Noninvasive unmanned aerial vehicle provides estimates of the energetic cost of reproduction in humpback whales

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Abstract. An animal's body condition will affect its survival and reproductive success, which influences population dynamics. Despite its importance, relatively little is known about the body condition of large whales and its relationship to reproduction. We assessed the body condition of humpback whales (Megaptera novaeangliae) at a breeding/resting ground from aerial photographs recorded using an unmanned aerial vehicle (UAV). Photogrammetry methods were used to measure the surface area of individual whales, which was used as an index for body condition. Repeated measurements of the same individuals were not possible; hence, this study represents a cross-sectional sample of the population. Intraseasonal changes in the body condition of four reproductive classes (calves, immature, mature, and lactating) were investigated to infer the relative energetic cost that each class faces during the breeding season. To better understand the costs of reproduction, we investigated the relationship between female body condition (FBC) and the linear growth and body condition of their dependent calves (CBC). We documented a linear decline in the body condition of mature whales (0.027 m²/d; n = 20) and lactating females (0.032 m²/d; n = 31) throughout the breeding season, while there was no change in body condition of immature whales (n = 51) and calves (n = 32). The significant decline in mature and lactating female’s body condition implies substantial energetic costs for these reproductive classes. In support of this, we found a positive linear relationship between FBC and CBC. This suggests that females in poorer body condition may not have sufficient energy stores to invest as much energy into their offspring as better conditioned females without jeopardizing their own body condition and survival probability. Measurement precision was investigated from repeated measurements of the same animals both from the same and different photographs, and by looking at residual errors in relation to the positioning of the whales in the photographs. The resulting errors were included in a sensitivity analysis to demonstrate that model parameters were robust to measurement errors. Our findings provide strong support for the use of UAVs as a noninvasive tool to measure the body condition of whales and other mammals.

Key words: baleen whales; bioenergetics; body condition; body morphometrics; breeding ground; drones; energy storage; energy transfer; life history; Megaptera novaeangliae; photogrammetry.

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INTRODUCTION

The body condition of animals in a population has important implications for individual survival and reproductive success, and consequently population dynamics. Body condition can be expressed through any physiological index that represents an individual’s energy reserves...
(Hanks 1981, Millar and Hickling 1990). Animals in good body condition generally have larger energy stores and therefore display more resilience and higher survival than individuals in poorer condition (Gaillard et al. 2000, Cook et al. 2004, Clutton-Brock and Sheldon 2010). Body condition is also related to the reproductive success in female mammals, and it influences factors such as the timing of reproduction (Cameron et al. 1993), the probability of conception (Loudon et al. 1983), fertility rates (Albon et al. 1983), fetal growth (Skogland 1984), offspring mass (Atkinson and Ramsay 1995), and calf survival (Festa-Bianchet 1998). The body condition of individuals constituting a population will strongly influence the population dynamics and, in turn, a population’s conservation status (Dobson 1992, Wauters and Dhondt 1995, Sæther 1997).

For capital breeding animals, where the costs of reproduction are met by endogenous energy stores during a period of fasting (Stephens et al. 2009), the link between body condition and reproduction is particularly strong (Festa-Bianchet et al. 1998, Bonnet et al. 2002). Baleen whales (mysticetes) are considered capital breeders because they finance the costs of reproduction in low-latitude breeding grounds with stored energy acquired at high-latitude feeding grounds (Lockyer 1987a, Kasuya 1995). A large body energy storage is a necessity for baleen whales as energy stores constitute the primary source of energy during the breeding season, when whales migrate to less productive equatorial waters (Lockyer 2007). Maternal body condition in baleen whales influences fecundity (Lockyer 2007, Williams et al. 2013) and fetal development (Lockyer 2007, Christiansen et al. 2014). Although not documented for baleen whales, maternal body condition in other marine mammals, such as pinnipeds, influences offspring birth and weaning mass (Boltnev and York 2001, Bowen et al. 2001), which, in turn, influences offspring survival (McMahon et al. 2000).

Much of the stored energy in baleen whales can be found in the muscle and adipose tissue (blubber and visceral fat), although a considerable amount is also stored in internal organs, bones, and other tissues (Lockyer 1986, 1987b, Vikingsson 1995, Næss et al. 1998, Miller et al. 2011, Christiansen et al. 2013). Several of these body tissues have been used as proxies for body condition in studies on baleen whale bioenergetics, including lipid concentration (Aguilar and Borrell 1990, Næss et al. 1998), blubber thickness and volume (Vikingsson 1990, Miller et al. 2011, Christiansen et al. 2013), and weight of different organs and tissues (Lockyer 1987b, Vikingsson 1995). However, a more commonly used metric for body condition in whales is body girth (Lockyer 1987b, Vikingsson 1990, Haug et al. 2002) or width (Perryman and Lynn 2002, Miller et al. 2012), which encompasses several of these tissues and, hence, provides a more holistic measure of body condition. Variation in girth and width in relation to prey abundance, seasonal fasting, feeding, and reproductive status has been measured in a number of baleen whale species, including minke (Balaenoptera acutorostrata), fin (Balaenoptera physalus), gray (Eschrichtius robustus), and right whales (Eubalaena sp.; Lockyer 1986, 1987a, b, Ichii et al. 1998, Næss et al. 1998, Haug et al. 2002, Perryman and Lynn 2002, Miller et al. 2012). These studies highlight that body girth and width measurements provide a reliable and good measure of body condition in baleen whales.

For migratory baleen whales, the temporal segregation between feeding and breeding is often reflected as seasonal changes in body condition, with an increase during the summer feeding season and a decrease during the winter breeding season (Lockyer 1987b, Vikingsson 1990, 1995, Næss et al. 1998, Konishi et al. 2008, Christiansen et al. 2013). Comparison of intraseasonal trends in body condition between different reproductive classes can provide valuable insights into the relative rates of energy acquisition and expenditure at different time periods. This includes variations in energy expenditure at different stages in their reproductive cycle (e.g., early and late gestation, and lactation; Lockyer 1986, Pettis et al. 2004, Miller et al. 2011, 2012). The strong relationship between energy storage and reproduction in baleen whales (Lockyer 1987a, Williams et al. 2013, Christiansen et al. 2014) makes it possible to estimate the energetic costs of reproduction by investigating the rate of decline in the body condition of a population throughout the breeding season, when whales are fasting. The cost of reproduction is one of the main drivers of the life history of species (Stearns 1992) and is a key component in any study attempting to
understand the bioenergetics of baleen whales (Lockyer 2007).

While several studies have shown that pregnant and lactating females both acquire and expend more energy than most other reproductive classes (Lockyer 1987a, b, Vikingsson 1990, 1995, Miller et al. 2012, Christiansen et al. 2013), relatively little is known about the direct relationship between female body condition and reproductive success in baleen whales. Lockyer (1987a) and Williams et al. (2013) reported that fecundity in fin whales was related to yearly variations in maternal body condition. In addition, Christiansen et al. (2014) documented that fetal growth was significantly affected by the relative body condition of females in minke whales. However, little is known about the relationship between maternal body condition and the growth, condition, and survival of their offspring postparturitions. Studies on pinnipeds highlight that the size of an offspring at birth and at weaning will strongly influence its survival probability (Boltnev et al. 1998, McMahon et al. 2000). Understanding how female body condition influences calf development and survival in baleen whales is therefore fundamental for our understanding of reproductive physiology and life history.

During every austral winter and spring, between May and November, humpback whales (Megaptera novaeangliae) from breeding stock D in the Southern Hemisphere migrate north from their summer feeding grounds in Antarctica (~56° S), along the Western Australian coastline to their tropical breeding grounds around Camden Sound (~15° S) in the Kimberley region (Chittleborough 1965, Jenner et al. 2001, Gales et al. 2010). Like most populations of large whales, breeding stock D was severely depleted through unsustainable whaling practices in the last century (Chittleborough 1965, Gibbs 2012). Following the cessation of whaling of humpback whales in the Southern Hemisphere in 1963, breeding stock D experienced a remarkable recovery of >10% increase per year (Hedley et al. 2011, Kent et al. 2012) and has almost rebounded to pre-exploitation numbers (>30,000 animals, Hedley et al. 2011, Bejder et al. 2016). As the population size approaches its carrying capacity (Braithwaite et al. 2012), density-dependent effect on body condition and reproduction is expected (Albon et al. 1983, Sæther 1997, Stewart et al. 2005). With the humpback whale being an important top predator, a better understanding of their body condition and its link to reproduction is fundamental to better understand the potential effects that these recovering populations will have on ecosystems in the coming decades.

The aims of this study therefore were to: (1) investigate intraseasonal variation in the body condition of four reproductive classes of humpback whales off northwestern Australia during the breeding season in order to determine the relative energetic costs that the different classes face; and (2) understand the relationship between the body condition of lactating females and the growth and condition of their dependent calves, to improve our understanding of the link between body condition and reproduction in baleen whales. To answer these questions, we used novel unmanned aerial vehicle (UAV) technology and photogrammetry methods to measure the body condition of individual whales. This is the first time that noninvasive methods have been applied to assess body condition within the family balaenopteridae, with this study also providing a feasibility study for this approach on free-ranging humpback whales.

**Methods**

**Study area**

Exmouth Gulf is located at the southern end of the breeding ground for stock D on the northwest shelf of Australia, between 21°45′ S–22°33′ S and 114°08′ E–114°40′ E (Fig. 1). The Gulf is approximately 3000 km² in size, with a mean depth of <20 m. Exmouth Gulf serves as an important breeding and resting area for breeding stock D humpback whales on their southwards migration returning from Camden Sound to their Antarctic feeding grounds (Jenner et al. 2001). While whales start to arrive in the Gulf in July during the northern migration, most of the whales enter the Gulf during the southern migration between late August and late October (Chittleborough 1953, Jenner et al. 2001). This time period corresponds to when the majority of calves are born, with the Gulf believed to serve as an important resting and nursing area for the whales. While females with calves can stay inside the Gulf for up to two weeks before continuing
their southern migration, mature males can remain for almost a month in search for females to mate with (Jenner and Jenner 2005). While in the Gulf, females with calves generally maintain a low level of activity at or near the surface, while mature males actively search and compete for females. This, together with calm weather conditions, allows the Gulf to act as an ideal site for UAV-based fieldwork on humpback whales.

**Sampling protocol**

All research was carried out under a research permit from the Department of Parks and Wildlife, Western Australia (SF010372), and an animal ethics permit from Murdoch University (R2736/15). The former permit allowed for a total of 200 whales to be sampled. The UAV was operated under a UAV Operator Certificate (CASA. UOC.0136) and a Remotely Piloted Aircraft System Licence in accordance with regulations by the Australian Civil Aviation Safety Authority.

Vertical aerial photographs of humpback whales were taken in Exmouth Gulf in August and September 2015. A 5.5-m research vessel surveyed the Gulf haphazardly in search of whales (Fig. 1). The boat was launched from either the town of Exmouth or the Learmonth Jetty, next to Learmonth airport (Fig. 1). Once a single or a group of whales were sighted, the boat approached to a distance of 100–300 m at idle speed. A small (50 cm diameter, 1.2 kg) water-proof “Splashdrone” quadcopter (www.swellpro.com) was deployed from a custom-made helipad at the bow of the boat and flown above the whales. Calibration of the gyro sensors of the UAV was made on land prior to launching the boat, and a dual battery system was used to keep the volatile memory of the gyro offsets throughout the day by not having to power down the UAV when switching batteries between consecutive flights. The UAV had a flight time of 8–10 min and could operate up to 1 km from the launch site. The distance between the UAV and the boat was usually kept to less than 300 m to provide a clear line of sight of the UAV and to facilitate positioning over the whales (also with a live video link—see below). The UAV was equipped with a Canon PowerShot D30 (Canon Inc., Tokyo, Japan) still camera, which took photographs at 2-s intervals, and a GoPro Hero4 (GoPro Inc., San Mateo, California, USA) continuously recording video. Both cameras were mounted vertically under the UAV. Typically, the UAV remained about 5 min above a whale resulting in, on average, 150 still images per individual. The UAV was initially flown at an altitude of 30–50 m, to obtain close-up photographs of the whale's body shape. A live video link, providing the UAV operator with direct feed from the GoPro camera, was used to correct the position of the UAV above the whale and also confirm that photographs of adequate quality had been obtained. Desired photographs were of a whale lying flat at the surface, dorsal side facing up, with a straight body axis and peduncle (that was nonarching; Fig. 2). The UAV was then flown to an altitude of 80–120 m, while the research vessel moved closer to the whale until both the whale and the boat were visible in the same photograph. The size of the research vessel was then used to scale the photograph (similar to Whitehead and Payne 1978). Once the scale photograph had been obtained, the UAV returned to the research boat and landed safely in the water.

**Morphometric measurements and scaling**

Photogrammetric methods were used to extract several morphometric measurements from the vertical close-up photographs of the whales.
CHRISTIANSEN ET AL.

(Fig. 2; Best and Rüther 1992, Perryman and Lynn 2002, Cosens and Blouw 2003, Miller et al. 2012), using a custom-written script in R (R Core Team 2014; Appendix S1 and Data S1). Length measurements (in pixels) included distance from the tip of the rostrum to: the notch of the tail fluke; the end of the dorsal fin; the position of the eyes (measured along the body axis of the whale); the beginning of the tail fluke (Fig. 2). The width of the whale (in pixels), measured perpendicular to the body axis, was measured at 5% intervals along the entire body of the whale, not including 0 and 100% of the body length (19 measurements in total), and also between the eyes. The relative measurements of the whale (in pixels) were converted to absolute measurements (in cm), using the scale photographs obtained for each animal.

Identification and classification of whales

Individual humpback whales were identified from the shape of their dorsal fin (Katona and Whitehead 1981), which were photographed from the research boat using a Nikon D300 camera with a 400-mm lens (Nikon Inc., Tokyo, Japan). Individual whales were classified into one of four reproductive classes: calves, immature, mature, and lactating whales. Calves and lactating females were classified based on their close and consistent association with each other. Immature and mature whales were separated based on their length, as sexual maturity in baleen whales can be determined by length rather than age (Sigurjónsson et al. 1990). From histological examination of testes from humpback whales from breeding stock D, Chittleborough (1955a) reported that the length of males at puberty

Fig. 2. (A) An example of desired aerial photograph of humpback whales captured by a unmanned aerial vehicle that was used in analyses. The whale is lying flat at the surface, dorsal side facing up, with a straight body axis and peduncle (nonarching). (B) Position of measurement sites of humpback whales recorded in this study. For clarity, only width (W) measurement sites located at 10% increments along the body axis are shown.
ranged from 10.15 to 12.44 m with a mean length of 11.20 m. From examinations of females captured during their first estrous cycle, Chittleborough (1955b) demonstrated that females at puberty ranged in size from 10.73 to 13.26 m, with a mean length of 11.73 m. Therefore, based on these estimates, a threshold length value of 11.2 m was used to separate immature whales from mature animals. In regard to sex determination, apart from lactating females the sex of individual whales was unknown.

Body site-specific changes in width

Intraseasonal changes in the body condition of baleen whales are not exhibited homogenously across the body of the animal, and the pattern of variability appears to be species specific (Vikingsson 1990, Folkow and Blix 1992, Naess et al. 1998, Miller et al. 2012, Christiansen et al. 2013). To assess which width measurements best capture intraseasonal changes in the body condition of humpback whales, we developed linear models (LMs) in R to test the effect of day (measured as Julian day) and length on each width measurement. Both linear and polynomial nonlinear models were developed to test the relationship between the dependent and independent variables. Comparison of model fit was made using Akaike’s information criterion (AIC). Separate models were developed for each reproductive class to explore whether variation in body condition varied between reproductive classes.

Body condition index

With the aim to develop a body condition index (BCI) that would capture the variation in width across the body of the humpback whales, we calculated the flat dorsal surface area for each individual (the area as seen from above) from the body morphometric data. The flat surface area of the body of the whales was modeled as a series of trapezoids connected to each other at each width measurement site. The surface area (m²) for each trapezoid segment, \(A_s\), was calculated:

\[
A_s = \frac{h}{2} \times (a+b)
\]

where \(a\) is the width (m) of the base (i.e., the anterior width measurement) and \(b\) is the width (m) of the top (i.e., the posterior width measurement) and \(h\) is the distance (i.e., length, m) between the two width measurements along the body axis of the animal. Because the head, fins, and tail fluke of cetaceans contain relatively little energy reserves (Brodie 1975, Koopman 1998), only segments \(s\) between the position of the eyes down to 80% of the body length from the rostrum were included in the BCI (i.e., surface area) (m²) estimate:

\[
BCI = \sum_{s=1}^{S} A_s
\]

where \(S\) is the total number of segments \(s\) between the position of the eyes and 80% of the body length from the rostrum. This quantitative index of body condition accounted for variation in width across the body of the whales and how it changed throughout the breeding season. A generalized additive model (GAM) with a thin plate regression spline smoother was used to investigate whether the size of the head in relation to total body length changed with respect to the length of the whale.

Intraseasonal changes in body condition

Linear models were developed to investigate intraseasonal changes in BCI of humpback whales for the four reproductive classes. In addition to day (Julian day) and reproductive class, length was included as a covariate to account for difference in the structural size between individuals, which will influence BCI (i.e., surface area). In the model selection process, covariates and interactions between covariates were added sequentially to the null model and different polynomial nonlinear factors were used to test the relationship between the dependent and independent variables. As above, model selection was made using AIC.

Effects of female body condition on calf condition and growth

From the best fitting model of BCI, the relative body condition of calves (CBC) was estimated as (Christiansen et al. 2014):

\[
CBC_i = \frac{BCI_{C,Obs,i} - BCI_{C,Exp,i}}{BCI_{C,Exp,i}} = \frac{\varepsilon_{C,i}}{BCI_{C,Exp,i}}
\]

where \(BCI_{C,Obs,i}\) is the observed BCI (i.e., surface area) of calf \(i\) (m²) and \(BCI_{C,Exp,i}\) is the expected (or predicted) BCI of a calf of the same length and at the same day in the season. A positive value of
CBC suggests that the calf was considered to be in a relatively better condition than an average calf, while a negative CBC value suggests that it was considered to be in a relatively poorer condition. The CBCs were compared to the relative body condition of their mothers (female body condition, FBC; Christiansen et al. 2014):

\[
FBC_i = \frac{BCI_{F,\text{Obs},i} - BCI_{F,\text{Exp},i}}{BCI_{F,\text{Exp},i}} = \frac{\epsilon_{F,i}}{BCI_{F,\text{Exp},i}}
\]

where \( BCI_{F,\text{Obs},i} \) and \( BCI_{F,\text{Exp},i} \) are the observed BCI and expected BCI (i.e., surface area) of the mother of calf \( i \) (m\(^3\)) at the same day in the season, respectively. Again, a positive value of FBC means that the mother was considered to be in a relatively better condition than the average mother, while a negative FBC value suggests that the mother was considered to be in a relatively poorer condition. LMs were then developed to investigate the effect of FBC on CBC (similar to Christiansen et al. 2014).

The effect of FBC on calf growth (i.e., length) was investigated using LMs. To account for the growth of calves through the breeding season, day (Julian day) was included as a covariate in the model. The effect of maternal size (i.e., length) was also assessed, as maternal length is often positively correlated to offspring size in mammals, including whales (Kovacs and Lavigne 1986, Best and Rüther 1992, Boltnev and York 2001, Perryman and Lynn 2002). Again, both linear and polynomial nonlinear relationships between calf length and maternal length were investigated and the best fitting model was selected using AIC.

**Model validation**

For all models, model validation tests were run to identify potential violations of the assumptions of the models. Homogeneity of variances was investigated from scatter plots of residuals vs. fitted values and residuals against each explanatory variable in the model. Normality of residuals was interpreted from quantile–quantile plots and from residual histograms. Influential points and outliers were identified using leverage and Cook’s distance. All model assumptions were fulfilled.

**Sensitivity analysis**

When measuring body morphometrics from aerial photographs, a number of potential measurement errors related to picture quality, measurement precision, and image distortion need to be investigated and, if necessary, accounted for.

To obtain accurate measurements of the body condition of the whales, the contour of the animal’s body in the water needs to be clearly visible in the photographs. Waves, water spray, and turbidity can distort the body contour in a photograph, resulting in a reduction in the accuracy of body morphometric measurements. Measurement precision within photographs was assessed by having three independent researchers measure the body morphometrics of the same whale from the same photograph. From these measurements, the coefficient of variation (COV) in “relative” body condition (the surface area in pixels) of each animal was calculated. To obtain a measure of accuracy of the “absolute” body condition (the surface area in m\(^2\)), measurement errors relating to the scaling of the photographs (the conversion from pixels to m\(^2\)) were also quantified. Again, three independent researchers scaled the same photograph for each whale, and the COV in “absolute” body condition was calculated. To minimize the risk of measurement errors affecting the body condition analyses, an upper threshold value of 0.05 was chosen for both COV values, with animals above this threshold being excluded from the main analyses.

To further investigate the effect of measurement errors, a sensitivity analysis was carried out to quantify the effect of measurement errors on the day parameter values (the intraseasonal effect) of the best fitting model. One thousand bootstrap iterations were run. For each of the iterations and for each individual, a random body condition value was drawn from a Gaussian distribution with the mean equal to the body condition of the individual and the standard deviation being estimated from the COV in “absolute” body condition (the surface area in m\(^2\)). The resulting density distributions of the day parameters and their associated standard errors (SEs) were visually examined to investigate the robustness of the model results to within-photographs measurement errors.

Depending on how the whale was positioned in the water (the degree of arcing or curving of the body), BCI (i.e., surface area) can be either positively or negatively biased. Similar to Perryman
and Lynn (2002), measurement precision (differences between repeated measurements of the same individual from different photographs) was assessed by calculating the COV for five whales that had each been photographed at least three times during the same encounter. From each photograph, the body condition of the whale was estimated, resulting in three independent body condition measurements of the same whale from different photographs. Subsequently, the COV in body condition for each of the five whales was then calculated. Based on this estimate, a sensitivity analysis was carried out to test the effect of between-photographs measurement errors on the day parameter estimates of the best fitting model. One thousand bootstrap iterations were run. Again, for each model iteration and for each individual, a random body condition value was drawn from a Gaussian distribution with the mean being equal to the body condition of the individual and the standard deviation being calculated from the COV in body condition resulting from the between-photographs measurement errors. The effect on the day parameter values of the best fitting model was visually examined from density distribution plots.

Potential measurement errors resulting from the positioning of the whale in the photograph (i.e., the distance from the midpoint of the photograph frame) was investigated by plotting the residuals of the best fitting model against its spatial coordinates (X and Y pixels) in the photograph.

**Results**

A total of 200 humpback whales were photographed vertically by the UAV in Exmouth Gulf between 3 August and 16 September 2015 (Fig. 1). Over this 44-d period, we spent 26 d on the water, equaling 186 h of research effort (Fig. 1). After initial filtering of photographs based on body position (removing laterally curved, arched, and animals rolling on their side) and picture quality (Appendix S2: Fig. S1), 134 animals remained for analyses’ purposes. This included 32 calves (body length [m]: mean = 5.64, SD = 0.81, min = 4.14, max = 7.76), 51 immature (body length [m]: mean = 9.74, SD = 0.85, min = 7.96, max = 10.95), 20 mature (body length [m]: mean = 11.86, SD = 0.81, min = 11.20, max = 14.42), and 31 lactating females (body length [m]: mean = 12.20, SD = 0.98, min = 10.77, max = 14.73) (Appendix S2: Fig. S2). Photograph identification records indicated that no individual was measured more than once during the study period. Hence, the body condition data represent a cross-sectional sample of the population and not repeated measurements of the same individuals. We did not observe any visual behavioral responses of the whales toward the UAV.

**Body site-specific changes in width**

The change in body width of humpback whales through the study period varied between measurement sites and also between reproductive classes. While calves and immature whales showed no intraseasonal change in body width, mature and lactating whales showed a decrease in width at a number of measurement sites (Fig. 3). For mature whales, the decrease was highest around 50–65% of the body length from the rostrum, while lactating females showed a decrease in width over a larger portion of their body, between 35% and 80% of the body length from the rostrum (Fig. 3). The proportional size of the head of humpback whales increased nonlinearly with the length of the animals ($F_{5,51,127.49} = 37.75$, $P < 0.001$, $R^2 = 66.8%$, $n = 134$), from 20% as calves (4–6 m body length) to 25% as late immatures/matures (>10 m body length) (Appendix S2: Fig. S3). As expected, the head of the whales showed no intraseasonal variation in width for any of the reproductive classes (Fig. 3). Similarly, the lower section of the peduncle (>80%) showed no significant change in width over the season.

**Intraseasonal changes in body condition**

Whale length, reproductive class, and the interaction between reproductive class and day explained 98.7% ($R^2$) of the variance in BCI (Model 9 in Table 1). Most of this variance was explained by length (98.1%), while the remaining 0.6% was explained by reproductive class (52.4%) and the interaction term (47.6%). The effect of length on BCI was best explained by a quadratic polynomial relationship ($F_{2,124} = 4712.1$, $P < 0.001$) (Appendix S2: Fig. S4). The overall body condition of humpback whales varied between reproductive classes ($F_{3,124} = 10.6$, $P < 0.001$), with calves having the smallest BCI (mean = 3.05 m$^2$, SD = 0.97, min = 1.58, max = 5.77), followed by
immature (mean = 7.98 m$^2$, SD = 1.36, min = 5.62, max = 10.31), mature (mean = 12.03 m$^2$, SD = 1.69, min = 9.90, max = 17.25), and finally lactating whales (mean = 12.64 m$^2$, SD = 1.76, min = 9.62, max = 16.74). The effect of day (intraseasonal effect) on BCI varied between reproductive classes ($F_{4,124} = 7.2, P < 0.001$) (Fig. 4). Similar to the site-specific changes in width, only mature and lactating whales showed a change in their BCI over the study period, while calves and immature whales showed no intraseasonal variation in BCI. Mature whales showed a decrease in BCI at a rate of 0.027 m$^2$/d (SE = 0.0083), while lactating females showed a decrease in BCI at a rate of 0.032 m$^2$/d (SE = 0.0076) (Fig. 4). The rate of change in BCI varied significantly between mature whales and lactating females ($t = -4.2, P < 0.001$).

Effects of female body condition on calf condition and growth

There was a positive linear relationship between FBC and CBC ($F_{1,22} = 4.5, P = 0.044$), with calves increasing in body condition at a rate of 0.594 m$^2$ (SE = 0.2786) per m$^2$ increase in FBC (Fig. 5). FBC explained 17.1% ($R^2$) of the variance in CBC. The lengths of the calves were affected by maternal length ($F_{1,21} = 22.0, P < 0.001$) and day ($F_{1,21} = 11.4, P = 0.003$) (Model 4 in Table 2). The model explained 61.4% of the variance in calf body length, with maternal length explaining 40.4% and day 21.0%. Calves showed an increase in length at a rate of 0.033 m/d (SE = 0.0097) through the study period and it was positively related to the size of their mothers, with calves increasing in length at a rate of 0.456 m (SE = 0.1005) per m increase in maternal length (Fig. 6). FBC had no effect on calf length (Models 3, 6, 7, 8, 9 in Table 2).

Sensitivity analysis

The day parameter values estimated from the bootstrapping procedure were relatively narrow in their distribution both within (Fig. 7) and between (Fig. 8) photographs. The residuals of the best fitting model (Model 9 in Table 1) showed no signs of spatial autocorrelation (spatial dependence) between data points (Appendix S2: Fig. S5). Finally, altering the body length threshold (to separate immature whales from...
mature whales) between 10.2 and 12.2 m (1 m below and above the chosen threshold value of 11.2 m, respectively) did not significantly affect the day parameter estimates (Appendix S2: Fig. S6).

**Discussion**

**Intrasessional changes in body condition**

The aim of this study was to investigate intraseasonal variation in the body condition of different reproductive classes of humpback whales. Because we were unable to make repeated measurements of the same individuals, this study represents a cross-sectional sample of the body condition of the population. We documented that the body condition of mature and lactating whales decreased significantly through the breeding season, while there was no change in the body condition of immature whales and calves. Similar differences in energy storage between reproductive classes have been documented in minke whales, fin whales, and right whales and are likely to reflect differences in energetic costs during the breeding season (Lockyer 1986, 1987b, Vikingsson 1990, 1995, Miller et al. 2012, Christiansen et al. 2013). In contrast, immature whales do not carry the added energetic costs of reproduction; however, they still rely on stored energy to support the costs of migration, daily field metabolic rates, growth, and body maintenance. As suggested by Miller et al. (2011), intraseasonal variation in the body condition of immature whales may not be detectable as they might rely on stored lipids in their blubber and other tissues to support the energetic costs during the breeding season. A decrease in lipid concentration would not necessarily be visible in the body shape (i.e., width) of the whales (Christiansen et al. 2013) and could therefore be a limitation when using photogrammetry methods to assess body condition.

The rate of decline in body condition was greater for lactating females than for other mature whales. Lactation is considered the energetically most costly part of the reproductive cycle in mammals (Gittleman and Thompson 1988), including large whales (Lockyer 1981), and to cover these high costs, pregnant females build up larger energy stores than any other reproductive class during the summer feeding season (Christiansen et al. 2013). As a consequence, pregnant whales early in the breeding season generally have the greatest body condition, while lactating females late in the breeding season...
season have the poorest body condition (Lockyer 1987a, Aguilar and Borrell 1990, Perryman and Lynn 2002, Miller et al. 2011, 2012). The high rate of decline in the body condition of lactating females in this study suggests that this is also the case for humpback whales.

That mature whales decreased significantly in BCI through the breeding season suggest that the energetic costs of reproduction were relatively high for this reproductive class. Catch data from Western Australia suggest that the majority of migrating mature (nonlactating) whales are males (Chittleborough 1965). Consequently, the cost of reproduction for male humpback whales is relatively high. High reproductive costs for mature males have been documented in mammalian species exhibiting female defense or scramble competition mating systems (Forsyth et al. 2005, Lane et al. 2010). On breeding grounds, male humpback whales actively compete for females where they physically fight and display aggressive behaviors toward each other in order to gain access to receptive females (Baker and Herman 1984). Such behaviors are likely to be energetically costly and could explain the observed difference in intraseasonal trends in body condition between mature and immature whales.

Some of the observed differences in absolute body condition (the intercepts in Fig. 4)
between reproductive classes are likely due to differences in the timing of migration. During the northern migration from Antarctica to the Kimberley region, immature whales and lactating females with calves born the previous year are the first to arrive, followed by anestrous females, mature males, and finally pregnant females (Chittleborough 1965). During the southern migration, the order is more or less the same, with immature whales arriving first, followed by mature whales and finally lactating females whom have recently given birth. At the time whales enter Exmouth Gulf, immature and mature whales should therefore have a relatively lower body condition compared with lactating females. This difference in timing of migration must be accounted for when calculating the absolute costs of migration and reproduction for different reproductive classes of whales (Christiansen et al. 2013). Measuring the body condition of humpback whales at different locations along their migratory route would help to further distinguish intraseasonal changes in body condition from potential differences caused by variation in the timing of migration between individuals and reproductive classes.

The decline in body condition for mature and lactating humpback whales was highest around the mid- and caudal regions of the body. In balaenopterids, the posterior region of the body plays an important role in energy storage (Lockyer 1987b, Næss et al. 1998, Christiansen et al. 2013). Næss et al. (1998) showed that during the feeding season the blubber thickness and

Table 2. Linear model selection results based on minimization of Akaike's information criterion (AIC) for humpback whale calf length.

<table>
<thead>
<tr>
<th>Model</th>
<th>Variables</th>
<th>$F$ (among)</th>
<th>$df$ (within)</th>
<th>$P$</th>
<th>$R^2$</th>
<th>AIC</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>CL ~ Day</td>
<td>6.7</td>
<td>1</td>
<td>22</td>
<td>0.0165</td>
<td>0.23</td>
<td>51.2</td>
</tr>
<tr>
<td>2</td>
<td>CL ~ Maternal length</td>
<td>14.9</td>
<td>1</td>
<td>22</td>
<td>0.0008</td>
<td>0.40</td>
<td>45.2</td>
</tr>
<tr>
<td>3</td>
<td>CL ~ FBC</td>
<td>0.0</td>
<td>1</td>
<td>22</td>
<td>0.9361</td>
<td>0.00</td>
<td>57.6</td>
</tr>
<tr>
<td>4</td>
<td>CL ~ Maternal length + Day†</td>
<td>16.7</td>
<td>2</td>
<td>21</td>
<td>&lt;0.0001</td>
<td>0.61</td>
<td>36.8</td>
</tr>
<tr>
<td>5</td>
<td>CL ~ Maternal length × Day</td>
<td>11.1</td>
<td>3</td>
<td>20</td>
<td>0.0002</td>
<td>0.62</td>
<td>38.0</td>
</tr>
<tr>
<td>6</td>
<td>CL ~ Maternal length × Day + FBC</td>
<td>10.6</td>
<td>3</td>
<td>20</td>
<td>0.0002</td>
<td>0.61</td>
<td>38.7</td>
</tr>
<tr>
<td>7</td>
<td>CL ~ Maternal length × Day + FBC</td>
<td>7.9</td>
<td>4</td>
<td>19</td>
<td>0.0006</td>
<td>0.63</td>
<td>40.0</td>
</tr>
<tr>
<td>8</td>
<td>CL ~ Maternal length × Day × FBC</td>
<td>8.1</td>
<td>4</td>
<td>19</td>
<td>0.0006</td>
<td>0.63</td>
<td>39.7</td>
</tr>
<tr>
<td>9</td>
<td>CL ~ Maternal length × Day × FBC</td>
<td>5.9</td>
<td>7</td>
<td>16</td>
<td>0.0016</td>
<td>0.72</td>
<td>38.9</td>
</tr>
</tbody>
</table>

Notes: Variable abbreviations: calf length (CL), Julian day (day), female body condition (FBC).
† The most parsimonious model (Model 4).

Fig. 6. Partial effect plots of calf length as a function of (A) maternal length and (B) day. The dashed lines represent 95% confidence intervals. In the left subfigure (A), day has been fixed at 240 (August 28), and in the right subfigure (B), length has been fixed at the mean length of lactating females (12.20 m). $n = 24.$
Fig. 7. Sensitivity analysis of within-photographs measurement errors showing the density distribution of the day parameter values (slope parameter) and their associated standard errors (SEs) for the best fitting model (Model 9 in Table 1) based on 1000 bootstrapping iterations. For each iteration and individual, a random body condition value was drawn from a distribution of values with the mean equivalent to the mean body condition of the individual and the standard deviation resulting from three independent body condition measurements (from the same photograph) for each whale. \( n = 134 \).

Fig. 8. Sensitivity analysis of between-photographs measurement errors showing the density distribution of the day parameter values (slope parameter) and their associated standard errors (SEs) for the best fitting model (Model 9 in Table 1) based on 1000 bootstrapping iterations. For each iteration and individual, a random body condition value was drawn from a distribution of values with the mean equivalent to the mean body condition of the individual and the standard deviation resulting from three independent body condition measurements (from three different photographs) from five whales. \( n = 5 \).
lipid content of minke whales increased the most at the caudal region of the body, just behind the dorsal fin (the posterior end of the dorsal fin of humpback whales in this study was located at ~70% of the body length from the rostrum). Christiansen et al. (2013) further confirmed that blubber deposition for both mature and pregnant minke whales was highest toward the posterior end of the body. Similarly in fin and sei whales (*Balaenoptera borealis*), Lockyer (1987b) reported that the caudal region posterior to the dorsal fin serves as the main area of lipid storage in both the blubber and muscle. While our findings demonstrate a significant decrease in body width in the caudal region for mature and lactating whales, the lower tail region of the whales (>80% of body length from the rostrum) showed no pronounced variation in width, which suggests that this region might play a more structural role in humpback whales, by providing aid during locomotion and streamlining the caudal body (Koopman et al. 1996, 2002, Struntz et al. 2004). Lactating females showed a decrease in width along a larger portion of their body (35–80%) compared with mature whales (50–65%). This is similar to lactating southern right whales, which displayed the highest decrease in width between 40% and 80% of the body length from the rostrum (Miller et al. 2012). Similarly, Perryman and Lynn (2002) found that the widest part of the body of pregnant and early lactating gray whales was located further back than that of other reproductive classes. We found that by modeling BCI as the surface area of humpback whales, this across body variation in width could be captured by a single metric of body condition. This, in turn, made it relatively easy to test the effect of different covariates on body condition, using standard statistical methods in ecology. We therefore highly recommend this single metric approach when studying the body condition of baleen whales.

**Effects of female body condition on calf condition and growth**

Newly born calves on the breeding grounds need to grow in size and build up a sufficiently thick blubber layer to survive the migration back to the feeding grounds in cold polar waters (Corkeron and Connor 1999). We documented a significant positive relationship between FBC and the condition of their calves. The iteroparous nature of baleen whales and the high costs of lactation (Lockyer 1981) suggests that female humpback whales with insufficient energy reserves should reduce their energetic investment into their offspring, by producing smaller (i.e., shorter) or poorer conditioned calves, to maintain their survival (Peacock 1991, Pontier et al. 1993, Lockyer 2007, Christiansen et al. 2014). Our results support this hypothesis and are further strengthened by the findings of Christiansen et al. (2014) who found that pregnant minke whales in poorer body condition reduced their energetic investment in their fetus proportionately to their own body condition. Thus, it would appear that female baleen whales throughout both gestation and lactation will prioritize their own body condition and survival, above that of their offspring, which is consistent with a K-strategist life history (MacArthur and Wilson 1967).

While the length of humpback whale calves increased throughout the breeding season, as expected, their BCI showed no intraseasonal variation. This was surprising, given that calves are born with relatively low fat reserves and need to accumulate these as quickly as possible to reduce heat loss. The BCI of calves increased with body length, meaning that the surface to volume area and therefore heat loss should decrease as the calf grows bigger. The best strategy for calves to reduce heat loss might therefore be to invest their excess energy into growth (i.e., length) rather than fat reserves, so that they can become larger overall and reduce their surface to volume area. While we found a positive relationship between maternal length and the length of the calves, which has also been found in other mammals (Skogland 1984, Kovacs and Lavigne 1986, Boltnev and York 2001, Lockyer 2007), including baleen whales (Best and Rüther 1992, Perryman and Lynn 2002), we found no significant relationship between FBC and calf length. Instead, females in better condition produced calves in better condition. An explanation for this could be that the growth rate of calves is always kept at its physiological maximum, irrespective of FBC (within the range of values observed in this study), to prepare the calf for the migration back to the cooler feeding grounds. While exceptionally good conditioned females can also afford to
fatten their calves, to provide extra insulation and an energetic buffer, poorer conditioned females will prioritize the growth of their calves in size (i.e., length) at the expense of calf condition, to yield a higher survival probability overall.

**Using unmanned aerial vehicles to assess body condition in baleen whales**

This study is the first to apply UAV technology and photogrammetry methods to assess body condition in a balaenopterid. Compared with conventional aircrafts, UAVs are less expensive and safer and can also be operated in more remote regions. Here, we demonstrate that even relatively inexpensive (<$1,000 USD) UAVs can be used to successfully measure body condition in baleen whales over relatively short time periods (i.e., 44 d). We show that even relatively small changes in condition of humpback whales can be reliably detected in measurements from vertical aerial photographs. We further show how measurement errors can be quantified and incorporated into analyses of body condition. Our sensitivity analysis demonstrated that our findings were robust to measurement errors both within and between photographs of the same whale and that there was no measurement bias associated with where in the photograph the whale was positioned. Apart from humpback whales, photogrammetry has so far been used to successfully measure the body condition of right whales (Miller et al. 2012) and gray whales (Perryman and Lynn 2002). We strongly encourage this approach to be extended further to other baleen whales, in an overall attempt to improve our understanding of large whale bioenergetics and reproductive biology.

**Management implications**

This study demonstrates how photogrammetry can be used to assess the body condition of humpback whales from aerial photographs recorded using UAV technology. This noninvasive approach provides a valuable tool to monitor the health of baleen whale populations globally. With most humpback whale populations recovering at an impressive rate, this approach can be used to measure density-dependent effects on body condition and reproduction (Fowler 1990, Stewart et al. 2005). Prey availability is likely to be a key determinant of body condition in baleen whales, and interannual variation in prey availability can be linked to changes in body condition and reproduction in baleen whales (Lockyer 1986, Ichii et al. 1998). Finally, developing a global health index for baleen whale populations will allow for comparison with other populations, which will provide a more holistic understanding of the status of baleen whale species and to aid in conservation.

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**Literature Cited**


**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1468/supinfo