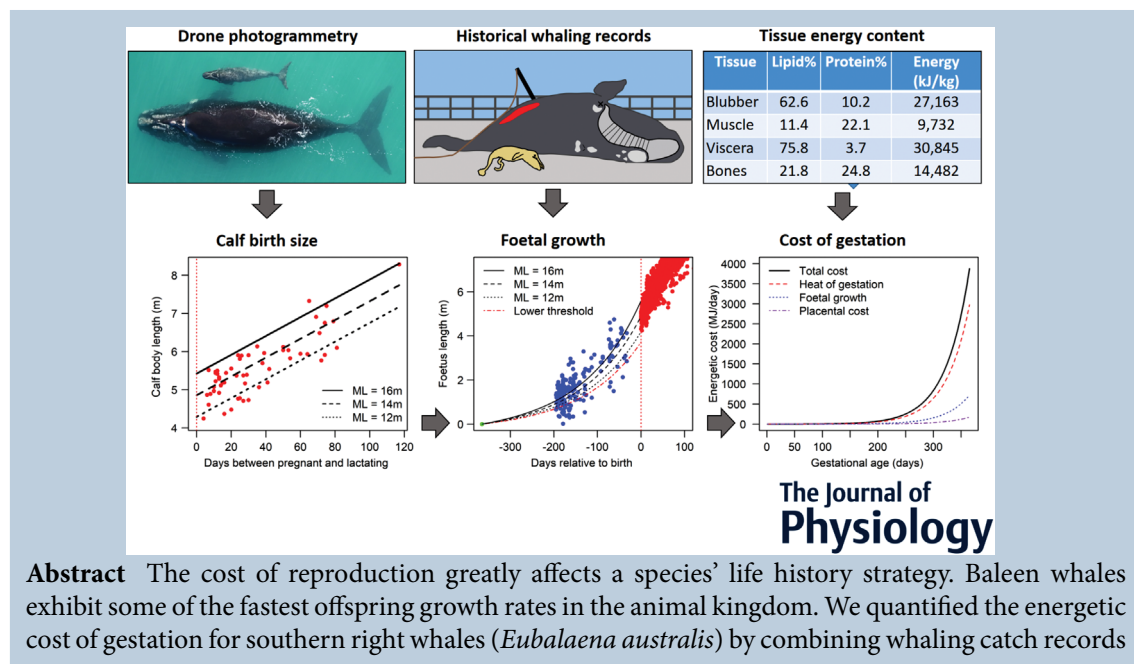[6]*Seastar Scientific, Vashon, WA, USA*
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Drone photogrammetry | **Historical whaling records** | **Tissue energy content**

Tissue	Lipid%	Protein%	Energy (kJ/kg)
Blubber	62.6	10.2	27,163
Muscle	11.4	22.1	9,732
Viscera	75.8	3.7	30,845
Bones	21.8	24.8	14,482

Calf birth size | **Foetal growth** | **Cost of gestation**

Abstract The cost of reproduction greatly affects a species' life history strategy. Baleen whales exhibit some of the fastest offspring growth rates in the animal kingdom. We quantified the energetic cost of gestation for southern right whales (*Eubalaena australis*) by combining whaling catch records

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of pregnant females with photogrammetry data on southern right whale mothers and calves from two breeding grounds in Argentina and Australia. The relationship between calf birth size and maternal length was determined from repeated measurements of individual females before and after giving birth. Fetal growth was determined from generalized linear models fitted to fetal length data from whaling operations between 1961 and 1967. Fetal length was converted to volume and mass, using the volume-to-length relationship of newborn southern right whales calves, and published tissue composition and energy content estimates. Fetal maintenance costs (heat of gestation) and the energy content of the placenta were predicted from published relationships and added to the fetal growth cost to calculate the total cost of gestation. Our findings showed that fetal growth rates and birth size increased linearly with maternal length, with calves being born at ∼35% maternal length. Fetal length increased curvilinearly through gestation, which resulted in an exponential increase in fetal volume and mass. Consequently, the cost of gestation was very low during the first (0.1% of total cost) and second trimester (4.9%), but increased rapidly during the last trimester (95.0%). The heat of gestation incurred the highest cost for pregnant females (73.8%), followed by fetal growth (21.2%) and the placental energy content (5.0%).

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Abstract figure legend The aim of this study was to estimate the energetic cost of gestation in southern right whales. First, drone photogrammetry was used to measure the size of newborn southern right whale calves on their breeding grounds. Birth lengths were found to be ∼35% of maternal lengths. Based on this, fetal growth curves were developed from historical whaling records. The fetus grew slowly in size during the first two trimesters, but increased rapidly during the final trimester. The growth rate of the fetus was positively affected by the size (length) of the mother, with larger females having faster growing fetuses. By converting fetal length to volume and mass, and using the energetic content of different tissues (blubber, muscle, viscera and bones), the cost of fetal growth through gestation could be estimated. Placental cost and heat of gestation were calculated from the fetal size, which together equalled the cost of gestation.

Key points

- Baleen whales exhibit some of the fastest fetal growth rates in the animal kingdom. Despite this, the energetic cost of gestation is largely unknown, as well as the influence of maternal body size on fetal growth rates and calf birth sizes.
- We combined historical whaling records and drone photogrammetry data to determine fetal growth rates and birth sizes in southern right whales (*Eubalaena australis*), from which we estimated the cost of gestation.
- Calf birth size, and consequent fetal growth rates, increased positively with maternal body size.
- The cost of gestation was negligible for southern right whale females during the first two trimesters, but increased rapidly during the last trimester.
- These results show that late gestation incurs a significant cost for baleen whale females, and needs to be accounted for in bioenergetic models.

Introduction

The cost of reproduction is a key component in determining a species' life history strategy, and in the trade-off in energy allocation between growth, survival and reproduction to maximize lifetime reproductive success (Bell, 1980; Reznick, 1985; Stearns, 1989). While the optimal allocation of energy is largely determined by age- (or size-) specific mortality (Charlesworth & Leon, 1976; Fisher, 1958; Michod, 1979), it also depends on the cost of reproduction, also known as reproductive effort (Audzijonyte & Richards, 2018; Charnov et al., 2007; Williams, 1966). In mammals, offspring birth mass generally increases with the body size of the mother (Blueweiss et al., 1978; Boltnev & York, 2001; Kovacs & Lavigne, 1986; Peters, 1983), while the relative investment in the offspring generally decreases with maternal size

(Parker & Begon, 1986; Reiss, 1991; Roff, 1992). The energetic costs of reproduction will also influence how environmental and anthropogenic factors may affect the reproductive parameters of a species, such as fecundity, gestation, litter/offspring size and reproductive rates, which in turn determine population dynamics.

Baleen whales, which comprise 16 species, are the largest animals on the planet (Lockyer, 1976), with many species undertaking annual migrations between summer feeding areas and winter breeding grounds, where foraging is largely absent (Kasuya, 1995; Lockyer, 2007). With their reproductive cycle being closely tied to their annual migratory cycle, baleen whales have evolved some of the fastest offspring growth rates among mammals (Frazer & Huggett, 1959, 1973), with both gestation and lactation being completed within approximately 1 year of conception and parturition, respectively (Best, 1994; Chittleborough, 1958; Hamilton, 1995; Huang et al., 2009; Laws, 1959; Rice, 1983). However, high offspring growth rates incur large maternal costs. While lactation is the most energetically costly phase in the reproductive cycle of baleen whales (Christiansen et al., 2018; Lockyer, 1981a), gestation also carries high energetic cost, especially during the later stages of pregnancy when females are migrating to the breeding grounds and are fasting (Christiansen, Rasmussen et al., 2014; Lockyer, 1981b; Villegas-Amtmann et al., 2015). In contrast, the early cost of gestation is considered to be negligible for baleen whales, as the relative mass (and energy requirement) of the fetus should be extremely small compared to maternal mass (Pirotta et al., 2019).

Fetal growth in mammals generally follows a curvilinear relationship, characterized by slow early growth followed by an exponential increase in fetal mass closer to parturition (Frazer & Huggett, 1974; Huggett & Widdas, 1951). In baleen whales, fetal growth rate estimates are generally based on fetal length data rather than weight, since fetal mass was not always recorded in scientific or commercial whaling operations (Laws, 1959). Based on data from humpback (*Megaptera novaeangliae*), blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), sei (*Balaenoptera borealis*), common minke (*Balaenoptera acutorostrata*) and grey whales (*Eschrichtius robustus*), Frazer and Huggett (1973) argued that baleen whale fetal length can be described by a single straight line through most of gestation. However, Laws (1959) demonstrated, using data from the same species (except grey whales), that fetal growth pattern in baleen whales follows a concave curve-like parabola, with initial linear slow growth followed by rapid exponential growth. This curvilinear pattern is supported by several other studies on the same species (Christiansen, Vikingsson et al., 2014; Ivashin & Mikhalev, 1978; Masaki, 1976; Nishiwaki, 1959; Rice & Wolman, 1971), with some studies (on grey whales) suggesting a deceleration in fetal growth towards

the end of pregnancy (Rice, 1983; Zimushko & Ivashin, 1980). With fetal mass increasing exponentially with fetal length in baleen whales (Laws, 1959), the energetic cost of fetal growth and maintenance should increase rapidly through gestation, especially during the latter part of pregnancy. While this is likely to have large implications for the reproductive strategy of baleen whales, no study to date has quantified the magnitude of this change using empirical data.

The aim of this study was to quantify the energetic cost of gestation in southern right whales (*Eubalaena australis*; SRWs) and the effect of maternal body size (length) and condition on fetal growth rates and energy investment. Based on other terrestrial (Gluckman & Hanson, 2004; Skogland, 1984) and marine mammals (Bowen et al., 1994; Pomeroy et al., 1999), we hypothesized that larger females should have faster-growing fetuses and give birth to larger calves compared to smaller females. We further hypothesized that females in poorer condition should have slower-growing fetuses and produce smaller offspring compared to larger females (Christiansen, Vikingsson et al., 2014). However, there should also be an upper limit for birth size due to maternal physiological constraints (Gluckman & Hanson, 2004; Huang et al., 2011) and temporal/geographical limitations (most females do not give birth outside of the breeding season/ground) (Christiansen, Vikingsson et al., 2014; Laws, 1959; Rice, 1983). Finally, we hypothesize that fetal growth, and hence the cost of gestation, should be low during the first two trimesters and then increase exponentially during the final trimester. We test these hypotheses using morphological data from historical whaling records and aerial photographs of SRWs obtained using unmanned aerial vehicles (UAVs).

Methods

Ethical approval

The UAV research in Argentina was carried out under permits from the Sub Secretaría de Conservación y Áreas Protegidas (no. 43-SsCyAP/18) and Dirección de Fauna y Flora Silvestres (no. 106/2018.SsG-M.P.), Chubut, Argentina. The UAV research in Australia was carried out under research permits from the Department for Environment and Water (DEW), South Australia (M26501-2, M26501-4, M26501-5 and M26501-6), and Marine Parks permits (MR00082-3-V, MO00082-4-R, MO00082-5-R and MO00082-6-R). The UAV was operated under UAV operator certificates with the necessary remotely piloted aircraft system licences in accordance with regulations by the Australian Civil Aviation Safety Authority. The UAV research in both Australia and Argentina was carried out under animal ethics permits from Murdoch University (O2819/16),

Western Australia, and DEW (4/2016), South Australia. Research has shown that the noise of the UAV used in this study (see model specifications in the next section) cannot be heard by the whales while close to the surface (Christiansen, Rojano-Doñate et al., 2016). Further, a behavioural impact assessment found no differences in the behaviour of SRW mother–calf pairs in the presence and absence of the UAV, even when flying at a very low altitude (5 m) (Christiansen, Nielsen et al., 2020).

Body morphometric data

Aerial photographs of SRW mother–calf pairs and late-pregnant females, were taken using a DJI Inspire 1 Pro UAV (Nanshan, Shenzhen, China) between late June and late September 2016–2019 at the Head of Bight (HoB), South Australia, and between early June and mid November 2018–2019 at Península Valdés (PV), Argentina (Fig. 1). For details about the data collection protocol and each study site, see Christiansen et al. (2018) for HoB and Christiansen et al. (2019) for PV. In both locations, a DJI Zenmuse X5 camera with a 25 mm lens was used to take vertical photographs of the dorsal side of SRWs as they surfaced to breathe. Photographs were quality-graded based on camera focus, body posture (straightness, roll, pitch and arch) and body length and width measurability (clarity of the body contour of the whales), following the protocol of Christiansen et al. (2018); only photographs of adequate quality were included in the analyses. Individual mothers were identified using the unique callosity pattern on their heads (Payne et al., 1983). Adult whales unaccompanied by a calf were classified as late-pregnant if they were subsequently observed with a dependent calf during the same breeding season.

From the aerial photographs, body length and widths (at 5% increments along the body) were measured using a custom-written script in R (R Foundation for Statistical

Computing, Vienna, Austria; Christiansen, Dujon et al., 2016). Measurements were converted from pixels to metres using the known altitude of the UAV (measured using a LightWare SF11/C laser range finder; Gauteng, South Africa), the camera sensor size, focal length and image resolution (for details, see Christiansen et al., 2018). The total body volume (V_{Total}) of each whale (i) was estimated using the formula of Christiansen et al. (2019):

$$V_{\text{Total},i} = \sum_{s=1}^{s=20} V_{s,i} \tag{1}$$

where V_s is the volume of each body segment (between two adjacent width measurement sites), given by:

$$V_{s,i} = \text{BL}_i \times 0.05 \times \int_0^1 \pi \times \frac{W_{A,s,i} + \left(W_{P,s,i} - W_{A,s,i}\right) \times x}{2}$$

$$\times \frac{H_{A,s,i} + \left(H_{P,s,i} - H_{A,s,i}\right) \times x}{2} dx \tag{2}$$

where BL_i is the body length of whale i, $W_{A,s,i}$ and $H_{A,s,i}$ are the anterior width and height measurements of body segment s for individual i, and $W_{P,s,i}$ and $H_{P,s,i}$ are the posterior width and height measurements of segment s for individual i, respectively. Height (dorso-ventral distance) measurements ($H_{A,s,i}$ and $H_{P,s,i}$) were predicted from the corresponding width measurements ($W_{A,s,i}$ and $W_{P,s,i}$) using the known height-width ratio of SRWs from Christiansen et al. (2019). The segments closest to the tip of the rostrum (0–5%BL from the rostrum; hereafter just '%BL') and the end of the tail region (85–100%BL) were modelled as elliptical cones (Christiansen et al., 2019). The body condition (BC_i) of SRW was calculated from the residual of the relationship between body volume
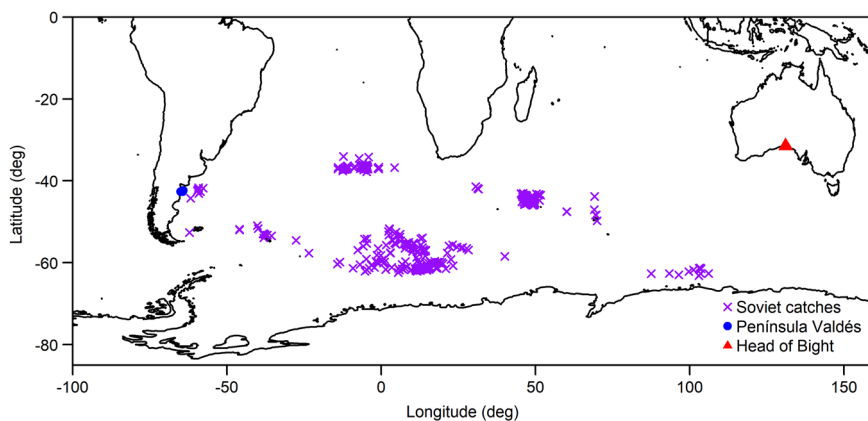

Figure 1. Sampling locations
Locations of the catches of pregnant southern right whales (purple crosses) and the two study sites, Península Valdés (blue circle), Argentina, and Head of Bight (red triangle), Australia, where the UAV photogrammetry data were collected. [Colour figure can be viewed at wileyonlinelibrary.com]

and body length (Christiansen et al., 2018; Christiansen, Dawson et al., 2020; Christiansen, Nielsen et al., 2020):

$$BC_i = \frac{BV_{obs,i} - BV_{exp,i}}{BV_{exp,i}} \qquad (3)$$

where $BV_{obs,i}$ is the observed body volume of whale i, in m^3, and $BV_{exp,i}$ is the expected (or predicted) body volume of whale i, in m^3, given by the log–log relationship between body volume and body length, using the HoB population as baseline (Christiansen et al., 2022):

$$\log\left(BV_{exp,i}\right) = -4.115 + 3.016 \times \log\left(BL_i\right) \qquad (4)$$

Calf birth size

Calf birth length (CBL) was estimated from the relationship between maternal body length and calf body length, using linear models (LM) in R version 4.0.3 (R Core Team, 2020). Paired UAV measurements of adult females that were first measured as late-pregnant and later on as early-lactating within the same breeding season were used for the analysis. Calf body length, measured at the first sighting of a mother–calf pair, was used as the response variable. Both absolute (in metres) and relative calf length (% of maternal length, hereafter just '%ML') were used in the analyses (two separate models). Maternal body length was used as the explanatory variable. To account for the growth of the calf since birth, the time in days between the last observation of the female as pregnant and the first observation of the female as lactating, was included as a covariate. Maternal body condition was included as a covariate in the model since it influences fetal growth rates in common minke whales (Christiansen, Vikingsson et al., 2014). Location was also included as a covariate since SRW calves in HoB are thinner than calves in PV (Christiansen, Dawson et al., 2020). Model selection was done using Akaike's information criterion (AIC), with covariates and interactions between covariates being added sequentially to the null model.

Calf volume at birth (CBV) was predicted from the log–log relationship between calf body volume and calf body length (eqn (4)). To account for the slender body shape of SRWs at birth (Christiansen et al., 2018), the predicted CBV was multiplied by the average body condition of SRWs at birth. To obtain the latter, the relationship between calf body condition and relative calf length (%ML) was determined using a generalized additive model (GAM) with a thin plate regression spline smoother, to account for the non-linear increase in body condition of calves over the first 3–4 months of lactation (Christiansen et al., 2018). Location was included as a fixed covariate in the model, to account

for differences in body condition of calves between HoB and PV (Christiansen, Dawson et al., 2020). The resulting GAM was then used to predict the birth body condition (BBC) of SRWs in the two locations from the predicted relative birth length.

For the LM and GAM, model validation tests included scatter plots of residuals *versus* fitted values and residuals against each explanatory variable (to test for homogeneity of variances), residual histograms (to test for normality of residuals) and estimation of leverage (to identify influential points) and Cook's distance (to identify outliers). All model assumptions were fulfilled.

Maternal volume loss at birth

The change in maternal body shape at birth was visually examined by plotting the mean absolute and relative body width at different measurement sites for females with paired measurements as late-pregnant and early-lactating in the same breeding season. Lactating females were further divided into those measured 0–20, 20–40 and 40–60 days after the last sighting of the female as pregnant. The mean loss in maternal body volume at birth (from pregnant to lactating) relative to CBV was also estimated for the same females. To minimize the effect of calf growth on the estimated maternal volume loss, we restricted the data to females that were re-measured as lactating within 20 days of being pregnant. The corresponding loss in maternal body condition at birth was also calculated.

Fetal length and volume

We used archived data of fetal length from 207 pregnant SRW females of known length that were caught (killed) in commercial catch operations by the Soviet whaling fleet *Yuri Dolgorukiy*, operating in the Southern Hemisphere between 1961 and 1967 (Fig. 1). Some of these data (155 of 207 measurements) were published in Best (1994) as References 7 (Best, Mikhalev & Brownell, in prep.) and 8 (Tormosov, pers. comm.) in Table 2 in that paper; the full data set is archived at the International Whaling Commission (Cambridge, UK). The full data set covered fetal lengths between the period from the 1 November (Julian day 304) to 12 April (Julian day 101). Blubber thickness (measured mid-laterally on the flank in line with the anus) was measured for 52 of the females, and standardized against their lengths to provide a measure of maternal body condition.

Fetal growth, expressed both as absolute (m) and relative (%ML), was investigated using generalized linear models (GLM), with fetal length as the response variable and day of year (Julian day) as the explanatory variable. Since conception and birth in SRWs occurs in the middle of the calendar year, fetuses measured in the second half

of the year will be younger than those measured in the first half. To account for this, the Day of year variable was recalculated for fetuses measured after day 182 (1 July), by subtracting 365 days. This resulted in the day of year variable being correlated with the gestation age of the fetuses. A log link was used in the GLMs to bind the fitted values above zero (fetal length cannot be negative) and to account for the exponential growth pattern in fetal length observed in other baleen whales (Christiansen, Vikingsson et al., 2014; Ivashin & Mikhalev, 1978; Laws, 1959; Masaki, 1976; Nishiwaki, 1959; Rice & Wolman, 1971). Maternal body length was included as a covariate since maternal size has a positive effect on fetal growth rates and birth size in mammals (Baker & Fowler, 1992; Boltnev & York, 2001; Byers & Hogg, 1995; Kovacs & Lavigne, 1986; Lockyer, 1990, 2007; McDonald et al., 2012; Skogland, 1984). The effect of maternal body condition, expressed as the relative blubber thickness (%BL) of pregnant females, was also investigated, since maternal condition influences fetal growth rates in common minke whales (Christiansen, Vikingsson et al., 2014) and fin whales (Lockyer, 2007). As before, model selection was done using AIC with covariates and interactions between covariates being added sequentially to the null model.

To estimate the growth rate of fetuses relative to the date of parturition, the GLM for relative fetal length was used to predict the day of year when the fetus reached the birth length of SRWs (based on the results of the LM in 'Calf birth size' section). Days to birth was then estimated by subtracting the calculated day of birth from the day of year. The two best-fitting GLMs for absolute and relative fetal length were then refitted by replacing day of year with days to birth. Fetal length, both absolute and relative, was then estimated as a function of days to birth, assuming a gestation period of 1 year for baleen whales (Best, 1994; Chittleborough, 1958; Laws, 1959; Rice, 1983). Model validation was done as described above (see 'Calf birth size' section) and all model assumptions were fulfilled.

Data on fetal volume do not exist for SRWs, and hence we assumed that the relationship between fetal volume (FV) and fetal length (FL) was the same as the relationship between calf volume and length (eqn (4), Christiansen et al., 2022):

$$FV_i = \exp\left(-4.115 + 3.016 \times \log(FL_i)\right) \times (1 + BBC)$$

(5)

where BBC is the body condition of SRW calves at birth. From the resulting fetal length and volume estimates, the daily growth rate in body length and volume of SRWs was calculated.

Fetal mass

Following the approach of Christiansen et al. (2022), fetal mass (FM) was estimated by summing together the mass of the various tissues comprising the body of SRWs, including muscle (FM_{Muscle}), visceral tissue (gut, intestines and organs, $FM_{Visceral}$), bones (FM_{Bones}) and blubber ($FM_{Blubber}$):

$$FM_t = FM_{Muscle,t} + FM_{Visceral,t} + FM_{Bones,t} + FM_{Blubber,t}$$

(6)

where FM_{Muscle}, $FM_{Visceral}$ and FM_{Bones} can be predicted directly from the structural size (body length) of right whales (Christiansen et al., 2022):

$$FM_{Muscle,i} = \exp\left(-4.115 + 3.016 \times \log(FL_i)\right) \times P_{Muscle} \times 10^3$$

(7)

$$FM_{Visceral,i} = \exp\left(-4.115 + 3.016 \times \log(FL_i)\right) \times P_{Visceral} \times 10^3$$

(8)

$$FM_{Bones,i} = \exp\left(-4.115 + 3.016 \times \log(FL_i)\right) \times P_{Bones} \times 10^3$$

(9)

where P_{Muscle} (0.282), $P_{Visceral}$ (0.102) and P_{Bones} (0.125) are the proportions of the body volume comprising muscle, viscera and bone tissue, respectively, based on Christiansen et al. (2022). This approach assumes that the relationship between fetal tissue mass and structural size in SRWs is the same as the relationship between tissue mass and structural size after birth. $FM_{Blubber}$ was estimated from the structural size (body length) together with the body condition (BBC) at birth (Christiansen et al., 2022):

$$FM_{Blubber,i} = \left[(1 + BBC_i) \times \exp\left(-4.115 + 3.016 \times \log(FL_i)\right) - \frac{FM_{Muscle,i}}{D_{Muscle}} - \frac{FM_{Visceral,i}}{D_{Visceral}} - \frac{FM_{Bones,i}}{D_{Bones}} \right] \times D_{Blubber}$$

(10)

where D_{Muscle} (960 kg m^{-3}), $D_{Visceral}$ (930 kg m^{-3}), D_{Bones} (720 kg m^{-3}) and $D_{Blubber}$ (700 kg m^{-3}) represent the average tissue densities of muscle, visceral, bones and blubber, respectively, based on published tissue densities from the UN Food and Agriculture organization (Charrondiere et al., 2012). The body condition at birth (BBC) was set to the mean birth condition of SRWs calves in HoB and PV (see 'Calf birth size' section). From the resulting fetal mass estimates, the daily growth rate in mass was estimated.

Energetic cost of gestation

Gestation costs (G) include fetal growth (FG), placental energy content (PE), and heat increment during gestation (Q) (Lockyer, 1981a, 1981b, 1987a, 2007; Villegas-Amtmann et al., 2015):

$$G = FG + PE + Q \qquad (11)$$

The cost of fetal growth (FG), in kJ day^{-1}, was estimated by multiplying the predicted fetal tissue mass estimates, in kg, with their respective energy contents, in kJ kg^{-1}, based on the assumed lipid (L) and protein (P) concentrations of the specific tissues (Lockyer, 1981a, 1981b):

$$
\begin{aligned}
FG_t = {} & FM_{Muscle,t} \; (L_{Muscle} \times E_L + P_{Muscle} \times E_P) \\
& + FM_{Visceral,t} \; (L_{Visceral} \times E_L + P_{Visceral} \times E_P) \\
& + FM_{Bones,t} \; (L_{Bones} \times E_L + P_{Bones} \times E_P) \\
& + FM_{Blubber,t} \; (L_{Blubber} \times E_L + P_{Blubber} \times E_P)
\end{aligned}
\qquad (12)
$$

where E_L and E_P are the assumed energy contents, in kJ kg^{-1}, for lipid and protein, respectively. Unfortunately, no empirical data exist on tissue energy content in SRWs fetuses. Lockyer et al. (1985) presented data on tissue energy content in a 2.05 m-long fin whale fetus, which had lipid and protein concentrations of 1.2 and 10.6% (wet weight) in the blubber (midlateral position), 2.4 and 6.6% in the muscle (midlateral position), and 1.8 and 6.0% in the visceral tissues (cardiac fat), respectively. These values are very low compared to the 75.7% mean lipid concentrations measured in the outer blubber layer (dorsal-anterior position) of dead young (<4 months old, $n = 59$) SRW calves in PV by Marón et al. (2021). In light of these limited data, we decided to follow the approach of Christiansen et al. (2022), who used the mean lipid and protein concentrations from different reproductive classes of fin, sei and common minke whales (Lockyer, 1987a; Lockyer et al., 1985; Vikingsson, 1990; Vikingsson et al., 2013). The mean lipid (L) and protein (P) concentrations were 62.6 and 10.2% in blubber ($L_{Blubber}$ and $P_{Blubber}$), 11.4% and 22.1% in muscle (L_{Muscle} and P_{Muscle}), 75.8% and 3.7% in visceral tissue ($L_{Visceral}$ and $P_{Visceral}$), and 21.8% and 24.8% in bones (L_{Bones} and P_{Bones}), respectively. The calorific equivalents (energy) of lipids (E_L) and protein (E_P) were assumed to be 39,539 kJ kg^{-1} (9450 kcal kg^{-1}) and 23,640 kJ kg^{-1} (5650 kcal kg^{-1}) wet weight, respectively (Brody, 1968; Lockyer et al., 1985).

Four approaches were used to model the resulting tissue energy content of SRW fetuses through gestation (assumed to be 365 days; Best, 1994). In the first (approach 1), we modelled the energy content of tissues to be fixed throughout gestation. In the second (approach 2), the energy content was modelled to increase proportionally to the mass of the fetus. In the third (approach 3), the tissue energy density was fixed at the mean calorific value

of whale muscle at 6276 kJ kg^{-1} (1500 kcal kg^{-1}) for all tissues, based on Lockyer (1981b). In the fourth (approach 4), the tissue energy density was based on the fin whale fetus measured in Lockyer et al. (1985). Since no values for lipid or protein concentrations were provided for the bones of the fin whale fetus, we used the same values as for fetal muscle. From the resulting tissue energy content, the daily cost of fetal growth (FG) was estimated.

To estimate the energy content of the placenta (PE), in kJ kg^{-1}, we used the approach of Villegas-Amtmann et al. (2015), who assumed that the energetic cost of fetal growth constituted $80.7 \pm 2.5\%$ of the total cost of reproductive tissue, with the remaining 19.3% representing the energy contained in the placenta and other tissues associated with pregnancy (Anderson & Fedak, 1987; Blaxter, 1989). Based on this, we calculated the daily cost of the placenta and other tissues (PE) from the daily growth cost of the fetus (FG) throughout gestation:

$$PE = FG_t / 0.807 \times (1 - 0.807) \qquad (13)$$

The daily cost relating to the heat increment during gestation (or heat of gestation, Q), in kJ day^{-1}, which constitute the daily metabolic energy expenditure of the female to maintain the growing fetus and associated tissues (including placenta), was calculated using the modified equation of Brody (1968):

$$Q\,(t) = \Delta FM_t / BM \times 18,410 \times BM^{1.2} \qquad (14)$$

where ΔFM_t is the daily growth rate in fetal mass, in kg day^{-1}, on day t and BM is the birth mass of the fetus, in kg.

Results

Calf birth size

A total of 57 females (HoB = 26, PV = 31) were sampled both as late-pregnant and early-lactating in the same season. The number of days between repeated samples ranged from 4 to 117 days, with a median of 26 days (SD = 25.4). Calf absolute body length was determined by maternal length ($F_{1,54} = 13.0$, $P < 0.001$) and the number of days between the last late-pregnant and first early-lactating sample ($F_{1,54} = 138.9$, $P < 0.001$) (model 6 in Table 1). The full model explained 73.8% (R^2) of the variance in calf length. There was a positive relationship between calf absolute body length (CL$_{Abs}$) and maternal body length (ML), with calves increasing in length at a rate of 0.283 m (SE = 0.079) per metre increase in maternal length (Fig. 2A). CL$_{Abs}$ also increased with the number of days passed between the last late-pregnant measurement

Table 1. Summary of linear model selection results based on minimization of Akaike's information criterion (AIC) for calf absolute (in metres) birth length (CBL)

Model	Variable	F	df (among)	df (within)	P	R^2	AIC	ΔAIC
1	CBL ∼ 1 (null)	–	–	56	–	–	133.9	72.3
2	CBL ∼ DPL	114.0	1	55	<0.001	0.67	72.0	10.3
3	CBL ∼ ML	4.0	1	55	0.050	0.07	131.9	70.3
4	CBL ∼ Location	2.9	1	55	0.093	0.05	133.0	71.3
5	CBL ∼ PBC	0.3	1	55	0.587	0.01	135.6	74.0
6	CBL ∼ DPL + ML[†]	75.9	2	54	<0.001	0.74	61.7	0.0
7	CBL ∼ DPL × ML	49.8	3	53	<0.001	0.74	63.6	1.9
8	CBL ∼ DPL + Location	62.4	2	54	<0.001	0.70	69.7	8.0
9	CBL ∼ DPL × Location	40.9	3	53	<0.001	0.70	71.6	9.9
10	CBL ∼ DPL + PBC	57.1	2	54	<0.001	0.68	73.2	11.5
11	CBL ∼ DPL × PBC	38.5	3	53	<0.001	0.69	74.1	12.4
12	CBL ∼ DPL + ML + Location	50.3	3	53	<0.001	0.74	63.2	1.5
13	CBL ∼ DPL + ML + PBC	50.6	3	53	<0.001	0.74	62.9	1.2

[†] The most parsimonious model (model 6). Abbreviations: df, degrees of freedom; DPL, days between mother was pregnant (last observation) and lactating (first observation); Location, study site (HoB *vs*. PV); ML, maternal body length; PBC, pregnant female body condition (last observation).

and the first early-lactating measurement (DPL), at a rate of 0.025 m (SE = 0.002) day^{-1} (Fig. 2*A*). CL$_{Abs}$, in metres, could hence be predicted from:

$$CL_{Abs,i} = 0.891 + 0.283 \times ML_i + 0.025 \times DPL \quad (15)$$

By fixing DPL at zero, calf absolute birth length (CBL$_{Abs}$), in metres, could be estimated from maternal

length (ML):

$$CBL_{Abs,i} = 0.891 + 0.283 \times ML_i \quad (16)$$

Maternal body length had no effect on the relative body length of calves (CL$_{Rel}$), with the only significant covariate being DPL ($F_{1,55} = 129.6$, $P < 0.001$) (model 2 in Table 2). The model explained 70.2% (R^2) of the variance in CL$_{Rel}$.
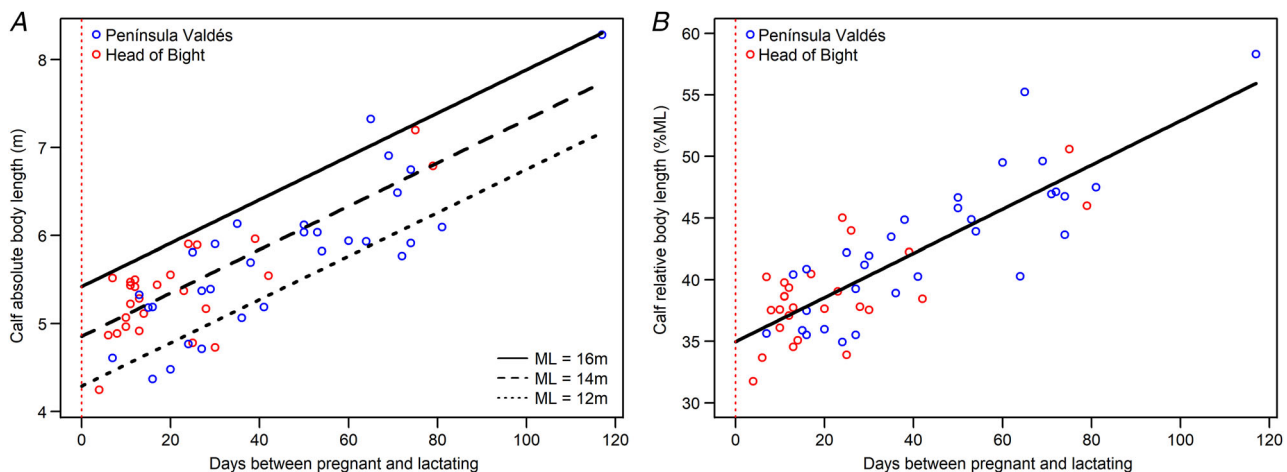
Figure 2. Calf birth size relative to maternal size
A, calf absolute body length as a function of maternal length and number of days between the last sample of the mother as late-pregnant and the first sample as early-lactating. The continuous lines represent the fitted values of the best fitting linear model (Model 6 in Table 1) for females of different body length (see bottom-right key). *B*, calf relative body length (%ML) as a function of number of days between the last sample of the mother as late-pregnant and the first sample as early-lactating. The continuous line represent the fitted values of the best fitting linear model (Model 2 in Table 2). The predicted birth lengths of calves can be derived from the intersects where the fitted lines cross the dotted vertical red lines. The colour of the data points shows the location where it was sampled (see top-left key). *n* = 57 mother–calf pairs (HoB = 26; PV = 31). [Colour figure can be viewed at wileyonlinelibrary.com]

Table 2. Summary of linear model selection results based on minimization of Akaike's information criterion (AIC) for calf relative (% maternal length) birth length (CBL)

Model	Variable	F	df (among)	df (within)	P	R^2	AIC	ΔAIC
1	CBL $\sim$ 1 (null)			56			−167.5	67.9
2	CBL $\sim$ DPL[†]	129.6	1	55	0.001	0.70	−234.6	0.8
3	CBL $\sim$ ML	0.7	1	55	0.411	0.01	−166.2	69.2
4	CBL $\sim$ Location	9.0	1	55	0.004	0.14	−174.2	61.2
5	CBL $\sim$ PBC	0.2	1	55	0.622	0.00	−165.8	69.6
6	CBL $\sim$ DPL + ML	68.3	2	54	0.001	0.72	−235.4	0.0
7	CBL $\sim$ DPL $\times$ ML	44.8	3	53	0.001	0.72	−233.5	1.9
8	CBL $\sim$ DPL + Location	63.7	2	54	0.001	0.70	−232.6	2.8
9	CBL $\sim$ DPL $\times$ Location	42.3	3	53	0.001	0.71	−231.2	4.2
10	CBL $\sim$ DPL + PBC	64.7	2	54	0.001	0.71	−233.2	2.2
11	CBL $\sim$ DPL $\times$ PBC	43.1	3	53	0.001	0.71	−231.9	3.5
12	CBL $\sim$ DPL + ML + Location	45.3	3	53	0.001	0.72	−233.9	1.5
13	CBL $\sim$ DPL + ML + PBC	45.6	3	53	0.001	0.72	−234.2	1.2

[†]The most parsimonious model (model 2). Abbreviations: df, degrees of freedom; DPL, days between mother was pregnant (last observation) and lactating (first observation); Location, study site (HoB *vs.* PV); ML, maternal body length; PBC, pregnant female body condition (last observation).

Calves increased in relative length at a rate of 0.179%ML day^{-1} (SE = 0.016) (Fig. 2*B*). CL_{Rel}, in %ML, could hence be predicted from:

$$CL_{Rel,i} = 34.96 + 0.179 \times DPL \qquad (17)$$

By fixing DPL at zero, the relative birth length of calves (CBL_{Rel}), in %ML, was:

$$CBL_{Rel,i} = 34.96 \qquad (18)$$

The mean relative birth length of calves was hence 34.97%ML (SE = 0.67) (Fig. 2*B*). Maternal body condition had no effect on calf birth length, and there was no difference in birth lengths between locations (Tables 1 and 2).

A total of 3558 measurements (HoB = 2566, PV = 992) of calf body condition were obtained from 1224 calves (HoB = 331, PV = 893). The body condition of calves increased curvilinearly with relative calf length (%ML) (GAM random effect: $F_{4.96,6.16} = 84.31$, $P < 0.001$), with BC increasing from 35% to 45%ML but then levelling off at larger sizes (Fig. 3). As expected, there was a significant difference in calf body condition between locations (GAM fixed effect: $F_{1,3557} = 221.7$, $P < 0.001$), with HoB calves (BC = −5.11%, SE = 0.455, at 34.97%ML birth length) on average being thinner compared to PV calves (BC = −0.61%, SE = 0.490, at 34.97%ML birth length) (Fig. 3). The model explained 17.4% of the deviance in calf body condition. By combining eqns (4) and (16) and multiplying them with the average body condition at birth

(BBC, specific for each location), calf birth volume (CBV) could be estimated from:

$$CBV_i = \exp\left(-4.115 + 3.016 \times \log\left(0.891 + 0.283 \times ML_i\right)\right) \times (1 + BBC) \qquad (19)$$

From 861 calves with known maternal lengths, 66 (7.7%) had observed lengths below that of their
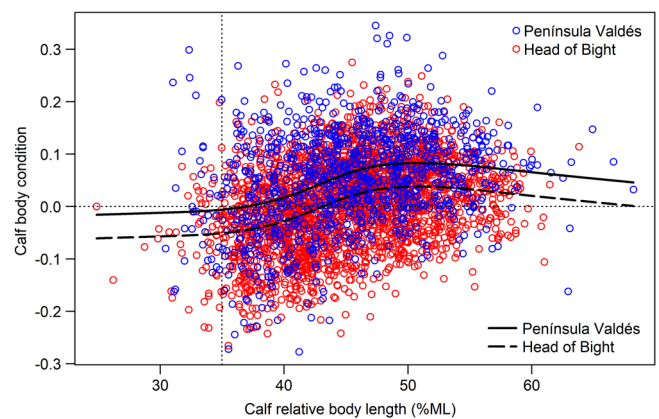

Figure 3. Calf body condition at birth
Calf body condition (BC) as a function of relative calf body length (CLR) for southern right whales in the two study sites (see top-right key). The continuous and dashed lines represent the fitted lines of the GAM for the two study sites (see bottom-right key). The vertical dotted line indicates the mean relative birth length (34.97% maternal length) for SRWs for both locations. The horizontal dotted line indicates an animal of average body condition (BC = 0). The mean body condition of calves at birth was (−0.61% in PV and −5.11% in HoB. *n* = 3558 measurements (HoB = 2566, PV = 992). [Colour figure can be viewed at wileyonlinelibrary.com]

predicted birth length. For these calves, the birth lengths were changed to the minimum observed lengths. After correcting for these smaller calves, the predicted birth lengths of calves (from eqn (16)) ranged from 3.72 to 5.47 m, with a mean of 4.75 m (SD = 0.247) (Fig. 4*A*). The corresponding relative birth length ranged from 24.9% to 36.3%ML, with a mean of 34.7%ML (SD = 0.79), which was close to the estimated mean birth length of 34.97%ML (Fig. 4*B*). The predicted birth volume (from eqn (19)) of calves ranged from 0.85 to 2.61 m^3, with a mean of 1.77 m^3 (SD = 0.266) (Fig. 4*C*). Maternal lengths ranged from 11.11 to 16.17 m with a mean of 13.70 m (SE = 0.822) (Fig. 4*D*).

Maternal volume loss at birth

From the 57 individually identified females (HoB = 26, PV = 31) that were measured both as pregnant and lactating within the same season, 23 gave birth within 20 days, 17 within 40 days and 8 within 60 days of last being seen as pregnant. The remaining nine were removed from analyses. There was a visible change in both the absolute and the relative body width of mothers after giving birth, with the animals getting visibly thinner around the region of 50−65%BL within 20 days of giving birth (Fig. 5). As the number of days between pregnancy and lactation increased, female body width decreased across a larger portion of the body, from 30 to 75%BL (Fig. 5). The decline in maternal body width observed over the first 20 days since giving birth corresponded to

a mean decrease in maternal body volume of 1.59 × CBV (SD = 0.651, n = 19) or 7.3 percentage points (SD = 2.37, n = 19) in maternal body condition.

Fetal length and volume

The fetal data set included 207 fetuses ranging in length from 0.017 to 4.75 m, extracted from pregnant females ranging in size from 12.4 to 16.8 m (Best, 1994). The most parsimonious GLM for absolute fetal length included day of year and maternal body length as covariates (model 6 in Table 3). The most parsimonious GLM for relative fetal length (%ML) included only day of year as a covariate (model 2 in Table 4), since maternal body length was already accounted for in the response variable. Maternal body condition had no effect on absolute or relative fetal length (Tables 3 and 4). Using the predicted relative birth length of SRW calves (34.97%ML) the predicted day of birth from the relative fetal length GLM was calculated to be Julian day 134 (14 May). The day of birth (and hence the time of conception) was not affected by maternal body length. From the refitted GLMs, the estimated days to birth (Julian day − 134) had a significant positive effect on relative fetal length ($F_{1,205}$ = 360.4, $P < 0.001$, Fig. 6*A*). The model explained 63.7% (pseudo-R^2) of the deviance in the data. Days to birth (DTB) had a positive log-linear effect (mean = 0.769%ML, SE = 0.037, on the log-scale) on relative fetal length (FL$_{Rel}$) (Fig. 6*A*). FL$_{Rel}$, in proportion of ML, could hence be predicted from:

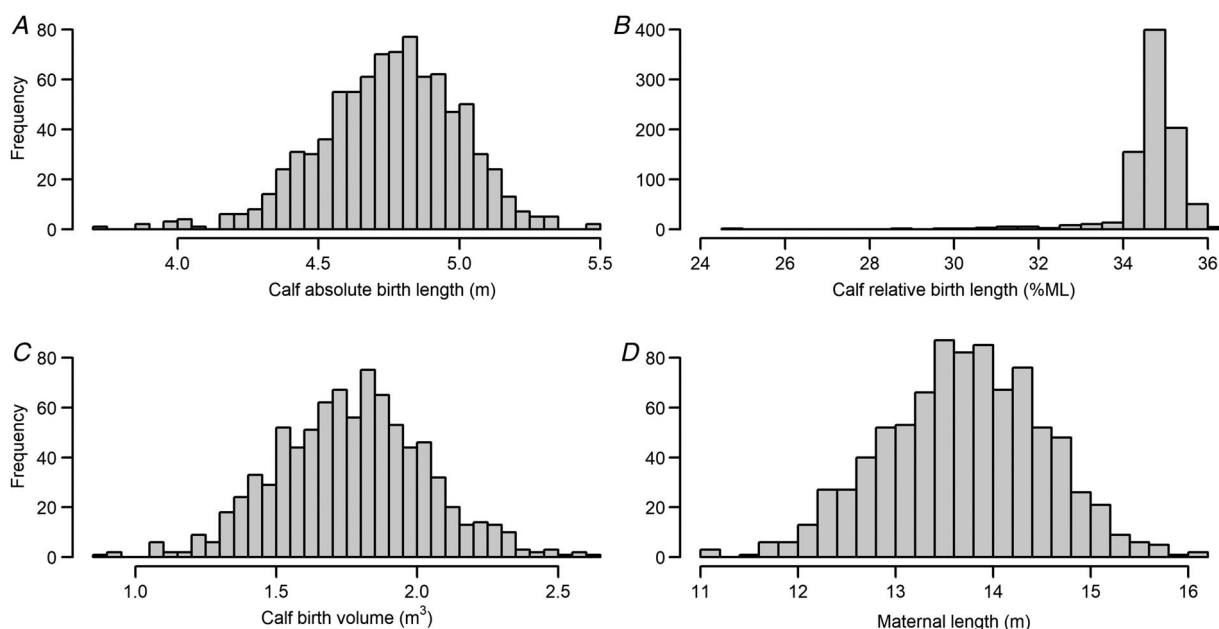$$FL_{Rel} = \exp\left(-1.050376 + 0.007685 \times DTB\right) \quad (20)$$

Figure 4. Calf size at birth
Frequency histograms of predicted calf absolute birth lengths (*A*), predicted calf relative birth lengths (*B*), predicted calf birth volumes (*C*) and measured maternal body lengths (*D*). n = 861 mother–calf pairs (HoB = 330, PV = 531).

Table 3. Results of the generalized linear model selection for southern right whale absolute fetal length (FL$_{Abs}$) based on minimization of Akaike's information criterion (AIC)

Model	Variable	Residual deviance	Null deviance	Pseudo-R^2	k	n	AIC	$\triangle$AIC
1	FL$_{Abs}$ ~ 1 (null)	19.31	49.70	0.00	0	51	147.4	49.7
2	FL$_{Abs}$ ~ Day	19.31	49.70	0.61	2	51	101.2	3.5
3	FL$_{Abs}$ ~ ML	38.23	49.70	0.23	2	51	136.0	38.3
4	FL$_{Abs}$ ~ Sex	49.34	49.70	0.01	2	51	149.0	51.3
5	FL$_{Abs}$ ~ MBC	49.70	49.70	0.00	2	51	149.4	51.7
6	FL$_{Abs}$ ~ Day + ML[†]	17.35	49.70	0.65	3	51	97.7	0.0
7	FL$_{Abs}$ ~ Day × ML	17.18	49.70	0.65	4	51	99.3	1.5
8	FL$_{Abs}$ ~ Day + Sex	19.21	49.70	0.61	3	51	102.9	5.2
9	FL$_{Abs}$ ~ Day × Sex	17.70	49.70	0.64	4	51	100.8	3.0
10	FL$_{Abs}$ ~ Day + MBC	19.31	49.70	0.61	3	51	103.2	5.5
11	FL$_{Abs}$ ~ Day × MBC	19.31	49.70	0.61	4	51	105.2	7.5
12	FL$_{Abs}$ ~ Day + ML + Sex	17.10	49.70	0.66	4	51	99.0	1.3
13	FL$_{Abs}$ ~ Day + ML × Sex	17.09	49.70	0.66	5	51	101.0	3.2
14	FL$_{Abs}$ ~ Day + ML + MBC	17.34	49.70	0.65	4	51	99.7	2.0
15	FL$_{Abs}$ ~ Day + ML × MBC	17.21	49.70	0.65	5	51	101.3	3.6

[†]The most parsimonious model (model 6). Abbreviations: Day, day of year (Julian day); k, number of parameters; MBC, maternal body condition (blubber thickness/ML); ML, maternal body length; n, sample size; Sex, the sex of the fetus.

Assuming a gestation period of 1 year (365 days), the size of the fetus (i.e. embryo) at the time of conception (DTB = −365) was:

$$FL_{Rel(conception)} = \exp(-1.050376 + 0.007685 \times -365)$$
$$= 0.021165 \quad (21)$$

A relative fetal (embryo) length of 2.1%ML at conception is unrealistic, and hence the following correction factor was added to eqn (20) to bind the size at conception (DTB = −365) to zero, while keeping the relative birth length at 34.97%ML (DTB = 0):

$$FL_{Rel} = \exp(-1.050376 + 0.007685 \times DTB)$$
$$+ (0.021165/365) \times DTB \quad (22)$$

The resulting model for absolute fetal length (FL$_{Abs}$), in metres, was (Fig. 6*B*):

$$FL_{Abs} = \big(\exp(-1.050376 + 0.007685 \times DTB)$$
$$+ (0.021165/365) \times DTB\big) \times ML \quad (23)$$
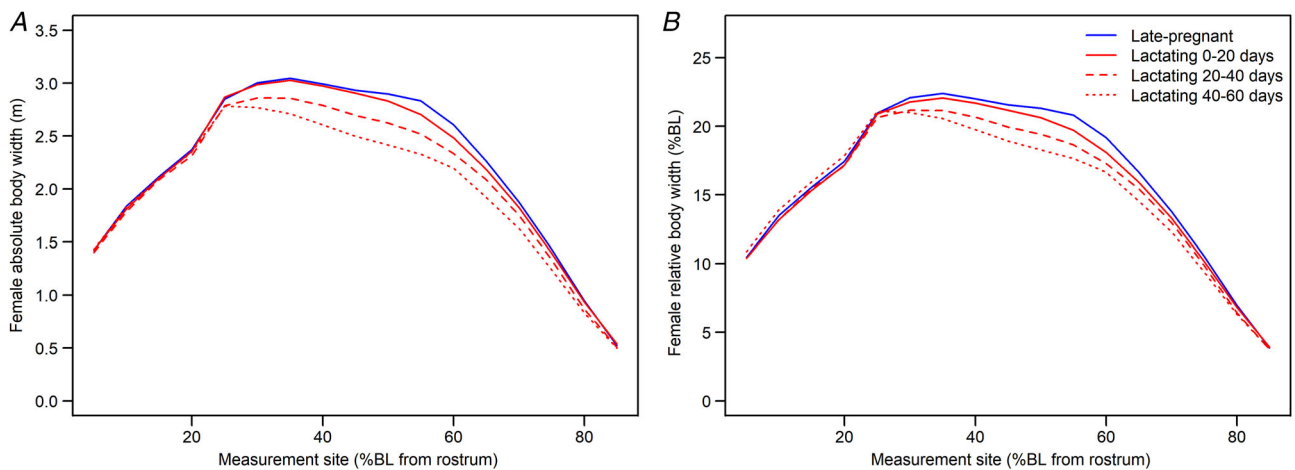

Figure 5. Change in maternal body shape at birth
Mean absolute (*A*) and relative (*B*) body width at different measurement sites for southern right whale females during late-pregnancy (blue continuous line, *n* = 57), after 0−20 days of lactation (red continuous line, *n* = 23), after 20−40 days of lactation (red dashed line, *n* = 17) and after 40−60 days of lactation (red dotted line, *n* = 8). [Colour figure can be viewed at wileyonlinelibrary.com]

Table 4. Results of the generalized linear model selection for southern right whale relative (%ML) fetal length (FL_Rel) based on minimization of Akaike's information criterion (AIC)

Model	Variable	Residual deviance	Null deviance	Pseudo-R^2	k	n	AIC	ΔAIC
1	$FL_{Rel} \sim 1$ (null)	0.081	0.206	0.00	0	51	−132.5	46.9
2	$FL_{Rel} \sim$ Day[†]	0.081	0.206	0.60	2	51	−177.8	1.6
3	$FL_{Rel} \sim$ ML	0.178	0.206	0.14	2	51	−137.9	41.5
4	$FL_{Rel} \sim$ Sex	0.205	0.206	0.00	2	51	−130.7	48.7
5	$FL_{Rel} \sim$ MBC	0.206	0.206	0.00	2	51	−130.5	48.9
6	$FL_{Rel} \sim$ Day + ML	0.080	0.206	0.61	3	51	−176.5	2.9
7	$FL_{Rel} \sim$ Day $\times$ ML	0.079	0.206	0.61	4	51	−175.0	4.4
8	$FL_{Rel} \sim$ Day + Sex	0.080	0.206	0.61	3	51	−176.3	3.1
9	$FL_{Rel} \sim$ Day $\times$ Sex	0.073	0.206	0.65	4	51	−179.4	0.0
10	$FL_{Rel} \sim$ Day + MBC	0.081	0.206	0.60	3	51	−175.8	3.6
11	$FL_{Rel} \sim$ Day $\times$ MBC	0.081	0.206	0.61	4	51	−173.8	5.6
12	$FL_{Rel} \sim$ Day + ML + Sex	0.079	0.206	0.62	4	51	−175.2	4.2
13	$FL_{Rel} \sim$ Day + ML $\times$ Sex	0.079	0.206	0.62	5	51	−173.2	6.2
14	$FL_{Rel} \sim$ Day + ML + MBC	0.080	0.206	0.61	4	51	−174.5	4.9
15	$FL_{Rel} \sim$ Day + ML $\times$ MBC	0.079	0.206	0.61	5	51	−172.9	6.5

[†] The most parsimonious model (model 2). Abbreviations: Day, day of year (Julian day); k, number of parameters; MBC, maternal body condition (blubber thickness/ML); ML, maternal body length; n, sample size; Sex, the sex of the fetus.

Assuming that the observed minimum calf birth length, 3.72 m, is close to the lower physiological limit for SRWs, the minimum absolute fetal length (FL_Abs.Min) through gestation was estimated from (Fig. 6*B*):

$$FL_{Abs.Min} = \big(\exp\left(-1.050376 + 0.007685 \times DTB\right)$$
$$+ (0.021165/365) \times DTB\big)$$
$$\times \big(CBL_{Abs,Min}/CBL_{Rel}\big) \quad (24)$$

where $CBL_{Abs,Min}$ is equal to the minimum observed absolute birth length of calves (3.72 m) and CBL_{Rel} is equal to the estimated relative birth length (34.97%ML) of SRWs. Based on the relationship between SRW body volume and body length (eqn (4)), fetal volume (FV) could be estimated from (Fig. 6*C*):

$$FV = \exp\big[-4.115 + 3.016 \times \log\big[(\exp\left(-1.050376\right)$$
$$+ 0.007685 \times DTB) + (0.021165/365) \times DTB)$$
$$\times ML]\big] \times (1 + BBC) \quad (25)$$

The equivalent minimum fetal volume (FV_Min) through gestation could be estimated from (Fig. 5*C*):

$$FV_{Min} = \exp\big[-4.115 + 3.016 \times \log\big[(\exp\left(-1.050376\right)$$
$$+ 0.007685 \times DTB) + (0.021165/365)$$
$$\times DTB) \times \big(CBL_{Abs,Min}/CBL_{Rel}\big)\big]\big]$$
$$\times (1 + BBC) \quad (26)$$

Fetal length increased curvilinearly through gestation (Fig. 6*A* and *B*). Based on an average sized SRW female

(14 m long), the model predicted the length of the fetus to be 0.00 m (0.00%ML) at conception (embryo, day = 0), 0.56 m (4.00%ML) at the end of the first trimester (day = 122), 1.82 m (12.99%ML) at the end of the second trimester (day = 243) and 4.90 m (34.97%ML) at the end of the third trimester (day = 365) at birth (Table 5, and Fig. 6*A* and *B*). This corresponded to a growth rate in fetal length of 0.31 cm day^{-1} at conception (Day 0), 0.66 cm day^{-1} at the end of the first trimester, 1.56 cm day^{-1} at the end of the second trimester and 3.83 cm day^{-1} at the end of the third trimester just before birth (Table 5, Fig. 6*A* and *B*). The relative growth in fetal length per trimester was 11.4, 25.7 and 62.9% for the first, second and third trimester, respectively (Table 6).

Fetal volume increased exponentially through gestation (Fig. 6*C*). Based on a maternal body length of 14 m and an average body condition at birth (BBC = 0), the fetal volume was estimated to be 0.000 m^{-3} at conception (embryo), 0.003 m^{-3} at the end of the first trimester, 0.099 m^{-3} at the end of the second trimester and 1.967 m^{-3} at the end of the third trimester at birth (Table 5 and Fig. 6*C*). The resulting growth rate in fetal volume was 0.00 litres day^{-1} at conception, 0.10 litres day^{-1} at the end of the first trimester, 2.59 litres day^{-1} at the end of the second trimester and 46.05 litres day^{-1} at the end of the third trimester just before birth (Table 5 and Fig. 6*C*). The relative growth in volume was 0.1, 4.9 and 95.0% for the first, second and third trimester, respectively (Table 6). Specific growth curves in volume for PV and HoB can be found at https://doi.org/10.6084/m9.figshare.17121446.

Fetal mass

Due to the difference in BBC between locations, the average body density (BD) of SRW fetuses in HoB (810.73 kg m^{-3}) was higher (lower proportion of blubber) compared to PV (805.72 kg m^{-3}). Assuming a BBC = 0, the average body density of the fetus was 805.07 kg m^{-3}. Based on this, fetal mass (FM) could be estimated from (Fig. 6*D*):

$$
\begin{aligned}
\text{FM} = \big(\exp\big[-4.115 + 3.016 \times \log\big[(\exp\left(-1.050376\right. \\
\left. + 0.007685 \times \text{DTB}\right) + (0.021165/365) \times \text{DTB}) \\
\times \text{ML}\big]\big] \times (1 + \text{BBC})\big) \times \text{BD}
\end{aligned} \quad (27)
$$

The equivalent minimum fetal mass (FM$_{\text{Min}}$) through gestation could be estimated from (Fig. 6*D*):

$$
\begin{aligned}
\text{FM}_{\text{Min}} = \big(\exp\big[-4.115 + 3.016 \times \log\big[(\exp\left(-1.050376\right. \\
\left. + 0.007685 \times \text{DTB}\right) + (0.021165/365) \\
\times \text{DTB}) \times \left(\text{CBL}_{\text{Abs,Min}}/\text{CBL}_{\text{Rel}}\right)\big]\big] \\
\times (1 + \text{BBC})\big) \times \text{BD}
\end{aligned} \quad (28)
$$

Following the pattern of fetal volume (Fig. 6*C*), fetal mass also increased exponentially through gestation (Fig. 6*D*). Based on a mean maternal body length of 14 m and an average body condition at birth (BBC = 0), the predicted fetal mass was 0.00 kg at conception (embryo), 2.28 kg at the end of the first trimester, 79.84 kg at the end of the second trimester and 1583.96 kg at the end of the third trimester at birth (Table 5 and Fig. 6*D*). The resulting growth rate in fetal mass was 0.000 kg day^{-1} at conception (embryo), 0.083 kg day^{-1} at the end of the first trimester, 2.084 kg day^{-1} at the end of the second trimester and 37.070 kg day^{-1} at the end of the third trimester just before birth (Table 5 and Fig. 6*D*). The relative growth in body mass per trimester was 0.1, 4.9 and 95.0% for the first, second and third trimester, respectively (Table 6). Specific growth curves in mass for PV and HoB can be found at https://doi.org/10.6084/m9.figshare.17121446.

Energetic cost of gestation

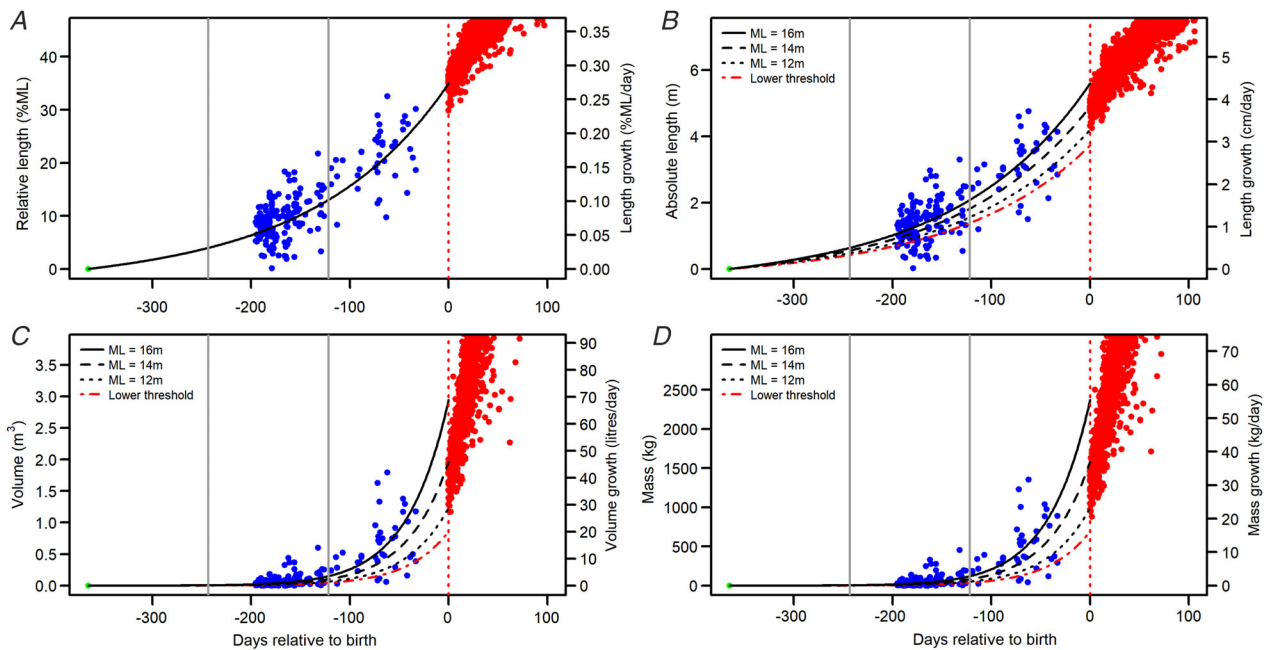Based on a maternal body length of 14 m and an average body condition at birth (BBC = 0), the cost of fetal growth

Figure 6. Southern right whale foetal growth through gestation
Relative fetal length (*A*), absolute fetal length (*B*), fetal volume (*C*), and fetal mass (left *y*-axis) and corresponding growth rates (right *y*-axis) (*D*) of southern right whales (blue symbols, *n* = 207), as a function of days to birth. The black fitted lines represent the predicted values from eqns (22), (23), (25) and (27), respectively. The red fitted lines represent the predicted values for a fetus to reach the minimum physiological birth length (3.72 m), given by eqns (24), (26) and (28), respectively. The line type (see key) indicates the effect of maternal length on absolute fetal length (*B*), volume (*C*) and mass (*D*). Calf length, volume and mass (red points, *n* = 3620) as a function of days since birth have been added to illustrate the close fit between fetal sizes and calf sizes at the time of birth (dotted vertical red lines). The green circle indicates the assumed time of fertilization (at which time the fetus, or embryo, length is 0), assuming a gestation period of 1 year. In this example, modelling approach 1 (assuming that tissue specific energy contents were fixed) was used and the calf body condition at birth (BBC) was fixed at 0 (average condition). The grey vertical lines split the gestation period of SRW into its three trimesters. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 5. Predicted mean length, volume, mass and energy content of southern right whale fetuses throughout gestation, and associated daily growth rates in length, volume, mass and energy (cost of fetal growth, placental costs and heat of gestation)

Fetal age (days)	Fetal length (m)	Fetal length growth (cm day^{-1})	Fetal volume (m^3)	Fetal volume growth (l day^{-1})	Fetal mass (kg)	Fetal mass growth (kg day^{-1})	Fetal energy content (MJ)	Fetal growth cost (MJ day^{-1})	Placental cost (MJ day^{-1})	Heat of gestation (MJ day^{-1})	Total gestation cost (MJ day^{-1})
0	0.00	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
10	0.03	0.33	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.01
20	0.07	0.35	0.00	0.00	0.00	0.00	0.07	0.01	0.00	0.05	0.06
30	0.10	0.37	0.00	0.00	0.01	0.00	0.26	0.03	0.01	0.12	0.16
40	0.14	0.39	0.00	0.00	0.03	0.00	0.67	0.06	0.01	0.24	0.31
50	0.18	0.42	0.00	0.01	0.07	0.01	1.44	0.10	0.02	0.43	0.55
60	0.22	0.44	0.00	0.01	0.14	0.01	2.76	0.17	0.04	0.70	0.91
70	0.27	0.47	0.00	0.02	0.25	0.01	4.84	0.26	0.06	1.08	1.40
80	0.32	0.50	0.00	0.02	0.41	0.02	8.01	0.39	0.09	1.61	2.09
90	0.37	0.54	0.00	0.04	0.65	0.03	12.66	0.57	0.14	2.32	3.02
100	0.42	0.57	0.00	0.05	0.99	0.04	19.31	0.80	0.19	3.29	4.28
110	0.48	0.61	0.00	0.07	1.46	0.06	28.64	1.11	0.27	4.57	5.94
120	0.55	0.66	0.00	0.10	2.12	0.08	41.51	1.52	0.36	6.25	8.14
130	0.61	0.70	0.00	0.13	3.02	0.11	59.03	2.06	0.49	8.46	11.01
140	0.69	0.75	0.01	0.18	4.22	0.14	82.62	2.76	0.66	11.34	14.75
150	0.76	0.81	0.01	0.23	5.83	0.19	114.09	3.67	0.88	15.06	19.60
160	0.85	0.86	0.01	0.31	7.97	0.25	155.77	4.84	1.16	19.87	25.87
170	0.94	0.93	0.01	0.40	10.77	0.32	210.60	6.34	1.52	26.06	33.92
180	1.03	0.99	0.02	0.53	14.44	0.42	282.33	8.28	1.98	34.00	44.26
190	1.13	1.07	0.02	0.68	19.21	0.55	375.71	10.75	2.57	44.17	57.49
200	1.24	1.14	0.03	0.88	25.40	0.71	496.79	13.91	3.33	57.15	74.39
210	1.36	1.23	0.04	1.14	33.40	0.92	653.20	17.94	4.29	73.71	95.94
220	1.49	1.32	0.05	1.47	43.71	1.18	854.65	23.07	5.52	94.79	123.37
230	1.63	1.42	0.07	1.88	56.94	1.51	1113.37	29.59	7.08	121.58	158.24
240	1.77	1.53	0.09	2.41	73.89	1.94	1444.87	37.87	9.06	155.59	202.51
250	1.93	1.64	0.12	3.07	95.56	2.47	1868.72	48.37	11.57	198.74	258.67
260	2.10	1.77	0.15	3.92	123.23	3.15	2409.65	61.67	14.75	253.41	329.83
270	2.28	1.90	0.20	4.99	158.47	4.02	3098.90	78.52	18.78	322.64	419.94
280	2.48	2.05	0.25	6.34	203.32	5.11	3975.87	99.83	23.88	410.23	533.94
290	2.69	2.20	0.32	8.05	260.31	6.48	5090.30	126.79	30.32	520.99	678.10
300	2.92	2.37	0.41	10.22	332.65	8.23	6504.91	160.85	38.47	660.97	860.29
310	3.16	2.56	0.53	12.95	424.39	10.43	8298.81	203.89	48.76	837.79	1090.44
320	3.43	2.75	0.67	16.40	540.62	13.21	10 571.74	258.22	61.76	1061.07	1381.05
330	3.71	2.97	0.85	20.76	687.78	16.71	13 449.45	326.81	78.16	1342.90	1747.87
340	4.02	3.20	1.09	26.26	873.98	21.14	17 090.41	413.35	98.86	1698.53	2210.74
350	4.35	3.45	1.38	33.19	1109.42	26.72	21 694.37	522.53	124.97	2147.16	2794.66
360	4.71	3.72	1.75	41.94	1406.97	33.76	27 513.01	660.23	157.90	2712.97	3531.10
Birth	4.90	–	1.97	–	1583.96	–	30 973.96	–	–	–	–

Estimates are based on an average sized southern right whale female (14 m long) and an average calf body condition at birth (BBC = 0). Specific costs relating to southern right whales at the Head of Bight and Península Valdés can be found at https://doi.org/10.6084/m9.figshare.17121446.

was 0.00 MJ day^{-1} at conception (embryo), 1.62 MJ day^{-1} at the end of the first trimester, 40.76 MJ day^{-1} at the end of the second trimester and 724.90 MJ day^{-1} at the end of the third trimester just before birth (Table 5 and Fig. 7A). The relative cost of fetal growth per trimester was 0.1, 4.9 and 95.0% for the first, second and third trimester, respectively, based on a fixed tissue energy density through gestation (approach 1, 3 and 4) (Table 6). Based on a gradual increase in energy tissue density (approach 2), the equivalent costs per trimester were 0.0, 1.9 and 98.1% for the first, second and third trimester, respectively (Table 6). The cost of placental growth followed the same pattern, with the daily cost being 0.00 MJ day^{-1} at conception, 0.39 MJ day^{-1} at the

Table 6. Predicted growth in length, volume, and mass of fetuses for each trimester during gestation (assumed to be one year in duration) for female southern right whales of different body length and the corresponding energetic costs of fetal growth, placental energy content and heat of gestation based on different modelling approaches of tissue energy

	Min			ML12			ML14			ML16		
	T1	T2	T3	T1	T2	T3	T1	T2	T3	T1	T2	T3
Fetal growth												
Fetal length (cm)	42.53	95.74	234.07	47.95	107.93	263.88	55.94	125.92	307.87	63.94	143.91	351.85
Fetal volume (l)	1.24	42.16	817.53	1.78	60.52	1173.64	2.83	96.34	1868.30	4.24	144.12	2794.79
Fetal mass (kg)	1.00	33.94	658.17	1.43	48.72	944.87	2.28	77.56	1504.12	3.41	116.03	2250.01
Approach 1: tissue specific energy content fixed												
Fetal growth cost (GJ)	0.02	0.66	12.87	0.03	0.95	18.48	0.04	1.52	29.41	0.07	2.27	44.00
Placental energy (GJ)	0.00	0.16	3.08	0.01	0.23	4.42	0.01	0.36	7.03	0.02	0.54	10.52
Heat of gestation (GJ)	0.07	2.31	44.83	0.10	3.57	69.18	0.18	6.23	120.86	0.30	10.10	195.96
Total gestation cost (GJ)	0.09	3.13	60.78	0.14	4.75	92.08	0.24	8.11	157.31	0.38	12.92	250.48
Approach 2: tissue specific energy content increasing												
Fetal growth cost (GJ)	0.00	0.25	13.30	0.00	0.36	19.09	0.01	0.57	30.39	0.01	0.86	45.47
Placental energy (GJ)	0.00	0.06	3.18	0.00	0.09	4.57	0.00	0.14	7.27	0.00	0.21	10.87
Heat of gestation (GJ)	0.07	2.31	44.83	0.10	3.57	69.18	0.18	6.23	120.86	0.30	10.10	195.96
Total gestation cost (GJ)	0.07	2.62	61.31	0.11	4.01	92.84	0.19	6.94	158.52	0.31	11.17	252.30
Approach 3: average tissue energy content fixed												
Fetal growth cost (GJ)	0.01	0.21	4.13	0.01	0.31	5.93	0.01	0.49	9.44	0.02	0.73	14.12
Placental energy (GJ)	0.00	0.07	1.42	0.00	0.07	1.42	0.00	0.12	2.26	0.01	0.17	3.38
Heat of gestation (GJ)	0.07	2.31	44.83	0.10	3.57	69.18	0.18	6.23	120.86	0.30	10.10	195.96
Total gestation cost (GJ)	0.08	2.58	49.95	0.12	3.95	76.53	0.20	6.84	132.56	0.32	11.01	213.46
Approach 4: tissue energy content based on fin whale fetus												
Fetal growth cost (GJ)	0.00	0.09	1.73	0.00	0.13	2.49	0.01	0.20	3.96	0.01	0.31	5.93
Placental energy (GJ)	0.00	0.03	0.60	0.00	0.03	0.60	0.00	0.05	0.95	0.00	0.07	1.42
Heat of gestation (GJ)	0.07	2.31	44.83	0.10	3.57	69.18	0.18	6.23	120.86	0.30	10.10	195.96
Total gestation cost (GJ)	0.07	2.42	46.98	0.11	3.73	72.27	0.19	6.49	125.77	0.31	10.48	203.30

The estimates are based on an average calf body condition at birth (BBC = 0). Specific costs relating to southern right whales at the Head of Bight and Península Valdés can be found at https://doi.org/10.6084/m9.figshare.17121446.

end of the first trimester, 9.75 MJ day^{-1} at the end of the second trimester and 173.36 MJ day^{-1} at the end of the third trimester just before birth (Table 5 and Fig. 7*A*). The heat of gestation equalled an energy expenditure of 0.00 MJ day^{-1} at conception, 6.65 MJ day^{-1} at the end of the first trimester, 167.48 MJ day^{-1} at the end of the second trimester and 2978.69 MJ day^{-1} at the end of the third trimester just before birth (Table 5 and Fig. 7*A*). Specific estimates of the costs of fetal growth for PV and HoB can be found at https://doi.org/10.6084/m9.figshare.17121446.

The daily cost of gestation increased exponentially through pregnancy (Table 5), with the relative cost per trimester being 0.1, 4.9 and 95.0% for the first, second and third trimester, respectively, based on a fixed tissue energy density through gestation (approach 1, 3 and 4) (Table 6). Based on a gradual increase in energy tissue density

(approach 2), the equivalent costs per trimester were 0.1, 4.1 and 95.8% for the first, second and third trimester, respectively (Table 6). Maintaining the growing fetus (the heat of gestation) constituted the largest relative cost, at 73.8% of total cost, followed by fetal growth at 21.2% and placental energy content at 5.0% (Fig. 7*A*). As maternal size (i.e. length) increased, so did the birth mass of the calf and the consequent cost of gestation, from 97.0 GJ at 12 m, to 165.7 GJ at 14 m, to 263.8 GJ at 16 m (Fig. 7*B*), assuming a BBC = 0 and tissue specific energy contents (approach 1 and 2). The minimum cost of gestation was 64.0 GJ based on the minimum observed birth size of 3.72 m (Fig. 7*B*). While the total cost of gestation was the same for modelling approach 1 (assuming a fixed tissue specific energy content through gestation) and 2 (assuming a gradual increase in tissue specific energy content through gestation), the maximum daily energy

cost of gestation was higher for approach 2 (Fig. 7*C*). Both the total cost and the maximum daily cost of gestation was lower for modelling approach 3 (assuming a fixed energy content for all tissues) and modelling approach 4 (assuming the same tissue energy content as a fin whale fetus), with the latter being slightly lower. The cost of gestation differed only slightly between locations (PV = 164.6 GJ, HoB = 156.5 GJ, based on a 14 m-long female) as a consequence of the higher BBC of calves in PV compared to HoB, and both estimates were similar to that of calves born at an average body condition (BBC = 0) (Fig. 7*D*).

Discussion

This study presents the first estimates of the cost of gestation in SRWs based on empirical data on fetal growth and calf birth sizes. We show that the daily cost of gestation can be high for baleen whales, and that maternal body size has a large influence on fetal growth rates and birth size. Further, we show that the

vast majority of gestation costs were incurred during the third trimester. Our estimates are based on 207 fetal length measurements obtained from pregnant females caught in whaling operations, 57 SRW females measured by aerial photogrammetry methods before and after birth, and 3558 morphometric measurements from 1224 calves in Argentina and Australia.

As hypothesized, larger females gave birth to larger calves compared to smaller females. While other studies of baleen whales (Christiansen, Dujon et al., 2016; Christiansen et al., 2021), including right whales (Christiansen, Dawson et al., 2020), have shown a positive relationship between maternal body length and calf size, this is the first study to demonstrate a direct relationship between maternal body length and calf birth length. With SRW calves being born at ~35%ML, this means that larger females had faster growing fetuses, which was supported by our fetal length analyses. While larger birth sizes could also be explained by larger females growing their fetus for a longer time, as reported for some terrestrial mammals (Huggett & Widdas, 1951), this is unlikely to be the case
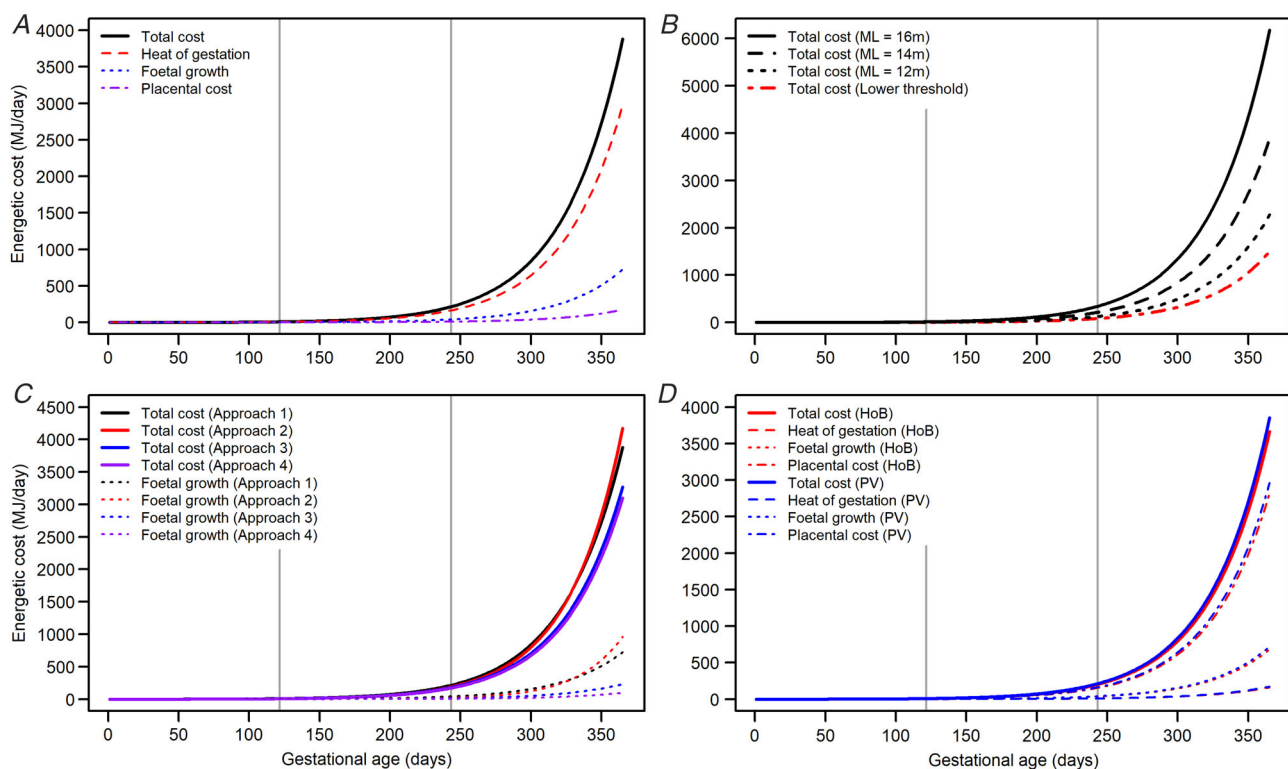
Figure 7. Cost of gestation in southern right whales as a function of gestational age
A, the cost of each energy component (fetal growth, placental energy content, heat of gestation, see key). *B*, the effect of maternal body length (ML) on cost of gestation. *C*, the result of different modelling approaches. *D*, differences in gestation cost between study location (differences in BBC). Approach 1: tissue specific energy contents were fixed; approach 2: tissue specific energy contents increasing gradually with fetal mass; approach 3: all tissues were fixed at the energy content of muscle; approach 4: tissue energy content based on fin whale fetus. Modelling approach 1 was used in *A*, *B* and *D*. Maternal length (ML) was fixed at 14 m in *A*, *C* and *D*. Calf body condition at birth (BBC) was fixed at 0 (average condition) in *A–C*. The grey vertical lines split the gestation period of SRW (assumed to be one year) into its three trimesters. [Colour figure can be viewed at wileyonlinelibrary.com]

for baleen whales since their reproductive cycle is tightly linked to their annual migratory cycle (Frazer & Huggett, 1959, 1973; Laws, 1959).

Maternal body condition had no effect on fetal growth or calf birth size. This is in contrast to the findings of Christiansen, Vikingsson et al. (2014), who found that common minke whale females in poorer condition had smaller fetuses. Effects of maternal condition on fetal growth rates has also been documented in a number of other mammal species, including ungulates (Byers & Hogg, 1995; Guinness et al., 1978; Skogland, 1984) and pinnipeds (Bowen et al., 1994; Kovacs & Lavigne, 1986; Pomeroy et al., 1999). In our study, 7.7% of the measured calves had lengths below their predicted birth lengths based on the size of their mother. These calves could either have been born prematurely, or been growing at a slower rate than expected. Gestation length varies naturally in mammals, even in species with relatively fixed gestation times (for a review, see Kiltie, 1982). Fetal (intrauterine) growth restriction is also common across mammalian species and can be caused by factors relating to the mother, the placenta or the fetus itself (for reviews, see McMillen et al., 2001; Morrison, 2008). Fetal growth restriction has been associated with poor perinatal health outcomes as well as increased risk of disease in adult life (McMillen & Robinson, 2005).

Alternatively, maternal body condition might have an effect on fetal growth and birth size in SRWs, but with our data set representing healthy (i.e. growing) SRW populations, it is possible that none of the measured females were in sufficiently poor condition to negatively affect fetal growth. When prey conditions are sufficient, SRW females generally have a 3-year reproductive cycle consisting of 1 year of gestation, 1 year of lactation and 1 year of resting (to recover energy stores) (Best, 1994). In contrast, common minke whales are considered annual breeders, with calving rates above 90% (Horwood, 1990; Jonsgård, 1951). This means that SRW females build up the energy reserves needed for reproduction over multiple feeding seasons, which could provide a buffer against poor prey conditions in a single year. In contrast, the body condition of common minke whale females will vary from year to year following the annual variation in prey conditions. It is also possible that a single measure of blubber thickness will not provide a good representation of the body condition of SRW females. In light of this, the reported birth lengths relative to maternal lengths in this study should be considered the optimal size for SRWs, whereas our minimum observed calf size of 3.72 m could be close to the species lower physiological limit. The latter is supported by the smallest reported right whale calves being 3.40 (dead 28 October 2009) and 3.54 m (dead 13 August 2013) for PV (Marón et al., 2015) and 3.65 for the closely related North Atlantic right whale (*Eubalaena glacialis*; Fortune et al., 2021).

There was no difference in birth length between locations. However, the body condition of newborn calves was 4.5 percentage points lower, on average, in HoB compared to PV. The same result was found by Christiansen, Dawson et al. (2020); they attributed this to local adaptations to different water temperatures, with calves in Australia being able to maintain a similar heat loss despite having a higher surface area to volume ratio, due to warmer waters experienced on their breeding grounds (15°C) compared to Argentina (11°C). While this difference in body condition was statistically significant, it had a negligible effect on the estimated cost of fetal growth and gestation, which was only 5.1% higher in PV compared to HoB.

Following parturition, SRW mothers had a reduction in their body volume equal to ∼1.6 times the birth volume of the newborn calf. That the volume loss of mothers exceeded the birth volume of the calves was likely due to the placenta and other tissues and fluids (e.g. amniotic fluid) associated with fetal development being ejected from the body during birth. The volume loss was visible just posterior of the mid-region of the body, from 50% to 65%BL. Additional loss in body volume following the first 20 days after birth was likely due to maternal costs of lactation, since the loss was visible across a wider portion of the body, from 30% to 75%BL, which corresponds to the area that is being metabolized during lactation (Christiansen et al., 2018). Quantifying the volume loss of mothers at birth is important, as this information can be used to correct morphological body condition estimates of pregnant females to obtain more accurate representations of their actual fat reserves relative to structural size. Furthermore, being able to identify late-pregnant females from their unique body shape (relative body width at 50−65%BL) is also beneficial for population monitoring, and potentially allows an estimation of the expected calving rate of a population in a given year.

Fetal length increased curvilinearly through gestation, which resulted in an exponential increase in fetal volume and mass for SRWs. This further supports the belief that baleen whales have a curvilinear fetal growth pattern (Christiansen, Vikingsson et al., 2014; Ivashin & Mikhalev, 1978; Laws, 1959; Masaki, 1976; Nishiwaki, 1959; Rice, 1983; Rice & Wolman, 1971; Zimushko & Ivashin, 1980) rather than linear growth as suggested by some authors (Best, 1994; Frazer & Huggett, 1973, 1974; Philo et al., 1992), although this may differ between species. Further, our growth model fitted well with the neonatal growth patterns measured for SRWs (Fig. 6, Christiansen et al., 2018; Christiansen et al., 2022). However, our results are in contrast to those reported by Best (1994), who used a straight regression line to represent the growth in fetal length of SRWs. While our study is partly based on the same data set, Best (1994) included 12 additional dubious measurements obtained between 1832 and 1937 from a

number of sources where the methods for measurement were unknown and possible only rough visual estimates of length. These additional measurements included some very large fetuses, >6 m in length, which were substantially larger than the measured birth sizes of SRWs in this study, or those predicted from eqn (16) for the largest observed mothers. Such large SRW fetuses are unlikely to occur in reality, as it would likely cause significant complication for the mother during labour. Furthermore, Best (1994) did not test for curvilinear patterns in his analyses, and did not include maternal length as a covariate in his growth model, which were both found to be significant in our analyses.

As a consequence of the exponential growth of the fetus, the cost of gestation was very low during the first (0.1%, of total cost) and second trimesters (4.9%), but increased rapidly during the last trimester (95.0%), as we had hypothesized. The gestation cost for an average-sized female (14 m long) during this period ranged from 126 to 159 GJ. This is significant when compared to other maternal expenses. For example, the cost of somatic growth is only ∼1.7 GJ for a similar sized female over the same time period (based on cost of growth of 13.9 MJ day^{-1}, Christiansen et al., 2022). In contrast, maternal costs for a lactating female of similar size over the same period is ∼300 GJ (based on an average blubber volume loss of 0.125 m^3 day^{-1}, Christiansen et al., 2018). Consequently, maternal costs during late gestation need to be accounted for in bioenergetic models.

The high relative cost experienced by pregnant females during the third trimester means that females with insufficient body condition are more likely to abort their fetus during this period. In support of this, Ichihara (1962) found that the rate of miscarriage in fin whales was about three times higher in the later stages of pregnancy than earlier on. This is likely to have implications for the reproductive strategy of baleen whales. Since early gestation costs are very cheap, it could be advantageous for females to mate and become pregnant, even if they are in moderate body condition. Whether the female completes gestation will then be determined by her foraging success during the following feeding season, and whether the female at the onset of the third trimester has acquired sufficient energy reserves to complete gestation and early lactation (the first 3−4 months after parturition until the female has returned to the feeding grounds). Since prey availability is a stochastic process, as evident from observed annual variations in the body condition of baleen whale populations (Gunnlaugsson et al., 2013; Leaper et al., 2006; Lockyer, 1987b), this reproductive strategy could be beneficial for SRW females since the cost of an aborted fetus prior to the third trimester would be very low compared to the potential fitness benefit of producing and weaning a viable offspring. Although empirical data are lacking to test this hypothesis,

a recent paper by Kershaw et al. (2021) found that the average annual pregnancy rate of humpback whales was considerably higher (∼37%) than the average annual calving rate (∼23%). This suggests that a large proportion of females either failed to maintain pregnancies to term or could not transfer enough energy to keep their calves alive throughout the lactation period. Furthermore, using a dynamic state model, Pirotta et al. (2019) showed that the optimal reproductive strategy of blue whales was for females to become pregnant whenever they could, since aborting a fetus or abandoning a calf early gave them the opportunity to become pregnant again soon after. The latter has also been shown for SRW females in PV, where early calf mortality often results in females being able to quickly build up sufficient energy reserves to become pregnant again already in the following breeding season, which results in a two-year calving interval rather than three (Maron et al., 2015).

Maintaining the fetus and associated tissues (including the placenta) represented the highest relative cost (73.8%, of total cost) of gestation for SRW females, followed by fetal growth (21.2%) and the energy contained in the placenta (5.0%). These estimates are similar to those reported for grey whales (Villegas-Amtmann et al., 2015), fin whales (Lockyer, 2007) and common minke whales (Lockyer, 1981b). However, all these studies relied on the same model equation by Brody (1968) to estimate heat of gestation, which has not been validated for baleen whales. To improve model estimates, attempts should be made to directly estimate this cost of gestation for marine mammals; such research might include studies of smaller species in captive facilities (Noren et al., 2015), or by using other metrics to infer energy expenditure, such as respiration rates (to infer oxygen consumption, Christiansen, Rasmussen et al., 2014) or rates of loss in morphological body condition (Christiansen et al., 2021), with comparisons of estimates between pregnant and non-pregnant animals. In addition, the costs of fetal growth are based on assumed tissue energy densities derived from juvenile and adult whales from other species, and might hence not be representative for SRW fetuses. Lipid and protein concentration in blubber, muscle and visceral tissues has been shown to vary significantly seasonally across the body of whales, and also between species and reproductive classes (Aguilar & Borrell, 1990; Lockyer, 1987a; Lockyer et al., 1984, 1985; Vikingsson, 1990; Vikingsson et al., 2013). Christiansen et al. (2000) demonstrated through model simulations that varying these tissue energy densities within their reported ranges can result in nearly a doubling in energy expenditure from the lowest to the highest values. This was also evident in our study when comparing the results from modelling approaches 1 and 2 with that of modelling approach 3 and 4 which assumed an overall lower tissue energy content. Which of these modelling approaches

is closest to the true cost of gestation in SRWs is unknown, and this uncertainty needs to be acknowledged (or incorporated) in bioenergetic models relating to fetal growth in baleen whales. With empirical data on fetal energy content lacking, we encourage researchers to measure this from either stranded pregnant females or animals accidentally caught in fishing gear. Finally, our estimates of growth in fetal volume and mass are based on the body volume to length relationship of newborn SRW calves, which might not be representative for a fetus throughout gestation. Lanzetti et al. (2020) used 3D landmarks to demonstrate changes in the cranial morphology of humpback whale fetuses relative to a juvenile specimen, and found significant differences. While a similar approach would have been desirable in our study, such data were not available for SRWs. Since we knew that the growing fetus would ultimately obtain a similar body shape to that of a newborn SRW calf (for which we had data), and we assumed that the absolute energetic cost of reaching those body proportions would be the same irrespective of how the body shape varied throughout gestation, we extrapolated the body volume to length relationship of newborn SRWs to the entire gestation period.

The cost of reproduction is important for studies of animal ecophysiology and bioenergetics, but also has important implications for management. We show that the vast majority of gestation costs were incurred during the third trimester, during which time pregnant females are migrating to their breeding grounds to give birth. Since females are fasting during this time, they are likely to be particularly vulnerable to anthropogenic disturbance. Larger females should be more resilient to disturbance, since they have larger energy reserves and can hence afford losing more energy before reaching the lower threshold for fetal growth. This valuable information should be incorporated into future bioenergetic models to assess the population consequences of disturbance (PCoD) on baleen whales (Pirotta et al., 2018), to benefit the management and conservation of baleen whale populations.

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Additional information

Data availability statement

The data that support the findings of this study are available from the corresponding author upon request.

Competing interests

The authors declare no conflicts of interest, financial or otherwise.

Author contributions

F.C. conceived and designed the study. F.C., M.M.U. and M.S. secured funding for the PV fieldwork, and F.C. and L.B. secured funding for the HoB fieldwork. F.C., N.L., M.M.U. and M.S. carried out the fieldwork in PV, and F.C. carried out the fieldwork in HoB. SRW fetal data was processed, collated and provided by P.C., Y.I. and D.T. Data processing, analyses and interpretation was carried out by F.C. F.C. wrote the manuscript with input from all authors. All authors have read and approved the final version of this manuscript and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved. All persons designated as authors qualify for authorship, and all those who qualify for authorship are listed.

Keywords

baleen whale, body condition, capital breeder, life history, photogrammetry, reproduction, reproductive effort

Supporting information

Additional supporting information can be found online in the Supporting Information section at the end of the HTML view of the article. Supporting information files available:

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