Maternal body size and condition determine calf growth rates in southern right whales

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ABSTRACT: The cost of reproduction is a key parameter determining a species' life history strategy. Despite exhibiting some of the fastest offspring growth rates among mammals, the cost of reproduction in baleen whales is largely unknown since standard field metabolic techniques cannot be applied. We quantified the cost of reproduction for southern right whales *Eubalaena australis* over a 3 mo breeding season. We did this by determining the relationship between calf growth rate and maternal rate of loss in energy reserves, using repeated measurements of body volume obtained from unmanned aerial vehicle photogrammetry. We recorded 1118 body volume estimates from 40 female and calf pairs over 40 to 89 d. Calves grew at a rate of 3.2 cm d^{-1} (SD = 0.45) in body length and 0.081 m^3 d^{-1} (SD = 0.011) in body volume, while females decreased in volume at a rate of 0.126 m^3 d^{-1} (SD = 0.036). The average volume conversion efficiency from female to calf was 68 % (SD = 16.91). Calf growth rate was positively related to the rate of loss in maternal body volume, suggesting that maternal volume loss is proportional to the energy investment into her calf. Maternal investment was determined by her body size and condition, with longer and more rotund females investing more volume into their calves compared to shorter and leaner females. Lactating females lost on average 25 % of their initial body volume over the 3 mo breeding season. This study demonstrates the considerable energetic cost that females face during the lactation period, and highlights the importance of sufficient maternal energy reserves for reproduction in this capital breeding species.

KEY WORDS: Baleen whales · Bioenergetics · Body condition · Energy transfer · Lactation · Offspring growth · Photogrammetry · Unmanned aerial vehicles

INTRODUCTION

The cost of reproduction is a key parameter determining a species' life history strategy (Stearns 1989) and population dynamics (Bell 1980). Baleen whales exhibit some of the fastest offspring growth rates among mammals (Frazer & Huggett 1973, Lockyer 1984) and are capable of producing and weaning a calf ranging in length from 4.5 (minke whale *Balaenoptera acutorostrata*) to 12.8 m (blue whale *B. mus-*

culus) in only 2 yr (for review, see Lockyer 1984). This rapid growth suggests considerable energetic costs for the mother, particularly during the lactation phase, which is considered the most expensive part of the mammalian reproductive cycle (Gittleman & Thompson 1988), including baleen whales (Lockyer 1981). The reproductive cycle of most baleen whales is closely linked to their migratory cycle. During summer they reside on high-latitude feeding grounds where they build up energy reserves, which they

then rely on during the winter breeding season when they migrate to low-latitude areas to mate and give birth (Lockyer 2007). Since feeding is absent (or limited, see Stockin & Burgess 2005) during the breeding season, lactating females rely on stored energy reserves to support their calves during the first months of life, while also supporting their own metabolic needs (Lockyer 2007, Christiansen et al. 2016a). Sufficient energy reserves are therefore critical for the survival of both the female and her calf. Despite lactation being the energetically most challenging phase in the reproductive cycle of baleen whales (Lockyer 1981), few studies have looked into the energetic cost of early calf development and the effect of maternal condition on calf growth rates.

In many mammalian and avian species, conditions experienced during early offspring development affect subsequent survival and reproductive performance (Lindström 1999, McMahon et al. 2000). With offspring size being positively related to survival (McMahon et al. 2000), females aim to increase their own fitness by maximizing the growth rates of their offspring to the extent that resources allow. The amount of energy that a baleen whale female can invest in her calf is limited by her absolute energy stores (Christiansen et al. 2013), which in turn are determined by her absolute size (i.e. body length) and body condition (Blueweiss et al. 1978, Lindstedt & Boyce 1985). Studies of terrestrial mammals show that maternal size and condition have a positive effect on fertility (Albon et al. 1983), litter size (Dobson & Michener 1995), foetal growth rates (Skogland 1984), size at birth (Atkinson & Ramsay 1995), offspring growth rates (Robbins & Robbins 1979) and survival (Festa-Bianchet 1998). In baleen whales, Lockyer (2007) documented that female body condition influenced the body weight–length relationship of fin whale *B. physalus* foetuses, with foetuses being leaner in years when females were in poorer body condition. Similarly, Christiansen et al. (2014) showed that foetal growth in minke whales was positively affected by maternal body condition. Christiansen et al. (2016a) found a positive relationship between calf and maternal body condition during postnatal development in humpback whales *Megaptera novaeangliae*. While these studies suggest that maternal body condition influences reproduction in baleen whales, no study to date has investigated the relationship between calf growth rate and maternal investment at an individual level.

The growth rate of a baleen whale calf during early development should be determined by the absolute amount of energy that its mother can transfer to it.

For a fasting female, this should be reflected in the rate of decline in her body condition (Christiansen et al. 2014, 2016a). To determine this relationship, however, repeated measurements of the same female and calf pair throughout the breeding season are needed. Because of their large size, measuring energy expenditure (e.g. cost of reproduction) in free-ranging whales is logistically difficult, and most standard methods (e.g. caloric intake, respirometry, doubly labelled water, isotope measurements of milk production) cannot be applied (Randolph et al. 1977, Oftedal 1984, Kurta et al. 1989). Baleen whales store most of their energy in muscle and adipose tissue (blubber and visceral fat), but a considerable amount is also stored in internal organs, bones and other tissues (Lockyer 1986, 1987, Vikingsson 1995, Christiansen et al. 2013). The body girth or width of a whale encompasses these different tissues, and can be used as a proxy for energy stores and body condition (Lockyer 1987, Best & Rüther 1992, Vikingsson 1995, Miller et al. 2012). The body width of free-living whales can be measured non-invasively (Christiansen et al. 2016b) using aerial photogrammetry methods (Miller et al. 2012, Christiansen et al. 2016a). Unmanned aerial vehicles (UAVs) have further made aerial photogrammetry more affordable and safer than using conventional aircraft, thus making this technique increasingly feasible for wildlife researchers (Christiansen et al. 2016a, Durban et al. 2016).

We investigated the growth rates of individual southern right whale *Eubalaena australis* calves in relation to the body size and condition of their mothers, by taking repeated photogrammetry measurements, via UAVs, of the same female and calf pairs over a 3 mo period on a breeding ground in South Australia. By estimating the body volume of whales from body length and width measurements, we tested the effect of maternal size (body length) and body condition on a proxy for the rate of energy investment (rate of loss in maternal body volume) into their calf. The absolute loss in maternal body volume over the breeding season was then used to estimate the cost of lactation in females.

MATERIALS AND METHODS

Study species and area

Every year between May and November, southern right whales migrate from summer feeding grounds in the sub-Antarctic and Antarctic (Bannister et al.

1997, 1999) to breeding grounds off the southern coast of Australia (Burnell 2008). The Head of Bight (HoB) (31° 29′ S, 131° 08′ E; Fig. 1) is a major calving ground for southern right whales in Australia, and most calves are born between late May and early September, with a peak in August (Burnell & Bryden 1997). Southern right whale females reach sexual maturity as early as 5 yr of age, with a mean age of first calving of 9.1 yr recorded for the Australian population (Burnell 2008). Like most baleen whales, right whales give birth to a single calf. The reproductive cycle of a southern right whale female is typically 3 yr (HoB = 3.38 yr; Burnell 2008) and consists of 1 yr of gestation (Best 1994), 1 yr of lactation (Thomas & Taber 1984, Tormosov et al. 1998) and 1 yr of recovery (replenishing energy reserves). Every year since 1991, shore-based research of southern right whales has been carried out at the HoB by the Great Australian Bight Right Whale Study (GABRWS, www.gabrightwhales.com) (Burnell & Bryden 1997). Combined with land-based photo-identification efforts, the study has collected demographic and life history data, including detailed information on the reproductive histories of individual females. The HoB photo-identification catalogue currently comprises 1186 individually identified adult and sub-adult whales, including 459 reproductive females (Charlton 2017).

Data collection

Vertical aerial photographs of southern right whale females with calves were taken at HoB between 24 June and 25 September 2016 using a DJI Inspire 1 Pro quadcopter UAV (56 cm diameter, 3.4 kg, www.dji.com; Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m592p267_supp/). The UAV was flown from land out to sea at altitudes of 5 to 120 m and within 2 km of the coast. Most southern right whale females at the HoB stay in shallow waters close to the coast (<2 km) to nurse their calves, and pairs could hence be photographed by the UAV. The Inspire 1 Pro has a mean flight time of 13 min and carries a 16 megapixel DJI Zenmuse X5 micro four-thirds camera with an Olympus M.Zuiko 25 mm f1.8 lens and a polarized filter. A gimbal was used to position the camera vertically down, while providing stability to account for the pitch and roll of the UAV. Photographs were triggered remotely by the pilot on shore. When photographing a whale, the UAV was flown at altitudes between 20 and 50 m. Once over a whale, the UAV could hover over it for up to 10 min, until photographs of adequate quality had been obtained. Desired photographs were of a whale situated flat at the surface, dorsal side facing up, with a straight body axis and peduncle that was non-arching (Fig. 2) (Christiansen et al. 2016a). A video link, providing the
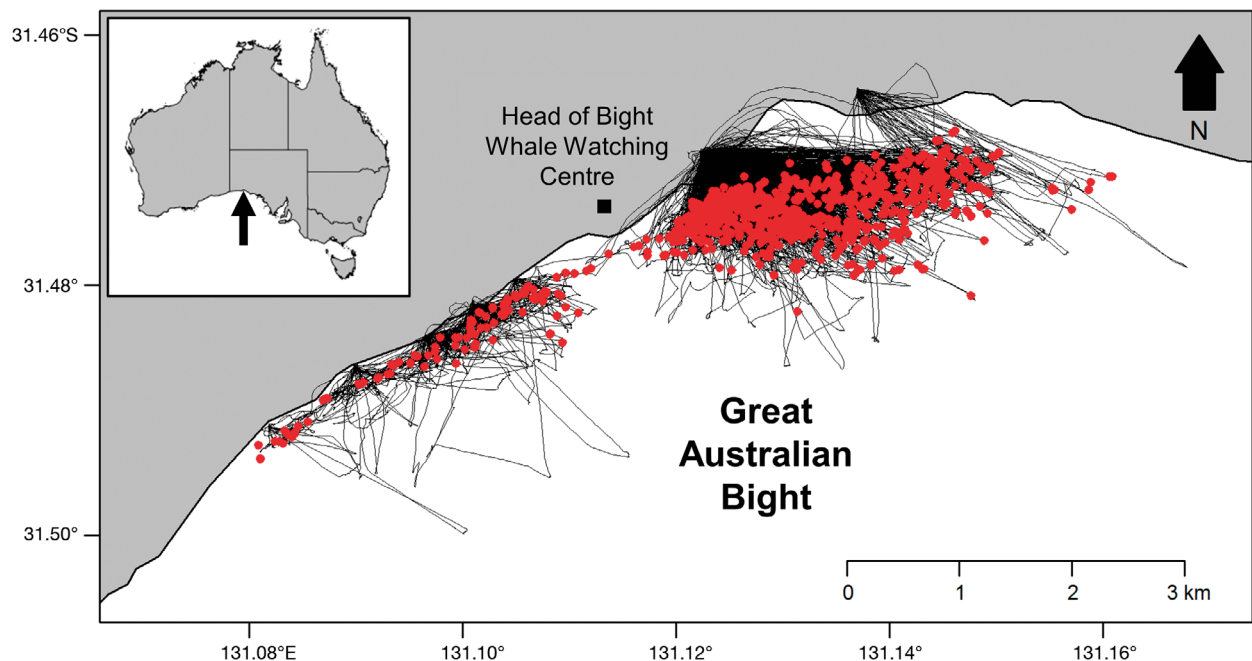

Fig. 1. Head of Bight study area in South Australia, displaying the unmanned aerial vehicle flight tracks (solid lines) during the study period (24 June to 25 September 2016) and the positions of the photographed southern right whale females and calves (red points) used in the analyses. n = 1118 measurements
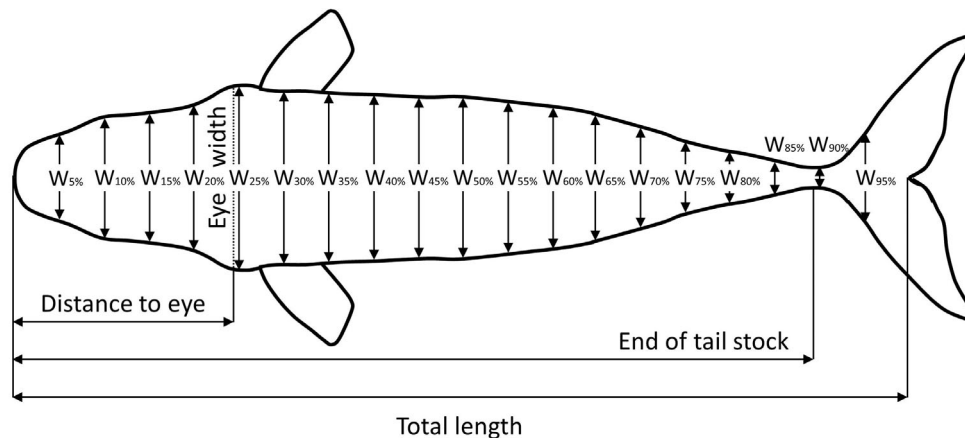
A

B

Fig. 2. (A) Example aerial photograph of a southern right whale used to measure body volume. Only photographs in which the whale was lying flat at the surface, with its dorsal side up and with a straight body axis and non-arching peduncle, were used in the analyses (Table S1, Fig. S2 in Supplement 1 at www.int-res.com/articles/suppl/m592p267_supp/). (B) Positions of measurement sites used in the study. The dotted line indicates the location of the eye width measurement, located at 25 and 20% body length from the rostrum for lactating females and calves, respectively (Fig. S4). W: width

UAV operator with live feed from the UAV camera through an iPad Air tablet, was used to correct the position of the UAV above the whale and also to confirm that photographs of adequate quality had been obtained. A LightWare SF11/C laser range finder (Lightware Optoelectronics, weight: 35 g) was used to measure the altitude of the UAV above sea level. The UAV and range finder setup was similar to that used by Dawson et al. (2017). The range finder has an accuracy of 0.1 m with a resolution of 1 cm and makes 20 readings per second using a 15 mW laser. The range finder was powered by the UAV battery and attached to the rear of the UAV with the sensors fixed downwards (Fig. S1). A compass and tilt sensor were connected to the range finder to record the pitch and roll of the UAV at the time of measurements. The range finder development, setup and testing was carried out by Global Unmanned Systems (www.gus-uav.com), Perth, Western Australia. The altitude, or height (H, in meters), of the UAV above sea level, was calculated from the measured range finder distance (Dist) by taking into account the pitch and roll of the aircraft at the time of measurement:

$$H = \cos(\text{pitch}) \times \cos(\text{roll}) \times \text{Dist} \quad (1)$$

where pitch and roll are given in radians and distance is given in meters. The range finder data were matched to the vertical photographs of the whales post hoc, using the GPS time stamps of the range finder and the Inspire 1 Pro.

Data filtering

For each flight, the best photographs of each individual whale were selected and graded based on several attributes: camera focus, straightness of body (horizontally), degree of body roll, degree of body arch, body pitch (vertically), body length measurability and body width measurability (Table S1, Fig. S2).

Each photograph was given a score of 1 (good quality), 2 (medium quality) or 3 (poor quality) for each attribute (Fig. S2). Photographs that were given a score of 3 for any attribute were removed from further analyses. In addition, photographs that obtained a score of 2 for both arch and pitch, pitch and roll or arch and roll were removed.

Morphometric measurements and scaling

Using photogrammetric methods, we extracted several morphometric measurements from the vertical photographs of the whales (Fig. 2) following the protocol of Christiansen et al. (2016a). Measurements were made using a custom-written script in R (R Core Team 2014; free download available from Christiansen et al. 2016a). Length measurements (in pixels) included the distance from the tip of the rostrum to the notch of the fluke, the distance from the tip of the rostrum to the position of the eyes (measured along the body axis of the whale), and the distance from the tip of the rostrum to the end of the tail stock (Fig. 2) (Christiansen et al. 2016a). We also measured the body width of the whales (in pixels) at 5% intervals along the entire body of the animals (19 measurements in total) perpendicular to the body axis (Christiansen et al. 2016a).

To convert the image pixel measurements to distance measurements, we first estimated the relative size of the whale in the photographs, in percent, based on the known resolution of the image (4608 × 3456 pixels). The size of the whale in the camera sensor, in meters, was calculated from this proportion and the known size of the camera sensor (17.3 × 13.0 mm). This measurement was then scaled to the actual size of the whale, in meters, by multiplying it with the scale factor C, which was calculated from:

$$C = \frac{H}{f} \qquad (2)$$

where H is the altitude (height) of the UAV above the waterline, in meters, and f is the focal length of the camera lens (25 mm), in meters.

Individual identification and life history data

Individual southern right whale females were identified from the aerial photographs, based on the unique callosity pattern on their heads (Payne et al. 1983), and matched to a photo-identification catalogue held by GABRWS. For females with known reproductive histories, the total number of calves produced by the female was extracted together with the average calving interval and the time since the last calving event. When possible, individual calves were sexed based on visual inspection of the genital area from the aerial photographs.

Site-specific changes in body width

Baleen whales deposit and metabolize fat reserves heterogeneously across their bodies (Lockyer et al. 1985, Miller et al. 2012, Christiansen et al. 2013, 2016a). To determine the metabolically active body area for southern right whale females and calves, we developed linear models in R to test the effect of Day of Year on each body width measurement. To account for the body length of the animal, the rate of change (slope parameter β) in relative body width (body width/body length) as a function of Day of Year was estimated for each individual and measurement site. Measurement errors in the body length of individual females (mean = 1.2%, upper 95% posterior density interval = 3.5%, max. = 7.3%) were accounted for by fixing the body length of each female to her own mean. The body width measurements were then recalculated based on the new body length measurements. Both linear and polynomial non-linear models were developed to test the relationship between relative body width and Day of Year. Model selection was based on Akaike's information criterion. Separate models were fitted for females and calves. The effect of sample size (total number of measurements of an individual) and sampling duration (number of days between the first and last measurement of an individual) on body width change was also investigated, to account for potential biases (Fig. S3).

Estimating body volume

Baleen whales deposit and metabolize fat not only laterally but all around their bodies. To quantify the amount of energy that lactating females lose throughout the breeding season as a function of the growth rate of their calves, the body volume of southern right whales was calculated from the body width and length data. The volume of the body of the whales was modelled as a series of frustums (a cone with the top cut off) connected to each other at each body width measurement site (similar to Christiansen et al. 2013). Assuming that the cross-section shape of

a whale is circular, so that the body girth (G) at each width measurement site can be calculated from $G = 2\pi \times r$, the body volume (m^3) of each frustum segment, V_s, was calculated:

$$V_s = \frac{1}{3}\pi h\left(r^2 + rR + R^2\right) \qquad (3)$$

where h is the height (i.e. distance, m) between 2 adjacent body width measurements along the body axis of the animal ($h = 0.05 \times$ total length), r is the radius of the smaller girth measurement (equivalent to half the anterior body width measurement), and R is the radius of the larger girth measurement (equivalent to half the posterior body width measurement). The total body volume, V_{total} (m^3), of the whales could then be estimated by summing the volume of the different frustum segments:

$$V_{total} = \sum_{s=1}^{S} V_s \qquad (4)$$

In baleen whales, relatively little energy is stored in the head, fins and tail fluke (Brodie 1975). Hence, for the body volume to represent the metabolically active area of lactating females, only segments (s) between the position of the eyes (~25% body length from the rostrum, Fig. S4) down to the end of the tail stock (~85% body length from the rostrum, Fig. S4) were included in the body volume estimate. For calves, the body volume was estimated for the entire body (except for the fins and tail fluke), from the tip of the rostrum down to the end of the tail stock (~85% body length from the rostrum, Fig. S4), so that the full growth in body volume could be quantified.

Calf growth in relation to maternal loss in volume

Linear models were used to determine the rate of change in body volume of lactating females and calves as a function of Day of Year. Separate models were fitted for each individual whale. Only individuals for which the model coefficient of determination (R^2) was higher than 0.5 (Fig. S5) were included in further analysis. Calf growth in body length was also investigated. From the resulting model parameters, the relationship between calf growth rates (both body volume and length) and maternal rate of loss in body volume was investigated. To distinguish between growth in calf body volume and length, calf body condition (CBC) was calculated from the residuals of the linear relationship between the rate of change in calf body volume and length (Fig. S6) and was modelled against maternal rate of loss in body

volume. Calf relative body width (proportion of body length) at 25% body length from the rostrum as a function of days since birth (described in next section) was also investigated using a generalized additive model (GAM).

Based on the estimated growth rates in body volume, the amount of change in absolute body volume of lactating females and calves over the breeding season was estimated. The mean residency time for lactating females with calves at the HoB calving ground was 71 d during 1992 to 1994 (Burnell & Bryden 1997) and 44 d during 2014 to 2016 (Charlton 2017), but some stayed as long as 108 d (Burnell & Bryden 1997). Based on the higher estimates, we set the residency time of lactating females to 90 d. Finally, the volume transfer efficiency (calf volume gain/maternal volume loss) between females and calves was quantified. To investigate if lactating females disproportionally allocate their energy investment into offspring of a specific sex, as seen in some mammals (Byers & Moodie 1990), the effect of calf sex on growth rates and volume transfer efficiency was tested.

Variables affecting maternal investment in calf

The effect of maternal size on offspring investment was investigated using linear models, by modelling maternal rate of loss in body volume as a function of maternal volume at calf birth (MVB), maternal body length and female body condition (FBC). To calculate MVB, the date of birth (DOB) of each calf was first calculated from the linear relationship between calf volume and Day of Year, by replacing calf volume with the known volume of calves at birth. At birth, southern right whale calves range in length between 4.5 and 6.1 m (Best & Rüther 1992). Based on this, we predicted the volume of an average 5.0 m long calf from the relationship between calf body volume and length (Fig. S7) and used this as the volume at birth. While we acknowledge that it is unrealistic to assume a common birth size for all calves measured in this study, fixing the body volume of calves at birth allowed us to standardize our maternal body volume estimates so that maternal investment could be compared against the same point in the development of their offspring. From the predicted calf volume at birth, we calculated the DOB for each calf from their body volume growth rates. From the calculated DOBs for the calves, MVB was calculated from the relationship between maternal volume and Day of Year. FBC was then calculated:

$$\text{FBC}_i = \frac{\text{MVB}_{\text{obs},i} - \text{MVB}_{\text{exp},i}}{\text{MVB}_{\text{exp},i}} \qquad (5)$$

where $\text{MVB}_{\text{obs},i}$ is the observed (i.e. calculated) volume of female i on the DOB of her calf and $\text{MVB}_{\text{exp},i}$ is the expected (or predicted) body volume of female i on the DOB of her calf, based on the linear relationship between maternal body volume and length (Fig. S8). A positive FBC means that the female was in relatively better condition than an average female, whereas a negative FBC means she was in a relatively poorer condition.

Model validation

To ensure that the model assumptions were met for each model, we ran model validation tests, including scatter plots of residuals versus fitted values and versus each explanatory variable in the model (to investigate homogeneity of variances), quantile–quantile plots and residual histograms (to investigate normality of residuals). We also calculated leverage and Cook's distance to identify influential points and outliers, respectively. For models containing multiple explanatory variables, collinearity (high correlation) between the explanatory variables in the model was investigated by estimating the variance inflation factor, with an upper threshold value of 3 indicating collinearity. All model assumptions were fulfilled, and no model showed signs of collinearity.

Sensitivity analysis

Measurement errors resulting from the range finder were investigated by measuring a known-sized object on land, a 1.45 × 1.55 m rubber carpet. The carpet was placed on a perfectly flat hard surface (a concrete helipad) and photographed at different altitudes ranging from 5 to 50 m at increments of 5 m and from 50 to 120 m at increments of 10 m (Fig. S9). Three independent measurements were made at each altitude using different UAVs and range finders. The errors in length and width of the object were estimated for each measurement and plotted as a function of altitude (Fig. S9). Additional error estimates inherent to the camera and range finder system can be found in Dawson et al. (2017). Measurement precision within photographs was assessed by having 3 independent researchers measure the body morphometrics of the same whale from the same photographs (Christiansen et al. 2016a). From these measurements, the coefficient of variation (COV) in body length and width was calculated for photographs of different body length and width measurability scores (Fig. S10). Measurement precision between photographs (differences between repeated measures of the same individual from different photographs) was assessed by taking 3 independent (i.e. different flights) measurements of the same whale within the same day and calculating the COV in body volume (Fig. S11) (Christiansen et al. 2016a). The mean COV of all repeated samples was then calculated as a measure of between-photograph precision.

To investigate the effect of measurement errors (described in the previous paragraph) on the final model parameters, resampling methods were used following the protocol of Christiansen et al. (2016a). One thousand bootstrap iterations were run. For each iteration and individual, new body length and width measurements were obtained from a distribution (Gaussian) of values, with the mean equal to the raw body width/length measurement of the individual and the standard deviation estimated from the COV in body width/length resulting from the different measurement errors (previous paragraph). Density distributions of the model parameters of the following relationships were obtained: growth rate in calf body volume, rate of decline in maternal body volume, relationship between rate of change in calf body volume and maternal body volume, relationship between CBC and maternal body volume, and relationship between maternal rate of decline and maternal body length and condition (Fig. S12).

RESULTS

Fieldwork was carried out between 24 June and 25 September 2016. Over this 93 d period, 49 d (52.7%) were spent collecting data. A total of 878 UAV flights (175.5 h) were conducted. The altitude of the UAV during photography ranged between 24.0 and 52.1 m (mean = 37.9 m, SD = 3.96). A total of 3354 aerial photographs of whales were taken (an average of 4 whales were photographed per flight), of which 2890 (86.2%) were successfully measured. After initial filtering based on picture quality (Table S1, Fig. S2 in Supplement 1), 1118 photographs remained. In total, 238 individual whales were identified throughout the study period (Fig. S13), including 89 lactating females, 91 calves and 58 non-lactating adults (both males and females). On average each female and calf pair was measured 10 times (SD = 5.7, min. = 1, max. = 29) over a mean period of 50 d (SD = 23.0, min. = 0, max. = 89; Fig. S14). A minimum of 4 meas-

urements over at least 20 d was needed to obtain accurate estimates of body width change (Fig. S3), and all individuals below these thresholds were removed from analyses. We further removed all individuals for which the model coefficient of determination (R^2) for body volume change was less than 0.5 (Fig. S5). After filtering, 40 female and calf pairs remained in the data set.

Site-specific changes in body width

The rate of change in relative body width of southern right whales throughout the breeding season differed between females and calves and also between measurement sites (Fig. 3). Lactating females decreased in relative body width over the middle to posterior part of their bodies, between 35 and 75% body length from the rostrum, whereas the head (<25% body length from the rostrum) and tail region (>80% body length from the rostrum) showed no change in body width (Fig. 3). In contrast, calves increased in relative body width at every measurement site (including the head region, <20% body length from the rostrum), apart from the tail stock (>80% body length from the rostrum), which showed no change in relative body width (Fig. 3). Most of the growth in relative body width of the calves occurred during the first month of lactation, after which the relative body width remained constant (GAM: $F_{3.62,4.53} = 56.84$, p < 0.001, $R^2 = 0.31$) (Fig. S15).

Calf growth in relation to maternal loss in volume

Calves increased linearly in body volume through the breeding season ($F_{1,591} = 5925$, p < 0.001, $R^2 = 0.91$) (Fig. S16A), while body length increased curvilinearly following a cubic polynomial relationship ($F_{3,589} = 1966$, p < 0.001, $R^2 = 0.91$) (Fig. S16B,C). The relationship between calf body volume and length was best described by a quadratic polynomial relationship ($F_{2,590} = 3587$, p < 0.001, $R^2 = 0.92$) (Fig. S7). Based on this, the average body volume of a calf of average body length at birth (i.e. 5.0 m) was calculated to be 1.6 m^3 (volume at birth). This was similar to the observed minimum volume of the sampled calves, which was 1.5 m^3. Calves increased in body volume at a rate of 0.081 m^3 d^{-1} (SD = 0.0108), with a range from 0.060 to 0.103 m^3 d^{-1} (Fig. 4B,D). The predicted volume of a calf at the end of the 90 d breeding season varied from 7.0 to 10.8 m^3, with an average of 8.9 m^3 (SD = 0.97). The maximum observed body volume of a calf was 11.7 m^3, similar to the upper range of predicted values. The relative increase in body volume of calves over the breeding season varied between 340 and 578%, with a mean of 455% (SD = 61).

The predicted body length of calves at birth ranged from 4.8 to 5.7 m, with an average of 5.3 m (SD = 0.23). The birth lengths corresponded to 33–41% of maternal body lengths, with a mean of 37% (SD = 1.7). The minimum observed calf body length was 4.7 m, or 34% of maternal length. The predicted body length at the end of the 90 d breeding season was 7.6 to 9.0 m, with a mean of 8.2 (SD = 0.34),
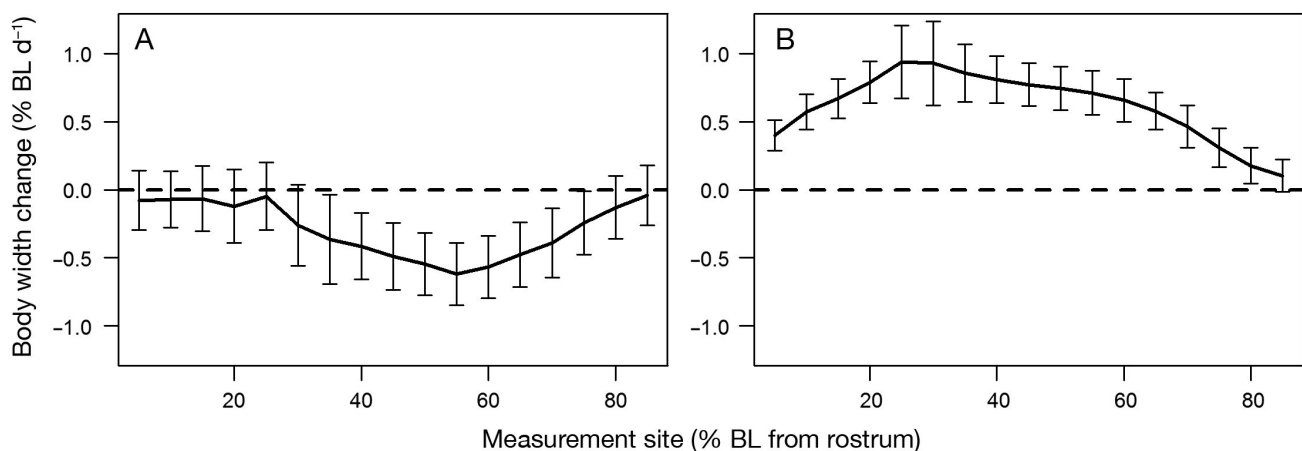

Fig. 3. Rate of change in relative body width (proportion of body length, BL) of southern right whale (A) females and (B) calves at different body width measurement sites (Fig. 2B). The solid black line represents the mean slope parameter (β) values of all measured female and calf pairs (n = 40) based on the linear model: body width/length = α + β × day. Error bars represent the mean of the lower and upper 95% CI of all individuals. The dashed lines represent the level where body width remains constant (β = 0) throughout the breeding season
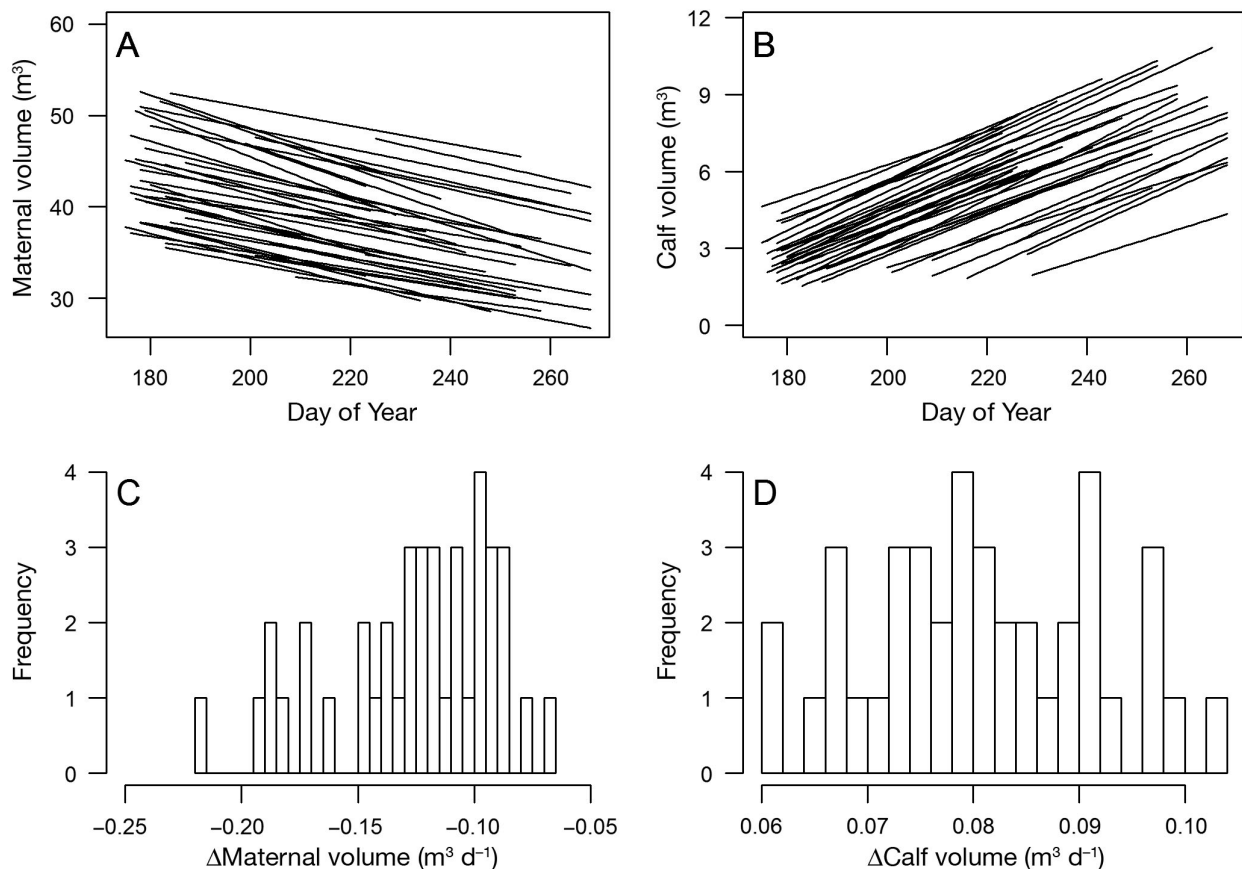
Fig. 4. Intra-seasonal change in body volume of southern right whale (A) females and (B) calves. Each solid line represents the fitted values of a linear model fitted to each whale in the data set. Frequency histograms of the rate of change (the corresponding slope parameter β of the linear models in [A] and [B]) in body volume of southern right whale (C) females and (D) calves. n = 40 female and calf pairs

which corresponded to 52–63% of maternal body length, with a mean of 57% (SD = 2.6). The maximum observed calf body length was 8.6 m, or 61% of maternal body length. The absolute increase in body length varied from 1.9 to 4.1 m, with a mean of 2.9 m (SD = 0.41), which equals an average growth rate between 2.2 and 4.6 cm d^{-1}, with a mean of 3.2 cm d^{-1} (SD = 0.45). This is similar to estimates reported from South Africa (2.8 cm d^{-1}; Best & Rüther 1992) and Argentina (3.5 cm d^{-1}; Whitehead & Payne 1981) and represents an increase between 35 and 83%, with a mean of 54% (SD = 9.3).

The size of lactating females ranged from 13.0 to 14.9 m in body length, with a mean of 14.2 m (SD = 0.53) (Fig. S17). This is similar to estimates from South Africa (13.9 m; Best & Rüther 1992), Argentina (13.7 m; Whitehead & Payne 1981) and Soviet catch records from the Southern Ocean (14.3 m; Tormosov et al. 1998). The predicted body volume of females at the time of birth varied from 33.2 to 56.2 m^3, with a mean of 44.4 m^3 (SD = 5.97). Similarly, the largest

measured body volume was 56.3 m^3. The rate of loss in maternal body volume varied between 0.069 and 0.219 m^3 d^{-1}, with a mean of 0.126 m^3 d^{-1} (SD = 0.0356) (Fig. 4A,C). At the end of the 90 d breeding season, the predicted body volume of the females was 25.4 to 46.3 m^3, with a mean of 33.0 m^3 (SD = 4.79). The lowest measured volume was 27.7 m^3. The absolute loss in body volume over the breeding season varied between 6.2 and 19.7 m^3, with an average of 11.3 m^3 (SD = 3.20). This corresponds to a relative loss in body volume of 14.6 to 37.0%, with a mean of 25.4% (SD = 5.53) (Fig. S18).

There was a significant negative relationship between calf growth in volume and maternal rate of change in body volume ($F_{1,38}$ = 7.85, p = 0.008, R^2 = 0.17) (Fig. 5A). For every 1 m^3 d^{-1} decrease in the rate of change in maternal volume, the growth rate of calves increased by 0.125 m^3 d^{-1} (SE = 0.0448). In contrast, maternal rate of change in volume did not affect the growth in body length of calves ($F_{1,38}$ = 2.95, p = 0.094, R^2 = 0.07) (Fig. 5B). Consistent with
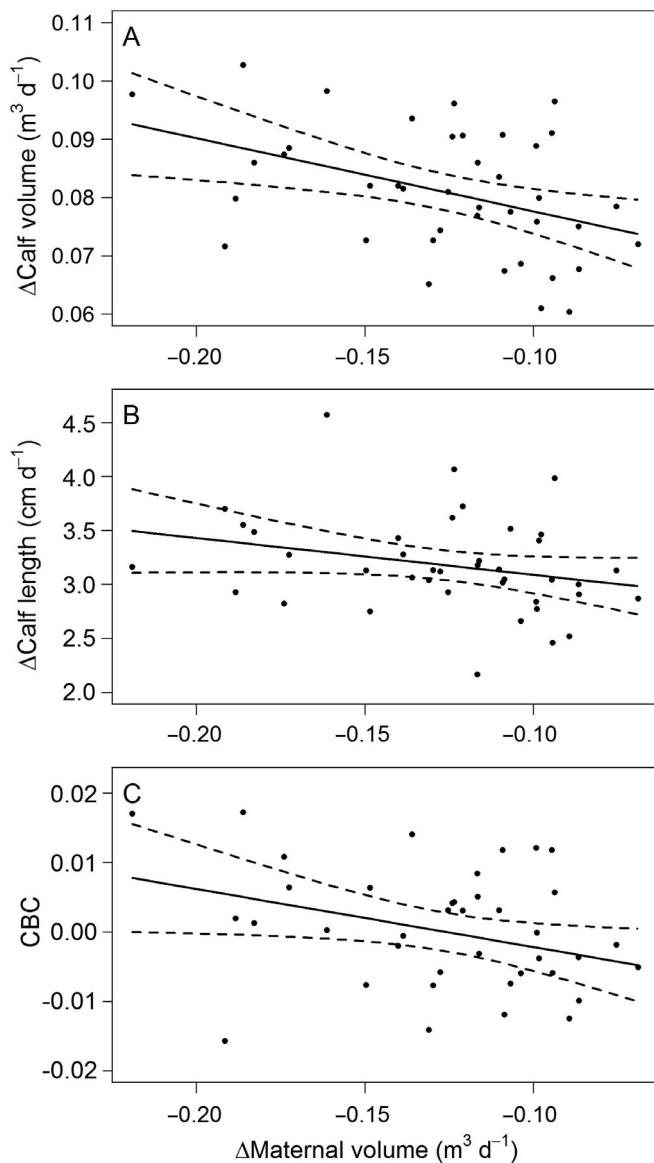
Fig. 5. Effect of maternal rate of loss in body volume on (A) calf growth in body volume, (B) calf growth in body length and (C) calf body condition (CBC). Solid lines represent the fitted values of the linear models; dashed lines represent 95% CI. n = 40 female and calf pairs

these results, calf body condition was negatively related to the rate of change in maternal volume ($F_{1,38} = 4.39$, p = 0.043, $R^2 = 0.104$) (Fig. 5C). The volume conversion efficiency between females and calves ranged from 37.4 to 105.0%, with a mean of 68.0% (SD = 16.91) (Fig. S19). The reproductive history (calves produced, average inter-calving interval and years since last calving event) of known females (n = 25) did not influence the volume conversion efficiency.

Of the measured calves, 13 were sexed by visual examination of the genital region from air. Of these, 7 (53.8%) were female and 6 (46.2%) were male. There was no difference in the growth rates of calves in body volume ($F_{1,11} = 0.85$, p = 0.376, $R^2 = 0.072$) or body length ($F_{1,11} = 1.38$, p = 0.265, $R^2 = 0.112$) and no difference in CBC ($F_{1,11} = 0.10$, p = 0.753, $R^2 = 0.009$) between sexes.

Variables affecting maternal investment in calf

The rate of change in maternal body volume was negatively related to MVB ($F_{1,38} = 21.3$, p < 0.001, $R^2 = 0.360$) (Fig. S20). With MVB being determined by maternal body length and condition, the rate of loss in maternal body volume was significantly affected by both maternal body length ($F_{1,37} = 14.5$, p < 0.001, $R^2 = 0.249$) and FBC ($F_{1,37} = 6.8$, p = 0.013, $R^2 = 0.117$). There was a negative relationship between the rate of change in maternal body volume and maternal body length, with the rate of loss in volume increasing by 0.033 m^3 d^{-1} (SE = 0.0087) for every meter increase in maternal body length (Fig. 6). Similarly, the rate of change in maternal volume was negatively affected by FBC, with the rate of loss in maternal body volume increasing by 0.015 m^3 d^{-1} (SE = 0.0058) for every 10% increase in FBC (Fig. 6). The full model explained 36.6% of the variance in the data, with maternal body length explaining 24.9% of the variance and FBC explaining 11.7%. There was no significant interaction between the 2 explanatory variables in the model.

While the absolute rate of loss in maternal body volume was affected by maternal body length and condition, the relative amount of body volume that the female lost over the 90 d breeding season was unaffected by maternal body length ($F_{1,37} = 0.99$, p = 0.327, $R^2 = 0.026$), condition ($F_{1,37} = 0.20$, p = 0.659, $R^2 = 0.005$) and reproductive history (calves produced, average calving interval, time since last calving event).

Sensitivity analysis

The measurement errors inherent from the UAV system varied with the altitude of the UAV (Fig. S9). Within the altitude range used to measure whales in this study (24.0 and 52.1 m), the measurement error was 0.73 cm (SD = 0.494) (Fig. S9). The COV in measurement error within photographs was estimated to be 0.30 and 0.38% in body length and 2.11 and
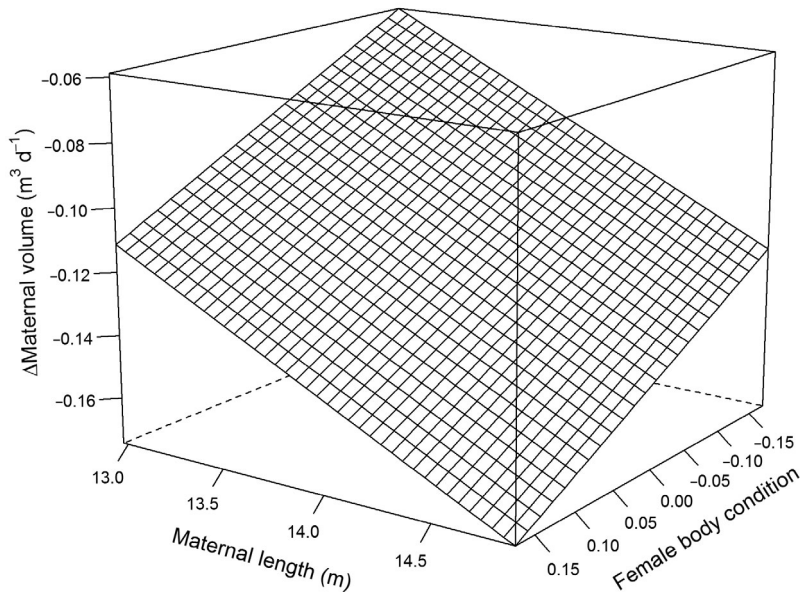
Fig. 6. Rate of loss in maternal body volume as a function of maternal body length and condition. n = 40 lactating females

2.31% in body width for photographs of quality 1 and 2, respectively (Fig. S10). The mean measurement error between photographs of the same whale within the same day was 4.75% (SD = 3.674) for lactating females and 3.11% (SD = 2.206) for calves (Fig. S11). The sensitivity analysis showed that all parameter values were robust to measurement errors (Fig. S12).

DISCUSSION

We investigated the relative cost of lactation in southern right whale females by estimating the loss in maternal body volume over the breeding season in relation to the growth rate of their calves. The positive relationship between calf growth rates and maternal body volume loss strongly suggests that the rate at which a female loses volume is proportional to the amount of energy she invests in her calf. Over the first 3 mo of lactation, females lost around 25% of their body volume. The relative loss in body volume was similar for females of different size and condition, suggesting that each female was investing as much energy as she could afford into her calf. Phocid seals lose between 16 and 42% of their mass during the lactation period (for review, see Bowen et al. 1992), whereas Antarctic fur seals *Arctocephalus gazella*, an otariid, and black bears *Ursus americanus*, a terrestrial capital breeder, transfer about 12 and 21% of maternal body energy into milk, respectively (Oftedal 2000). While the cost of lactation has

never been directly measured in baleen whales, it was indirectly calculated (from mammary gland mass and calf growth over 6 mo) for blue whales to be 32% of maternal energy reserves (Lockyer 1984, Oftedal 2000). If we for simplicity assume that the loss in body volume of southern right whales is proportional to the loss in body mass and energy content, our estimate is similar to these. This highlights the substantial costs that baleen whales face during the lactation period and the importance of a large body size and good maternal condition for the growth and possible survival of their calves. However, care should be taken when comparing different proxies for energy until future studies have managed to establish the relationship between body volume, mass and energy content.

To produce an average-sized (8.2 m, 8.9 m^3) calf over a 3 mo breeding season, a female of average body length (14 m) needs to invest 10.7 m^3 of body volume. For every 1 m^3 growth in calf volume, a female hence needs to invest 1.47 m^3 of her own body volume, which is equal to a volume conversion efficiency of 68%. This rate is similar for phocid seals, which have a mass transfer index ranging from about 45 to 75% (for review, see Bowen et al. 1992). Our estimate, however, also includes changes in volume related to the female's own metabolism, maintenance and growth (Lockyer 2007, Christiansen et al. 2016a). To estimate the cost of lactation alone, the rate of loss in maternal body volume can be compared to that of resting (non-pregnant/non-lactating) adult females. Unfortunately, we only obtained repeated measurements from 2 resting females (Fig. S21 in Supplement 1). Their rate of loss in body volume was 0.042 (SE = 0.023) and 0.070 m^3 d^{-1} (SE = 0.040), which corresponds to 33.2–55.3% of that of lactating females (0.126 m^3 d^{-1}), respectively. While these estimates suggest that lactation adds significantly to the energy expenditure of females, more data are needed to accurately quantify the cost of lactation in southern right whales. Further, differences in activity level between lactating and resting females also must be accounted for.

The rate of decline in body width of lactating southern right whales was highest around the middle and caudal regions of the body, which corresponds well with other studies of right whales (Miller et al. 2012) and also humpback whales (Christiansen et al.

2016a). The fact that the caudal region plays an important role for energy storage has also been reported for minke, fin and sei whales *Balaenoptera borealis* (Lockyer et al. 1985, Lockyer 1987, Christiansen et al. 2013), whereas the head and tail regions of baleen whales serve a structural role (Brodie 1975) as evident from the lack of body width change in those areas. In contrast, calves increased proportionally in width across the length of their bodies as they grew. At birth, southern right whale calves are relatively slender, with their maximum body width (at 25% body length from the rostrum) corresponding to about 17% of their body length. During the first month of their lives, calves grew rapidly in relative body width to about 21% of their body length, after which their relative body width remained constant. This early fattening is likely to have thermoregulatory benefits for the calves, by quickly reducing their surface area to volume ratio. Maternal investment, however, did not influence the growth of calves in body length. The same has been documented for humpback whales (Christiansen et al. 2016a) and suggests that growth in calf body length might be more resilient to reduced maternal condition compared to calf body volume.

Maternal investment was dictated by her absolute body volume at the time of giving birth, which in turn was a function of her absolute size (body length) and relative body condition. Maternal body size is perhaps the most important predictor of reproductive output in mammals (Blueweiss et al. 1978), with the amount of energy a female is able to store in her body generally increasing with her size (Lindstedt & Boyce 1985), while the relative cost of milk production decreases with size (Oftedal 2000), as does her mass-specific metabolic rate (Kleiber 1947). Although body length did not vary much between females in this study (13.0 to 14.9 m), it still had a strong effect on their total body volume and the amount of volume invested in their calves. Because calf growth is determined by the absolute, rather than relative, energy investment of the female, a larger (i.e. longer) female needs to invest less of her relative energy stores to produce a similar-sized calf compared to a smaller female. Larger females will hence be more resilient to stressors, both natural (e.g. prey productivity) and anthropogenic (e.g. disturbance), that could reduce their body condition. For example, a 15 m female would be able to sustain a loss in relative body condition of up to 54% and still be able to invest the minimum amount of volume observed in this study (0.069 m^3 d^{-1}) into her calf, while a 13 m female would only be able to sustain an 11% decrease in body condition.

Females in better condition appeared to invest more energy into their calves compared to females in poorer condition. Similar relationships have been documented in humpback whales (Christiansen et al. 2016a), pinnipeds (Arnbom et al. 1997, Wheatley et al. 2006) and terrestrial mammals (Skogland 1984, Keech et al. 2000). Producing larger calves is likely to bring direct fitness benefits for females, since offspring survival generally increases with size (Lindström 1999, McMahon et al. 2000). Larger calves are faster and stronger and have better breath-holding ability, which may make them less vulnerable to predation. A larger body size will also reduce heat loss in calves, which is beneficial during the southern migration and on the colder, high-latitude feeding grounds. Larger calves are also likely to be more resilient to environmental variability (e.g. periods of food shortages). However, a high energy investment in a calf might result in a future loss in survival and/ or fecundity of the female (Williams 1966). Baleen whales are long-lived iteroparous organisms, which should strive towards maintaining their own survival above that of their offspring to maximize lifetime reproductive success (Lockyer 2007, Christiansen et al. 2016a). A female in poor body condition might therefore reduce the energy investment in her calf to maintain a high maternal survival probability. Lower maternal investment also means that the female will recover her body reserves faster and be able to reproduce again sooner. Finding out where the optimal balance between current and future offspring investment lies will require further research using multi-year data on body condition and calving rates.

While our body volume metric provided a more comprehensive estimate of energy content compared to dorsal surface area (Christiansen et al. 2016a) or body width alone (Durban et al. 2016), it assumed a circular body shape of the whales, which we could not confirm. Although Miller et al. (2012) found no difference in body width measured at 30% body length from the rostrum in free-swimming North Atlantic right whales *Eubalaena glacialis* and calculated diameters from girth measurements on carcasses, this needs to be investigated across the entire body of the animals. Further, while our UAV photogrammetry approach was able to capture changes in the body shape of whales, as a proxy for energy content, it is not able to capture within-tissue variation in energy (i.e. lipid) content. Many baleen whale species show intra-seasonal trends in lipid concentration in their blubber, muscle and other tissues (Lockyer 1986, 1987). In addition to lipids, marine mammals also catabolize some lean tissue while fast-

ing (Houser & Costa 2001). While blubber lipid concentrations should be possible to obtain through biopsy sampling, determining which tissue is being utilized (lean versus adipose tissue) will be more challenging in free-living whales.

Like most baleen whale populations, the Australian southern right whale population was hunted to the brink of extinction by commercial whaling operations during the 19th and early 20th centuries (Dawbin 1986) and illegal Soviet whaling in the 1950s to early 1970s (Yablokov 1994, Tormosov et al. 1998). Although the population in southwestern Australia is recovering at a promising rate (5.55% growth per annum and a population size of about 2200 animals in 2016; Bannister 2016), the species is still listed as endangered in Australia under the Commonwealth Environmental Protection and Biodiversity Conservation Act (DSEWPaC 2012). Right whales around the world continue to face multiple anthropogenic threats, including ship strikes, shipping noise and entanglements in fishing gear (Knowlton et al. 2001, van der Hoop et al. 2017). Monitoring the body condition of right whale populations over time will allow us to better understand the health of populations and how much they fluctuate naturally, so that environmental (e.g. prey productivity) and anthropogenic (e.g. disturbance) effects can be disentangled. Interannual variations in the body condition of southern right whales can also provide valuable information about ocean productivity on their feeding grounds, as an indicator of ocean health (Burek et al. 2008). Finally, this study provides valuable baseline data of the body condition of a healthy right whale population, which serves as a comparison to less healthy populations, such as the North Atlantic right whale, where reproductive failure resulting from malnutrition might be a contributing factor to their slow recovery (Kraus et al. 2001). Further, the high mortality of female North Atlantic right whales has skewed their age range to a significantly lower average age than that of southern right whales (Pace et al. 2017). As a result, many of the North Atlantic females never get pregnant, and those that do will on average be younger than southern right whales. Hence, female North Atlantic right whales will be relatively deprived of the advantage of having a larger body size (both body length and volume), which would lower the relative cost of lactation, as shown in the present study.

Data archive. The data set used in the analyses can be found in Supplement 2 at www.int-res.com/articles/suppl/m592 p267_supp/.

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